

## DIPLOCYNODON MUELLERI COMB. NOV., AN OLIGOCENE DIPLOCYNODONTINE ALLIGATOROID FROM CATALONIA (EBRO BASIN, LLEIDA PROVINCE, SPAIN)

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**ABSTRACT**—The study of more than 100 skeletal remains of *Hispanochampsia muelleri* Kälin, 1936, from the Oligocene of El Talladell (Lleida Province, Catalonia, Spain), has been decisive in revealing misinterpretations about its anatomy and phylogenetic position. *Hispanochampsia muelleri* is shown to be a member of the clade Diplocynodontinae, and is here considered a junior synonym of *Diplocynodon*. This analysis provides strong evidence for this monophyletic grouping, which is made up of the species *Baryphracta deponiae*, *Diplocynodon darwini*, *Diplocynodon muelleri*, *D. tormis*, *D. ratelii*, and *D. hantoniensis*. All of these species bear ventral osteoderms with paired ossifications, and a deep posterior tip of the iliac blade, which are synapomorphies of Diplocynodontinae. However, the interrelationships of the Diplocynodontinae remain unresolved. *D. muelleri* shares with *D. hantoniensis*, *D. tormis*, and *D. ratelii* the presence of an enlarged jugal foramen, and the particular dentary occlusion in line with the maxillary tooth row. It is highly likely that the two Spanish species, *Diplocynodon muelleri* and *Diplocynodon tormis*, were close relatives.

### INTRODUCTION

In 1936, Otto Kälin described the Oligocene crocodylian species *Hispanochampsia muelleri*, from the quarry of El Talladell (Tàrrrega, Lleida Province, Catalonia) in northeastern Spain. Kälin erected the new species on the basis of two skulls (which he referred to as ‘T1’ and ‘T2’), the holotype and paratype, which are housed in the Natural History Museum of Basel in Switzerland (Fig. 1). The locality of El Talladell is a famous fossil Lagerstätten known to scientists and amateurs since 1900. Two limestone quarries, Talladell and Cervera, were being exploited by industry at that time, and a large collection of thousands of fossil plant, gastropod, fish, turtle, crocodylian, and mammal remains was unearthed in the course of this activity (Coma Torres, 1999). Specimens from these two nearby localities form part of the collections of several Catalonian and national institutions, and several specimens were also deposited in Basel and London (Natural History Museum) (Appendix 1).

Before Kälin’s description, the reptilian assemblage discovered at Tàrrrega (La Pedrera del Ramón) was the focus of attention of Catalonian and French palaeontologists. Vidal and Deperet published several papers on the exceptional remains from this early Oligocene locality (Vidal & Deperet, 1906). Deperet (1906) was the first to provide a description of a crocodylian skull in ventral view, attributing it to *Diplocynodon* sp., and noting the presence of double caniniform teeth on the mandible. In fact, the historical collection of the Martorell Museum at Barcelona retains the original Deperet attributions. Kälin was prompted to describe the material collected by a Swiss amateur that was deposited at the Museum of Basel. Kälin rejected the attribution of *Diplocynodon* because he was not able to observe the ‘double caniniform teeth’ in the Basel specimens. Thus, he erected a new genus and species, *Hispanochampsia muelleri*, being confident that it was a fossil caiman closer to *Melanosuchus* than to *Diplocynodon*.

The donation by the Clua collection of new crocodylian material to the Martorell Museum allowed Bataller (1941) to propose two *Diplocynodon* species: *D. marini* (IGME 745N, IGME1568N) and *D. guerini* (IGME1565N). Bataller did not

highlight differences between *D. guerini*, *D. marini*, and *Hispanochampsia* nor did he make any reference to Kälin’s work. Bataller (1956) subsequently suggested the synonymy between *D. guerini* and *Hispanochampsia* without actually making any anatomical comparison but noting the similarities between the two holotypes (Fig. 2). Bergonioux (1958) furnished a brief description of *Hispanochampsia* and *D. marini*, professing serious doubts about the validity of the latter taxon. A revision of *Hispanochampsia* was carried out by Buscalioni (1986), in which she proposed a new reconstruction of the skull (Fig. 1), discussed the synonymy of *D. marini* and *D. guerini*, and referred both specimens to *Hispanochampsia*. The most recently published article containing information on this taxon is that of Brochu (2004), who produced a tentative phylogenetic analysis based on Kälin’s photographs, and on fragmentary specimens housed at London’s Natural History Museum (BMNH R3942-44). He placed *Hispanochampsia* within Alligatorinae as the sister taxon of *Arambourgia* and *Procaimaoidea*.

Herein, we revise the osteology of *Hispanochampsia muelleri* and propose a character matrix including data from the whole skeleton. We regard *Hispanochampsia* as a junior synonym of *Diplocynodon*, and provide a revised diagnosis of the genus *Diplocynodon*. We also discuss the relevance of this species to our understanding of the evolutionary history of basal alligatoroids.

### MATERIALS

The collected material of *Hispanochampsia* is housed in several public institutions and private collections. J. Gallemì and S. Moyà-Solà (archives of Museu Comarcal de l’Urgell, Tàrrrega, Spain) compiled the first unpublished catalogue of the Talladell fossils, and Gómez-Alba (1997) included the material from *Hispanochampsia* in his official catalogue of the Martorell Museum (Barcelona, Spain). Approximately 150 specimens have been revised in this study, all of them from El Talladell, except for one that was discovered in the early Oligocene locality of Soses, 15 km from Lleida (Barcelona, Spain) (Lacasa Ruiz, 1998). Here, to our knowledge, we document the first comprehensive list to include all known specimens attributed to the species *Hispano-*

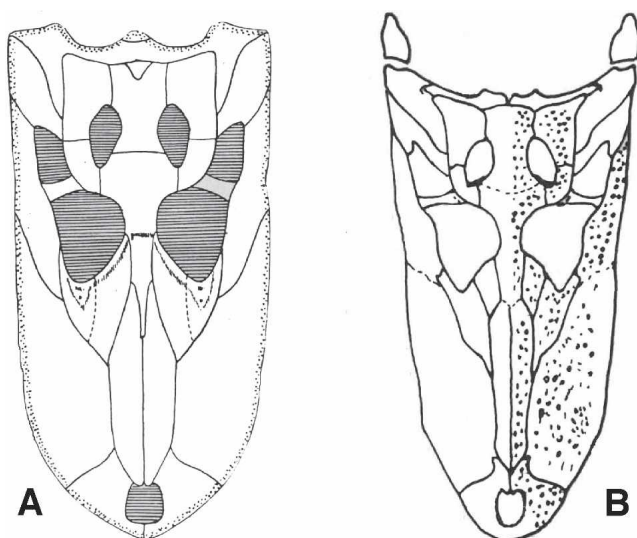


FIGURE 1. Schema of the skull of *Hispanochampsia muelleri* from the Oligocene of El Talladell (Lleida, Spain). **A**, after Kälin, 1936; **B**, after Buscalioni, 1986.

*champsia muelleri*, located in 13 different institutions and collections. Each specimen was photographed, and the entire collection of documents deposited in the Urgell Museum in Tàrrrega (Lleida Province).

The specimens are flattened by compression; thus, most are two-dimensional fossils embedded in a limestone. Some are preserved as slab and counter-slab. Only two specimens have been cleaned up to allow a three-dimensional observation. The majority of the specimens are cranial remains, because skulls were the best fossils of those identified by the quarry operators. We also describe postcranial remains from the same locality of El Talladell that can be attributed to *Hispanochampsia*. One complete individual has been preserved, corresponding to IGME 1568N and formerly attributed to *D. marini*. Thus, we include in this study the material described by J. R. Bataller, namely *D. guerini* (IGME 1565N) and *D. marini* (IGME 1568N and IGME 745 N), which were found in the same locality as *Hispanochampsia muelleri*, the Oligocene outcrop of El Talladell. He

erected the two species on the basis of the reduced size of *D. marini* (total body length about 30 cm). The attribution to the genus *Diplocynodon* was based on “the presence of a palatal and lateral notch to lodge the third and fourth lower teeth” (Bataller, 1941:p. 27) and on “the shape and disposition of osteoderms” (Bataller, 1941:p. 29) (without any explicit mention of the presence of paired ventral osteoderms). The conclusion that ‘*D. guerini*’ is in fact *Hispanochampsia* is founded on the following features (Fig. 2): snout bearing parallel rounded maxillae; maxillae rather low and not constricted mid-length; premaxillary-maxillary without external notch; orbital outline showing anterolateral embayment; premaxillary contour rounded, bearing wide external naris (Buscalioni, 1986).

**Institutional Abbreviations**—**AS**, Ajuntament, Soses, Lleida, Spain; **BMNH**, Natural History Museum, London; **CEP**, Col·lecció Escolars Pias, Tàrrrega, Lleida, Spain; **CLFC**, Col·lecció Luis Ferrer y Condal, La Fuliola, Tàrrrega, Lleida, Spain; **CM**, Col·lecció Montmelo, Barcelona, Spain; **DPUAB**, Departament de Paleontologia Universidad Autònoma de Barcelona, Spain; **IEI**, Institut d’Estudis Ilerdencs, Lleida, Spain; **IGME**, Instituto Geológico y Minero de España, Madrid; **IPS**, Institut de Paleontologia ‘Miguel Crusafont’, Sabadell, Barcelona, Spain; **MCT**, Museu Comarcal de l’Urgell, Tàrrrega, Lleida, Spain; **MGS**, Museu Geològic del Seminari, Barcelona, Spain; **MMB**, Museu de Geologia de Barcelona ‘Martorell’, Spain; **NMB**, Naturhistorisches Museum Basel, Switzerland.

#### SYSTEMATIC PALEONTOLOGY

CROCODYLIFORMES Hay, 1930, sensu Benton and Clark, 1988

EUSUCHIA Huxley, 1875

CROCODYLIA Gmelin, 1789, sensu Benton and Clark, 1988

ALLIGATOROIDEA Gray, 1844, sensu Brochu, 2003

DIPLOCYNODONTINAE Brochu, 1999

*DIPLOCYNODON* Pomel, 1847

**Diagnosis**—Unambiguous synapomorphies of the genus are as follows: largest dentary alveolus immediately caudal to fourth is 10, 11 or 12 (character 167, state 2); medial jugal foramen large (character 120, state 1). Since the latter trait is unknown in *Baryphracta* the character could also be a synapomorphy of Diplocynodontinae.

*DIPLOCYNODON MUELLERI* (Kälin, 1936), comb. nov.

**Holotype**—NMB Spa 4 (= ‘T1’) housed in Basel. Kälin (1936: 5) identified this specimen as the holotype of his species *Hispanochampsia muelleri*; skull exposed in dorsal view.

**Type Locality and Horizon**—El Talladell, Lleida, Spain. Lower Oligocene, Calcaries de Tàrrrega Formation (Coma Torres, 1999), zone of *Theridomys major*, Agustí et al., 1987; MP23.

**Referred Material**—NMB, Spa 4; NMB, Spa 73; IGME, 1565N; 1567N; IEI, 74; MMB, 28129; MCT, 1531; MCT 1528.

**Diagnosis**—Small crocodylian (adult skull length ca. 250 mm). Characters occurring in combination: skull profusely ornamented, and dorsoventrally flattened. Snout with linear and parallel maxillary edges. Dentary teeth (3+4) occluding in an inner pit between premaxilla and maxilla. 3rd and 4th mandibular teeth almost the same size and with confluent alveoli. Dentary symphysis short (reaching third alveolus). Splenial excluded from mandibular symphysis, and with anterior tip passing dorsal to Meckelian groove. Smallest mandibular alveoli: 8th and 9th. Largest mandibular alveoli: 11th and 12th. Dentary teeth occluding lingually at premaxilla and interfingering at mid-maxillae. Largest maxillary alveoli: 4th and 5th, almost same size. External naris with rim at posterior border. Nasals not contributing to

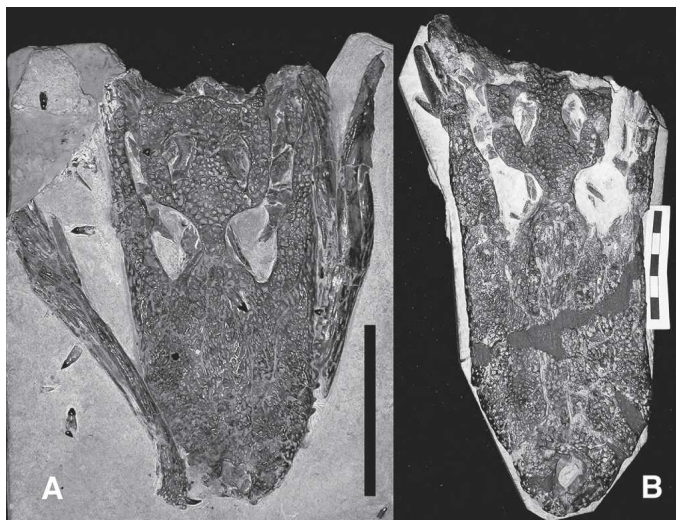


FIGURE 2. **A**, Spa 4 T2, the holotype of *Diplocynodon muelleri* (Kälin, 1936); **B**, IGME 1565N, *Diplocynodon guerini*. Scale bar equals 5 cm.

narial margin. Lacrimal longer than prefrontal. Transverse prefrontal interorbital ridge. Orbital contour anteriorly notched. Parietals expanded in shelf visible in dorsal view at supratemporal fossa. Frontoparietal suture entering supratemporal fossae. Palatine fenestrae long and wide. Lateral edges of palatines with anterior projections into suborbital fenestrae. Supraoccipital slightly exposed in dorsal view at skull table. Occipital condyle procumbent. Steep squamosal prongs. Small quadratojugal spine. Subrectangular dorsal osteoderms with shallow keels. Ventral osteoderms paired with double ossifications. Iliac blade deep posteriorly.

### DESCRIPTION

Sixty percent of the specimens studied are individuals with skull lengths of 100 to 160 mm. The other 40% have skull lengths of approximately 190 to 230 mm. In general, the specimens are excellently preserved in dorsal and ventral views, with details at sutures. Compression means that there is no detailed information in the lateral view and accurate dimensions cannot be determined. However, some cleaned specimens (CM1, CM2, CM3) allow a partial three-dimensional description of the lateral part of the basioccipital and basisphenoid lateral region, and of the infratemporal fenestra and otic recess. In most cases, the lower jaw is fractured.

### Cranial Osteology

**General Morphology**—The skull is wide, short and low (Figs. 3, 4). In dorsal view, the general morphology of the skull reveals an almost linear maxillary margin without any lateral festooning; as a consequence, the profile is rather square. The dorsal surface is profusely and completely ornamented with shallow, circular

pits. The quadratojugal bears the same ornamentation, and the skull table has a more regular pattern than the rostrum. Even in the smallest individuals, there is a distinct prefrontolacrimal ridge along the orbital margin.

Caudally, the paraoccipital process and the quadrate deviate laterally so that the medial edge of the quadrate ramus is aligned with the paraoccipital process. The quadrates do not extend backwards and almost do not extend beyond the occipital condyle. The anterior contour of the skull table is curved. The skull table represents less than 20% of the total skull length. The lateral sides of the skull table are curvilinear. The infratemporal fenestra, although collapsed on most specimens, is subtrapezoidal, higher than long. The supratemporal fenestra has an anterior notch and its main axis diverges laterally slightly. A pronounced medial parietal shelf that reduces the fenestral width dorsally is a distinctive feature of *D. muelleri*. The medial inner surface of the fossa constitutes a nearly horizontal shelf. At the fossa the quadrate does not separate parietal and squamosal ventrally at the posterior supratemporal foramen (Fig. 5). The orbits are drop-shaped with an anterior notch within the lacrimal. The interorbital space is slightly shorter than that between the supratemporal fossae. The nasals are excluded, at least dorsally, from the external naris but almost reach the border of the narial aperture. The external naris is not bisected.

The paratype (SPA 73 = T2) is well preserved in ventral aspect. The shape of the palatine fenestra is peculiar in *Diplocynodon muelleri*: it is proportionally very long (approximately one third of the total length of the reconstructed skull). The choana is located within the pterygoids, bears a short, thin inner septum, and the choana is broader than it is long. The posterior and anterior rims of the choana lie at the same height. The choana projects posterovertrally.

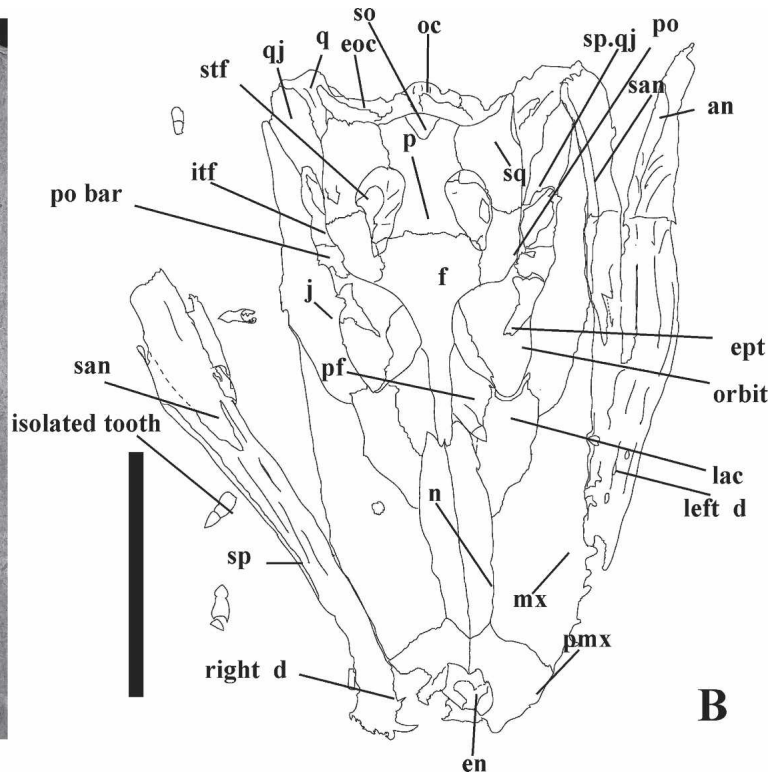


FIGURE 3. The holotype of *Diplocynodon* (= *Hispanochampsia*) *muelleri* (Spa 4 T2) from the Oligocene of El Talladell outcrop at Tárrega (province of Lleida) housed at Basel (Switzerland). Skull in dorsal view. **Abbreviations:** an, angular; d, dentary; eoc, exoccipital; ept, ectopterygoid; f, frontal; j, jugal; lac, lachrymal; mx, maxilla; n, nasal; oc, occipital condyle; p, parietal; pmx, premaxilla; po, postorbital; po bar, postorbital bar; prf, prefrontal; q, quadrate; qj, quadratojugal; san, surangular; so, supraoccipital; sq, squamosal; sp. qj, spina quadratojugal; stf, supratemporal fenestra. Scale bar equals 5 cm.

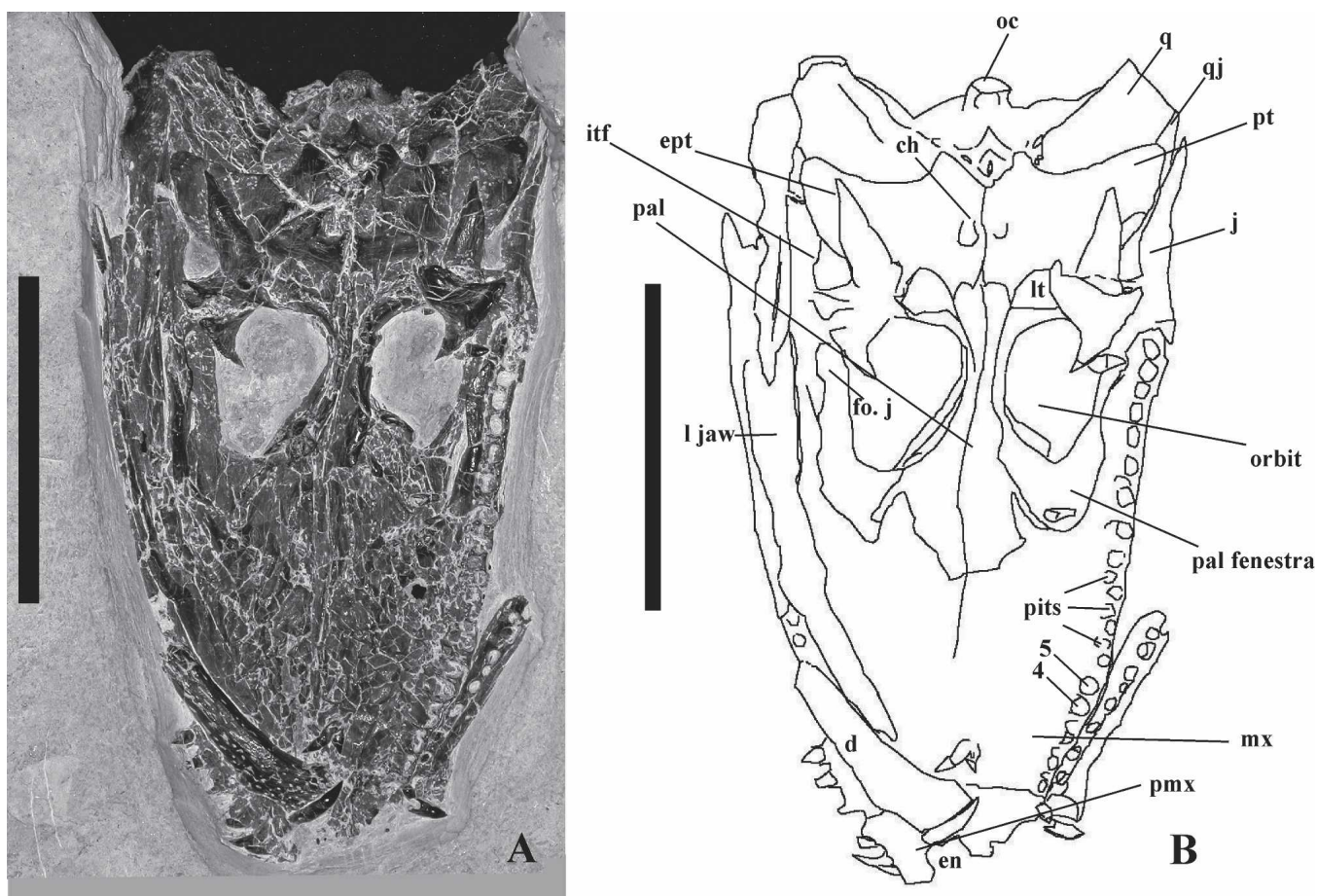


FIGURE 4. The holotype of *Diplocynodon* (= *Hispanochamps*) *muelleri* (Spa 4 T2) from the Oligocene of El Talladell outcrop at Tárrega (province of Lleida). Skull in ventral view. **Abbreviations:** **ch**, choana; **d**, dentary; **en**, external naris; **ept**, ectpterygoid; **fo.j**, anterior jugal foramen; **itf**, infratemporal fenestra; **j**, jugal; **lt**, laterosphenoid; **l jaw**, lower jaw; **mx**, maxilla; **oc**, occipital condyle; **pal**, palatine; **pmx**, premaxilla; **pt**, pterygoid; **q**, quadrate; **qj**, quadratojugal. 4th and 5th maxillary teeth are labeled, as well as the reception pits of mandibular dentition. Scale bar equals 5 cm.

**Premaxilla**—Dorsally, the posterior premaxillary processes reach a point that is level with the third maxillary alveolus. The external naris is longer than it is wide. The naris is posterolaterally surrounded by a rim, generating a sharp notch at an equivalent position to that in *Alligator* in which the notch is behind and parallel to the premaxillary-maxillary suture. The bone sculpture differs from the rest of the skull although but not so pronounced as in *Alligator*. This rim is also perceptible in *D. tormis* and *D. gracilis*. The rear border of the external naris is level with the lateral premaxillo-maxillary suture. Since nearly all known specimens are dorsoventrally flattened and/or longitudinally sectioned, it is difficult to evaluate the ventral premaxillomaxillary [I'd make all these the same] suture. MCT 1528 is the specimen that best exposes this view, revealing a linear suture, at least in its lateral part. There are five premaxillary alveoli and a series of tiny lingual foramina along the tooth row. There are three lingually placed pits for receiving mandibular teeth. The first pit is located between the first and second premaxillary alveoli, the second between the third and fourth, and the third at the premaxillomaxillary suture. The incisive foramen is rather small, keyhole-shaped, and located posterior to the two most anterior pits. The foramen abuts the premaxillary pits without entering tooth row. In dorsal view, the narial fossa is well developed anteriorly.

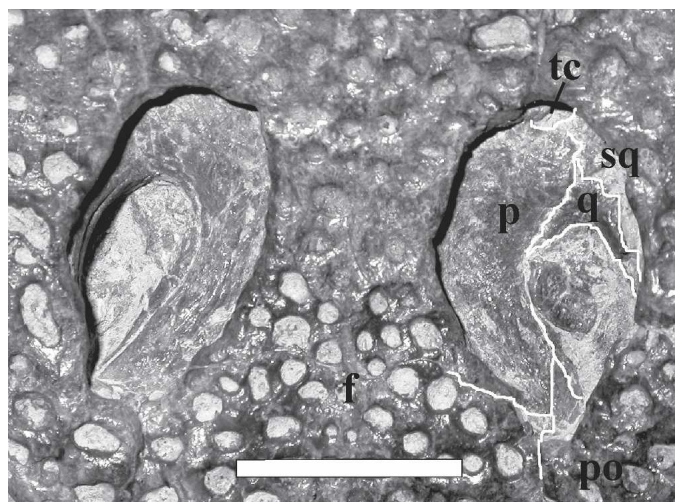


FIGURE 5. *Diplocynodon* (= *Hispanochamps*) *muelleri* from the Oligocene of El Talladell, Spain, specimen MMB 28129. Close view of the supratemporal fenestra. Note how the quadrate does not enter the temporal canal (**tc**) and how the parietal (**p**) and quadrate (**q**) contact each other. Abbreviations as in Figure 3. Scale bar equals 1 cm.

**Nasals**—In the original description and reconstruction by Källin (1936), the nasals enter the external naris (Källin, 1936:Fig. 5). ‘T1’ and ‘T2’ are not as well preserved and the process interpreted by Källin as a nasal projection is due to the compression of the narial rim of the premaxillae. The observation of the specimen IGME 1565N housed at the Instituto Geológico y Minero de España (Madrid, Spain) and that of Montmelo (CM 6) confirmed that the nasals do not enter the naris. The nasals are relatively short and narrow compared with the maxillae. The anterior portion of the nasomaxillary suture is linear. The nasals contact the lacrimals, prefrontals and the frontal process. The contact with the prefrontal is simple, and the nasal sends a short posterior process between the frontal and prefrontal. The suture with the lacrimals is rather long, being approximately one-third of the length of the lateral nasal suture from the point of contact with the prefrontal to that with the premaxilla. This suture is oblique and posterolaterally oriented.

**Maxilla**—The maxilla does not present *Caiman*-like festoons. The rostrum is like that of *Alligator*. Consequently, the profile is not triangular, as in *Diplocynodon tormis* or *D. gracilis*, but rather the lateral edges are comparatively linear and parallel, even in smaller individuals. The maxilla contacts the lacrimal and jugal. The triple-point of contact with these bones is located in front of the orbit, lateral to the main anteroposterior axis of the orbit, as in *Diplocynodon tormis*. The tooth row features a reduced interalveolar distance, which is almost reduced to a thin lamina. The 4th and 5th maxillary alveoli are the largest. This character is evident in the holotype SPA 73 (=‘T2’ in Källin, 1936), in CM 7, in the Luis Ferrer y Condal collection, and in MCT 1528 at the Tarrega Museum). This character differs in *Diplocynodon* and *Baryphracta deponiae* (with 3rd and 4th as the largest; Frey et al., 1987). The total number of alveoli is approximately 20. The alveolar series starts at the level of the posterior margin of the palatal fenestra, while the anterior margin of the palatal fenestra is approximately at the level of the 10th maxillary alveolus.

The maxillary dental series changes in size. The 4th and 5th alveoli have the greatest diameters, and the 6th to 8th alveoli are situated more laterally toward the edge of the maxilla. Alveoli exhibit their maximum diameter from the 10th alveolus to the end of the maxillary series. These largest are slightly compressed laterally.

All mandibular teeth occlude in pits located almost semi-lingually to the maxillary tooth row. In other words, pits anterior to the 4th and 5th are in line with the maxillary alveoli, but slightly displaced lingually, while behind the 5th the three successive caudal pits are in line with the maxillary. Pits are slightly smaller than the alveoli. The maxilla separates the ectopterygoid from the tooth row. The palatal shelf of the maxilla located laterally to the ectopterygoid is a thin lamina at the level of the last two alveoli (almost touching the alveolar rim) and enlarges to equal the alveolar width along the lateral borders of the palatal fenestra. In all specimens, the palate surface is flat, and the alveolar rims are not very high. Corresponding with the 4th and 5th maxillary alveoli there is a large boss on the dorsal maxillary surface that involves both alveoli.

**Prefrontal**—Lacrimals are longer than prefrontals. The relation between the two bones was not properly reconstructed by Källin (1936), giving the impression that the prefrontal was longer than the lacrimal. IGME 1565N and the holotype itself clearly show that the prefrontal is shorter than the lacrimal; the prefrontal has a nearly sub-trapezoidal shape. The suture between the lacrimal and prefrontal is linear. In none of the known specimens has a complete prefrontal pillar been preserved.

**Lacrimal**—The suture between the lacrimal and nasal is actually longer than that of the nasoprefrontal (Fig. 1). The anterior border of the lacrimal tapers toward the midline, unlike in *Caiman* and *Alligator*, which both have a transverse anterior

outline. In most adult specimens (IGME 1565N, SPA 73) preorbital ridges and a transverse step are visible. These ridges cannot be seen in immature individuals. Lacrimal and prefrontal contribute approximately equally to the anterior orbital border.

**Frontal**—The anterior frontal process is thin and leans out slightly before the anterior margin of the orbit. The frontal-prefrontal suture enters the orbit just anterior to the most medial point of the opening. The frontoparietal suture is linear (crossing the interparietal space transversely). The frontal-postorbital suture enters the supratemporal fossa at its anterior tip. The frontal dorsal surface is flat, and there is no rim along the orbital edge.

**Parietal**—The parietal constitutes the posterior margin of the skull table. It comprises the space between supratemporal fenestrae that is equivalent to that between the orbits. The parietal constitutes most of the inner medial surface of the supratemporal fenestrae. The medial inner surface of the fossa is a subhorizontal shelf. Although the quadrate sends a small dorsal projection towards the posterior temporal fenestra, as in other *Diplocynodon* species, the extension of the parietal shelf within the fossa ensures that the quadrate does not separate the parietal and squamosal ventrally to the posterior supratemporal foramen (Fig. 5). A small surface of the supraoccipital is exposed behind and medially at the skull table in dorsal view.

**Squamosal**—The parietosquamosal suture is linear at the skull table that enters the supratemporal fenestra behind the cranial aperture of the posttemporal canal (Fig. 5). The squamosal enlarges medially at the posterolateral edge of the supratemporal fossa and is visible in dorsal view. The posterior squamosal projections slightly diverge from the lateral contour of the cranial table, the quadrate branches being located laterally to them. The squamosal prong is rather short, unornamented, and does not completely cover the lateral margin of paraoccipital processes. The squamosal and quadrate at the paraoccipital process form a singular, steep, right-angled contour when observed in lateral view. This structure is also seen at least in *Diplocynodon darwini*, *D. ratelii*, and *D. tormis*. The arrangement of the structure is made by a sharp dorsal projection of the quadrate that sutures with the squamosal laterally and by a prominent lamina of the paraoccipital process that contacts the quadrate laterally (Fig. 6).

**Postorbital**—The postorbital bar is slender, short, and is shifted posteriorly relative to its placement in many alligatoroids. In all specimens the postorbital bar is collapsed and flattened but, despite this, it is evident that it inserts from the lateral surface of the jugal just caudally to the ridge exhibiting the jugal at its orbital margin. The anterolateral border of the postorbital has a curved but angular contour, unlike that of *Brachychamps* and *Acynodon*, in which the skull table and frontal follow the outline of a single curvature.

**Quadrate**—The quadrate (Figs. 3, 4, and 6) diverges posteriorly and has a short caudal ramus. The medial hemicondyle is the smallest. The plane formed by the two quadrate hemicondyles is oriented mediocaudally and lateroanteriorly. At the dorsal surface of the caudal ramus, the air-filled duct opens through a large oval opening (approximately 0.7 mm), forming a depressed area on the bone surface. Mainly in large specimens (IEI 74; MCT 1531), the quadrates bear a longitudinal dorsal lamina that extends as far as the region posterior to the auditory meatus. This lamina constitutes the suture with the squamosal (Fig. 6). The otic region is compressed in all the specimens. *Diplocynodon muelleri* appears to have an invaginate otic recess, and the quadratosquamosal suture probably lies along the posterior wall of the external otic recess. Ventrally, the quadrate has developed a ridge that runs parallel to the rear margin of the exoccipitals. The quadrate lateral condyle contacts the quadratojugal. The medial hemicondyle of the quadrate does not bend ventrally, as occurs in *Alligator*.

**Quadratojugal**—This bone is proportionately large compared with the condition observed in living crocodylians and is pro-

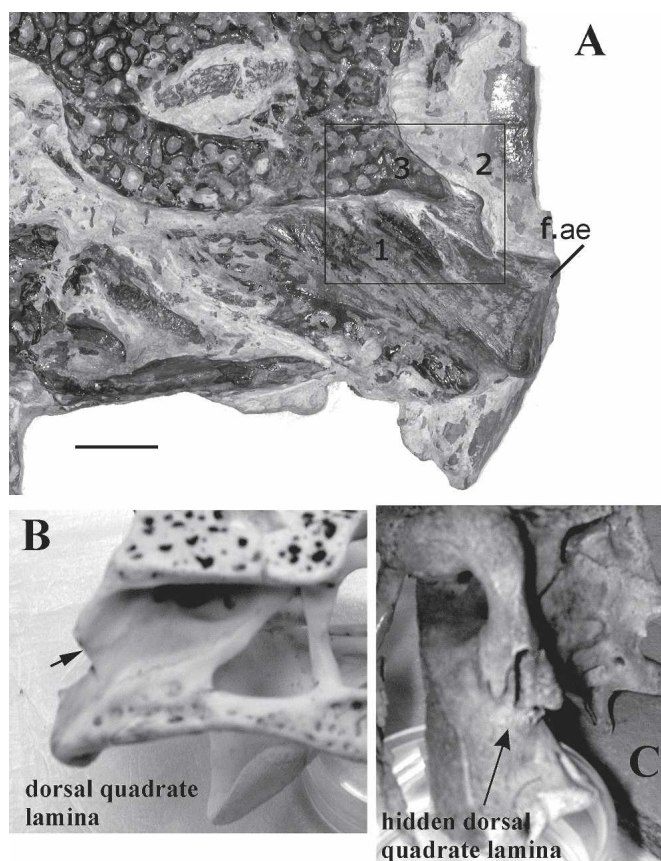


FIGURE 6. *Diplocynodon* (= *Hispanochamps*) *muelleri* from the Oligocene of El Talladell, Spain (specimen IEI74). **A**, detail of the squamosoquadrate suture at the paraoccipital process, showing the position of the foramen aereum (**f. ae**). Note the sharp dorsal lamina of the quadrate (1), the prominent lateral lamina of the paraoccipital process (2), and the short squamosal prong (3). Scale bar equals 1 cm; **B**, detail of the squamosal-quadrate suture of the alligatorine *Melanosuchus*, showing the development of the dorsal quadrate lamina; **C**, the quadrate dorsal lamina is hidden and between a ventral projection of the squamosal (with a long prong) and paraoccipital process in *Crocodylus rhombifer* (skull in laterocaudal view).

fusely ornamented. The spina quadrato jugalis is not always preserved but can nonetheless be appreciated in the holotype 'T1,' in the Montmelo (CM2) and IEI 74 specimens, where it is small and slender and located high up on the dorsocaudal margin of the fenestra. The quadratojugal forms a dorsal projection that seems to prevent contact between the postorbital and the quadrate.

**Jugal**—The jugal forms the inferior border of the infratemporal fenestra and becomes deeper on its anterior orbital border. The posterior jugal process is not rod-like but compressed. A large anterior jugal foramen at the medial side can be observed in the holotype. The jugal-quadratojugal suture is V-shaped in lateral view, and the rear part of the jugal lies beneath the quadratojugal. In ventral view the jugals are exposed laterally to the ectopterygoids throughout their contact, as in *D. darwini*. The quadratojugal-jugal suture is located dorsally, anterior to the posterior corner of the infratemporal fenestra.

**Palatine**—The palatine tube is narrower than the palatine fenestra. The lateral margins of the palatines are linear. Palatines are fully exposed in the Tàrrega specimen (MCT 1528) and also in the holotype. The suture with the pterygoids seems to be located anterior to the posterior tip of the palatine fenestra. The anterior suture between the palatine and maxilla is U-shaped,

with the convexity extending cranially and significantly beyond the anterior margin of the palatal openings. The palatines flare posteriorly as in many *Diplocynodon* species, and anteriorly they feature a 'wing-shaped' process that expands laterally along the medial border of the palatal fenestrae.

**Ectopterygoid**—The ectopterygoid is clearly visible on the paratype (Spa 73), the Montmelo largest skull (CM 6), and in the MCT 1528 specimen housed at Tàrrega. It is a massive bone with a short, sharp anterior process. Its posterior descendent process is robust and its tip does not reach the end of the lateral pterygoid flange. There is no trace of a flexure between the two bones. The posterior projection is shorter than its anterior equivalent. The posterior ectopterygoid process that lies on the medial side of the jugal does not exceed the level of the postorbital bar. The medial ascending projection of the ectopterygoid is hidden in all the specimens.

**Pterygoid**—This bone is compressed and distorted in most specimens. The paratype, T2, exposes its ventral view, while the pterygoids are three dimensionally exposed in Montmelo CM 8 specimen. The pterygoid wings are divergent and vertical, with two pronounced posterior parasagittal projections. A short space separates the posterior pterygoid rim from the choana, which is surrounded entirely by pterygoids and is circular and slightly elongated anteroposteriorly. The pterygoids make up most of the posterior corner of the palatal fenestra. Their anterior suture with palatines is anteriorly concave.

**Occiput and Basicranium**—The description of the occipital region (Fig. 7) is based on CM 1 specimen in the Montmelo collection. Comments on all other specimens are limited by their compression and by their inclusion in the matrix. The supraoccipital is rather short and low, and bears a thick sagittal crest. The occipital region is characterised by the backward extension of the occipital condyle. Exoccipitals show a slight concave curvature in caudal view. The paraoccipital process and the quadrate condyle diverge laterally. Exoccipitals do not overhang the ventral edge of the quadrate, so they are not laterally exposed at the caudal end of the braincase.

The ventral exoccipital processes do not reach the base of the basioccipital. The median eustachian foramen is ventral to the lateral eustachian openings. The basioccipital tubera are angled. A median crest divides the ventral portion of the basioccipital, but not as sharply as in *Diplocynodon tormis*. The basisphenoid, although broken, is visible in posterior view, emerging ventral to the basioccipital as a thin lamina. It also seems to rise posteriorly and dorsal to the pterygoids as a narrow edge.

## Mandible

The most striking feature of the lower jaw (Fig. 8) is the length of the symphyseal suture, and the morphology of the 3rd and 4th teeth: their alveoli are confluent so that there is no alveolar wall between them, and of almost an equal size.

**Dentary**—The dentary is a robust element with a square transverse section in the ramus. It is profusely ornamented laterally and ventrally. In lateral aspect the dentary has two vertical waves, with one peak at the level of the 3rd and 4th teeth, and the other between the 9th and 11th teeth. The 8th and 9th alveoli are the smallest, while the 11th and 12th have the greatest diameter. The interalveolar space is slightly smaller than the alveolar width. The dentary series is rectilinear (instead of sigmoid as in *Brachychamps* or *Allognathosuchus*). The mandibular symphysis is very short, reaching the level of the third alveolus. In occlusal view the most anterior portion of the dentary expands medially at the symphyseal area, forming a shelf that extends posteriorly up to the fifth alveoli.

**Splenial**—The splenial does not participate in the mandibular symphysis, and its anterior tip passes dorsally to the Meckelian groove.

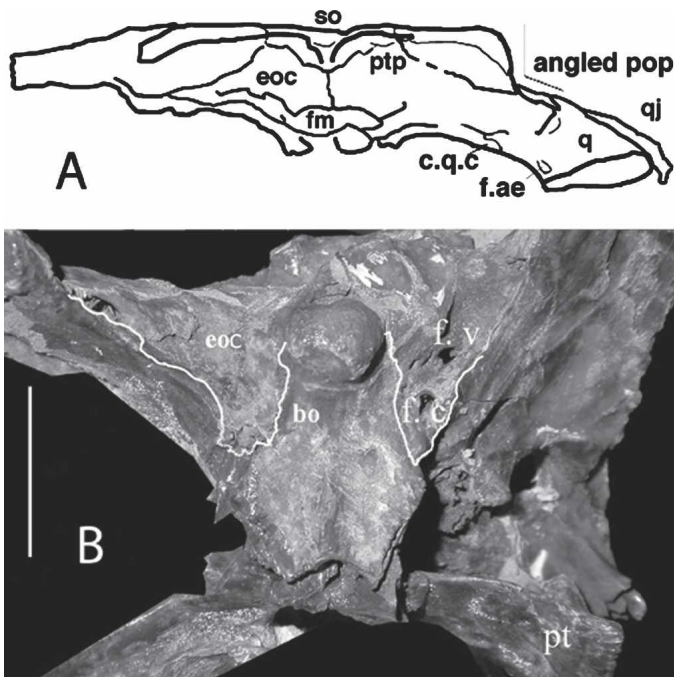


FIGURE 7. *Diplocynodon* (= *Hispanochamps*) *muelleri* from the Oligocene of El Talladell, Spain. **A**, schematic drawing of the dorsal part of the occiput on a specimen from Montmello collection; **B**, specimen CM1 from the Montmello collection showing the ventral part of the occipital view. Scale bar equals 2 cm. **Abbreviations:** **bo**, basioccipital; **c.q.c**, cranioquadrate canal; **eoc**, exoccipital; **f. ae**, air-filled duct; **fm**, foramen magnum; **f.c.**, carotid foramen; **f.v.**, vagus foramen; **ptp**, posttemporal process. Other abbreviations as in figures 3 and 4.

**Angular and Surangular**—The surangular has a thick dorsal edge for muscular attachment. Its lateral and dorsal surfaces are delimited by a sharp crest. In its anterior dorsal suture with the dentary, the surangular probably bears two subequal anterior processes. This feature is also seen in the holotype and in a specimen from the Tàrraga Museum. In the glenoid area, the suture between the surangular and articular is probably not bowed. The retroarticular-surangular suture is anteroposteriorly oriented and the surangular lacks a crest covering the lateral contour of the glenoid area. The surangular expands laterally, forming a platform dorsally and a knob laterally, and is pinched off anteriorly to the tip of the retroarticular process.

The angular-surangular suture contacts the external mandibular fenestra at its posterior angle; the fenestra is rather small and its main axis is nearly parallel to the mandible elongation.

**Articular**—Its air-filled duct is on the dorsal surface of the retroarticular process located at its medial border. The retroarticular process curves dorsally, although its posterior tip does not exceed the height of the posterior glenoid crest. The medial retroarticular flange has a linear contour except in its anterior portion that is convex. The surface of the retroarticular process has a ventral bend posteriorly and laterally to the crest behind the glenoid articular area, forming a rough area for muscular attachment confluent with the lateral knob of the surangular.

#### Dentition

The dental formula is 5+17/19-20. All the teeth have proportionately short crowns that are conical in shape. They are largely homodont. The anterior teeth are especially acute, with slender crowns. Nonetheless, the last teeth on the maxilla, despite ending with a sharp apex, have more bulky mid-crowns.

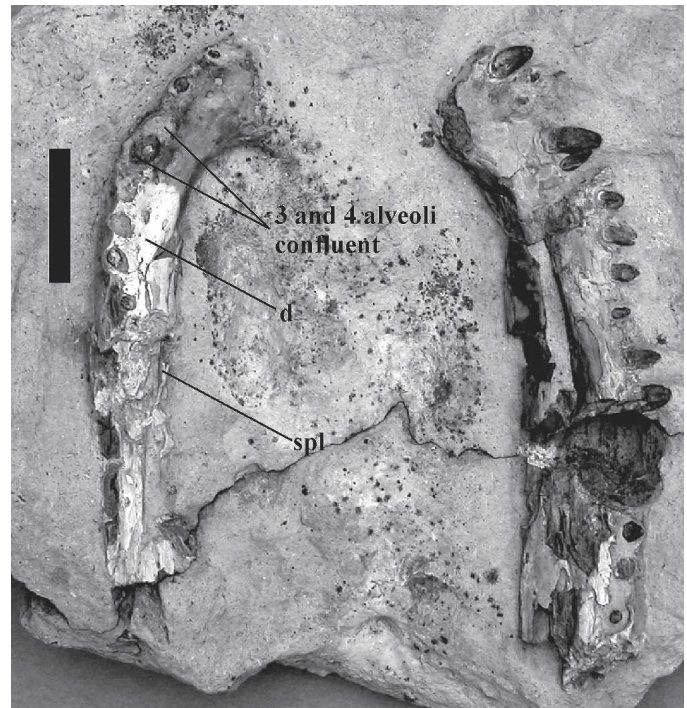


FIGURE 8. *Diplocynodon* (= *Hispanochamps*) *muelleri* from the Oligocene of El Talladell (MCT 1529). Lower jaw. Scale bar equals 2 cm. Note the shortness of the symphyseal area. **Abbreviations:** **d**, dentary; **spl**, splenial.

#### Postcranial Osteology

**Dermal Armor**—*Diplocynodon muelleri* has an armored body with dorsal and ventral osteoderms. According to Brochu (1997), ventral armor is typical of living, very short-snouted taxa: *Alligator sinensis*, all caimans, and *Osteolaemus tetraspis*. Basal alligatoroids such as *Diplocynodon* (with a skull length equivalent to that of *A. sinensis*) and *Baryphracta deponiae* (with a skull length as long as that of *Osteolaemus*) are also covered by complete ventral and dorsal armor. Nonetheless, differences in the degree of development of the armor have been described, for instance, among the *Diplocynodon* species and the extensive osteodermal skeleton with pholidosis in tail and limbs of *Baryphracta* (Frey et al., 1987). The extension of caudal ventral osteoderms cannot be given for *Diplocynodon muelleri* because the tail is not preserved.

The paravertebral osteoderms are almost square. The only specimen on which the dorsal armor is completely preserved is IGME 745N and its counterslab IGME 1568 N. On this specimen the osteoderms have a length to width ratio of 5:6. They are rectangular but more squared than in *D. ratelii*. Osteoderms are ornamented with pits that enlarge from the centre to the external margins. They are rather flat with very low but thick keels. The anterior margin of dorsal midline osteoderms has a smooth strip without any process.

The IGME specimen appears to have six contiguous dorsal osteoderms (3+3), as do *Baryphracta* and *D. darwini*. *Diplocynodon muelleri* may bear one further accessory lateral row. In general, it is peculiar to Alligatoridae to have tall keels at the dorsal and nuchal osteoderms, and even nuchal osteoderms in alligatoridae may bear a gaussian crest. Keels are not generally prominent among *Diplocynodon* species. However, nuchal osteoderms in *D. darwini* lack acute crests, while the crest is sharp in *D. ratelii* and *D. gracilis*. This sharp crest is maintained along paravertebral osteoderms in *D. ratelii*, while these of *D. darwini*

and *Baryphracta* have a thick, smooth anteroposterior area in relief. *D. muelleri* has a rather low crest compared with these latter two genera.

Ventral osteoderms are more rectangular than the dorsal ones. *D. muelleri*, like *Baryphracta* and other *Diplocynodon*, has paired ossifications that suture together. In all of them, the submodule (cranial part) exhibits a posterior sutural area, which connects with the anterior edge of the principal module (posterior part), and a smooth and thin anterior area (articular surface), which lies over the dorsal surface of the principal module at its posterior edge. Double ossifications of the ventral armor can be characterised by considering the relationship between the posterior and anterior parts (Fig. 9). *Baryphracta*, *Diplocynodon darwini*, and *D. muelleri* show the same disposition between modules, but they nevertheless differ in anterior part width, which are, respectively, one-fifth, one-third, and one-half the size of the posterior part. Double ossifications have never been described in *D. muelleri* because few specimens with complete and fully exposed ventral armor have been preserved. The internal view of the ventral series is exposed in the IGME 1568 N specimen, revealing a succession of sutured and overlapping osteoderms (Fig. 9).

### Vertebral Series

Specimens do not show well-preserved vertebrae. The centra are procoelous. No detailed structure can be discerned. The only particular feature that may be observed is the broad transverse

extension of their neural arches along the dorsal and lumbar series.

### Pectoral and Pelvic Girdles

Preparation and removal from the matrix of the scapula (CM 10) and coracoid (MGS 26428) (Fig. 10) yield no information about whether they were found in association with each other or with other skeletal parts. The scapula has a broad blade (nearly two thirds of the length) (Fig. 10). The dorsal blade flares anteriorly and posteriorly. It has an anterior convex outline and a pronounced concave posterior contour. The dorsal margin is as large as the ventral border. The deltoid crest of the scapula has a broad margin.

The iliac blade is a thin, non-twisted lamina. The anterior iliac process is absent. The iliac blade has a rounded dorsal contour that ends posteriorly with a deep, straight edge. In general, the anterior portion of the dorsal profile resembles that of *Alligator sinensis*, although it is more continuous and less irregular, as in *Crocodylus acutus*. The posterior end, however, shares the condition exhibited by *Allodaposuchus* and other *Diplocynodon*, with a deep blade margin. An almost complete pelvic girdle (ilium, ischium, and a fragment of the pubis) corresponds to the MCT 1537 slab housed at the Museu Comarcal de l'Urgell, in Tàrrrega (Fig. 10). These elements were found in isolation.

### Appendicular Skeleton

The best-preserved hind limb bones are those of the MCT 1533 specimen from the Museu Comarcal de l'Urgell. The deltoid crest of the humerus shows a concave profile, having a conspicuous ventral tip (Fig. 10). A large area is occupied by the deltoid crest, which comprises one-third of the humeral length, as occurs in *Diplocynodon tormis*. The hindlimb bones are relatively more robust than forelimb bones, especially the femoral and tibial shafts. In particular, the femur shows a pronounced sigmoid curvature, so that the distal third of its shaft bends ventrally. The femur is consistently thick along its shaft.

### PHYLOGENETIC ANALYSIS

A heuristic search using random addition with 100 replicates and the branch-swapping algorithm (TBR) (PAUP 4.0B 10 from Swofford, 2001) yielded 2007 equally optimal trees of length 261. This was obtained using the data matrix of Brochu (2004) on alligatorine phylogeny. It has been analyzed using 40 taxa and 167 characters (see Appendix 2). The close relationships of *Hispanochamps muelleri* with members of *Diplocynodon* (*D. darwini*, *D. ratelii*, *D. hantoniensis*) have prompted us to include other species, including *D. tormis*, in this analysis. The latter species, from the Eocene of the Duero Basin, has been coded following Buscalioni and colleagues (1992). All characters were treated as unordered, and *Borealosuchus sternbergii* and *Asiatosuchus germanicus* were used as successive outgroups. *Hispanochamps muelleri* is shown to be a member of the clade Diplocynodontinae in the resulting cladograms (Fig. 11). The major topologies found in relationships of Alligatoroidea (Brochu, 2004) are maintained in the consensus tree, except for the phylogenetic position of *Hispanochamps muelleri*.

Our result differs drastically from Brochu's (2004) hypothesis, in which *Hispanochamps*, *Procaimanoidea*, and *Arambourgia* form a clade. Direct observation of abundant and previously unstudied material has been decisive in our study, not only in revealing the autapomorphies shared with other members of Diplocynodontinae, but also in revising Kálin's misinterpretations. This is the case of the suture and the relationship between the prefrontal and lacrimal that is otherwise a decisive character that places *Hispanochamps* within Alligatorinae. Although we agree to some extent with Brochu's (2004) interpretation that

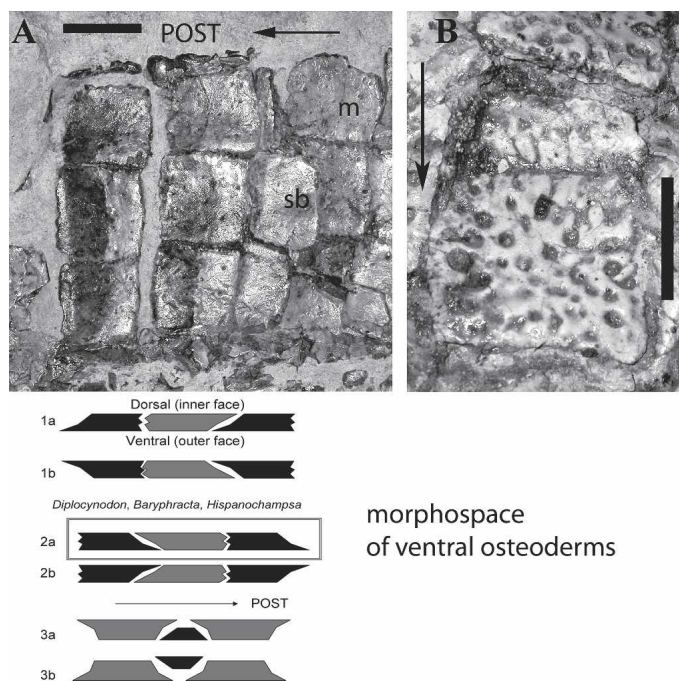


FIGURE 9. **A**, Ventral osteoderms in internal view, specimen IGME 1568N; **B**, ventral osteoderm showing the double ossification, external view. Specimen at the Ajuntament Soses (Lleida). Scale bars equal 1 cm. **Abbreviations:** sm, submodule (cranial part) (grey square in the schema) and m, main module (caudal part) (black square in the schema). Below, schema of ventral osteoderms with double ossifications showing in a combinatory morphospace all the possible combinations of the following traits: suture anterior and dorsal overlap (1a); suture anterior and ventral overlap (1b); suture posterior and dorsal overlap (2a) (condition in Diplocynodontinae and equivalent to the condition in caimans, *Borealosuchus* and *Procaimanoidea kayi*); suture posterior and ventral overlap (2b); ventral extra ossification (3a); dorsal extra ossification (3b). Except for condition 2a, the remainder are unknown for Crocodylomorpha. Arrows point in posterior orientation.



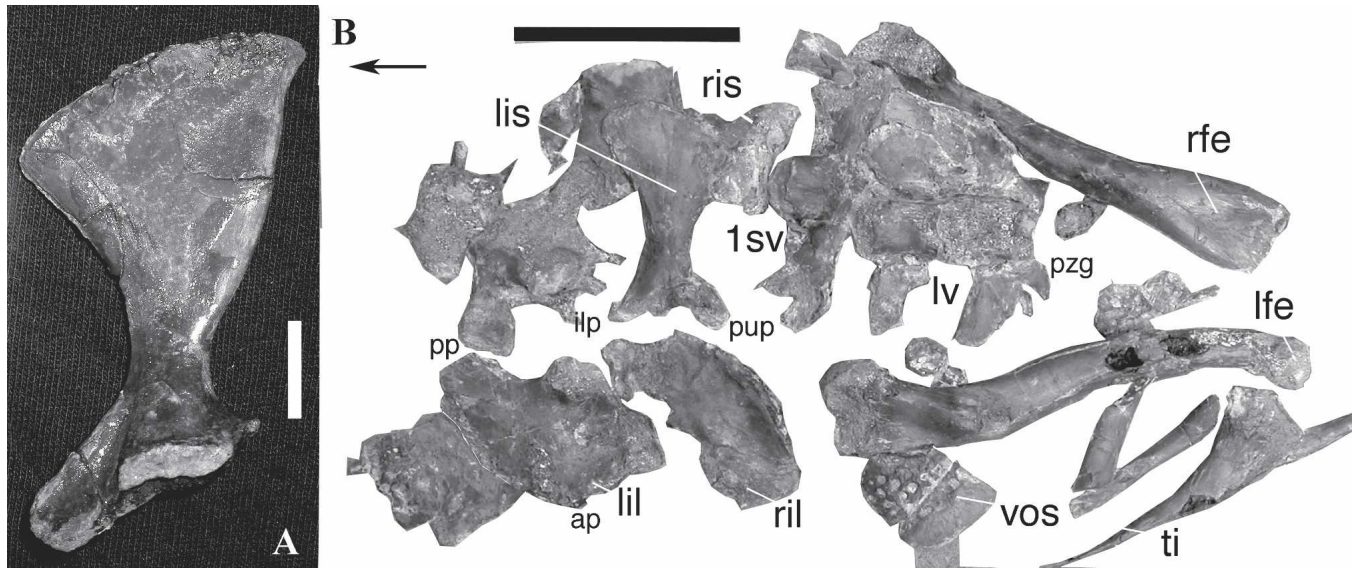


FIGURE 10. Pectoral and pelvic girdles of *Diplocynodon* (= *Hispanochampsia*) *muelleri* from the Oligocene of El Talladell **A**, isolated scapula (CM10). Scale bar equals 1 cm; **B**, specimen MCT 1537. Right iliac blade in medial view (**ril**); note that the acetabular area is broken off). Left iliac blade (**lil**) in lateral view. Both the anterior (**ap**) and posterior (**pp**) processes of the iliac blade are visible. Right ischium (**ris**). Left ischium (**lis**) in lateral view (note the pubic (**pup**) and iliac (**ilp**) processes). Lumbar (**lv**) and first sacral vertebra (**1sv**) in ventral view. Anterior view of the right femur (**rfe**), and posteromedial view of the left femur (**lfe**). Other abbreviations: **pzy**, prezygapophysis; **ti**, tibia; **vos**, bipartite ventral osteoderm. Arrow points caudally. Scale bar equals 5 cm.

particular features of *Hispanochampsia* show a singular combination of traits, such as the shortness of the symphysis, the large and rather compressed posterior maxillary alveoli, the rim and notch around the external nares, the rather flat and compressed skull, and the rather wide incisive foramen, some of these features can also be observed in several species of *Diplocynodon*. For instance, symphyseal length varies in species of *Diplocynodon* from the 4th to the 6th dentary alveoli. *Diplocynodon ratelii* and *D. tormis* also have a rim and notch associated with the contour of the external nares. A dorsoventrally flattened skull is also present in *D. darwini*. Other features concerning alveolar dimensions show a certain degree of variation as well. The smallest mandibular alveolus for *Diplocynodon* is the 9th, for *Hispanochampsia muelleri* the 8th and 9th. The 11th and 12th alveoli are the largest in *Hispanochampsia muelleri*, *D. hantoniensis*, *D. tormis*, and *D. ratelii*, but in *D. darwini* the 12th followed by the 13th are the largest. The data matrix in Appendix 2 contains the coding for three new characters following Brochu's revised matrix (2004) for all the diplocynodontine members. The variation observed in *Diplocynodon* has led to some discrepancies with Brochu's original character scores for *Hispanochampsia* (see Appendix 2). Such observations reinforce the phylogenetic position of *Hispanochampsia* as a member of Diplocynodontinae.

The significance of this monophyletic group (Diplocynodontinae) is based on synapomorphies shared by *Baryphracta deponiae*, *Hispanochampsia muelleri*, and *Diplocynodon* (*D. tormis*, *D. hantoniensis*, *D. darwini*, and *D. ratelii*): the construction of the iliac blade with a rounded and smooth dorsal border but a deep posterior tip (#28(4), Fig. 10), the posteriorly shifted axial keel of the spinal process (#6(0), unknown for *Hispanochampsia*), the ventral armor with bipartite ventral osteoderms (#39(2)), and a linear frontoparietal suture (#86(1), reverted in *D. ratelii*). Even coding significant postcranial characters in the data matrix as missing (#28 and #39) for *Hispanochampsia*, on the suspicion that fragmentary postcranial remains could potentially belong to a more complex crocodylian assemblage comprising a mixed sample of *Hispanochampsia* and *Diplocynodon*, the resulting cladograms place the Talladell species within Diplocynodon-

tinae, with *D. darwini* in a basal position as the sister group of the remaining *Diplocynodon* and *Hispanochampsia*. With the inclusion of *Hispanochampsia* and *Diplocynodon tormis*, the diagnosis of Diplocynodontinae is the same as was subscribed by Brochu in his monograph on Alligatoroidea (1999).

There is strong evidence for several characters to unite *D. hantoniensis*, *D. tormis*, and *D. ratelii*. These include an enlarged jugal foramen (#120), and the particular dentary occlusion of *Diplocynodon*, in line with the maxillary tooth row (#78), and are both shared by *Hispanochampsia muelleri*. The inclusion of this species within the clade *Diplocynodon* results in the blurring of the (*D. hantoniensis* + *D. ratelii*) diagnosis. Evidence supporting this clade is weakened without unique characters to diagnose the group (see also Brochu, 1999). The consensus tree reveals a polytomy in the definition of *D. hantoniensis*, *D. ratelii*, *D. tormis*, and *Hispanochampsia*. This latter taxon may be classified either as the sister group of (*D. tormis* + (*D. hantoniensis* + *D. ratelii*)) or as the closest relative of *D. tormis*.

To be consistent with the present result, the simplest solution would be to consider *Hispanochampsia* a synonym of *Diplocynodon* (i.e., *D. muelleri*). In so doing, we would relocate the Tàrrrega crocodile within its first attribution, suggested by Deperet (1906) and Bataller (1941). With *D. muelleri* and *D. tormis* in the definition of the genus *Diplocynodon*, its diagnosis differs from that given in Brochu (1999). *Diplocynodon muelleri* also possesses a set of characters that can be ascertained as derived: (#94) palatine anterior contour, and (#43) splenial excluded from mandibular symphysis with anterior tip passing dorsal to Meckelian groove. Additionally, specific differences between *D. muelleri* and *D. ratelii* or *D. tormis* can be endorsed. The premaxillary is laterally elevated rather than being low. Pits in the premaxillae for the reception of the mandibular teeth are lingually situated as opposed to those pits placed interlocked between premaxillary teeth, as in the species *D. tormis* and *D. ratelii*.

Bascalioni and colleagues (1992) argued against the monophyly of *Diplocynodon*. Although the consensus trees of their analysis was consistent with subsequent analyses (Brochu, 1997, 1999, 2004), which suggested a basal position for *D. darwini* relative to most other species of *Diplocynodon*, they were not



strongly supported because of the small sample size. Instead, the present analysis demonstrates the existence of a larger diplocynodontid clade that inhabited Europe during the Cenozoic. Nonetheless, the monophyly of *Diplocynodon* might not be sustained if one of the possible results on the phylogenetic interrelationships of diplocynodontines is taken into account in which *Baryphracta*, *D. darwini*, and *Hispanochampsia* could be the stem group of the remainder and species of *Diplocynodon*. In such a case, the proper solution should be the transferral of *D. darwini* to a new genus (instead of *Hispanochampsia*), leaving *Diplocynodon* as a genus that would have a natural meaning as well. Therefore, a revision of other Palaeogene European alligatoroids attributed as *Diplocynodon* sp. is still required.

In this sense, Buscalioni and colleagues (1992), Ginsburg and Bulot (1997), Pereda-Suberbiola and colleagues (2001), and Hua (2004) have compared specimens found in different localities, ranging in age from Palaeocene to Miocene, addressing the variation and variability of features of *Diplocynodon*. A robust solution is required to the long-standing problem of the monophyly of *Diplocynodon*, not only through the revision of all its putative species (*D. darwini*, *D. ratelii*, *D. gervaisi*, *D. hantonienensis*, *D. tormis*, *D. stryriacus*, *D. levantinum*, and *D. dalpiazii*, etc.; Franco et al., 1992; Rauhe & Rossmann, 1995; Ginsburg & Bulot, 1997) within a phylogenetic framework, but also by reassessing character definitions and character states for the sake of clarifying their phylogenetic interrelationships. The diversification of the Diplocynodontinae was significant in European freshwater ecosystems for more than 60 million years, thus providing a vast fossil record that can be stratigraphically traced.

On the scale of the Iberian Peninsula, diplocynodontines have been recorded throughout the Duero and Ebro Basin localities. The species *Diplocynodon tormis* ranges from the lower Eocene to the lower Oligocene in the Duero Basin (Ortega & Buscalioni, 1992). Localities from the Ebro Basin ranging from the Oligocene to the lower Miocene have provided crocodylian material attributed to '*Diplocynodon* sp.' as in the cases of the material from Tudela and Bardenas Reales in Navarra (Lower Miocene) (Crusafont et al., 1966; Pereda-Suberbiola et al., 2001; Murelaga et al., 2002). The material from Tudela (an almost complete skull) and Navarra (isolated cranial and mandibular fragments) shows striking similarities to that of *Diplocynodon muelleri*. The shortness of the mandibular symphysis, reaching the third alveolus, is a good example. On a local scale, the hypothesis of two related species inhabiting different Basins of the Iberian Peninsula, those of the Ebro and the Duero, should be not discounted.

Finally, *Diplocynodon muelleri* provides evidence about the diversification of European Diplocynodontinae, contributing to the debate about vicariant versus dispersal paleobiogeographical hypotheses in Europe and North America during the Cenozoic (Buscalioni et al., 1997, 1999, 2003; Brochu, 1999, 2003, 2004; Kotsakis et al., 2004). Since *Diplocynodon muelleri* can no longer be considered an alligatorine, the evolutionary history and biogeography of the Tertiary European Alligatorinae (*Arambourgia* and *Allognathosuchus haupti*; Brochu, 2004) must be explained independently. Whether any dispersal event from North America to Europe took place or not depends on the final understanding of the phylogenetic relationships of *Acynodon polyodon* and *Musturzabalsuchus buffetauti*. These Late Cretaceous taxa were considered as basal Globiodonta. The affinities of *Acynodon* and *Stangerochampsa* and the basal position of *Musturzabalsuchus* within Alligatoridae suggested the occurrence of an ancient European stock, and a vicariant event between North America and Europe during the Late Cretaceous (Buscalioni et al., 1999).

#### LIFE RESTORATION OF *DIPLOCYNODON MUELLERI*

The Oligocene macroflora from Tàrrrega and Cervera (Ebro Basin) has allowed the restoration of the Oligocene Ebro Basin

palaeoclimate. The main vegetal community corresponds to tropical-deciduous forest (Sanz de Siria, 1996a,b). *Diplocynodon muelleri* inhabited lakes and ponds of fresh to oligosaline waters, which evolved under a subtropical, warm climatic regime with an average temperature between 22° C and 26° C, and closed drainage conditions.

*Diplocynodon muelleri* was a small alligatoroid, covered by thick dorsal and ventral dermal armor (Fig. 9). Largest individuals are approximately 1.5 m in total length, with skull lengths of approximately 180 to 250 mm. The hind limbs are more massive than the forelimbs. Pedal digits show massive phalanges and digits, which are large in comparison with manus phalanges and digits. The trunk is wide and dorsoventrally compressed, and correspond to 25% of the body length. As in *Diplocynodon darwini*, the trunk is slightly less than twice the skull length. There is no indication about either the shape or size of the tail.

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APPENDIX 1. Specimens attributed to *Diplocynodon muelleri* (= *Hispanochampsia muelleri*) studied in this article.

**AS:** 1. Plate with nearly complete, entirely fractured skeleton. **CEP:** (The first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá records three specimens without serial number; we examined four specimens in this collection): 1. Skull table in dorsal view; 2. Skull table in ventral view; 3. Undetermined limb-bone fragment; 4. Skull fragment. **CLFC:** 2301. Skull in dorsal view. **CM.** This material is not mentioned in the first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá. Official cataloguing of this material is being undertaken by Oriol Saula, curator of the Museu Comarcal de l'Urgell, Tárrega, Lleida, Spain. Montmelo collection (Barcelona, Spain) comprises, among other specimens: CM1. Skull; CM2. Skull lacking the rostral part; CM3. Basioccipital; CM4. Posterior fragment of skull; CM5. Occipital region; CM6. Skull; CM7. Maxilla; CM8. Skull; CM9. Skull table; CM 10. Scapula. **DPUAB.** The first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá records five specimens: 30736, 30740, 30748, 30760, 30766. The collection actually contains the following material without serial number and no other material of *Hispanochampsia* belonging to the Department collection is known (personal observation at DPUAB and Pons-Muñoz, pers. comm.): 1. Right femur. **IEI:** 74. Skull without rostrum in dorsal view and lower jaw fragments. **IGME:** 1565N. Slab with skull in dorsal view (holotype of *Diplocynodon guerini*); 1567N. Slab with lower jaw and skull fragments; 1764N. Lower jaw fragments; 1568N. Slab bearing a compressed skeleton of a juvenile individual with skull turned upside down in dorsal view and ventral osteoderms exposed; 745N. Counter-slab of 1568N specimen (holotype of *Diplocynodon marini*); 712 N. Lower jaw fragments; 7N. Fattened skull and lower jaw fragments. **IPS.** The first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá records three specimens

without serial number. The collection actually features only the following material and no other material is known (personal observation in Sabadell and Angel Galobart, pers. comm.): 5804. Skull in dorsal view, left lower jaw and osteoderms. **MCT**: 1521. Osteoderms; 1522. Osteoderms and cranial fragments; 1523. Cranial fragments; 1524. Portion of rostrum; 1525. Osteoderms fragments and fragmented right lower jaw; 1526. Osteoderms and fragmented vertebrae; 1527. Lower jaw fragments; 1528. Skull in ventral view and portion of the right lower jaw; 1529. Left and right lower jaw disarticulated; 1530. Fragmented maxilla; 1531. Skull in dorsal view and right lower jaw; 1532. Dorsal posterior osteoderms; 1533. Disarticulated lower jaw, osteoderms, ribs, limb bones; 1534. Ventral maxillary portion; 1535. Skull in ventral view and fragmented lower jaw; 1536. Counter-slab of the previous specimen with fragments of lower jaw; 1537. Left and right femora, pubic bones, osteoderms, sacral vertebrae; 1553. Bone fragments; 1555. Bone fragments. **MGS**: 26422 and 26423. Isolated teeth and osteoderms; 26424. Anterior portion of skull in dorsal view; 26425. Skull in dorsal view; 26426. Lower jaw in ventral view; 26427. Skull fragments in dorsal view; 26428. Bone fragments, osteoderms and left coracoid; 26429. Skull in ventral view and associated tortoise fragments; 26430. Osteoderms and bone fragments (three plates); 26432. Osteoderms; 26433. Bone fragments. **MMB**. An official catalogue of the Martorell Museum has been published (Gómez-Alba, 1997). The first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá records ten specimens attributed to *Hispanochamps* in this collection that were not found during our examination of the collection: 4157-1, 4157-2, 4189, 9300, 9351, 9360, 9408, 9424, unnumbered-1, unnumbered-2. Conversely, three specimens not mentioned in this catalogue have been observed: 33147, 33146, 9438. The collection currently consists only of the following material. No other *Hispanochamps* material belonging to the MMB collection is known (personal observation at the Museu de Geologia "Martorell" in Barcelona, and Julio Gómez-Alba, pers. comm.). One asterisk refers to specimens not mentioned in the Gallemì-Moyá catalogue, but mentioned in the published catalogue (Gómez-Alba, 1997) and observed by us. Two asterisks refer to specimens that are mentioned in the published catalogue but have not been studied. Three asterisks refer to all specimens mentioned also by the Gallemì-Moyá catalogue: \*\*4157-1. Plate with skull portion in ventral view, mandible and vertebral fragments; \*\*4157-2/3. Cranial fragment; \*\*\*9289. Right posterolateral cranial fragment; \*\*\*9292. Skull fragment; \*\*\*9294. Skull fragment. \*\*9300. Vertebral centrum; \*\*\*9303. Skull fragments; \*\*9351-1/2. Bone fragments and isolated teeth labelled as "*Diplocynodon* 690. Oligoceno. Tàrraga."; \*\*9360. Cranial fragment in ventral view; \*\*\*9390. Lower jaw fragment; \*\*\*9406. Skull and lower jaw fragments; \*\*\*9420. Lower jaw fragment; \*\*9424. Skull in dorsal view; \*\*\*9426. Two cranial fragments. (divided in the published catalogue (1997) into 9426-1 and 9426-2); \*\*9428. Posterior cranial half in dorsal view, \*\*\*9429. Skull in ventral view; \*\*\*9430. Osteoderms and limb bones; \*\*\*9431. Skull in ventral view lacking the anterior part of rostrum; \*\*\*9433. Bone fragments; \*\*\*9434. Skull and both left and right lower jaw; \*\*\*9434-1. Palate fragment; \*\*\*9435. Left and right lower jaw; \*\*\*9437. Skull in ventral view and lower jaw; \*9438. Skull in ventral

view; \*\*\*9440. Skull in dorsal view; \*\*\*9441. Right maxillary fragment; \*\*\*20.823. Skull fragments; \*\*\*20.826. Skull fragment with lower jaw fragment; \*\*\*20.827. Maxillary fragment; \*\*\*25.924. Osteoderms; \*\*27150. Bone fragments; \*\*\*28.126. Skull in dorsal view; \*\*\*28.127. Skull in ventral view (probably the counter-slab of the next specimen); \*\*\*28.128. Skull and both left and right lower jaw; \*\*\*28.129. Skull in dorsal view without rostrum; \*\*\*28.130. Skull in dorsal view; \*33145. Skull in dorsal view and disarticulated lower jaw; \*33146. Skull in ventral view (probably in the unpublished catalogue it is "s/n: crani en vista ventral"), \*33147. Lower jaw fragment showing mandibular fenestra; \*\*33148. Cranial bone fragment and teeth; \*\*33149-1/3. Isolated teeth. **NMB**. The first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá records four specimens: 4, 73, 74, 76. The collection currently contains the material described below. No other material of *Hispanochamps* is known (personal observation in Basel and Engesser, pers. comm.): Spa 4 = "T1". Holotype (Kälin, 1936:5). Plate with skull in dorsal view; ventral view also preserved; Spa 73 = "T2". Paratype: dorsoventrally compressed skull with associated lower jaw. **CJFV**. The first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá records four specimens from the private collection, "Collecció Josep de Villalta, Barcelona, Spain"; all of which lack a serial number: 1. anterior skull fragment in dorsal view. 2. anterior skull fragment in ventral view. 3. rib fragment, osteoderms and distal portion of a femur. 4. isolated teeth. This material has not been examined. **BMNH**: The first palaeontological catalogue of El Talladell fossils compiled by Gallemì and Moyá reports no *Hispanochamps* specimens from the London Natural History Museum. However, material belonging to *Hispanochamps* has been observed at BMNH: R3942, skull in dorsal view; R3943, skull fragments; R3944, lower jaw in lateral inner view; R3945, skull and lower jaw in ventral view; osteoderms with associate postcranial elements. It was described the frontoparietal suture as not entering the supratemporal fenestra in BMNH R3492 (Brochu, 1999:80). The frontoparietal suture of all observed *Hispanochamps* specimens deeply penetrates the supratemporal fenestra; in BMNH R3942 is actually difficult the evaluation of frontoparietal suture.

APPENDIX 2. Character coding is based on Brochu's 2004 matrix (including his new characters 165, 166 and 167). Together with the character coding of *Diplocynodon muelleri* here we provided for the first time the one of *Diplocynodon tormis*. It has been revised the coding of characters 165–167 for *D. darwini* [012] based on: 1) ME5360 (Hessisches Landesmuseum, Darmstadt, Germany), and 2) Berg (1966, fig 2, pag. 25). *D. ratelii* [012] based on 1) Vaillant (1872, PL 4), 2) SG549 (Musée National d'Histoire Naturelle, Paris, and 3) Buscalioni (1986). *D. hantoniensis* [012] based on BMNH R30392 mandible, and Berg (1966:fig. 9).

#### *Diplocynodon muelleri*

????? ????? ????? ?1?? ?01?? 1?4?? ?011 0??21 ??200 ?0111 101??  
 ????? 11?00 ?0111 00?0 12100 0?011 01311 1012? 00?00 ?0001 00000  
 101?0 00111 ?1000 ?0??2 1??0? ?011 00001 00100 01?? ???? 0 0??01 2

#### *Diplocynodon tormis*

????? ????? ????? ?1?? ???? ???? ???? ???? ???? ???? ???? ???? ????  
 1?0?0 00111 00101 12100 00011 01311 1002? 0?000 1000? ?0000 101?? 00111  
 01000 00?12 0010? 1?011 00001 0?100 01?? ???? ?0?01 2