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First cranial remains of *Cheirogaster richardi* (Testudines: Testudinidae) from the late Miocene of Ecoparc de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula): taxonomic and phylogenetic implications

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Abstract

Although skulls of extinct Testudinidae are generally much scarcer than shell remains, when available they provide important data for resolving taxonomic and phylogenetic problems. This is illustrated here based on two well-preserved giant tortoise skulls from the early Vallesian (MN9, late Miocene) of Ecoparc de Can Mata (ECM; els Hostalets de Pierola, Vallès-Penedès Basin, NE Iberian Peninsula). These specimens, referable to the extinct genus *Cheirogaster*, differ significantly from *Cheirogaster bolivari* and are assigned to *Cheirogaster richardi*, whose cranial morphology was previously unknown. This nominal taxon had been considered a junior subjective synonym of *C. bolivari*, due to a previous neotype designation for the former, based on shell remains, that did not met the requirements of the *International Code of Zoological Nomenclature*. Such designation is here considered invalid because it was based on material from a different geographic area, even though remains from the original type locality area were available. Given that the holotype of *C. richardi* (from the early Vallesian of els Hostalets de Pierola) had been destroyed, to clarify the taxonomic status of this taxon we designate one of the two ECM skulls as the neotype of the species. On its basis, an emended diagnosis is provided, which leads us to conclude that two different species are recorded from the Iberian Miocene: *C. bolivari*, from the middle Aragonian of inner Iberian basins; and *C. richardi*, from the latest Aragonian and Vallesian of the Vallès-Penedès Basin. Additional cranial material of *Cheirogaster* from inner Iberia would be required to clarify whether these species display a distinct geographic distribution and/or a different chronostratigraphic range. A cladistic analysis of the Testudinidae based on cranial morphology supports a sister-taxon relationship between *Cheirogaster* and *Centrochelys*. Overall, our results highlight the significance of cranial morphology for attaining a better understanding of turtle taxonomy and phylogenetic relationships.

Keywords: giant tortoises; testudinids; taxonomy; phylogeny; *Cheirogaster bolivari*; early Vallesian.

Introduction

Testudinids

There are 331 extant species of turtles (order Testudines), of which 250 belong to the suborder Cryptodira and 81 to the Pleurodira (Turtle Taxonomy Working Group 2012). Cryptodires are not only more diverse than pleurodires, but also geographically more widespread and adapted to a wider range of habitats (Marmi & Luján 2012), including marine, freshwater and terrestrial environments. Recent molecular analyses suggest that Testudines as a whole constitute a monophyletic clade, sister-taxon of the Archosauria, from which they would have diverged about 255 Ma (Crawford et al. 2012), although their oldest fossil record corresponds to the early Late Triassic, ca. 220 Ma (see review in Marmi & Luján 2012). Phylogenetic uncertainties remain regarding many groups of both extant and especially extinct turtles (Marmi & Luján, 2012). Thus, although Guillon et al. (2012) constitutes a huge effort to reconstruct the phylogeny of extant taxa based on molecular data, additional research is required to better resolve the relationships of some groups of living turtles at the genus level (Turtle Taxonomy Working Group, 2012).

With about 181 extant species (Turtle Taxonomy Working Group 2012), the cryptodire superfamily Testudinoidea constitute the most diverse group of turtles. They originated and began to radiate during the Cretaceous, with the several modern families having radiated early in the Paleocene (Lourenço et al., 2012). Among them, the exclusively terrestrial Testudinidae, with an almost world-wide distribution (except Australia and Anctarctica), have an excellent fossil record, although the lack of cranial material for basal representatives of several testudinid genera sometimes hampers a good resolution of their phylogenetic relationships (Marmi and Luján, 2012). Cranial remains of fossil testudinids, due to preservational reasons, are generally much scarcer than postcranial remains (especially shells or shell fragments). As a result, many extinct species are only known based on shell remains, which may hamper an adequate evaluation of their phylogenetic relationships as well as alpha-taxonomy. The fragmentary nature of fossil remains therefore explains why the taxonomy of many extinct testudinids is biased in favour of shell features. When available, however, cranial morphology arguably provides a very valuable source of phylogenetic information, and it further has the potential to help in the resolution of long-lasting taxonomic problems. This is illustrated here on the basis of two remarkably-complete skulls of the giant extinct testudinid genus *Cheirogaster* Bergounioux, 1935 (preliminarily reported by Luján et al. 2010, 2011), which were recovered thanks to the palaeontological intervention that was carried out during the construction of a road and a recycling plant (Ecoparc de Can Mata, ECM) in els Hostalets de Pierola (Alba et al. 2011, 2012; Carmona et al. 2011; Luján et al. 2010, 2011), close to the Abocador de Can Mata (ACM; Alba et al. 2006, 2009, 2011).

The genus *Cheirogaster*

The evolution of gigantism among tortoises is clearly a homoplastic phenomenon, generally regarded as an adaptation to either local or global environmental changes (Kear, 2010). In particular, the evolution of giant tortoises has been related to climatic cooling and associated changes in vegetation, since larger body masses enable the maintenance of a higher metabolism through inertial homeothermy and further provide space for the voluminous fermentative gut necessary for the consumption of grasses (Kear, 2010). In spite of this, giant testudinids are currently restricted to oceanic islands, so that in Western Europe only three small-sized species of testudinids (belonging to the genus *Testudo*) can be found. In contrast, medium to large-sized terrestrial tortoises are frequently recorded from Cenozoic deposits of Europe. Most of them are currently classified in the extinct genus *Cheirogaster*, of which fourteen distinct species may be recognized (see Tables 1 and 2). *Cheirogaster* species are generally represented by shells and other postcranial remains, and only more exceptionally by cranial remains (see Tables 2 and 3).

The genus *Cheirogaster* is apparently restricted to Europe (Lapparent de Broin 2002), whereas both extinct and extant large terrestrial tortoises from mainland Africa and Asia are classified into different genera (Lapparent de Broin 2002): *Centrochelys* Gray, 1872 and *Stigmochelys* Gray, 1873 from Africa, and *Manouria* Gray, 1854 and *Geochelone* Fitzinger, 1835 from Asia. Even though the earliest representatives of *Cheirogaster* correspond to the Late Eocene and Oligocene of France (Broin, 1977; Lapparent de Broin, 2001; Danilov, 2005), the genus mostly diversified during the Miocene, becoming widespread throughout Europe. Such diversification was accompanied by an increase in size and the development of a tough armour constituted by a large number of osteoderms (Lapparent de Broin 2002). During the late Miocene and Pliocene, the geographic distribution of *Cheirogaster* was mostly restricted to southern Europe (Lapparent de Broin 2002). They also colonized several Mediterranean islands, where they evolved insular adaptations (loss of osteoderms, and lightening and modification of the plastron and carapace; Lapparent de Broin 2002). The largest forms correspond to the mainland species (Kear 2010), and appear more or less simultaneously between the late Miocene and the Pleistocene in several places, suggesting that this was an adaptive response to environmental deterioration that occurred independently in several lineages (Kear & Georgalis 2009).

The genus *Cheirogaster* in the Iberian Peninsula

Two different species are customarily recognized in the fossil record of mainland Iberian Peninsula (see Table 3 and Fig. 1), *C. bolivari* Hernández-Pacheco, 1917b and *C. richardi* (Bergounioux, 1938), although the taxonomic status of the latter has been questioned during the last decade (Jiménez Fuentes et al. 2000). *Cheirogaster bolivari* was erected on the basis of remains from the middle Miocene (MN5-MN6) of Alcalá de Henares in the Madrid basin (Hernández-Pacheco 1917b; Royo y Gómez 1935b), whereas *C. richardi* was erected somewhat later on the basis of material from the late Miocene (MN9) of els Hostalets de Pierola (Bergounioux 1938, 1958). Both taxa were originally erected within the genus *Testudo*, which at that time hosted a group of taxa now considered paraphyletic (for the current definition of *Testudo*, see Fritz &

Bininda–Emonds 2007). Loveridge and Williams (1957) suggested that all European giant tortoises should be transferred into the genus *Geochelone*, originally erected for the extant species *Geochelone stellata* (Schweigger, 1812), a junior synonym of *Geochelone elegans* (Schoepff, 1795) (see Fritz & Havaš 2007). For the two Iberian taxa, such taxonomic proposal was subsequently adopted by several authors during the following decades (Auffenberg 1974; Jiménez Fuentes & Carbajosa Tamargo 1982; Cuesta et al. 1983; Jiménez Fuentes 1984). Bourgat and Bour (1983) first suggested that these species, together with *Testudo perpiniana* Depéret, 1885, should be transferred to the genus *Cheirogaster* s.l., even though they did not formally propose the new combinations. Jiménez Fuentes (1984) still attributed the two Iberian species to *Geochelone*, but subsequently he soon transferred them to *Cheirogaster* s.l. (Jiménez Fuentes et al. 1986, 1988c), a proposal that has been followed by most subsequent researchers.

Over the years, abundant fossil remains of *Cheirogaster* have been recovered from the Aragonian and Vallesian (middle to late Miocene) of the inner Iberian basins (Hernández-Pacheco 1917a,b, 1921; Gómez-Royo 1935a,b; García & Alberdi 1968; Jiménez Fuentes 1971, 1984, 2000; Jiménez Fuentes & Carbajosa Tamargo 1982; Cuesta et al. 1983; Jiménez Fuentes et al. 1986, 1988a, 1988b, 1989, 1990). These remains mainly consist in shell and other postcranial material, generally attributed to *C. bolivari* (Aragonian remains) or *C. richardi* (Vallesian remains) (see Table 3). The cranial morphology of *C. bolivari* is known on the basis of a partial cranium from the middle Miocene (MN5-MN6) of Ciudad Universitaria (Madrid Basin), which has the same age than the original type locality, being described and figured by Royo y Gómez (1935b). The latter author further mentioned, but did not describe or figure, a partial cranium including the orbit from the late Miocene (MN9) of Arévalo in the Duero Basin, which he attributed to the same species. The knowledge on *Cheirogaster* from the Vallès-Penedès Basin is more restricted, being mainly limited to the citations provided by Bergounioux (1938, 1958; see also Bataller 1956), since subsequent finds from this basin (see Table 3) remain mostly unpublished (Checa Soler & Rius Font 2003; Alba et al. 2006, 2009, 2010; Blaya Martí 2007; Oró Badia et al. 2008; Rotgers et al. 2008; Luján et al. 2010, 2011; Carmona et al. 2011).

After a contorted nomenclatural and taxonomic history, more recently *C. richardi* has been considered either as a valid taxon (e.g., Lapparent de Broin 2002) or as a junior subjective synonym of *C. bolivari* (Jiménez Fuentes et al. 2000). Here we provide a detailed description of the *Cheirogaster* skulls from ECM, together with extensive comparisons with the available cranial material of other species of the genus *Cheirogaster*. The taxonomic implications of these skulls are discussed, with particular emphasis on the putative synonymy between *C. bolivari* and *C. richardi*. The remains described in this paper are therefore important for two related reasons: first, because they enable the first description of the cranial anatomy for *C. richardi*; and second, because the morphological details they provide indicate that this taxon is not a junior synonym of *C. bolivari*. Furthermore, an emended diagnosis of *C. richardi*, based on cranial features, is provided, and a phylogenetic analysis is performed to discern the phylogenetic relationships of the genus *Cheirogaster*.

Age and geological background

The local stratigraphic series of ECM (els Hostalets de Pierola, Catalonia, Spain) is situated in the Vallès-Penedès Basin (NE Iberian Peninsula; Fig. 2), a NNE-SSW-oriented, asymmetric half-graben, situated between the two Catalan Coastal Ranges (Cabrera & Calvet 1990; Bartrina et al. 1992; Roca & Guimerà 1992; Roca et al. 1999). The thick middle to late Miocene sedimentary sequences of the area of els Hostalets de Pierola mainly consist of red to brown mudstones, sandstones, breccias and conglomerates, which were deposited in the distal to marginal, inter-fan zones of two major coalescing alluvial fan systems (Moyà-Solà et al. 2009). Regarding age, the 170 m-thick local stratigraphic series of ECM (Carmona et al. 2011; Alba et al. 2012) is stratigraphically situated above the nearby ACM series (Alba et al. 2006, 2009, 2011; Moyà-Solà et al. 2009; Fig. 3), which corresponds to the latest middle Miocene (ca. 12.5 to 11.5 Ma; MN7+8, or MN7 and MN8 sensu Mein and Ginsburg 2002, latest Aragonian). Moreover, the ECM series overlaps with the nearby stratigraphic series of the Riera de Claret (Moyà-Solà et al. 2009), which records the MN8/MN9 (Aragonian/Vallesian) and middle to late Miocene transitions. In the area of els Hostalets, the Aragonian/Vallesian boundary is recorded between the two classical localities of Can Mata I and Can Mata III (Moyà-Solà et al. 2009; Fig. 3), both of which are stratigraphically situated below the ECM series (Luján et al. 2010, 2011; Carmona et al. 2011; Alba et al. 2012), thus indicating an early Vallesian (MN9, late Miocene) age for all the ECM localities. This is confirmed by magnetostratigraphic data from ECM, which indicate that all the stratigraphic series can be correlated to chron C5n (Alba et al. 2012), which is characteristic of the early Vallesian. On biostratigraphic grounds, it should be taken into account that latest Aragonian and earliest Vallesian faunas from the Vallès-Penedès Basin are virtually indistinguishable except for the presence in the latter of the hipparionin equid *Hippotherium* (Agustí et al. 1997, 2001; Casanovas-Vilar et al. 2006), which dispersed into this basin at 11.1 Ma (Garcés et al. 1996; Agustí et al. 1997, 2001). As such, the fact that this taxon has not been recorded yet at ECM (Carmona et al. 2011; Alba et al. 2012) would apparently stand in contradiction with the Vallesian age indicated by both litho- and magnetostratigraphic data. This taxon, however, was apparently quite rare during the earliest Vallesian, and in fact the presence of *Hispanomys aragonensis* at ECM confirms the Vallesian age of this series (Carmona et al. 2011; Alba et al. 2012). On the other hand, the lack of *Cricetulodon*, which dispersed into the Vallès-Penedès Basin at 10.4 Ma (Garcés et al. 1996; Agustí et al. 1997), would indicate a correlation of the ECM series to the local biozone MN9a of Agustí et al. (1997). On the basis of average sedimentation rates for the nearby ACM series, the ECM series would represent a time span of ca. 0.5 myrs, ranging from about 11.0 to 10.5 Ma (Carmona et al. 2011; Alba et al. 2012), which is consistent with the available biostratigraphic data. On this basis, the stratigraphic position of IPS43809a and IPS43810a (102 and 128 m along the 170 m-thick ECM series) would indicate estimated ages of 10.7 and 10.6 Ma, respectively.

Materials and methods

Nomenclature and taxonomy. The anatomical nomenclature employed in this paper is mainly based on Gaffney (1972), whereas the taxonomy used broadly follows Fritz & Havaš (2007), except for *Geochelone sulcata* (Miller, 1799), which is referred to the genus *Centrochelys*, following Lapparent de Broin (2002).

Abbreviations. CRARC: Centre de Recuperació d'Amfibis i Rèptils de Catalunya (Catalonia, Spain); **ICP**: Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona (Catalonia, Spain); **IPS**: acronym of the collections of the ICP (formerly Institut de Paleontologia de Sabadell); **NHMW**: Naturhistorisches Museum Wien (Paläontologogische Abteilung, Austria); **MN**, Mammal Neogene units; **MNCN-CSIC**: Museo Nacional de Ciencias Naturales – Consejo Superior de Investigaciones Científicas (Madrid, Spain); **MP**, Mammal Palaeogene units; **MSCB**: Museu del Seminari Conciliar de Barcelona (Spain); **STUS**: Sala de las Tortugas, Facultad de Ciencias de la Universidad de Salamanca (Spain); **MNHN**: Muséum National d'Histoire Naturelle (Paris, France).

Studied material and comparative sample. The studied material includes a skull with lower jaw (IPS43809a) and associated postcranial remains from a young individual and another skull with lower jaw preserved in two parts (IPS43810a) from an adult, which are housed at ICP. Both fossil and extant material from the following collections was examined by one of the authors (AHL) as comparative material: CRARC, IPS, NHMW, MNCN-CSIC, MSCB, STUS and MNHN. This comparative sample is mainly restricted to the genera included in the phylogenetic analysis (see Online Supplementary Material Appendix 1 for a complete list of specimens and bibliographic citations employed in the morphological comparisons). Particular emphasis was placed on the cranial fossil material of *Cheirogaster* spp.

Measurements and morphometric comparisons. To compare the shape of the two crania described here with those of other species of *Cheirogaster*, we performed two Principal Components Analysis (PCA). The total sample included six skulls: the two ECM crania (IPS43809a and IPS43810a), *Cheirogaster* sp. nov. from Epanomi, *C. perpiniana*, *C. schafferi* and *Cheirogaster* sp. from Thessaloniki. Material of *C. bolivari* could not be examined and published measurements were not available. To describe skull shape we used twelve metrical variables (A–F and H–M), shown in Fig. 4 and listed in Table 4. The PCA analyses were computed in the statistical package PAST (Hammer et al., 2001) for both the original raw variables and Mosimann shape variables. The latter are generated by dividig the original measurement by the geometric mean of all the measurements in each taxo or individual being analyzed (Mosimann 1970; Jungers et al. 1995). Minimum Spanning Trees (MST) were also computed in PAST with the PCA analyses.

Computed tomography. Computed tomography (CT) was employed to recognize internal anatomical structures of the two skulls described here. Several skulls from extant cryptodires, with particular emphasis on testudinids, were also CT-scanned for comparison. CT-scans were performed with a medical CT (Sensations 16, Siemens) at the Hospital Mútua de Terrassa (Barcelona, Spain). Scans were performed at 140

kV and 220 mA, obtaining 0.391 mm of pixel size and an output of 512x512 pixels per slice with an inter-slice space of 0.3 mm.

Phylogenetic analysis. We compiled a data matrix with 22 taxa and 66 cranial characters, to conduct a cladistic analysis at the genus level for deciphering the phylogenetic relationships of *Cheirogaster*. The data matrix includes 20 genera of Testudinidae (18 extant ones, plus the extinct *Cylindraspis* and *Cheirogaster*), as well as the geoemydids *Heosemys* and *Batagur*, which were included as outgroups. The data matrix was mainly based on that published by Gerlach (2001), with some modifications; the latter included the addition of *Cheirogaster*, based on the various species for which cranial remains are available (*C. bolivari*, *C. perpiniana*, *C. richardi*, *C. schafferi* and *Cheirogaster* sp. nov. from Greece), as well as the fusion of different species of the same genus—including *Testudo horsfieldi* Gray, 1844 and *Testudo kleinmanii* Lortet, 1883, together with *Testudo graeca* Linnaeus, 1758, into *Testudo* s.l.; furthermore, several character states were modified on the basis of observations on the comparative sample. Character statements have been reported in the Online Supplementary Material Appendix 2, whereas the data matrix employed (with 22 taxa and 66 characters) is reported in Online Supplementary Material Appendix 3 (see also Online Supplementary Material Appendix 4 for the corresponding nexus file). Two parsimony-uninformative characters (#12 and #59) were removed from the analysis. The analysis was performed with PAUP* 4.0b10 for Unix (Swofford 2003), by using maximum parsimony and the 'branch-and-bound' option; characters were treated as unordered, and multiple state characters were treated with the default option 'uncertain', which picks the character state that minimizes tree length. A strict consensus tree was computed, and clade stability was also assessed by means of Bremer's support (i.e., the extra steps required to collapse a clade in the consensus of near-most-parsimonious trees). The Consistency Index (CI), Retention Index (RI) and Rescaled Consistency Index (RCI) are reported to evaluate the level of homoplasy.

Systematic palaeontology

Order **Testudines** Linnaeus, 1758

Suborder **Cryptodira** Cope, 1868

Superfamily **Testudinoidea** Batsch, 1788

Family **Testudinidae** Batsch, 1788

Subfamily **Testudininae** Batsch, 1788

Genus ***Cheirogaster*** Bergounioux, 1935

Type species. *Cheirogaster maurini* Bergounioux, 1935.

Other included species. *Cheirogaster gigas* (Bravard, 1844), *C. eurysternum* (Gervais, 1848), *C. perpiniana* (Depéret, 1885), *C. leberonensis* (Depéret, 1890), *C. gymnesica* (Bate, 1914), *C. schafferi* (Szalai, 1931), *C.*

phosphoritarum (Bergounioux, 1935), *C. ginsburgi* (Broin, 1977), *C. bolivari* (Hernández-Pacheco, 1917b), *C. vitodurana* (Biedermann, 1863), *C. richardi* (Bergounioux, 1938), *C. steinbacheri* Hans-Volker, 1996, *Cheirogaster* sp. nov. (see Vlachos 2011).

Emended diagnosis. Medium to large-size testudinid with a triangular and broad cranium, and a long preorbital region relative to total cranial length. Distinguished from other testudinids (including *Centrochelys*) by the following autapomorphies: lower cranium; apertura narium externa anterodorsally oriented; posteriorly-situated zygomatic arch; and anteroposteriorly short fossa temporalis superior. Further distinguished from *Centrochelys* by several plesiomorphic shell features—including the marginal 4 less developed than marginal 5, the wider xiphiplastron, the non-projecting gulars, and the lack of xiphiplastral spykes—for which *Centrochelys* is autapomorphic.

Cheirogaster richardi (Bergounioux, 1938)

(Figs. 5–11)

1937 *Testudo richardi* Bergounioux; 793, nomen nudum.

1938 *Testudo richardi* Bergounioux; 271–282, figs 5–6.

1956 *Testudo richardi* Bergounioux; Bataller: 21.

1957 *Testudo richardi* Bergounioux; Bergounioux: 40.

1958 *Testudo richardi* Bergounioux; Bergounioux: 179–183, fig 17, pl. XXXIV.

1972 *Ergilemys richardi* (Bergounioux); Chkhikvadze: 54.

1974 *Geochelone (Geochelone) richardi* (Bergounioux); Auffenberg: 158.

1976 *Geochelone (Ergilemys) richardi* (Bergounioux); Mlynarski: 101–102, pl. 94–1.

1977 *Geochelone* ‘s.l’ (Bergounioux); Broin: 242.

1984 *Geochelone richardi* (Bergounioux); Jiménez Fuentes: 160–163, figs 1b–b’.

1986 *Cheirogaster* (s.l.) *richardi* (Bergounioux); Jiménez Fuentes et al.: 313–322, 3 figs.

1989a *Centrochelys richardi* (Bergounioux); Chkhikvadze: 48–50.

1989b *Centrochelys richardi* (Bergounioux); Chkhikvadze: 429–432.

1991 *?Cheirogaster richardi* (Bergounioux); Jiménez Fuentes & Martín de Jesús: 100.

1992 *?Cheirogaster richardi* (Bergounioux); Jiménez Fuentes: 88–99, fig. 3.

1993 *?Cheirogaster richardi* (Bergounioux); Jiménez Fuentes et al.: 12, fig. 7.

2000 *Cheirogaster bolivari* (Hernández-Pacheco); Jiménez Fuentes: 110–113.

2002 *Cheirogaster richardi* (Bergounioux); Lapparent de Broin: 126.

2003 *Cheirogaster bolivari* (Hernández-Pacheco); Jiménez-Fuentes: 193, fig 7.

2006 *Cheirogaster bolivari* (Hernández-Pacheco); Alba et al.: 303.

2010 *Cheirogaster* sp.; Luján et al.: 166–167, fig. 2.

Neotype. IPS43809a, skull (cranium with mandible; Figs. 5, 6, 9, 11) and associated postcranial remains from a young individual (Table S1 and Fig. S1), housed at the ICP.

Other referred specimens. IPS43810a, skull (cranium, preserved in two parts, with mandible; Figs. 7, 8, 10, 11) and associated postcranial remains from an adult individual (Table S1 and Fig. S1), housed at the ICP.

Emended diagnosis. Large-sized *Cheirogaster* species characterized by the following cranial apomorphies (as compared to species with known skull remains): elliptical premaxillary pit; very slender zygomatic arch; marked mediolaterial constriction of the prefrontal and frontal at the orbital level; larger and more dorsally-oriented fossa orbitalis; and straight and upwardly-inclined cranial dorsal profile (including the supraoccipital ridge). Plastron with a trilobate anterior margin (with a median protrusion), long gulars and straight pectoro-abdominal groove.

Differential diagnosis. *Cheirogaster richardi* differs from other species of this genus except *C. bolivari* in the trilobate anterior margin of the plastron with a median protrusion—instead of regularly concave to convex (not evaluable in *C. schafferi* and *Cheirogaster* sp. from Thessaloniki). It differs from other species of this genus for which the cranium is known (*C. bolivari*, *C. perpiniana*, *C. schafferi*, *Cheirogaster* sp. from Thessaloniki and *Cheirogaster* sp. nov. from Epanomi) in the five autapomorphies of the genus mentioned in the emended diagnosis. *Cheirogaster richardi* further differs from *C. shafferi* and *Cheirogaster* sp. from Thessaloniki in the smaller cranial size; and from *C. perpiniana* and *Cheirogaster* sp. nov. from Epanomi in the longer gulars and the straighter (instead of curved) pectoro-abdominal groove. Regarding species for which the cranium is unknown, *C. richardi* differs from most of them (except *C. vitodurana*, *C. steinbacheri* and *C. leberonensis*) in the larger shell size. It also differs from *C. maurini*, *C. gigas* and *C. vitodurana* in the obliquely-oriented (instead of transversely-aligned) humero-pectoral groove. It further differs from *C. maurini* in the regularly alternating octagonal and hexagonal neurals, the triangular (instead of rectangular) epiplastron, and smaller pectoral scutes; from *C. gigas*, in the more posteriorly situated anterior margin of the femoral scute (at the level of the inguinal axilla); from *C. phosphoritanum*, in the less developed nuchal notch; from *C. ginsburgi*, in the shorter pectoral scutes; from *C. steinbacheri*, in the triangular (instead of rectangular) pygal; from *C. leberonensis*, in the longer gulars and straighter (instead of posteriorly curved) pectoro-abdominal groove, and from *C. gymnesica*, in the more dorsally-orientedanterior margin of the plastron and the more developed osteoderms.

New type locality. Local stratigraphic series of Ecoparc de Can Mata (ECM; Figs. 1 and 3), sector VCE-B (els Hostalets de Pierola, Barcelona, Catalonia, Spain), metre 102 of the local stratigraphic series.

Occurrence. The neotype has an estimated age of 10.7 Ma (*Hipparion* s.l. + *Megacritetodon ibericus* Concurrent range zone, early Vallesian, late Miocene; see Casanovas-Vilar et al. 2011), and the known range

of the species (see Table 3) includes the latest Aragonian (MN7+8, middle Miocene) and the Vallesian (MN9-MN10, late Miocene). The species is recorded in the Vallès-Penedès Basin (see Table 3), whereas its occurrence in inner Iberian basins is currently uncertain.

Description

Preservation. The neotype IPS43809a (Figs. 5, 6) is a well-preserved, slightly dorsoventrally-flattened skull including both the cranium and the mandible. The left portion of the cranium is damaged, because the quadratojugal, parietal and frontal have been partially eroded, whereas the prootics are almost not preserved at all, and the quadrate and squamosal are completely missing; the left opisthotic and vomer have been only partially preserved posterolaterally. The mandible is well preserved, but attached to the cranium and laterally displaced to the left (the right dentary is interpenetrated for a few millimetres with the left maxilla). This hinders the evaluation of some anatomical structures on the right side of the cranium in palatal view. This cranial remain was found articulated with cervical vertebrae (see Table S1 and Fig. S1), as well as in close spatial association with plastron and carapace fragments (in such a poor condition that they cannot be even prepared) and several forelimb bones (see Table S1 and Fig. S1), which presumably belong to the same individual.

IPS43810a (Figs. 7, 8) is a complete skull, preserved in two parts, which was found on the same stratigraphic level than IPS43809a. The basal portion further preserves the mandible attached to the base of the cranium. The left squamosal, quadrate, jugal, and quadratojugal are missing, whereas the left maxilla and mandible are partially eroded. The left otic region has been preserved relatively well, including the prootic, supraoccipital, quadrate and opisthotic, in spite of the fact that these bones are quite fractured and have a superficially eroded surface. The right side of the cranium only preserves the squamosal well. The mandible is preserved, but not in perfect condition, further being partially covered by sediment. This skull was also found associated with a several postcranial remains (see Table S1 and Fig. S1), which presumably belong to the same individual.

Measurements. The skulls are about 10 cm long; see Table 4 for cranial measurements.

Skull roof elements. The skull roof elements, formed by the prefrontals, frontals, parietals and a small portion of the supraoccipital, define a very low and triangular skull, with the roofline of the braincase descending anteriorly.

The prefrontals are preserved in the two specimens (Figs. 6C, 8C), although on the right side of IPS43010a this bone is quite damaged and deformed (Figs. 7C, 8C). This element contacts the maxilla laterally, the frontal dorsoposteriorly, the premaxilla anteriorly, and the vomer and palatine

ventrally. The dorsal plate of the prefrontals, which forms the dorsal rim of the apertura narium externa, is reduced by the anterior development of the frontals (Figs. 6C, 8C). The prefrontal forms the anteromedial portion of the orbital margin. The descending process of the frontal forms the posterolateral wall of the fossa nasalis and the anterior wall of the fossa orbitalis (Figs. 5E, 6E), which is large. In the fossa nasalis, the descending posterior walls are separated in the lower portion, and in IPS43809a, despite the considerable amount of matrix still present, it is clear that it forms a wide ethmoid fissure (Fig. 9A–B). The frontals are well preserved in the two available skulls (Figs. 6C, 8C). This bone contacts the prefrontal anteriorly, the parietal posteriorly and the postorbital posterolaterally. In dorsal view, the frontals display an approximately triangular shape (they become narrower posteriorly), deeply entering the prefrontals (Fig. 5C, 6C, 8C, 8C). The former constitute most of the dorsal margin of the orbit. On the ventral surface of the frontals, the ventromedial process defining the sulcus olfactorius by parasagittal ridges is covered by sediment (Fig. 10B,C) and the CT-scans do not allow us to determine its shape (Figs. 9D–E, 10C), although most likely it was opened ventrally.

The parietals are well preserved, although the descending flanges are highly eroded and fractured (Figs. 5C, 7C). The parietals contact the frontals anteriorly, the postorbitals anterolaterally, the supraoccipital posteriorly and each other medially. Dorsally, the posterolateral process extends from the postorbital to the long supraoccipital spine (Figs. 6C,E, 8C,E). The parietal does not overhang the upper temporal fossa, but only contributes in forming the zygomatic arch (Figs. 6C, 8C). The descending process of the parietal contacts the pterygoid and the prootic dorsolaterally, and laterally it does not overlap the prootic and does not contact the squamosal (Figs. 6C, 8C, 11C).

The jugals are preserved (Figs. 6E,F, 8E,F), although badly damaged in IPS43010a (Figs. 5E,F, 7E,F). This bone contacts the maxilla anteroventrally, the postorbital dorsolaterally and the quadratojugal posteriorly, forming the anteroventral orbital rim, the posteroventral rim of the zygomatic arch and the anterodorsal rim of the cheek emargination (Fig. 6E,F, 8E,F).

The quadratojugal is poorly preserved in the two available skulls from ECM (Figs. 5E,F, 7E,F). This bone, which constitutes the dorsal rim of the cheek emargination, contacts the jugal anteroventrally, the postorbital dorsoanteriorly, the quadrate laterally, and the squamosal posteriorly. Dorsally, the quadratojugal overlaps the quadrate, contacting the squamosal, but does not contribute to the tympanic cavity (Figs. 6E, 8E).

In both available specimens, the squamosals are only partly preserved (Figs. 5C, 7C). This bone, which forms the lateral portion of the temporal emargination, contacts the quadratojugal anteriorly, the quadrate dorsoanteriorly, the opisthotic dorsomedially, and the pterygoid ventromedially. The

CT-scans enable us to observe that the antrum postoticum is very large, being largely constituted by the squamosal (Fig. 9F).

The postorbitals, which are well preserved in the two skulls (Figs. 5C, 7C), contact the frontal anterodorsally, the parietal dorsoanteriorly, the jugal anteroventrally and the quadratojugal posteroventrally. This bone constitutes most of the zygomatic arch, which is slender and quite posteriorly situated (6C, 8C).

Palatal elements. The premaxillae are preserved in both specimens, although only partially on the right side of IPS43010a (Fig. 7A). They contact the maxilla laterally and the vomer posteriorly, forming the anterior portion of the triturating surface. In dorsal view, the premaxillae slightly (but clearly) protrude from the anterior profile of the cranium, because their anterior surface is thickened and swollen at the level of the interpremaxillary suture (Figs. 5C, 7C). On the triturating surface, the premaxillary ridge is absent (Figs. 5D, 11A). An ellipsoidal, moderately deep premaxillary pit can be discerned in IPS43809a, being surrounded by the labial ridge anteriorly and by the transverse ridges posterolaterally (Fig. 11A). The foramen praepalatinum, only visible in IPS43809a (Fig. 11A), is located on the posterior portion of the premaxilla, outside the triturating surface of palate, and is larger than the nutritive foramina of the cranium. The transverse ridges are well developed in IPS43809a (not visible in IPS43810a), being located close to the maxilla-premaxilla suture (Fig. 11A), instead of clearly on the premaxilla. Despite the breakage of the ventral rim of the premaxilla, the probable presence of a central premaxillary cusp is betrayed by the above-mentioned thickening and general robustness of the medial portion of the premaxillae along the midline suture (Fig. 11A). The cusp corresponding to the premaxillary-maxillary suture is not clearly visible, but again, the robustness of the area surrounding the suture (Figs. 5A, 7A) indicates the possible presence of such cusp. Although the ventral edge of the premaxilla is not perfectly preserved, a crenate notch is discernible in IPS43809a (Figs. 5A, 7A).

The maxilla is relatively well preserved in the two available specimens (Figs. 5A,E, 7A,E), although in IPS43010a it is partially broken and obscured by sediment. It contacts with the premaxilla anteromedially, the palatine medially, the pterygoid posteromedially, the jugal posterolaterally and the prefrontal dorsally. The triturating surface of the maxilla widens posteriorly to a notable extent (Fig. 6F). On the triturating surface of IPS43809a, three different ridges can be appreciated (Fig. 11A): labial, median maxillary and lingual. The median maxillary ridges develop longitudinally between the labial and lingual ridges, being restricted to the maxilla and meeting the transverse ridge onto the premaxillary-maxillary suture. These ridges are clearly denticulate (Figs. 5D, 7D, 11A). The lingual ridge becomes wider in posterior direction, being developed on the maxilla between the palatine and the medial maxillary ridge, and merging with the transverse ridge

at the premaxillary-maxillary suture. Moreover, in the ECM specimens these lingual ridges further display, like the median maxillary ones, a denticulate morphology. In the two available crania, the labial ridges constitute the lateral borders of the triturating surface (Fig. 11A). It is unclear whether the small serrations shown by the maxillary portion of the labial ridge (Figs. 5E, 7E) reflect the original morphology or whether they are at least partly the result of erosion. In lateral view, the ventral edge of the maxilla is moderately concave in the two available specimens. The posterior maxillary process is well developed in the two specimens (Figs. 5E, 6E, 7E, 8E).

The vomer is not well preserved in any of the two specimens (Figs. 5D, 7D, 11A): in IPS43810a, the anterior margin is missing, whereas in IPS43209a half of it is lacking. This bone contacts the premaxilla anteriorly, the maxilla ventrolaterally, the prefrontal anterodorsally, the palatine laterally and the pterygoid posteriorly. The medial vomerine ridge, situated in the middle of the ventral portion of the vomer, is very narrow and quite high (Fig. 11A). The vomer divides the palatine but not the pterygoid (Fig. 6D). Although the contact vomer-basisphenoid is absent from both skulls, among land tortoises this character apparently shows a high degree of intraspecific variability (À.H.L., pers. obs. based on the comparative sample). The preservation of the palatines is poor: they are partially broken off in IPS43810a (Fig. 7D), and only partially preserved and fractured in IPS43809a (Fig. 5D). This bone contacts the prefrontal anteriorly, the maxilla laterally, the vomer medially, and the pterygoid posteriorly. The medial edges of the palatine form the anterior and medial rim of the internal choanae (Figs. 5D, 6D, 11A). The palatine is divided into two distinct areas (Figs. 5D, 11A): an anteromedial plate that contacts the maxilla and participates in the formation of the foramen orbito-nasale; and a wider posterolateral plate that participates in the formation of a small posterior palatine foramen. Towards posterior, the maxillary-palatine suture does not follow the medial limit of the trituration surface, but is more laterally situated (Figs. 5D, 11A). As a result, the portion of the posterolateral plate bearing the posterior palatine foramen is situated on the same plane than the rest of the trituration surface, instead of being more dorsally situated. The posterior palatine foramen is small and elongate, being completely enclosed by the palatine (Figs. 6D, 11A).

The pterygoids have been partially preserved in both specimens (Figs. 5D, 7D). This bone contacts the vomer and palatine anteriorly, the maxilla anterolaterally, the parietal dorsally, the basisphenoid and basioccipital posteromedially, the quadrate posterolaterally and the prootic posterodorsally. The anterolateral portion of the bone is represented by a very thin projection that forms the medial rim of the fenestra subtemporalis and contacts the maxilla for a few millimetres (Figs. 5D, 6D, 11A). Although the posterior part of the pterygoid is poorly preserved, in IPS43810a the processus interfinestralis of the opisthotic is covered by the pterygoid (Figs. 7F, 11B). The

pterygoid ridge, located on the parietal, the pterygoid and quadrate, dorsally merges with the processus inferior parietalis (Fig. 11C). At the anterolateral margin of the pterygoid, the external pterygoid process is quite small (Figs. 5D, 7D, 11C). The medial part of the preserved pterygoid (Figs. 5D, 6D) shows the typical dorsal concavity found in tortoises with a highly vaulted palate (Meylan & Sterrer 2000). No foramen caroticum laterale is present on the pterygoid.

Palatoquadrate and braincase. The quadrates are in relatively poor condition in both specimens (Figs. 5C, 7C); thus, the left quadrate of IPS43809a is partly broken away, and the condylus mandibularis is displaced anteromedially in both sides. This bone contacts the quadratojugal anterodorsally, the opisthotic posteromedially, the squamosal posteriorly, the prootic dorsoanteriorly and the pterygoid ventrally. The quadrate does not contact the parietal dorsally, in front of the foramen stapedio-temporale. The dorsal surface of the quadrate hosts a large part of the fossa temporalis superior, the foramen stapedio-temporale and the trochlear process (Fig. 6C, 8C). In IPS43810a, the quadrate contributes entirely to the processus trochlearis, excluding the prootic, and ventrally it terminates in the condylus mandibularis (Figs. 7C, 8C). Furthermore, the quadrate forms the wall that divides the middle ear into distinct regions, the cavum tympani and the cavum acustico-jugulare (Fig. 10C–F). The cavum tympani, which is wider than high, is continued posterodorsally by the large antrum postoticum (Fig. 9F). The latter is constituted by the quadrate and the squamosal. The medial wall of the quadrate contributes to the formation of the lateral wall of the cavum acustico-jugulare (Fig. 10F). It is formed basically by the quadrate and pterygoid. The incisura columellae auris is enclosed by the quadrates (Figs. 5E, 6E, 7E, 8E). The anterior region of the quadrate, together with a small portion of the prootic, constitute the relatively large trochlear process (Figs. 7C, 8C, 11E). The opisthotic and supraoccipital are excluded from the formation of the foramen stapedio-temporale, which is quite large and situated on the suture between the quadrate and the prootic (Figs. 8C, 11E). It can be observed that this foramen communicates with the cavum acustico-jugulare through the canalis acustico-jugulare (Fig. 10F). The processus epipterygoideus of the quadrate laterally overlaps the pterygoid below the foramen nervi trigemini, and contacts the processus inferior parietalis, forming a well-developed crista pterygoidea apparently without intervention of the epipterygoid (Fig. 11C). The foramen nervi trigemini, only observable in IPS43810a, is situated quite anteromedially (Fig. 11C), being apparently double (constituted by a posterior foramen trigemini laterally and an anterior foramen trigemini medially). A very short processus articularis is located below the cavum tympani, developing into the condylus mandibularis (Figs. 5E, 9C). The condylus mandibularis is divided into two facets by a parasagittal groove (Fig. 11B). The fenestra postotica has been only preserved on the left side of IPS43810a (Fig. 11B), despite being infilled with sediment; it is situated in the ventromedial margin of the

quadrate, contacting the pterygoid ventrally, the opisthotic dorsally and possibly the basisphenoid posteromedially.

The prootics are well preserved only in IPS43810a (Fig. 7C), although the right one is covered by sediment; IPS43809a only preserves the posterior part of the prootic dorsal margin, which contributes to the foramen stapedio-temporale. The prootic contacts the quadrate dorsolaterally, the parietal dorsomedially, the supraoccipital posteromedially, the opisthotic posteriorly and the pterygoid ventrally. The dorsal exposure of the prootic shows a rectangular outline, being about thrice longer than wide (Fig. 8C).

The opisthotics are significantly deformed (Fig. 5C, 7C). This bone contacts the prootic dorsoanteriorly, the quadrate laterally, the supraoccipital medially and the squamosal posterolaterally; in palatal view, the opisthotic contacts the exoccipital but apparently not the basioccipital. The opisthotics are directly involved in the formation of the fenestra postotica, but they do not participate in the foramen stapedio-temporale (Figs. 8D, 11E).

The exoccipitals are well preserved in IPS43810a (Fig. 7B), whereas they are quite eroded in IPS43809a (Fig. 5B). This bone contacts the supraoccipital dorsally, the opisthotic anterodorsally, and the basisphenoid ventromedially. The exoccipital constitutes the lateral part of the foramen magnum and part of the condylus occipitalis (Figs. 6B, 8B). There are two openings on its posterior surface (Figs. 8B, 11D): the larger and more lateral foramen jugulare posterius, and the smaller and more medial foramen nervi hypoglossi. The foramen jugular posterius is completely enclosed in the occipital, being located near the opisthotic-exoccipital suture (Figs. 8B, 11D). In turn, the foramen nervi hypoglossi emerges directly from the cranium, being located between the condylus occipitalis medially and the foramen jugular posterior laterally (Fig. 11D).

The basioccipital is generally visible (Figs. 6D, 8D), although in IPS43809a it cannot be observed well due to the superposition of the mandible. This bone, approximately triangular and located posterior to the basisphenoid, contacts the basisphenoid anteriorly, the exoccipital posteriorly and the pterygoid laterally.

The supraoccipitals are generally well preserved in the two specimens from ECM (Figs. 5E, 7C), although the posterior end of the supraorbital ridge is missing in IPS43810a. This bone contacts over a large posteromedial area with the parietal, with the prootic anterolaterally, the opisthotic laterally and the exoccipital posteroventrally. The suture between the supraoccipital, prootic and opisthotic is Y-shaped (Figs. 6C, 8C). The supraoccipitals constitute the dorsal portion of the foramen magnum, the posterior half of the roof of the braincase, a portion of the cavum labyrinthicum and most of the supraoccipital ridges (Fig. 10D). The supraoccipital spine is long, extending posteriorly beyond the quadrates (Figs. 6C, 8C). IPS43809a preserves two evident

longitudinal ridges, developed one below the other, on each side of the spine (Figs. 5E,F). Approximately three-quarters of the posterior portion of supraoccipital spine form a blade-like structure. The supraoccipital spine is pointed upwards, following the same inclination of the remaining skull roof elements in lateral view (Figs. 5E,F, 7E,F).

The basisphenoids are well preserved in the two available skulls (Figs. 5D, 7D). This bone contacts the pterygoid anterolaterally and the basioccipital posteriorly, but does not display any distinctive structure.

Cranial fenestrae and openings. The apertura narium externa, encircled by the premaxillae, maxillae and prefrontals, is relatively large (Figs. 5A, 7A). In the best-preserved skull (IPS43809a), it opens in an anterodorsal direction and displays a subrectangular shape. The orbits, delimited by the maxilla, prefrontal, frontal, postorbital and jugal, are larger than the apertura narium externa (Figs. 6C, 8C). They are separated by a thin zygomatic arch from the upper temporal fossa, which is slightly wider than the orbit (Figs. 5C, 7C). The fossa temporalis superior is anteroposteriorly shorter than the orbit, and also proportionally short relative to overall cranial size (Figs. 5C, 7C). The temporal emargination, delimited anteriorly by the postorbital, medially by the parietal, and laterally by the squamosal, displays roughly parallel medial and lateral rims (Figs. 6C, 8C). The development of the cheek emargination is difficult to interpret because of preservation reasons in the two skulls—especially given the anterior displacement of the quadrates in IPS43809a (Fig. 5A)—although it was probably smaller than the orbit and dorsally developed up to about the level of the inferior orbital rim. The rim of the internal choanae is only partially preserved, although they are delimited by the vomer and palatine (Fig. 11A). The fenestra subtemporalis, delimited by the maxilla, pterygoid, quadrate, jugal and quadratojugal, is partly covered by matrix or encircled by distorted bones (Figs. 6C, 8C); its original shape cannot be therefore confidently evaluated, although it is about as large as the orbit. The foramen magnum, constituted by the exoccipital and supraoccipital, and oval in shape, is much larger than the occipital condyle (Figs. 6B, 8B). The right cavum tympani is sufficiently preserved in IPS43809a to evaluate its morphology, being wider than tall, slightly smaller than the apertura narium, and completely enclosed by the quadrate (Figs. 5E, 6E).

Mandible. The dentaries (Figs. 5F, 7E,F) contact each other anteriorly at the mandibular symphysis, and each one further contacts the coronoid posterodorsally, the angular posteroventrally, the surangular posterolaterally and the prearticular posteromedially. On the triturating surface of IPS43809a (this region is not visible in IPS43810a), the lingual and labial ridges are denticulate and equally developed, slightly converging anteriorly and being separated by a deep groove that is filled by sediment (Fig. 5C). They join medially, just lateral to the symphysis, to form a single broad,

distinct dorsal denticle at the symphysis (Fig. 5A). As seen in right lingual view of IPS43809, the labial surface of the dentary is smooth but displays multiple foramina, including the foramen dentofaciale majus, together with several nutritive foramina (Fig. 5D); the fossa meckeli is relatively well developed. The dentary is quite shallow, further becoming shallower towards its anterior portion (which displays a concave lower profile), except at the symphysis, which is higher (Fig. 5F).

The coronoids are poorly preserved in IPS43809a (Figs. 5F, 6F) and in IPS43810a, further being partially covered by matrix on the later (Fig. 7E,F). This bone, which displays a triangular shape, contacts the dentary anterolaterally, the surangular posterolaterally and the prearticular posteromedially. The coronoid process is comprised of the coronoid boen alone (Figs. 5F, 6F). In IPS43809a, the right surangular is well preserved although fossilized in contact with the skull, whereas the left one is eroded both laterally and dorsally (Figs. 5F, 6F). The suture between the surangular and the dentary is interdigitated (see Jones et al. 2011, their Fig. 2), with the dorsal portion of the former extending much anteriorly towards the dentary than the basal one (Fig. 6F). The surangular further contacts the coronoid dorsally, the prearticular and angular ventrally and the articular posteriorly. In the two available skulls from ECM, the postdentary elements are relatively lightly built (Figs. 5F, 7E,F).

The articular, which is preserved on the right side of both IPS43809a (Fig. 6D) and IPS43810a (Fig. 7E), contacts the surangular anterolaterally, the angular ventrally and the prearticular medially. The articular forms the area articularis mandibularis that, in IPS43809a, is about as wide as long, and shows a moderately shallow medial concavity and a nearly flat lateral area (Fig. 5B,C).

In IPS43809a, the right prearticular is well preserved (Fig. 5D), although fossilized in contact with the base of the cranium, whereas the right one is only incompletely preserved. This bone contacts the coronoid dorsally, the articular posterolaterally and the angular ventrolaterally. The foramina intermandibularis caudalis and oralis are not recognizable in any of the available mandibles from ECM. Both angulars are well preserved in IPS43809a (Fig. 5F), whereas they are eroded in IPS43810a. This bone contacts the dentary anteriorly, the prearticular dorsomedially, the articular posteriorly and the surangular dorsally.

Morphometric comparisons

The results of the PCA have been reported in Fig. 12 and Table S2. The ECM crania (IPS43809a and IPS43810a) plot reasonably close to one another and are linked by the Minimum Spanning Trees (MST) in both PCA analyses. In the first PCA analysis (Fig. 12A), which used the raw measurements, PC1 (96% of total variance) separates the ECM skulls from *C. schafferi*, Thessanolini, the Epanomi skull (EPN102) and,

to a lesser extent, *C. perpiniana*. This axis is largely influenced by size differences, since all the PC have positive loadings—except variable H (or skull width/length ratio), which has a zero loading (see Table S2). Therefore, the lower PC1 scores of the ECM skulls mainly reflect their smaller absolute size. In the second PCA analysis, based on the Mosimann shape variables (Fig. 12B), PC1 (47% of variance) separates the ECM skulls and from *C. perpiniana*, Thessaloniki, *C. schafferi* and, to a lesser extent, the Epanomi skull. The lower PC1 scores of the former are mostly attributable to their high values of variables B* and D* (skull and splanchnocranium relative lengths), as well as to the low values of M* and K* (skull and interorbital relative widths). The PC2 (29% of variance) mainly separates the Epanomi skull (with a negative score) and the adult ECM skull (IPS43810a, with a positive score) from both the juvenile ECM (IPS43809a) and the remaining skulls. The higher score of IPS43810a mostly refects its moderately high values of variable M* (skull relative width) combined with its low values of A* (relative total skull length). A larger sample of skulls would be required to provide more reliable statistical results. Moreover, the lack of published measurements for *C. bolivari* precludes extending the comparisons to the other Iberian Miocene species. However, our preliminary morphometric analyses are consistent with the taxonomic distinctiveness of the ECM skulls—further supported in this paper on the basis of qualitative morphologic features.

Discussion

Taphonomy

None of the two available skulls from ECM is associated with a shell in anatomical articulation, but they were found in close spatial association with partial shell elements and some postcranial bones that might belong to the same individuals. Sedimentologic evidence suggests deposition under terrestrial and strongly aerated conditions within an alluvial fan depositional context (Carmona et al. 2011), perhaps being associated to a mudflow event that might have caused a rapid burial. Experimental models have demonstrated that disarticulation times are longer in terrestrial than in aquatic environments (Brand et al. 2000, 2003), although both in aquatic and in terrestrial environments, the skull, vertebrae, ribs and limbs bones separate from the body early, whereas the shell is the last to disarticulate. This pattern, coupled with the smaller size and higher fragility of cranial remains, explains why many findings consist in shells only. Regarding the specimens reported here, it should be noted that recovery of articulated skulls is exceptional in ECM, where dozens of shells (still unprepared) were recovered with no associated skull. This suggests that the cranial specimens described here must have been exposed during a shorter time than average at ECM. This is confirmed by the fact that there is no evidence of scavenging, weathering or abrasion on the surface of the skulls and shell bones (weathering stage 0 of Behrensmeyer 1978), whereas abrasion is also absent to moderate in the articulation surfaces of isolated bones and plates associated to the crania (weathering stages 0-2 of Beherensmeyer 1978; see also Brand et al. 2000). The close spatial association and the lack of both significant weathering and abrasion therefore indicate that these specimens were exposed for a moderate interval of time, having been buried relatively close to the place of death. When the carcasses of tortoises are

exposed in terrestrial environments, the flesh is degraded by insect larvae, although under dry conditions the bones and skin may remain articulated for quite long periods of times (Brand et al. 2003). This might have prevented the skulls of these individuals from being disarticulated from the shell during the short transport by mudflows that surely preceded burial. This is confirmed by the fact that both specimens here described preserve not only the cranium but the mandible as well, and especially that IPS4309a also preserves the stapes and hyoid, thereby indicating that the skin was still attached to the skull when deposition occurred. To sum up, it can be inferred that, after death, the carcasses of these tortoises were exposed on the ground and remained unburied for a relatively short interval of time (probably less than twenty weeks, see Brand et al. 2003), being rapidly buried after little transport, which together with the preservation of skin at the time of burial would have prevented the crania and several limb elements from being carried away from the shell fragments.

Taxonomy

The genus *Cheirogaster* has been historically diagnosed on the basis of postcranial features, including traits such as the lack of cervical horny shield, the undivided supracaudal horny shield, the elongate epiplastral lip, the presence of a posterior epiplastral excavation, and the alternating octagonal and quadrangular neural bony plates (Broin 1977; Danilov 2005; Lapparent de Broin 2001; Claude & Tong 2004). The above-mentioned features, however, are variously present in other genera of giant tortoises. For example, the cervical horny shield is also lacking in *Stigmochelys*, *Centrochelys* and *Geochelone* (Lapparent de Broin, 2000). Similarly, the epiplastron with a posterior excavation and a long epiplastral lip is characteristic of most giant tortoises (Lapparent de Broin, 2000), and the greater development of these features in *Cheirogaster* might be related to the attainment of generally larger sizes. Overall, to our knowledge the genus *Cheirogaster* does not display any clear-cut shell apomorphy distinguishing it from other giant tortoises. Its shell morphology more closely resembles that of *Stigmochelys*, *Geochelone* and *Centrochelys*, including the morphology of the nuchal and pygal plates. Several shell features enable the distinction of *Cheirogaster* from its putative sister-taxon (*Centrochelys*), but in these regards the former merely displays a more primitive condition. Thus, *Cheirogaster* lacks the following shell autapomorphies of *Centrochelys* (Bour 1984; Lapparent de Broin 2000): marginal 4 more developed than marginal 5; anteriorly-projecting and diverging gulars (more developed in male specimens); xiphiplastral narrowing behind the anal scutes; posteriorly-projecting, narrow and pointed xiphiplastral spykes (more marked in female specimens).

In addition to shell morphology, cranial remains also provide a valuable source of data both for taxonomic discrimination and for phylogenetic inference. Besides the new remains of *C. richardi* described in this paper, cranial specimens have been previously reported for several *Cheirogaster* species (Table 2), namely *C. bolivari*, *C. perpiniana*, *C. schafferi*, *Cheirogaster* sp. from Thessaloniki, and *Cheirogaster* sp. nov. from Epanomi (Arambourg & Piveteau 1929; Szalay 1931; Royo y Gómez 1935b; Bourgat & Bour 1983; Vlachos 2011). Based on this skull material, we conclude that a clear-cut distinction of the genus *Cheirogaster* from other testudinids is only possible on the basis of several cranial autapomorphies of the

former, as reported in the new emended diagnosis provided in this paper: lower cranium; more dorsally-oriented apertura narium externa; posteriorly-situated zygomatic arch (situated at or behind cranial mid-length); and anteroposteriorly short fossa temporalis superior. Among giant tortoises, the cranial morphology of *Centrochelys* is the most similar one to *Cheirogaster* (Bourgat and Bour 1983; Bour 1984; Lapparent de Broin 2002), including the triangular and broad shape of the cranium, the long preorbital region relative to cranial length, the long and anteriorly-wide vomer. However, the above-mentioned cranial derived features of *Cheirogaster* enable its distinction not only from other testudinids, but from *Centrochelys* as well.

Although skull characters provide additional data for resolving the taxonomy of this genus, difficulties arise with respect to differentiating between species, because several were established on postcranial remains and lack skull material. This is the case of *C. richardi*, which was previously described on the basis of shell material from the same age and geographic area than the ECM skulls. However, based on the published remains for the various species of *Cheirogaster*, *C. richardi* can be distinguished by a unique combination of shell features (including the anterior morphology of the plastron) from all other species of the genus except *C. bolivari* (see our differential diagnosis of *C. richardi* for further details). When the cranial morphology is taken into account, it emerges that *C. richardi* can be further distinguished from the other species of the genus for which the skull is known (including *C. bolivari*, see Royo y Gómez 1935b) by the presence of five features that are apparently autapomorphies of the former. As summarized in the emended diagnosis of *C. richardi* provided in this paper, these characters include: (1) premaxillary pit elliptical, instead of circular in *C. bolivari*; (2) much slenderer (instead of robust) zygomatic arch than in *C. bolivari*; (3) prefrontal and frontal region markedly constricted mediolaterially at the level of the orbits (thus becoming much narrower from anterior to posterior), instead of remaining approximately of the same width as in *C. bolivari*; (4) larger and more dorsally-oriented fossa orbitalis than in *C. bolivari*; and (5) generally straight and upwardly-inclined cranial dorsal profile and supraoccipital ridge, whereas in *C. bolivari* the former is convex (the supraoccipital ridge is not preserved in the latter).

The above-mentioned differentiating cranial features of *C. richardi* as compared to other species of *Cheirogaster*, *including C. bolivari*, justify a distinct species status for the former. The distinct taxonomic status of the ECM remains is further supported by the morphometric comparisons performed in this paper on the basis of skull measurements—although it should be taken into account that *C. bolivari* could not be included, due to the lack of published cranial measurements for this taxon. Given the above-mentioned differences with regard to other species of *Cheirogaster* for which cranial remains have been reported, two different taxonomic attributions are possible for the ECM material: either these two skulls represent a new, previously undescribed species; or they correspond to *C. richardi*, erected on the basis of shell remains from the same age and area, but for which no cranial remains were previously known. Evaluating these competing taxonomic alternatives is however hampered by several taxonomic and nomenclatural issues regarding the Iberian Miocene remains of *Cheirogaster*. Particularly problematic is the purported synonymy between *C. bolivari* and *C. richardi*, with the former having priority if the two nominal taxa are considered to belong to the same species.

Nomenclature

Cheirogaster bolivari was originally erected as *Testudo bolivari* by Hernández-Pacheco (1917b) on the basis of shell and other postcranial remains from the middle Miocene of Barranco de los Mártires in Alcalá de Alcalá de Henares (MN5 or MN6; see also Hernández-Pacheco 1917a, 1921; Royo y Gómez 1935b). Hernández-Pacheco (1917b) did not designate a holotype, nor figured or described the type material, which was subsequently described in detail by Royo y Gómez (1935b). According to Jiménez Fuentes and co-authors, the "neotype" (Jiménez Fuentes et al. 1988c) or "lectotype" (Jiménez-Fuentes and Martín de Jesús 1991) would be lost. In fact, the type material consists of several syntypes, from which—to our knowledge—a lectotype was never designated.Additional finds from the inner Iberian Peninsula during the early 20th Century, such as those from the MN5 or MN6 of Calle de Moret (Royo y Gómez 1921) and Ciudad Universitaria (Royo y Gómez 1934, 1935a,b), the MN6 or MN7 of Cerro del Otero (Hernández-Pacheco 1921; Royo y Gómez 1935b), and the MN9 of Arévalo (Royo y Gómez 1933, 1935b), were also attributed to *C. bolivari* by Royo y Gómez (1935b). Most of this material is currently lost, including—given the unsuccessful efforts by the senior author of this paper to locate this material while visiting the MNCN-CSIC in 2010—the syntypes from Alcalá de Henares and the partial cranium from Ciudad Universitaria, having been probably lost during the Spanish Civil War (Patricia Pérez Dios, pers. com. to À.H.L., 2010).

Cheirogaster richardi was originally described by Bergounioux (1938) within the genus *Testudo*, on the basis of a plastron that he incorrectly attributed to the Oligocene of Tàrrega (Bergounioux 1837, 1838)—incidentally, Bergounioux (1937) first used the binomen '*Testudo Richardi* sp. nov' as a new taxon but without describing the species, designating a holotype or figuring it, and hence the species was not formally erected until Bergounioux's (1938) formal description. In the latter paper, Bergounioux justified the erection of this species largely on the erroneous (supposedly older) geological age of the material as compared to *T. bolivari*, further failing to provide clear diagnostic criteria with regard to the latter. In fact, the holotype of *T. richardi* (figured and described by Bergounioux 1938, 1958), which was lost during the Spanish Civil War (Jiménez Fuentes et al. 1988c; Jiménez Fuentes & Martín de Jesús 1991), came from late Miocene (MN9) levels of els Hostalets de Pierola (Bataller 1956; Bergounioux 1958), i.e. from the same area and age from where the ECM specimens described in this paper come from. Bergounioux (1958) reported additional photographs and descriptions of the holotype, further providing a shell-based, emended diagnosis of the species and maintaining the species distinction between *C. bolivari* and *C. richardi*—still within the genus *Testudo*. In contrast, in the same paper Bergounioux erected a new species of *Cheirogaster*, *C. arrahonensis* Bergounioux, 1958, on the basis of fragmentary shell remains from the Vallesian of Subsòl de Sabadell (Barcelona, Spain). Jiménez Fuentes & Martín de Jesús (1991) considered that the latter remains, too fragmentary to be identified at the species level, might be attributable to *Cheirogaster* sp. However, as noted by Lapparent de Broin et al. (2006), the preserved morphology of the holotype and only specimen indicates that it should be attributed instead to the genus *Testudo*. Given that the available morphology from the holotype specimen is too limited to provide an adequate diagnosis at the species level, the nominal taxon

Cheirogaster arrahonensis Bergounioux, 1958 is best considered a nomen vanum—i.e., based on a type inadequate for definitive diagnosis (see Mones 1989 for the distinction between nomina dubia and nomina vana).

The distinction between the two Iberian species of Miocene giant tortoises remained neither disputed nor further justified, until Jiménez Fuentes (1984) supported it on the basis of the morphology of the anterior portion of the plastron. Jiménez Fuentes (1984) observed that a specimens attributed to *C. bolivari* from the MN8 of Coca in Segovia (Jiménez-Fuentes 1971) displayed a marked epiplastral excavation and a uniformly-pointed anterior margin of the plastron, whereas those from the nearby MN9 locality of Arévalo in Ávila (García and Alberdi 1968; Jiménez Fuentes and Carbajosa Tamargo 1982) lacked such excavation and further displayed a trapezoidal anterior margin with protuberances. In these regards, the Arévalo remains resembled the holotype of *C. richardi* from the MN9 of els Hostalets, leading to the conclusion that both species were distinct and displayed a different chronostratigraphic range (Jiménez Fuentes 1984). Jiménez-Fuentes et al. (1988c) interpreted such taxonomic opinion to be an implicit neotype designation for these species, and explicitly recognized the partial shell and associated postcranials STUS 352 (described by Jiménez Fuentes 1971, and figured by Jiménez Fuentes & Carbajosa Tamargo 1982; Jiménez Fuentes 1984) from the lower levels of Coca as the neotype of *C. bolivari*, and the partial plastron STUS 2414 (described and figured by Jiménez Fuentes & Carbajosa Tamargo 1982; Jiménez Fuentes 1984) from El Lugarejo in Arévalo as the neotype of *C. richardi* (see also Jiménez Fuentes & Martín de Jesús 1991). As recognized by Jiménez Fuentes & Martín de Jesús (1991), such designations did not fulfil the requirements of the International Code of Zoological Nomenclature regarding the proximity between the original type locality and the provenance of the neotype.

In the case of *C. bolivari*, the lectotype was from a much older (MN5-MN6) locality from Madrid, whereas the neotype would be from the MN8 of Segovia; in the case of *C. richardi*, the holotype was from the MN9 of els Hostalets de Pierola in the Vallès-Penedès Basin, whereas the neotype would be from the similarly-aged locality of Ávila. According to the current edition of the International Code of Zoological Nomenclature (ICZN 1999), one of the qualifying conditions for a neotype to be valid requires that the authors designating it must state ‘the author's reasons for believing the name-bearing type specimen(s) … to be lost or destroyed, and the steps that had been taken to trace it or them’ (Article 75.3.4). Jiménez Fuentes et al. (1988c) did not completely fulfil such requirement, because they merely asserted that the two holotypes had been lost. Jiménez Fuentes & Martín de Jesús (1991) further specified that they had visited the MSCB, concluding that the holotype of *C. richardi* had been destroyed (not merely lost) during the Spanish Civil War. While seminarists had left the MSCB to avoid anticlerical attacks, the crowds invaded the museum and burnt the vitrines, with many fossils being thrown through the windows (S. Calzada, pers. com. to À.H.L., 2010). Therefore, it is most likely that the holotype was destroyed, and we fully agree with Jiménez Fuentes et al. (1988c) on the need to erect a neotype to clarify the taxonomic identity of *C. richardi* as compared to *C. bolivari*.

There is reason to question the previous neotype designation for *C. richardi* by Jiménez Fuentes et al. (1988c). For such a designation, the International Code of Zoological Nomencalture requires 'evidence that the neotype came as nearly as practicable from the original type locality […] and, where relevant, from the same geological horizon or host species as the original name-bearing type' (ICZN 1999, Article 75.3.6). As already stated, the correct type locality of *C. richardi* is els Hostalets de Pierola, and although Bataller (1956, p. 21) was unable to precise whether it came from Aragonian or Vallesian levels, Bergounioux (1958, p. 179; our translation from the French) further clarified that 'Dr. Crusafont has kindly noted to me that it was found in the Vallesian levels, where numerous additional remains from giant tortoises have been found to date […]. Elements from the plastron or carapace are currently at the Seminary of Barcelona and at the Museum of Sabadell'. Bataller (1956) also asserted that six additional more or less complete specimens had been collected from els Hostalets by that date. Thus, although neither Bataller (1956) nor Bergounioux (1958) gave any indication regarding the loss of the holotype, they clearly stated that additional specimens from the same area and age as the original type locality were available during the 1950s, which even enabled Bergounioux (1958) to refine the original diagnosis of *C. richardi*. Hence, the neotype designation for *C. richardi* by Jiménez Fuentes et al. (1988c) clearly failed to fulfil the requirements of the Code (Jiménez Fuentes & Martín de Jesús 1991), since in spite of the similar MN9 age, it came from a different geographic area that was not so close as possible (see Bergounioux 1958) to the type locality. We therefore infer that the previous neotype designation *C. richardi*, based on STUS2414 from Arévalo, must be deemed invalid.

Nomenclatural problems aside, the neotype designation for *C. richardi* by Jiménez-Fuentes et al. (1988c) has caused additional taxonomic confusion, leading to the doubtful conclusion that the *C. richardi* and *C. bolivari* are synonymous. Thus, Jiménez Fuentes et al. (2000) noted that the neotype of *Cheirogaster bolivari*, originally attributed to a male, belonged in fact to a female individual—the purported differences between both taxa regarding epiplastral excavation in *C. bolivari* being in fact attributable to sexual dimorphism within a single species. Jiménez Fuentes et al. (2000) further considered that the anterior contour of the plastron (proposed as a diagnostic feature by Jiménez Fuentes 1984) was variable within a single locality, thereby concluding that all Aragonian and Vallesian giant tortoises from Iberia were attributable to a single species, *C. bolivari*, with *C. richardi* being considered it junior subjective synonym. Jiménez Fuentes et al. (2000), however, failed to comment on the diagnostic features provided by Bergounioux (1958) in his emended diagnosis of *C. richardi*. The purported synonymy between these two nominal taxa is largely based on the invalid designation of a neotype for *C. richardi* by Jiménez Fuentes et al. (1988c), since this material is geographically much closer to the type locality of *C. bolivari*—either the original locus typicus from Alcalá de Henares (MN5-MN6) or the neolocus typicus of Coca (MN8)—than to the original locus typicus of *C. richardi* (Vallesian levels of els Hostalets de Pierola). Moreover, such synonymy is contradicted by the cranial differences reported in this paper between the material from Ciudad Universitaria (attributable to *C. bolivari* on postcranial grounds as well as on the basis of both geographic and chronostratigraphic provenance) and the new material from els Hostalets de Pierola (with the same age and geographic provenance than the lost holotype of *C. richardi*).

In our opinion, it is not possible to clarify the taxonomic status of the nominal taxon *C. richardi* as a potentially distinct species from *C. bolivari* on the basis of the previously available data, the holotype being destroyed and their putative synonymy based on an invalid neotype designation. The two skulls from the early Vallesian of els Hostalets de Pierola reported here therefore provide the opportunity to objectively clarify the status of the nominal taxon *C. richardi* by designating a neotype. It should be taken into account that els Hostalets de Pierola, as recognized by Bataller (1956), does not correspond to a single locality. Although more than twenty classical sites are known from this region (Crusafont & Truyols 1954; Golpe-Posse 1974), most of them are loosely-defined areas that do not correspond to a single stratigraphic level of a palaeontological locality in a strict sense (Agustí et al. 1985), and many finds from the 20th Century either correspond to isolated finds or have no recorded exact provenance. Classical Hostalets 'localities' were grouped into Hostalets Inferior (Aragonian levels) and Hostalets Superior (Vallesian levels) (Crusafont & Truyols 1954; Golpe-Posse 1974; Agustí et al. 1985, 1997), and it was not until the last decade that more two hundred new localities, accurately dated thanks to detailed litho-, bio- and magnetostratigraphic control, have been discovered in the same area of els Hostalets de Pierola. The latter include the Aragonian levels of the ACM series (Alba et al. 2006, 2009, 2011; Moyà-Solà et al. 2009) as well as the Vallesian levels of the ECM series (Luján et al. 2010; Alba et al. 2011, 2012; Carmona et al. 2011). The *Cheirogaster* cranial remains described in this paper came from the latter and, as such, our neotype designation fulfils the requirements of Article 75.3.6 of the Code, according to which the neotype must come from nearly as practicable from the original type locality and the same geological horizon, namely the Vallesian levels of els Hostalets de Pierola.

Our neotype designation further fulfils the requirements of Article 75.3.2 of the Code—according to which it is necessary to state the differentiating features from other taxa in the nominal species-group taxon—since our emended diagnosis provides several morphologic features enabling the distinction of *C. richardi* from *C. bolivari* and other species of the genus, as further discussed above. On the basis of these morphologic characters, we conclude that *C. richardi* is not a junior synonym of *C. bolivari*. On the basis of material from their respective type localities and adjacent areas, the two Iberian species of *Cheirogaster* would be recorded in different areas of the Iberian Peninsula and different time intervals (Table 3). However, given the previous confusion between these two species, the taxonomic attribution of latest Aragonian and Vallesian remains of *Cheirogaster* from inner Iberian basins (e.g. Chañe, Toril, Coca, Los Valles de Fuentidueña, Arévalo, Autovía A6, Batallones) remains to be clarified, being here merely assigned to *Cheirogaster* sp. As such, it is currently uncertain whether these two distinct species merely displayed a different geographic distribution, a different chronostratigraphic range, or both.

Phylogeny

In order to infer the phylogenetic relationships of *Cheirogaster*—a taxon absent from several previous cladistic analysis of testudinids (e.g., Crumly 1982; Meylan & Sterrer 2000; Gerlach 2001; Takahashi et al. 2003)—we incorporated the cranial features revealed by the two ECM skulls, together with previously-

published data on other Miocene *Cheirogaster* species, into a pre-existing matrix (Gerlach 2001) of cranial characters for extant testudinid genera (see Materials and methods for further details). A cladistic analysis based on maximum parsimony yielded two most parsimonious trees (see the strict consensus in Fig. 13), merely differing in the relative branching order of the genera *Stigmochelys* and *Aldabrachelys*. For the remaining taxa, our analysis yields very similar results to those previously obtained by Gerlach (2001), but shows several inconsistencies regarding the molecular phylogeny recovered by Le et al. (2006). Nevertheless, our analysis recovers a sister-taxon relationship between *Cheirogaster* and the extant African large-bodied testudinid *Centrochelys*.

This agrees with previous views by some authors (Lapparent de Broin 2002; Lapparent de Broin et al. 2006), but contrast with the results of a previous cladistic analysis by Kear (2010), based on a combined data matrix of molecular data for extant taxa as well as the cranial and postcranial of morphologic (both cranial and postcranial) features already employed by Takahashi et al. (2003). According to the preliminary report published by Kear (2010), his analysis would place *Cheirogaster* in a much more basal position (less nested within the tree) than our analysis. The two analyses would further markedly differ regarding the position of *Manouria*, deeply nested in our cladogram but occupying a more basal position in Kear's (2010; see also Takahashi et al., 2003). In the two most parsimonious trees obtained by our analysis, we recover a *Centrochelys+Cheirogaster* clade, which is also supported by the bootstrap analysis with a bootstrap value of 58% (Fig. 13). This clade is characterized by the following synapomorphies: tuberculae present on the posterior margin of the pterygoids (independently evolved in *Kinixys+Chersina*); and basioccipital tuberculae projecting beyond posterior margin of opisthotic (also present in other taxa). According to this topology, *Cheirogaster* would autapomorphically differ from *Centrochelys* by the presence of a curved instead of straight maxilla in lateral view, although such character has independently evolved more than once (despite many similarities, these two genera can be distinguished on the basis of shell morphology, such as the narrowing of xiphiplastra of *Centrochelys*: Lapparent de Broin 2002). *Centrochelys*, in turn, would autapomorphically differ from *Cheirogaster* by the presence of tooth-like tubercles on the maxillary alveolar ridges (also present in many other taxa), the maxillae projecting posteriorly beyond the postorbitals (a condition also present in *Geochelone* and *Malacochersus*) and the anterior process of the surangular not interdigitating with the dentary (a condition also present in other taxa).

The nesting of *Cheirogaster* within a clade otherwise composed by African, Madagascan and Indo-oceanic taxa suggests that, from a palaeobiogeographic viewpoint, *Cheirogaster* might be of African origin, although a taxonomic revision of Palaeogene *?Cheirogaster* from Europe (for which no cranial remains are currently known) would be required to test this hypothesis. Additional cranial remains of *Cheirogaster* spp. would be required to further clarify the internal phylogeny of this genus at the species level.

Conclusions

New fossil testudinid skull material confirms that there were two species of giant tortoise in Iberia during the Miocene, rather than just one as previously suggested. The specimens, from the early Vallesian (MN9, late Miocene) of Ecoparc de Can Mata (ECM) in the Vallès-Penedès Basin, differ significantly from *Cheirogaster bolivari* from the MN5-MN6 of inner Iberian Peninsula and can be referred to *C. richardi*, thereby improving the diagnosis of the latter species as well as for this widespread extinct genus. An attribution of the ECM skulls to *Cheirogaster* is justified by several morphological features autapomorphic of this genus. Moreover, the ECM skulls further display several characters previously unknown among *Cheirogaster* species for which cranial material is known, including *C. bolivari*. *Cheirogaster richardi* had been considered a junior subjective synonym of *C. bolivari* by some authors, given the lack of cranial material for *C. richardi* as well as previous invalid neotype designations for the two species. In our opinion, the neotype designation for *C. richardi* must be deemed invalid, because it does not fulfil the criterion of maximum possible proximity to the original locus typicus. To clarify the taxonomic status of *C. richardi*, one of the EMC skulls is designed as the neotype of this species, and an emended diagnosis of the species is provided. On this basis, the specific distinction between *C. bolivari* (from the MN5-MN6 of inner Iberian basins) and *C. richardi* (from the MN9-MN10 and, probably, MN7+8 of the Vallès-Penedès Basin) is clearly supported. Additional cranial material from the latest Aragonian and Vallesian of inner Iberian basins would be necessary for clarifying whether these species have a distinct geographic and/or a temporal distribution. Finally, a cladistic analysis of testudinids at the genus level, based on cranial features, supports a sister-taxon relationship between *Cheirogaster* and *Centrochelys*. Further examination of the cranial material referred to *C. bolivari* is necessary to better resolve the phylogenetic relationships among species of the genus *Cheirogaster*. Overall, our results stress the need of erecting neotypes for extinct species only when material from the same area and age than the original type locality is available (in order not to introduce additional taxonomic confusion), and further highlight the significance of cranial morphology for attaining a better understanding of chelonian taxonomy and phylogenetic relationships.

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Figure legends

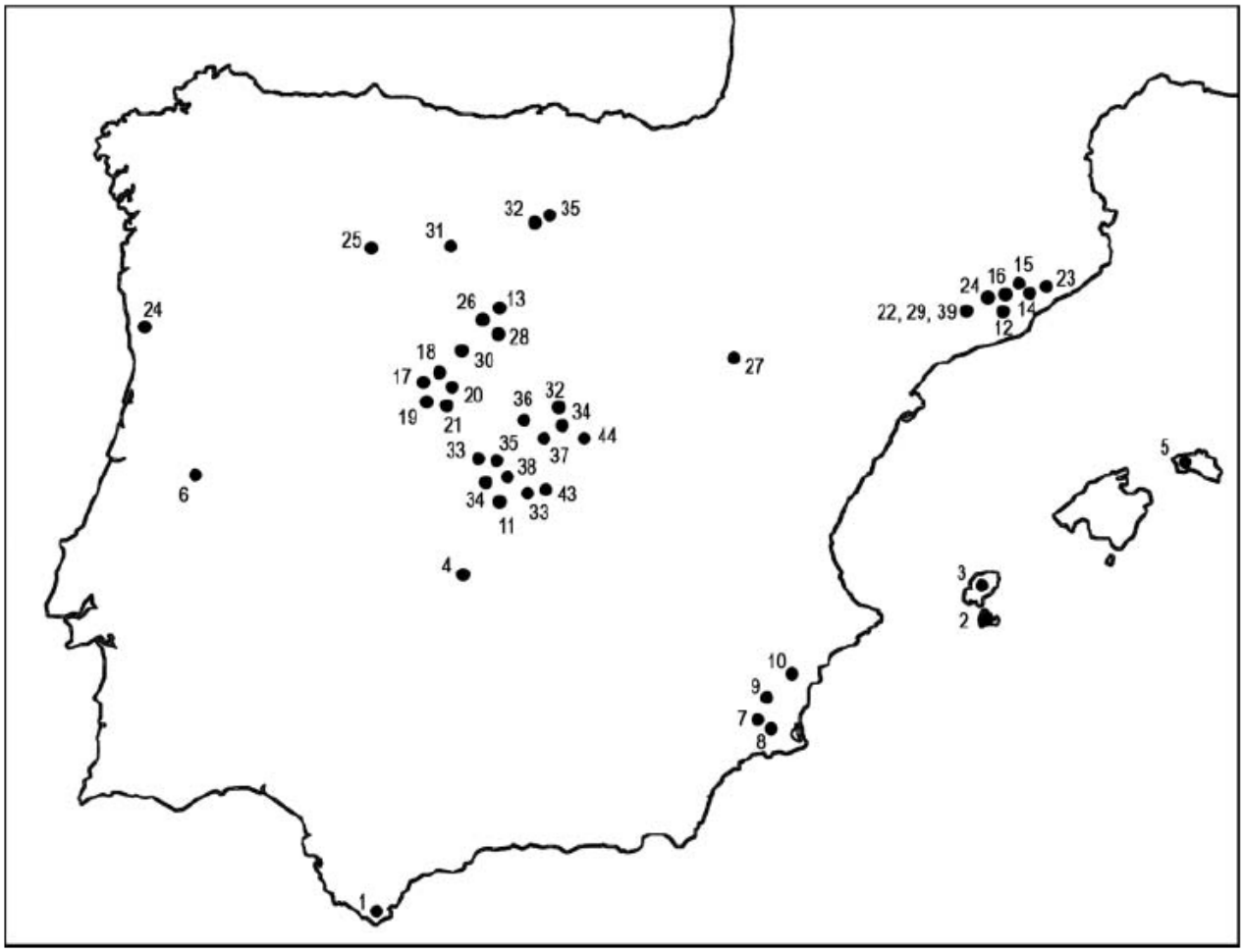

Figure 1. Location map of palaeontological sites with *Cheirogaster* remains in the Iberian Peninsula, according to published sources (see locality numbers and further details in Table 2).

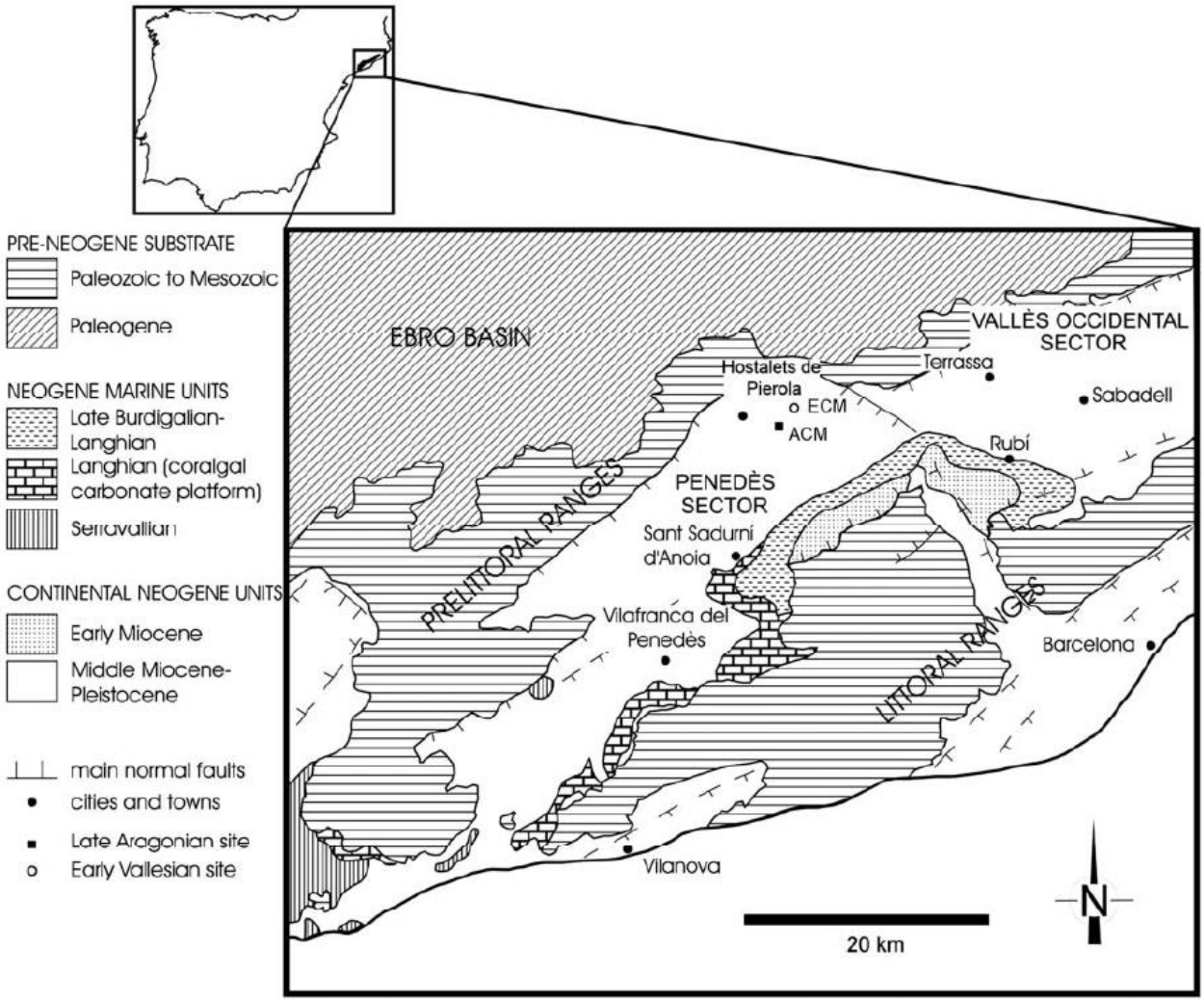

Figure 2. Schematic geological map of the Vallès-Penedès Basin, showing the main geological units and the situation of Abocador de Can Mata (ACM) and Ecoparc de Can Mata (ECM). Modified from Casanovas-Vilar et al. (2008).

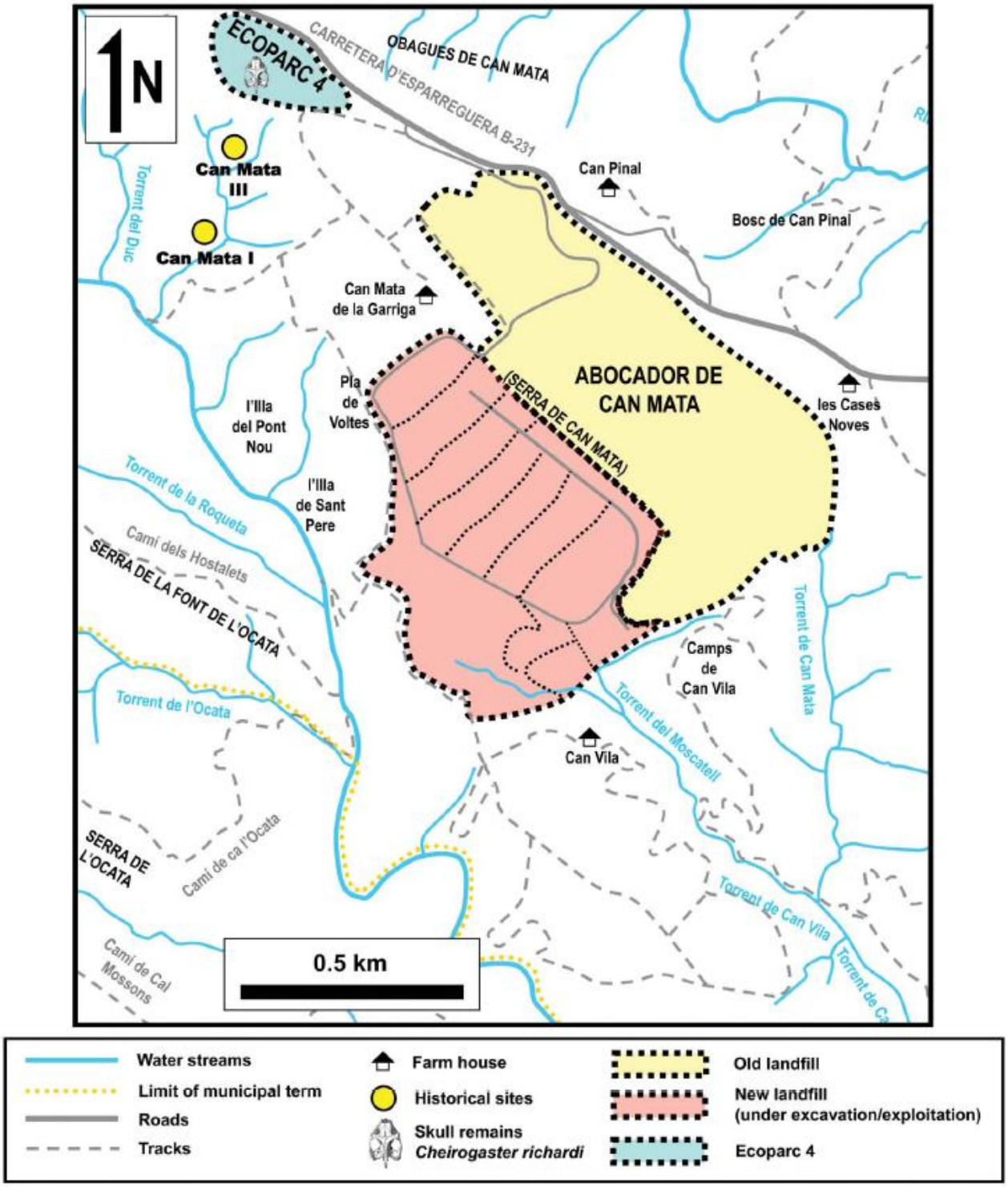

Figure 3. Map of situation of Ecoparc de Can Mata (Ecoparc 4) and Abocador de Can Mata. The extension of the old landfill whereas as well as the area currently under exploitation and/or excavation are indicated, together with the location of the skulls of *Cheirogaster richardi* and that of two classical Can Mata localities. Modified after Moyà-Solà et al. (2009).

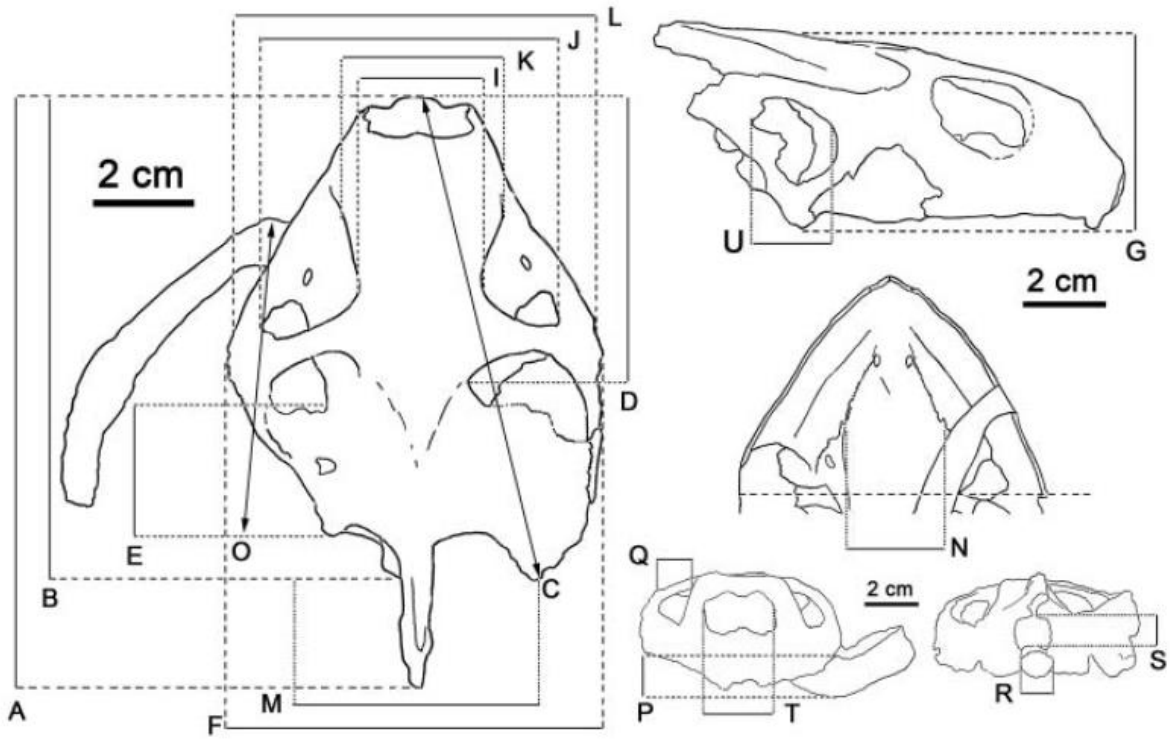

Figure 4. Cranial measurements (in mm) taken in this study, exemplified in the skull of *Cheirogaster richardi* (IPS43809a, neotype). **A**, total skull length; **B**, skull length (excluding the supraoccipital crest); **C**, skull diagonal length; **D**, splanchnocranium length; **E**, neucrocranium length; **F**, greatest skull width; **G**, greatest skull height; **H**, skull width/length ratio, not shown in the figure but indicated here because it is computed as F/B; **I**, interorbital width between the internal orbital margins; **J**, interorbital width between the external orbital margins; **K**, interorbital width between the posteroventral projections of the maxilla; **L**, skull width at the orbital region; **M**, skull width between the squamosals; **N**, width of the palatal fossa; **O**, length of the lower jaw; **P**, depth of the mandibular symphsysis; **Q**, mediolateral greatest orbital width; **R**, width of the occipital condyle; **S**, height of the foramen magnum; **T**, nasal aperture width; **U**, ear opening length.

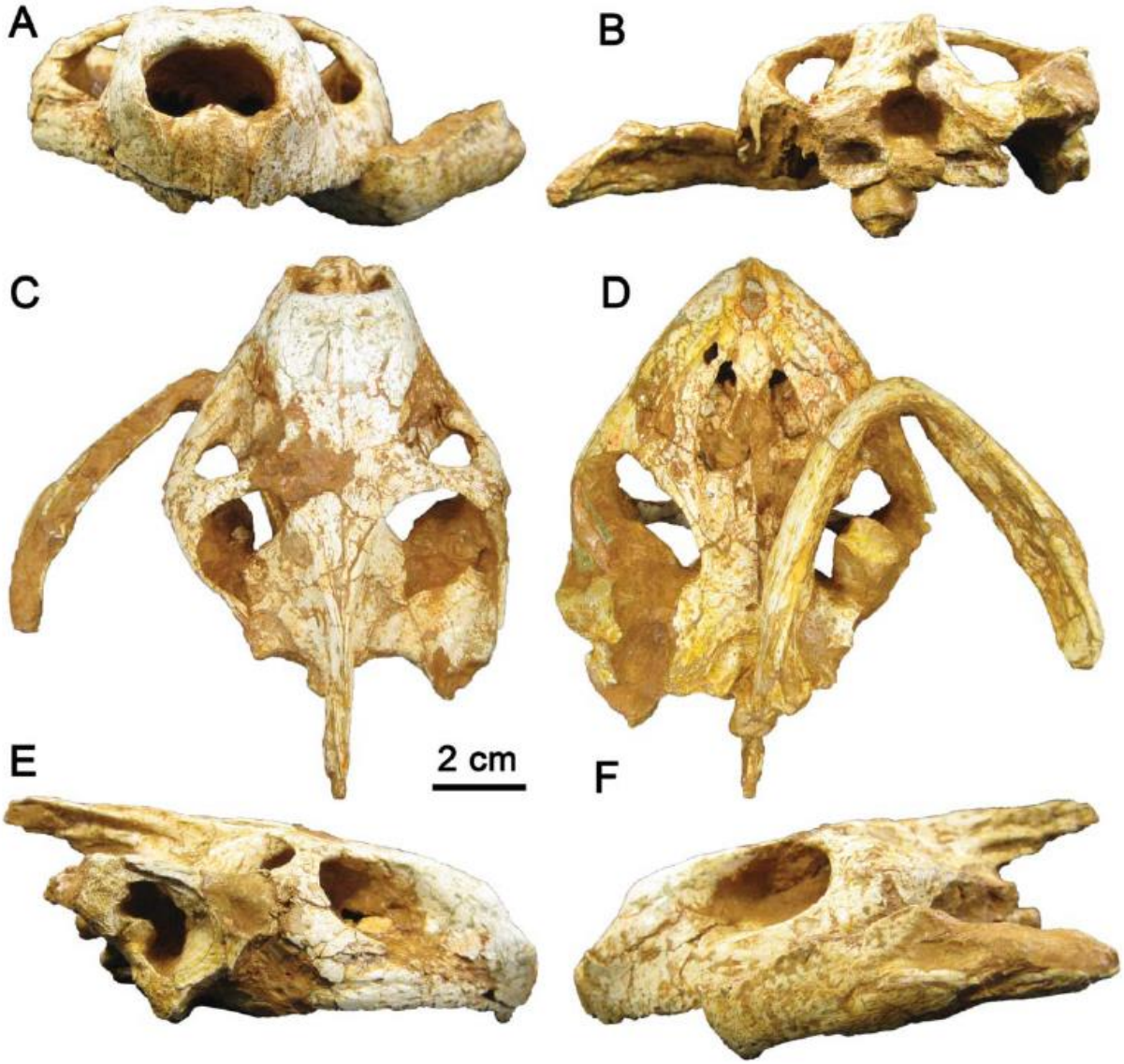

Figure 5. Skull of *Cheirogaster richardi* (IPS43809a, neotype), in **A**, frontal, **B**, occipital, **C**, dorsal, **D**, ventral, **E**, right lateral and **F**, left lateral views.

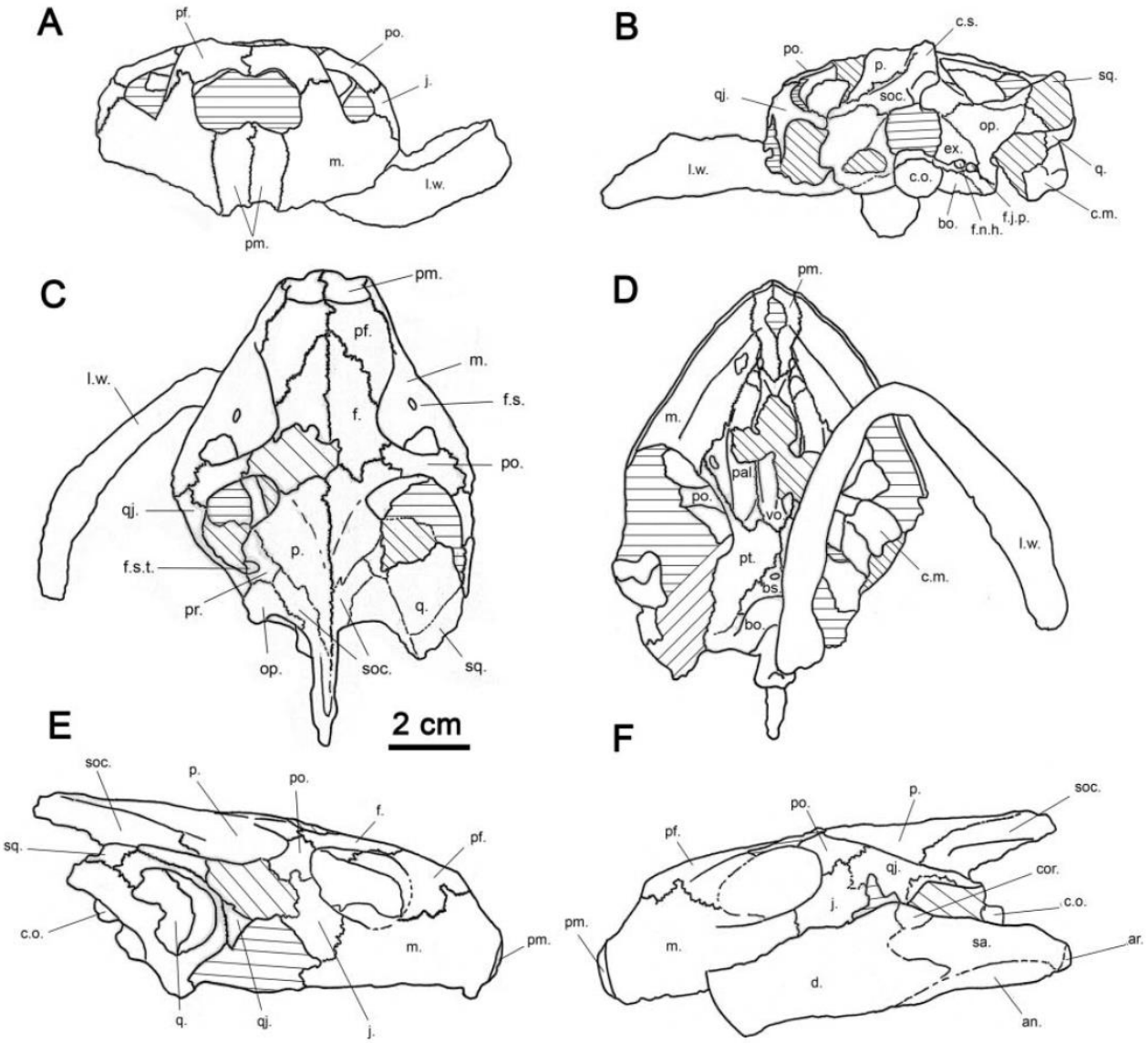

Figure 6. Drawing of the skull of *Cheirogaster richardi* (IPS43809a, neotype), in **A**, frontal, **B**, occipital, **C**, dorsal, **D**, ventral, **E**, right lateral and **F**, left lateral views. Oblique lines indicate broken areas, whereas horizontal lines denote unremovable matrix. Abbreviations: an., angular; ar., articular; bo., basioccipital; bs., basisfenoide; c.m., condylus mandibularis; c.o., condylus occipitalis; cor., coronoid; c.s., crista supraoccipitalis; d., dentary; ex., exooccipital; f., frontal; f.j.p., foramen jugulare posterius; f.n.h., foramen nervi hypoglossi; f.p., fenestra postotica; f.s., foramen supramaxillare; f.s.t., foramen stapediotemporale; j., jugal; l.w., lower jaws; m., maxilla; op., opistotic; p., parietal; pal., palatine; pf., prefrontal; pm., premaxillary; po., postorbital; pr., prootic; pt., pterygoid; q., quadrate; qj., quadratojugal; sa., surangular; soc., supraoccipital; sq., squamosal, vo., vomer.

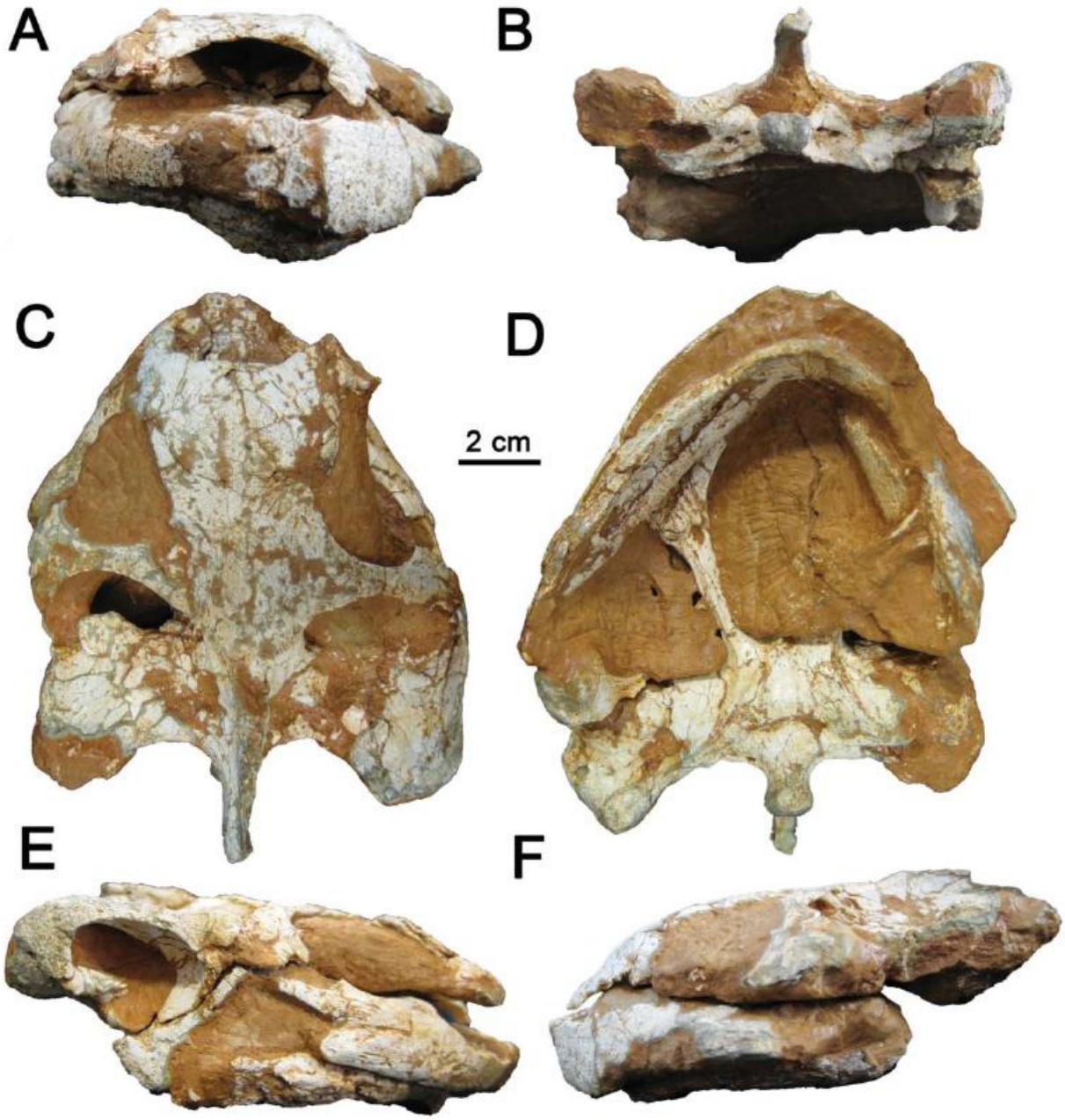

Figure 7. Skull of *Cheirogaster richardi* (IPS43810a), in **A**, frontal, **B**, occipital, **C**, dorsal, **D**, ventral, **E**, right lateral and **F**, left lateral views.

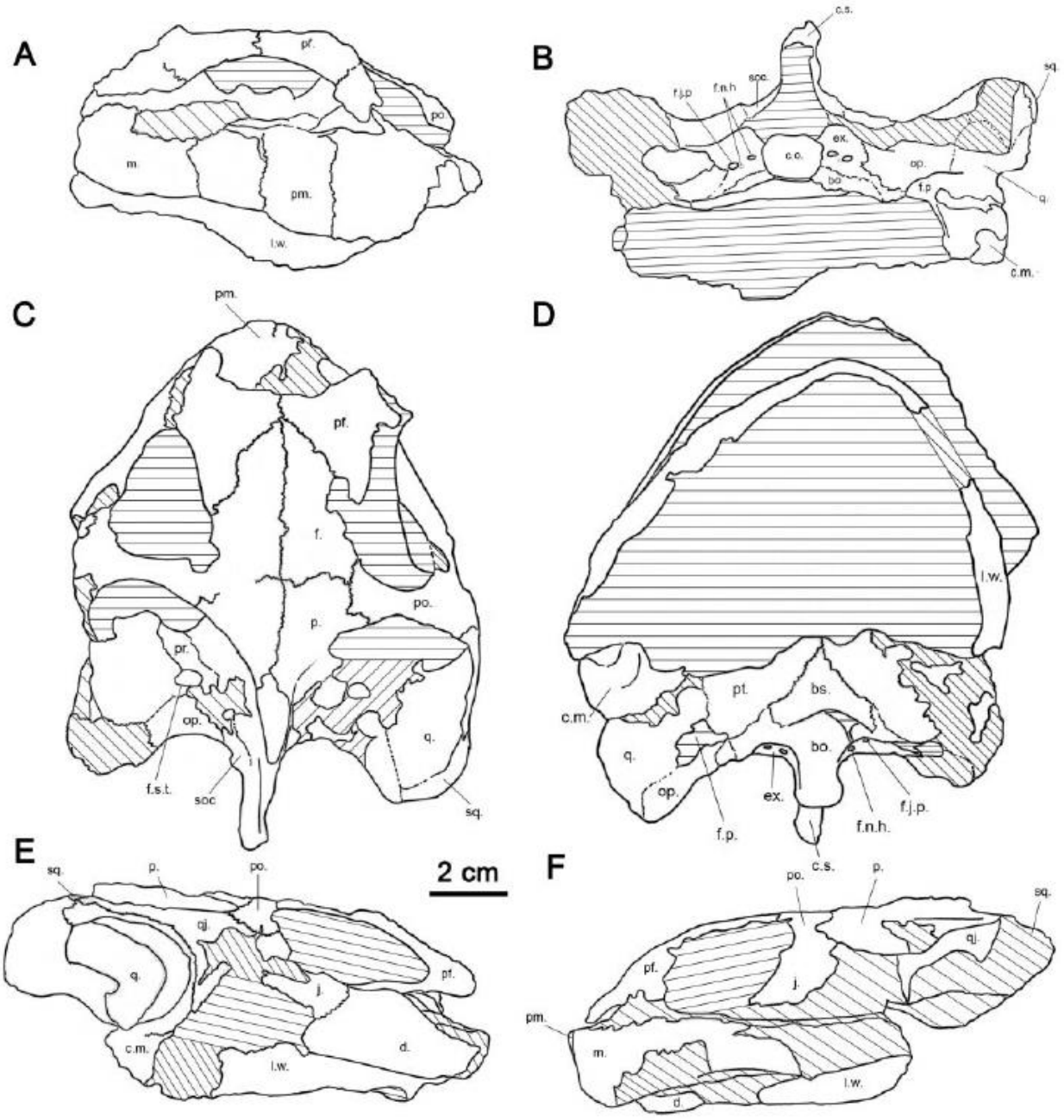

Figure 8. Drawing of the skull of *Cheirogaster richardi* (IPS43810), in **A**, frontal, **B**, occipital, **C**, dorsal, **D**, ventral, **E**, right lateral and **F**, left lateral views. Oblique lines indicate broken areas, whereas horizontal lines denote unremovable matrix. Abbreviations as in Fig. 7.

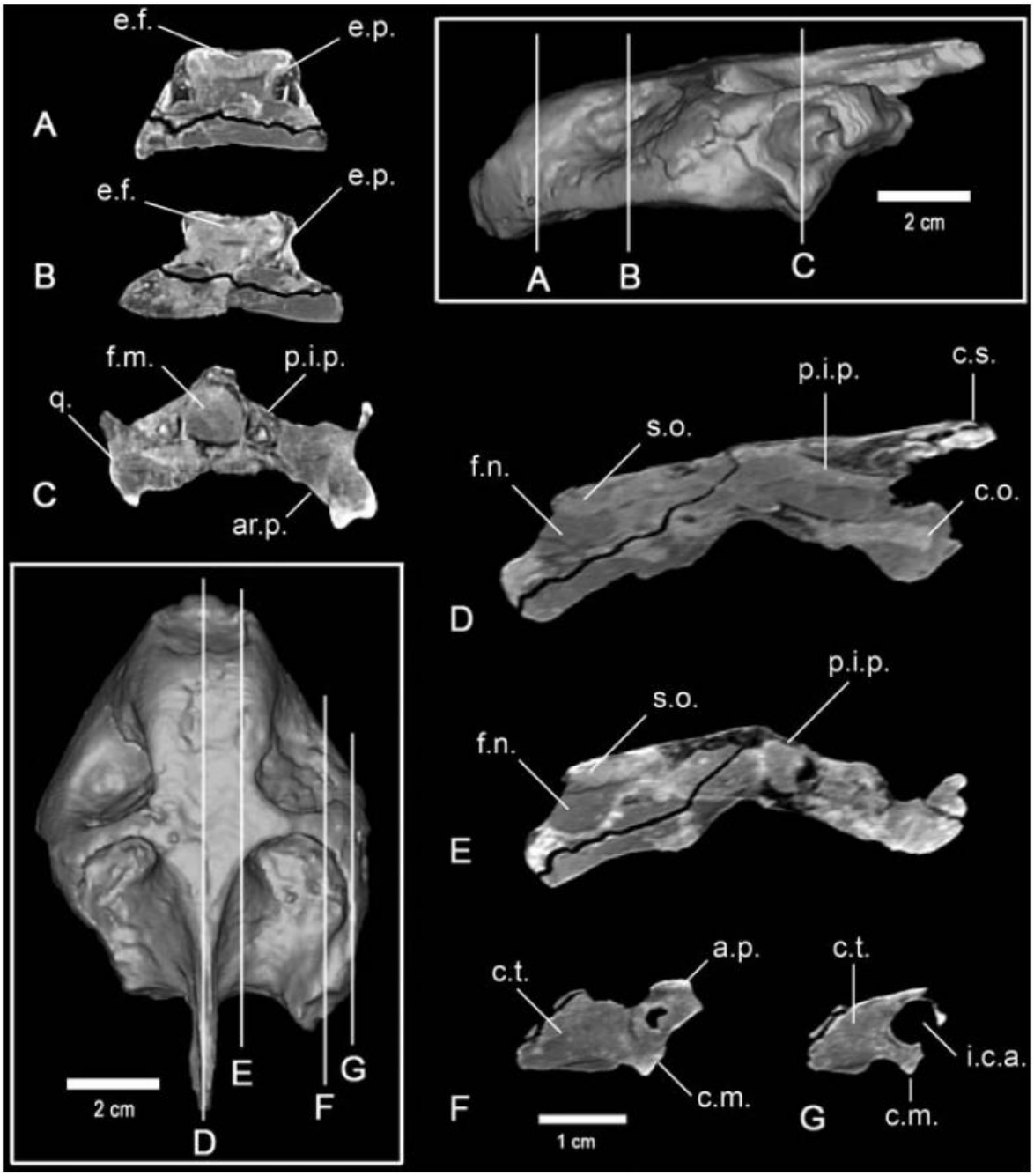

Figure 9. CT-scans of the skull of *Cheirogaster richardi* (IPS43809a, neotype). **A–B**, coronal sections through the nasals; **C**, coronal section through the oticum chamber; **D**, sagittal section; **E**, parasagittal section; **F–G**, parasagittal sections through the oticum chamber. Abbreviations: a.p., antrum postoticum; ar.p., articular process; c.a.j., cavum acustico-jugulare; c.m., condylus mandibularis; c.t., cavum tympani; c.o., condylus occipitalis; e.f., ethmoidal fissure; e.p., ethmoid processes; f.m., foramen magnum; f.n., fossa nasalis; f.s.t., foramen stapedio-temporale; i.c.a., incisura columellae auris; l.c., labiryntic chamber; p.i.p., processus inferior parietalis; q., quadrate; s.o., sulcus olfactorius; t.p., trochlear process; v.p., ventromedial process.

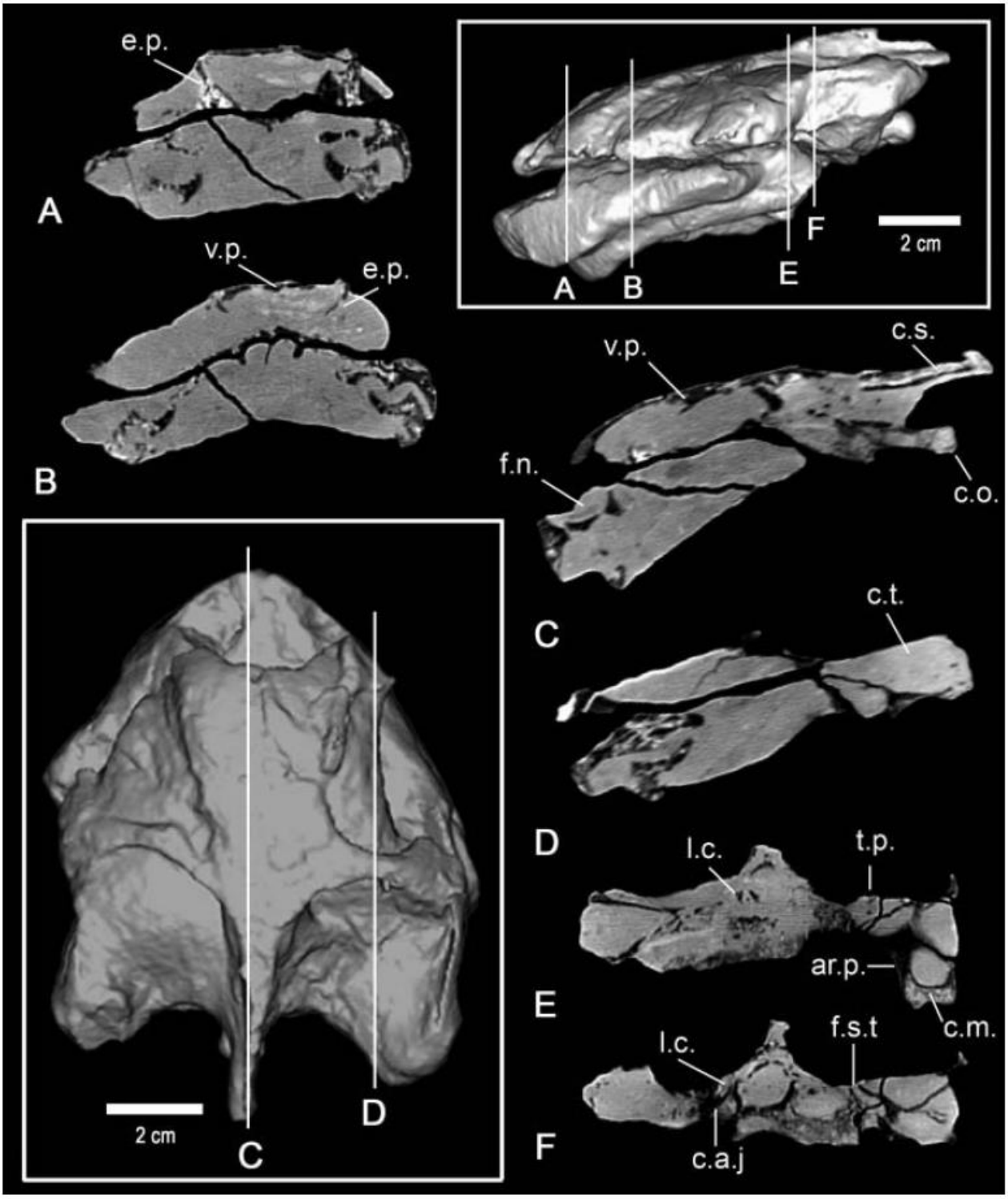

Figure 10. CT-scans of the skull of *Cheirogaster richardi* (IPS43810a). **A–B**, coronal sections through the nasals; **C**, coronal section through the oticum chamber; **D**, sagittal section; **E**, parasagittal section; **F–G**, parasagittal sections through the oticum chamber. Abbreviations as in Fig. 9.

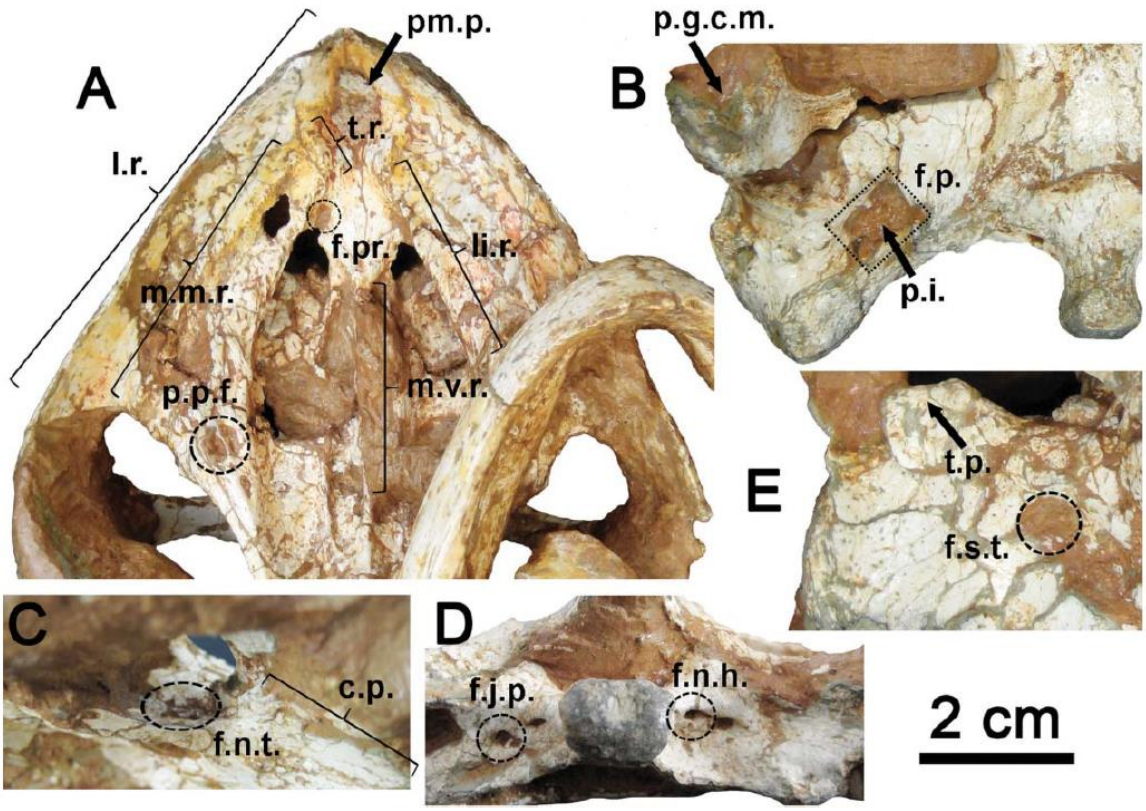

Figure 11. Close up photographs illustrating several details of the cranial morphology in *Cheirogaster richardi*. **A**, Detailed ventral view of the palate in IPS43809a, showing the several ridges of triturating surface as well as several cranial foramina and the premaxillary pit; **B**, Detailed ventral view of the right posterior portion of the skull in IPS43810a, showing the fenestra postotica and the mandibular condyle; **C**, Detailed oblique view of the left palatoquadrate of IPS43810a showing the relative position of the crista pterygoidea and the foramen nervi trigemini; **D**, Detailed posterior view of the occipital region in IPS43810a, showing the position of the foramina; **E**, Detailed dorsal view of the left posterior portion of the skull in IPS43810a, showing the auditory region. Abbreviations: c.p., crista pterygoidea; f.j.p., foramen jugulare posterius; f.n.h., foramen nervi hypoglossi; f.n.t., foramen nervi trigemini; f.p., fenestra postotica; f.pr., foramen praepalatinum; f.s.t., foramen stapedio-temporale; l.r., labial ridge; li.r., lngual ridge; m.m.r., median maxillary ridge; m.v.r., medial vomerine ridge; p.g.c.m., parasagittal groove of the condylus mandibulares; pm.p., premaxillary pit; p.p.f., posterior palatine foramen; t.r., tranverse ridge; t.p., trochlear process.

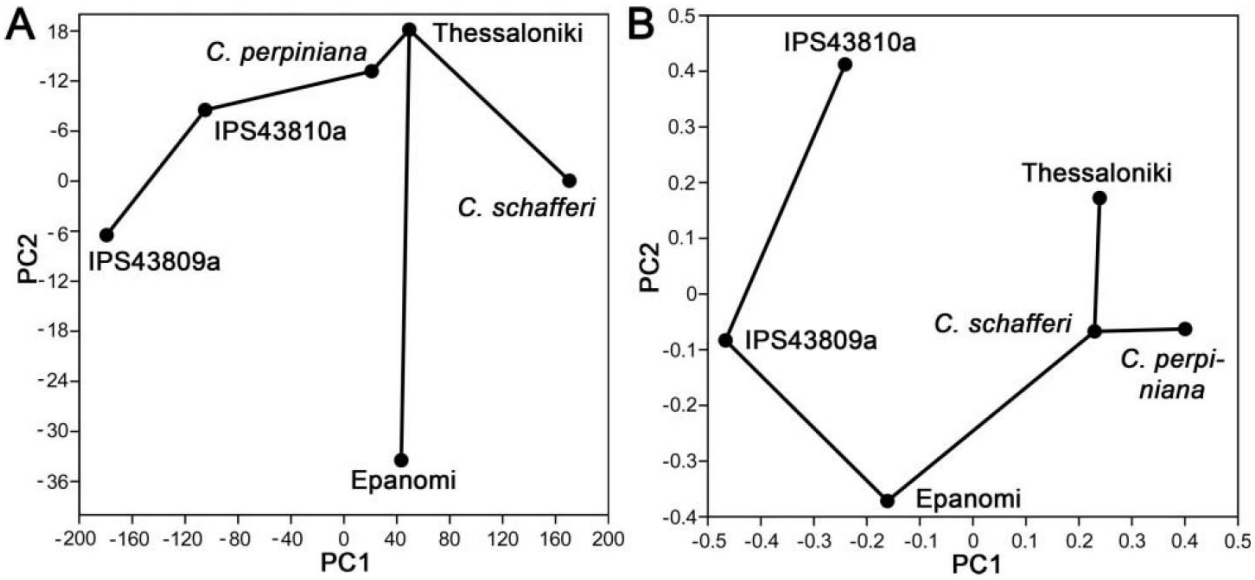

Figure 12. Results of the Principal Components Analysis (PCA) performed on the basis of cranial measurements on selected *Cheirogaster* species (see also Table S2). **A**, PCA based on the original measurements (reported in Table 4); **B**, PCA based on the Mosimann shape variables computed on the basis of the original ones.

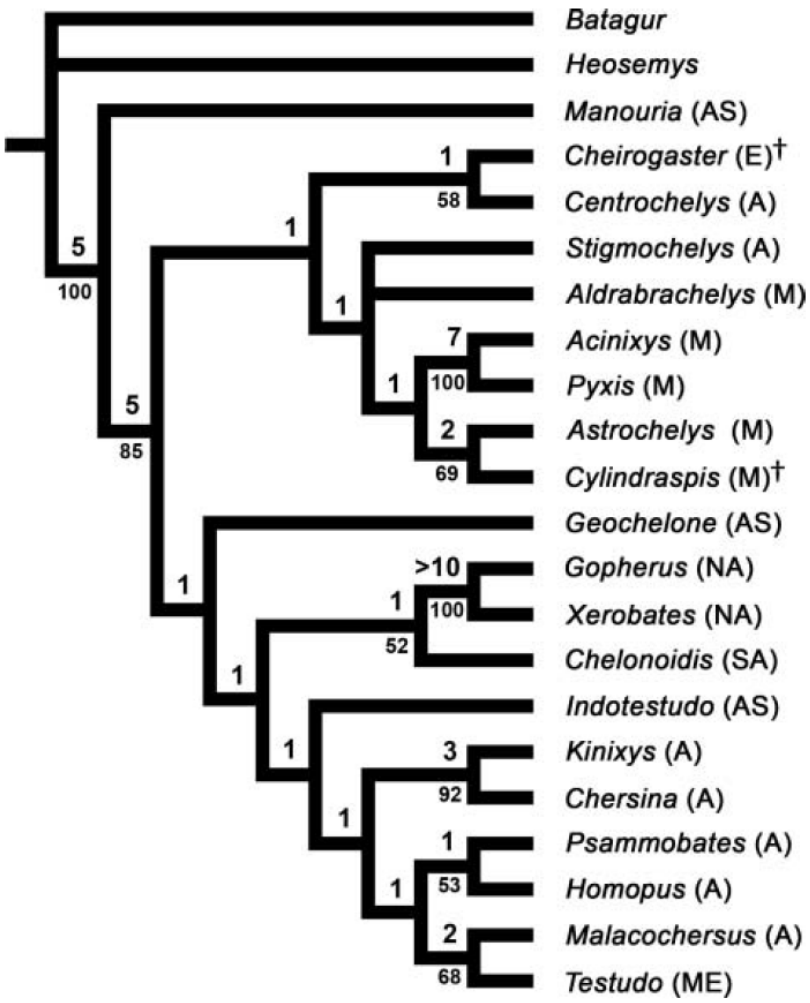

Figure 13. Phylogeny of eighteen testudinid genera (including the extinct *Cylindraspis* and *Cheirogaster*) on the basis of cranial features; *Cheirogaster* was coded on the basis of published descriptions of *Cheirogaster* spp. (see text for further details), as well as the two crania of *C. richardi* described in this paper. The strict consensus cladogram of the two most parsimonious trees of 147 steps (CI = 0.47, RI = 0.68, RCI = 0.32) obtained by the parsimony analysis is shown; the geoemydids *Heosemys* and *Batagur* were treated as outgroups. Numbers above nodes refer to Bremer's support index, whereas numbers below supports refer to bootstrap values. Extinct taxa are denoted by a dagger. The geographic distribution of testudinid genera is also depicted: A, Africa; AS, Asia; E, Europe; M, Madagascar or adjacent islands; ME, Mediterranean region; NA, North America; SA, South America and/or Galápagos Islands.

Online Supplementary Material

Figure S1. Postcranial and shell material associated to the two crania of *Cheirogaster richardi* described in this study (see catalogue numbers and anatomical identification in Table S1).

Table S1. List of postcranial and shell material associated to the two crania of *Cheirogaster richardi* described in this study.

Table S2. Results of the Principal Components Analysis (PCA) performed on the basis of cranial measurements of *Cheirogaster* species as well as on the Mosimann shape variables computed on their basis (see also Fig. 12).

Appendix 1. Complete list of specimens examined and bibliographic citations employed in the morphological comparisons.

Appendix 2. Character statements (modified from Gerlach 2001) employed in the cladistic analysis. The resulting data matrix with character scoring for the various taxa is reported in Appendix 3.

Appendix 3. Data matrix employed in the cladistic analysis performed in this paper for testudinid genera and *Cheirogaster*; *Batagur* and *Heosemys* are included as the outgroup. Missing data are represented by '?'; A = (0,1); B = (0,2).. See character definition in the Online Supplementary Material Appendix 2.

Appendix 4. Nexus file corresponding to the data matrix employed in the cladisc analysis performed in this paper (see also Appendix 3).