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Tetraconodont dental remains (Suidae, Tetraconodontinae) from the Middle Miocene site of Ca l'Almirall (Vallès-Penedès Basin, NE Iberian Peninsula)

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The suid dentognathic remains from the Middle Miocene (late Aragonian, MN6) site of Ca l'Almirall (formerly 'Can Almirall'; Vallès-Penedès Basin, NE Iberian Peninsula) were originally assigned to *Hyotherium soemmeringi* and subsequently to *Conohyus steinheimensis* (currently *Versoporcus steinheimensis*). However, such a taxonomic attribution is not backed by published descriptions or adequate iconography. Here we figure and describe the material to substantiate its taxonomic assignment and revisit the age of the site. We conclude that most of the material belongs to a tetraconodont that can be readily distinguished from *Conohyus simorreensis* and *Parachleuastochoerus valentini* in premolar size and proportions and shows greatest similarities with *Versoporcus* spp. Some authors have synonymised *Versoporcus grivensis* with *Versoporcus steinheimensis*, which overlaps in chronostratigraphic range and geographic distribution. However, based on size we tentatively support the distinction of the two species and assign the studied material to the former—while noting that the attribution of other *Versoporcus* remains from the Vallès-Penedès Basin is in need of revision. With an estimated age of ~14.0–13.5 Ma, the Ca l'Almirall material is roughly coeval with the oldest record of both *Versoporcus* spp., supporting the view that they are not successive chronospecies of a single evolving lineage.

Keywords: Artiodactyla; fossil suids; *Versoporcus*; taxonomy; Aragonian; Spain

Introduction

The first mention of fossil vertebrate remains from the site of Ca l'Almirall (formerly incorrectly spelled 'Can Almirall') was the citation of *Sus major* by Almera (1898: p. 254), who referred to the site as “el cerro de casa Almirall de Castellví de la Marca” (i.e., “the hill of Almirall house in Castellví de la Marca”, our translation from the Spanish original). Almera (1898) did not specify on what specimen the citation of *Sus major* (currently in *Hippopotamodon*; e.g., Pickford 2015) was based, but his find was subsequently echoed by Hernández-Pacheco (1914) and Bataller (1918). The latter

author figured the specimen (Bataller 1918: fig. 4), which is housed at the Geology Museum of the Barcelona Seminary (catalog number MGSB 31262), and concluded that it belonged to a sirenian (see also Bataller 1924; Pilleri et al. 1989: fig. 42). The find apparently faded into oblivion until Miquel Crusafont and Jaume Truyols rediscovered the site in 1957 (see Crusafont Pairó and Golpe Posse 1975). Soon thereafter, Crusafont Pairó (1959) reported the first faunal list for the site, which included two suids (*Listriodon splendens* and *Hyotherium soemmeringi*). Sporadic surveys between the 1960s and early 1970s expanded the faunal list (Crusafont Pairó and Golpe Posse 1975), but in Golpe-Posse's (1971) PhD dissertation on Spanish suiforms and subsequent publications (Golpe-Posse 1972, 1974; Crusafont Pairó and Golpe Posse 1975) all the suid material was referred to *H. soemmeringi*. Later, micromammal samplings were performed at Ca l'Almirall (Agustí et al. 1985), but no further suid remains have been recovered ever since. Some conditioning and building works during the 2010s unearthed some vertebrate fossil remains and motivated a visit by the Archaeological and Palaeontological Survey of the Generalitat de Catalunya, which inventoried the site. Ca l'Almirall was visited again by a team from the Institut Català de Paleontologia Miquel Crusafont (ICP) in 2016 (Casanovas i Vilar et al. 2019), who located the main fossiliferous layer but concluded it was threatened by future building works.

Golpe-Posse (1971) attributed a total of five dentognathic specimens from Ca l'Almirall to *H. soemmeringi*, including both upper and lower cheek teeth, while Crusafont Pairó and Golpe Posse (1975) reported four additional isolated teeth, mostly fragmentary, assigned to the same taxon. Crusafont Pairó and Golpe Posse (1975) considered that the previous citation of *L. splendens* was doubtful and might correspond to the older species *Listriodon lockharti*. They also speculated—apparently unaware

that Bataller (1918) had figured Almera's (1898) material—that the citation of *Sus major* likely corresponded to *H. soemmeringi*. Neither Golpe-Posse (1971) nor Crusafont Pairó and Golpe Posse (1975) described the material in detail, but merely reported dental measurements and figured the most complete specimen (a mandibular fragment with p3–m3). Eventually, Van der Made (1990) concluded that most of the material assigned by Golpe-Posse (1971, 1972) to *Hyotherium soemmeringi* belonged in fact to *Conohyus steinheimensis*, and reassigned the Ca l'Almirall remains to the latter species, which was later transferred to *Parachleuastochoerus* (Fortelius et al. 1996; Van der Made 1997, 1999). Van der Made (1990) noted that the Ca l'Almirall fossils seemed to be too advanced for the MN6 age supported by Agustí et al. (1985) but did not describe them either.

More recently, Pickford (2014) described multiple tetraconodontine fossil remains from the Vallès-Penedès Basin. Those from the younger (MN7+8) site of Sant Quirze previously assigned by Golpe-Posse (1971, 1972, 1974) to *H. soemmeringi* and *Hyotherium palaeochoerus* (the latter currently in *Propotamochoerus*), and subsequently reassigned to *C. steinheimensis* by Van der Made (1990), were included by Pickford (2014) in the hypodigm of *Parachleuastochoerus valentini*—then a new combination based on a long forgotten nominal species originally described by Filhol (1882) from Valentine Quarry in Saint-Gaudens, France (MN7+8). Pickford (2014) further erected the genus *Versoporcus* for the species previously known as *Parachleuastochoerus steinheimensis* (i.e., *Versoporcus steinheimensis*; type locality Steinheim, Germany, early MN7+8) and distinguished a second species of the genus (*Versoporcus grivensis*; type locality La Grive-Saint-Alban, France; late MN7+8; see the Discussion for further details about the age). Even though Pickford (2014) did not mention the Ca l'Almirall material, in the framework of a wider revision of European

Tetraconodontinae, Pickford (2016) assigned it to *V. steinheimensis* without additional justification. In the meantime, Van der Made et al. (2014) still included the Ca l'Almirall material in *P. steinheimensis*, and most recently Van der Made (2020) questioned Pickford's (2014, 2016) taxonomy and considered that *P. valentini*, *Versoporcus*, and *V. grivensis* are subjective junior synonyms of *Conohyus simorreensis*, *Parachleuastochoerus*, and *P. steinheimensis*, respectively. Except for the different taxonomic opinions about the validity of *Versoporcus*, there seems to be a consensus about the species assignment of the Ca l'Almirall suid material (Pickford 2016; Van der Made 2020). Nevertheless, such consensus is only apparent, for these two authors also have a different taxonomic concept of the nominal species and the boundaries of its variation. This casts doubts on the species attribution of the Ca l'Almirall suid, which cannot be independently evaluated based on the published literature, because descriptions are lacking and the iconography is very poor. To remedy this situation, here we figure and describe in detail the suid material from Ca l'Almirall and, on this basis, revisit its taxonomic assignment by means of qualitative and quantitative comparisons with the relevant material available from the literature.

Geographical location and geological background of the site

The fossil site of Ca l'Almirall is located in the Penedès Sector of the Vallès-Penedès Basin (NE Iberian Peninsula; see Casanovas-Vilar et al. 2016a for a review of the fossil vertebrate record from the basin). The site is close to the village of la Múnia (formerly also called 'l'Almúnia') within the municipality of Castellví de la Marca, next to the private trackway that goes from road BV-2128 to the farmhouse of Ca l'Almirall de Puigdespí. Despite the fact that the site has traditionally been referred to as 'Can Almirall' (e.g., Crusafont Pairó 1959; Golpe-Posse 1972, 1974; Crusafont Pairó and Golpe Posse 1975; Agustí et al. 1985) or, at most, 'Ca n'Almirall' (with the orthography

corrected; Casanovas-Vilar et al. 2016a), both spellings are at odds with the official toponym—‘Can’ and ‘Cal’ are both contractions of ‘casa’ (house) and the article that precedes the name of a person in Catalan—and should be replaced by ‘Ca l’Almirall’. The UTM (ETRS89) coordinates of the site are 31N 383589 E – 4578192 N (Casanovas i Vilar et al. 2019).

From a geological viewpoint, the locality of Ca l’Almirall is located in marine transitional layers toward the top of the Marine and Transitional Unit of the Vallès-Penedès Basin (Agustí et al. 1985; Casanovas-Vilar et al. 2016a). The main fossiliferous level that has yielded mammal remains is a coquina located below a siltstone that crops out at the northern and southern slopes of the small hill where the farmhouse is located (Crusafont Pairó and Golpe Posse 1975; Casanovas i Vilar et al. 2019). The fossil assemblage contains a mixture of terrestrial mammals along with elements from brackish and marine water, such as cerithioid gastropods, ostreids, and sirenians (Crusafont Pairó 1959; Golpe-Posse 1974; Crusafont Pairó and Golpe Posse 1975; Santafé Llopis 1978; Agustí et al. 1985; Casanovas i Vilar et al. 2019), and the stratigraphy of the area indicates alternating continental to marine sediments (see Santafé Llopis 1978 for further details), suggesting that the depositional environment of the mammalian remains was a palustrine or estuarine wetland (Golpe-Posse 1974; Crusafont Pairó and Golpe Posse 1975; Santafé Llopis 1978).

In agreement with Crusafont Pairó (1959), Golpe Posse (1971) assigned the site to the ‘early Vindobonian’, and Golpe-Posse (1974) more specifically considered it to be roughly equivalent to Sansan–La Grive (i.e., MN6–MN7+8). Agustí et al. (1985) dated the site to MN6, which was only tentatively accepted by Van der Made (1990), who subsequently referred it to MN7+8 (Van der Made 1997). Similarly, Steininger et al. (1990, 1996) correlated the site to MN8 (~11.9 Ma) following Aguilar (1982), who

considered it equivalent in age to Castell de Barberà (nowadays considered earliest Vallesian; Alba et al., 2019). Most recently, Casanovas-Vilar et al. (2011a, 2015, 2016a) tentatively supported a correlation with MN6, whereas Pickford (2016) considered it ‘MN8’ (i.e., late MN7+8) again. Rodents, which comprise the basis for late Middle Miocene regional biochronology (e.g., see Casanovas-Vilar et al. 2016b and references therein), may help to refine the correlation of Ca l’Almirall, but these turned out to be relatively scarce. Only 20 identifiable rodent cheek teeth have been recovered from the site, and many of them belong to taxa with little biochronologic value. Cricetids, which are diagnostic for Middle Miocene regional biozones (and also for MN zones; see Agustí et al. 2001; Hilgen et al. 2012) are represented by only 10 specimens that do not permit a confident species identification (contra Agustí et al. 1985). These include a medium-sized Cricetodontini indet. but only lower molars have been recovered, so it is impossible to conclude if the material belongs to *Cricetodon* or to *Hispanomys*. Other cricetids include a few molar fragments of a large species of *Democricetodon* (the size of *Democricetodon larteti*) and a few upper molars of a *Megacricetodon* species that agrees in size and morphology with the members of the *Megacricetodon collongensis*–*Megacricetodon gersii* lineage (see Oliver Pérez 2015). The remaining rodent fauna includes scarce material of the glirid *Muscardinus* cf. *hispanicus* and of various sciurids, the latter described by Aldana Carrasco (1992a, 1992b) and attributable in our opinion to *Miopetaurista* sp., *Heteroxerus* cf. *grivensis*, and *Csakvaromys* sp.

The rodent fauna from Ca l’Almirall suggests a correlation to either MN6 or MN7+8, as most of the reported species occur in their respective reference localities Sansan and La Grive-Saint-Alban. Hilgen et al. (2012) dated the lower boundary of MN7+8 to ~13.1–12.6 Ma based on the first historical appearance of *Megacricetodon*

crusafonti; in contrast, Casanovas-Vilar et al. (2016b), following Agustí et al. (2001), dated it to 12.4 Ma at the Vallès-Penedès Basin, based on the first historical appearance of *Megacricetodon ibericus*. The *Megacricetodon* species present at Ca l'Almirall is clearly different from *M. ibericus*, which discounts a correlation to MN7+8 and implies an age older than 12.4 Ma. Indeed, the *Megacricetodon* material from Ca l'Almirall better agrees in size and morphology with *Megacricetodon gersii*, which is characteristic of Sansan (Maridet and Sen 2012), the reference locality of MN6, as well as of local zones Dd (late half) and E of the Calatayud-Montalbán Basin (east-central Spain), where this species is recorded from 14.4 to 13.8 Ma (Oliver Pérez 2015). Given that Hilgen et al. (2012) defined the lower boundary of MN6 by the first historical appearance of *Megacricetodon gersii*, this supports a correlation of Ca l'Almirall to MN6 and suggests an age between 14.4 and 13.8 for the site.

Furthermore, *Cricetodon*—the first cricetodontin genus recorded in the Iberian Peninsula—first occurs at zone E (14.06–13.80 Ma; boundaries after Van der Meulen et al. 2012). Therefore, the presence of a *Cricetodontini* indet. at Ca l'Almirall argues against an age older than 14.0 Ma, overall resulting in an estimated age of 14.0–13.8 Ma. Considering the scarce rodent fauna recovered at Ca n'Almirall, this correlation must be regarded as tentative until a richer sample is available. Nevertheless, an early MN6 age for Ca l'Almirall is consistent with the regional context, given that this site is located in the upper transitional facies of the Marine and Transitional Unit of the Vallès-Penedès Basin (Agustí et al. 1985; Casanovas-Vilar et al. 2016a). This unit predates the Upper Continental Units of this basin, corresponding to at least three episodes of transgression-regression dated to the late Burdigalian, Langhian, and early Serravallian (Casanovas-Vilar et al., 2016a). However, given the regional diachronism

of rodent bioevents, even among different Iberian basins (Casanovas-Vilar et al. 2016b), the age of the site should probably be only broadly estimated around 14.0–13.5 Ma.

Materials and methods

The described suid material from Ca l'Almirall is housed at the ICP, Sabadell, Spain. The material mentioned by Golpe-Posse (1971) or Crusafont Pairó and Golpe Posse (1975) has been found among the ICP collections except for a single specimen (an M1–M2 series; see Table 1). Catalogue numbers are preceded by acronym 'IPS' (Institut de Paleontologia de Sabadell, the name of the ICP predecessor). The catalogue numbers given by Golpe-Posse (1971) are different from those currently valid, so in Table 1 we have specified their equivalences. The currently available material was remeasured, but the measurements previously reported by Golpe Posse (1971) and Crusafont Pairó and Golpe Posse (1975) have been provided for the sake of comparison. For single specimen that has not been located, given the lack of descriptions and iconographic material to validate their identification, we have refrained from using its measurements in the comparisons.

Dental terminology generally follows Van der Made (1996: figs. 1–15) and Fujita et al. (2000: fig. 7)—except that the 'paraconid' of lower premolars is referred to as 'prestylid' and that the 'tetracone' and 'tetrapreconule' of upper molars are respectively termed 'hypocone' and 'hypopreconule' (Thaung-Htike et al. 2006: fig. 2). Furthermore, Smith and Dodson's (2003: fig. 7) recommendations for the orientation of teeth and dental axes are also followed, except that 'buccal' instead of 'labial' was used for cheek teeth. Measurements of maximum mesiodistal length (L) and labiolingual/buccolingual breadth (B) of the studied material were taken to the nearest 0.1 mm with a digital calliper for all the available tooth loci. For molars, labiolingual breadth was taken separately at the mesial lobe (Bm) and the distal lobe (Bd), and then

the highest value was selected as maximum BL. A breadth/length index was computed (in %) as $BLI = B / L \times 100$. Tooth size and proportions of the described material were compared with those of other species by means of scatter plots of B vs. L. Systematics follows Pickford (2014, 2016)—see Van der Made (2020) for alternative views regarding the discussed tetraconodontines.

Dental measurements for the comparative sample were taken from the literature for the following species and fossil sites: *V. steinheimensis* from La Grive-Saint-Alban and Steinheim, *V. grivensis* from Anwil, Gratkorn, and La Grive-Saint-Alban, and *P. valentini* from Charmoille, Hinterauerbach bei Wartenberg, Hollabrunn, Klein Hadersdorf, Pitten, Kleineisenbach, Mira, Saint-Gaudens (including Valentine Quarry), Sant Quirze, Tutzing, and Wartenberg bei Erding (Pickford 2014, 2016); *C. simorreensis* from Alhambra, Carpetana, Channay, Käpfnach, Le Fousseret, Pischelsberg, Przeworno 2, St. Oswald, Urlau, and Villefranche d’Astarac (Ginsburg 1977; Kubiak 1981; Van der Made 1989, 1998, 2020; Van der Made and Morales 2003; Pickford 2013a, 2016); and *Conohyus doati* from Gaiselberg, Gau-Weinheim, El Buste, Fonte do Pinheiro, and Nuri Yamut (Van der Made 1989; Van der Made and Tuna 1999; Pickford 2013b, 2016). Both *P. valentini* and *C. doati*, which are recorded in MN7+8 and MN9 sites (Pickford 2016), were considered by Van der Made (2020) junior subjective synonyms of *C. simorreensis*, which sensu Pickford and Laurent (2014; see also Pickford 2014, 2016) would be mainly recorded at MN6 and MN7+8 sites (except for the MN9 site of Doué-la-Fontaine; Pickford 2016). In turn, the two species of *Versoporcus* are mostly recorded in MN7+8 sites, although some of them might be alternatively correlated with MN9 (Pickford 2016) and at least *V. steinheimensis* is considered to be present at Castell de Barberà (e.g., Van der Made 1997; Pickford 2016), which is currently

conclusively correlated with earliest MN9 (Alba et al. 2019)—see the Discussion for further details about the chronostratigraphic range of *Versoporcus* spp.

Systematic palaeontology

Order Artiodactyla Owen, 1848

Superfamily Suoidea Gray, 1821

Family Suidae Gray, 1821

Subfamily Listriodontinae Gervais, 1859

Listriodontinae indet.

Referred material

A lower incisor germ fragment (IPS126409; Fig. 1e), see Table 2 for measurements.

Description and remarks

The lower incisor germ fragment available from Ca l'Almirall displays three distinct mamelons on the incisal edge, preserving the cervix at the mesial or distal end (where a moderately developed anticlinid is present), and no portion of the endocristid can be observed. Overall these features indicate that the germ fragment belongs to a brachyodont and labiolingually compressed crown. This morphology is inconsistent with a tetraodont lower incisor (which would be much higher-crowned and mesiodistally shorter; e.g., see the i1–i2 of the *V. grivensis* holotype in Pickford 2014: fig. 32) and more closely resembles that of a listriodont lower incisor (e.g., Van der Made 1996: Pl. 19 fig. 16).

Subfamily Tetraodontinae Lydekker, 1876

Genus *Versoporcus* Pickford, 2014

Versoporcus grivensis (Gaillard, 1899)

Holotype

Associated maxillary and mandibular fragments from a single individual, including the left maxilla with P2–M3 (CCECL LGr 649), the right maxilla with P1–M1 and the mandibular symphysis with right and left i1–i2 partial right male c1 (CCECL LGr 650), the left mandibular corpus with p3–m3 (CCECL LGr 651), and the right male C1 (CCECL LGr 1527), housed in the Centre de Conservation et Études des Collections, Lyon, France. Gaillard (1899: Pl. III figs. 6, 8–9) figured part of the holotype (the two maxillary fragments, the mandibular corpus fragment, and the male c1) and noted that all these remains belong to a single individual, while Pickford (2014: figs. 30–33) figured all the specimens except the c1 and provided dental measurements.

Type locality

La Grive-Saint-Alban, Saint-Alban-de-Roche, France (MN7+8, late Aragonian, Middle Miocene). The site of La Grive includes multiple fissure fillings of different age (Mein and Ginsburg 2002), and unfortunately the exact provenance of the remains assigned by Pickford (2014) to the species was not reported. However, it is most likely that the holotype described by Gaillard (1899) comes from Peyre et Beau Quarry fissure A, which is correlated to late MN7+8, with an estimated age of 11.9–11.2 Ma (Casanovas-Vilar et al. 2011b, 2016b; see Discussion for further details).

Referred material

See Table 1 for a list of specimens of *V. grivensis* from Ca l'Almirall and Table 2 for measurements.

Description

Upper dentition

An isolated upper premolar crown fragment with root (Figure 1a) is interpreted as a mesial fragment of left P1. It is smaller and displays a more advanced degree of wear than the isolated left P2 (Figure 1b). As far as it can be ascertained, it shows a similar occlusal morphology, characterized by a marked lingual cingulum and a more restricted mesiobuccal one, except that the paracone appears more mesially positioned and gives rise to a comparatively shorter paraprecrista. The P2 preserves a moderately worn crown (with dentine exposure at the apex of the paracone) and two roots with moderate waisting at the cervix. The crown is elongate (much longer than wide, BLI = 45%) and somewhat wider distally than mesially. The lingual contour is rather straight, whereas the labial one displays a median constriction separating the moderately convex mesiobuccal contour from the more marked distobuccal extension of the crown. The paracone is centrally located at about crown midlength and originates two mesiodistally oriented crests. The paraprecrista curves mesiolingually toward the prestyle located on the mesiolingual end of the crown and displays an irregular course with some bifurcations that delimit several small foveae. In particular, the paraprecrista bifurcates before reaching the prestyle, giving rise to two distinct arms that ultimately merge with one another. Furthermore, a shorter and thinner secondary crista also descends from the paraprecrista in mesiobuccal direction, splitting the mesiobuccal cingulum in two distinct portions. The parapostcrista is straighter than the paraprecrista but of similar length, ending close to the distal end of the crown, forming a mildly distinct poststyle. There is a relatively well-developed cuspule (metacone) attached to the buccal side of the parapostcrista at about two-thirds of its length. The crown walls are moderately bulging at the level of the paracone, and otherwise mesially and distally concave,

particularly on the lingual side. The buccalcingulum is clearly discontinuous and restricted to the mesial and distal ends of the crown. The lingual cingulum, in contrast, is only partly interrupted at the base of the paracone, being well marked and beaded mesiolingually and similarly marked but wide (almost ledge like) on its distolingual portion. The mesial root is slightly longer than the distal one. Both are slightly waisted at the cervix, buccolingually compressed, and tilted toward another, being separated by a very narrow space that is filled by maxillary bone—giving the false impression that they are partially fused.

The right maxillary fragment IPS1733 (Figure 1c) preserves the P4–M1, and although some maxillary bone is preserved mesially from the P4, it is so damaged that no alveoli of the P3 can be discerned. The two preserved tooth crowns display a moderately advanced degree of wear with dentine exposure at the apices of the main cusps. The P4 displays a suboval and lingually tapering occlusal contour that is buccolingually wider than mesiodistally long (BLI = 134%). The lingual side is much more markedly convex than the buccal one, whereas the mesial and distal contours are quite straight. The protocone is located at about crown midlength on the buccal half of the crown, being somewhat more peripheral than the labial cusps. The paracone and metacone are represented by a single dentine lacuna, but originally their tips must have been placed very close to one another, as no vertical groove can be discerned on the crown separating their bases. There are no distinct lingual or buccal cingula, whereas mesial and distal ones are relatively well developed, particularly along the course of the protocone cristae. Both the protoprecrista and the protopostcrista are thick and long, reaching the mesial and distal cingula, respectively. Moderately developed prestyle and poststyle can still be discerned on the buccal half of the crown despite of wear. The profossa is mesially narrow (apparently due to the presence of a protoconule that has

been worn away) but much wider and deeper, being distally enclosed by the thickened end of the protopostcrista and the distal cingulum.

The M1 displays a subrectangular occlusal outline that is slightly longer than wide (BLI = 97%). It displays two distinct (mesial and distal) lobes separated by marked buccal and lingual constrictions. Well-developed mesial and distal cingula can still be ascertained, the distal one being more clearly ledge-like and somewhat distally protruding. There are four main cusps of conical shape and remnants of Fürchen can still be ascertained despite the heavy degree of wear. The two mesial main cusps are transversely aligned, whereas the hypocone is more distally located than the metacone. No protopreconule can be discerned on the mesial end of the crown, probably due to wear. In the middle, the hypopreconule is extensive but somewhat smaller than the main cusps, and slightly located toward the lingual half of the crown (i.e., closer to the protocone than to the paracone). The transverse groove separating the mesial and distal lobes is lingually blocked by a large hypoectoconule that is mesially bounded by a very deep crevice. An upper molar crown fragment (IPS31217; Figure 1d), larger than the M1 and identified as a mesiolingual fragment of right M2, might belong to the same taxon, although it is too worn to be diagnostic. As in the M1, there is no distinct metaectaconule (just small folds of enamel) between the two lobes, but in contrast there is a more marked style on the mesiobuccal corner of the crown, which we interpret as the buccal end of the mesial cingulum. Given the presence of a lower incisor fragment attributable to a listriodont (see above), we only tentatively assign this partial molar crown to *V. grivensis*.

Lower dentition

The left mandibular fragment IPS31238 (Figure 1f) preserves the p3–m3 series with a very slight degree of wear (i.e., with very limited dentine exposure on the cusp apices of

all teeth except the m3, which shows no apparent wear). The inferior portion of the corpus up to the alveolar level below p3 and the buccal side of the p4 were reconstructed with plaster decades ago, so it does not reflect the original depth of the mandible. Based on the uppermost original portion preserving the mandibular bone, the corpus becomes wider buccally from m1 (maximum preserved width of the corpus = 19.8 mm) to m3 (25.3 mm at the mesial level of m3, where the anterior end of the ramus is located, such that the lower portion of the anterior margin of the ramus overlaps with the distalmost portion of the m3 crown in lateral view). The preserved lower cheek teeth series (p3–m3) is 103 mm long, and the portion corresponding to the lower molars measures 67 mm.

A damaged (reconstructed) isolated lower premolar crown with mesial root IPS3612 (Figure 1g) is interpreted as a left p3, as it generally resembles in shape and proportions the p3 from the mandibular fragment (Figure 1f) and, despite being slightly smaller, it appears too large for a p2. Given that IPS3612 shows a more advanced degree of wear, the description of this tooth locus will be based on IPS31238. Furthermore, IPS3612 has not been included in the dental plots (see below) because originally the crown was probably longer (not only the prestylid is completely worn away but the present reconstruction of missing crown portion is somewhat uncertain). Based on IPS31238, the p3 is high-crowned, rather sectorial, and mesiodistally elongate (BLI = 52%), being somewhat broader distally than mesially. The occlusal contour is convex buccally, whereas on the lingual side it displays a mild concavity followed by a distolingual convex expansion of the crown base. The crown relief is dominated by the centrally located protoconid; from its apex, two sharp and steeply inclined cristids originate in a mesiodistal direction, resulting in a trenchant profile in buccal/lingual views. The protoprecristid is straight and descends mesially until reaching a distinct and

cuspid-like prestylid located on the mesialmost end of the crown and surrounded by well-developed mesiobuccal and mesiolingual cingulids that do not extend distalward. Distally from the protoconid apex, the protopostcristid displays a faint cuspid-like thickening (which may be interpreted as a rudimentary metaconid) and then markedly curves distolingually until ending close to the crown base. Distally from it there is a distal cuspid (hypoconid) that is higher but less distinct than the mesial prestylid. The buccal and lingual crown walls are slightly bulging at the level of the protoconid, but display more or less marked concavities at the level of the two cristids (more accentuated on the distal half of the crown).

The p4 is slightly lower-crowned than the p3, with the protoconid apex slightly tilted anteriorly, although it should be taken into account that the p4 is slightly more worn than the p3 distally from the protoconid. The p4 is mesiodistally shorter than the p3, but much broader buccolingually in relative terms (BLI = 67%). It displays a suboval occlusal contour somewhat wider distally than mesially. The buccal contour is convex and distolabially protruding, whereas the lingual one displays a slight constriction. As in the p3, the relief of the crown is dominated by a centrally located protoconid, with two mesiodistal cristids that originate from its apex. The protoprecristid similarly ends on a cuspid-like mesial prestylid, which is somewhat less distinct than in the preceding premolar but also surrounded by distinct cingular developments; due to the broader crown, these cingular developments constitute small verticalised foveae on each side. The protopostcristid is less steep than the protoprecristid. As in the p3, remnants of a rudimentary metaconid can still be observed despite wear on the distal aspect of the protoconid apex. Distally from it, the protopostcristid bifurcates at about its midlength, originating a verticalised distolingual cristid (as in the p3) and a more subhorizontal and distobuccally oriented one (not

clearly visible in the p3). The latter cristid ends on a hypoconid that is located on the distalmost end of the crown and is subequal in size to the mesial prestylid. The crown walls are convex and bulging on the mesial aspect of the protoconid, but markedly concave distally, where the buccal and lingual clefts are deeper than in the p3 (albeit they do not interrupt the protopostcristid). The distobuccal portion of the crown is surrounded by a distinct cingulid (more marked than that on the distolingual side) that encloses a small fovea.

The m1 and the m2 display a subrectangular occlusal outline longer than wide (BLI = 75% and 70%, respectively). The m1 is slightly broader distally than mesially and slightly constricted at the junction between the mesial and distal lobes, whereas the m2 is larger in absolute terms, slightly more elongate, and displays straighter buccal and lingual contours. The m3 is longer than the preceding molars and relatively narrower (BLI = 55%), with a distally tapering occlusal contour. The m1 displays a moderate degree of wear with dentine exposure at the apices of the main cuspids, whereas in the m2 there is almost no dentine exposure, and the m3 displays only very slight wear. Fürchen are best ascertainable in the m3 but can also be recognised in the preceding lower molars; enamel wrinkling is not well developed even in the slightly worn m3. The occlusal structure of the m1 and m2 is very similar. The protoconid and metaconid are transversely aligned, with the metaconid being higher and more extensive, whereas the apex of the entoconid is just slightly more mesially located than that of the hypoconid but similar in extension. The hypopreconulid and the pentaconid are centrally located and well developed, the former being slightly larger. On the buccal side, between the two lobes, there is a distinct hypoectoconulid, which is better developed in the m2 (almost contacting the hypopreconulid but being slightly more mesially located). There is a very narrow mesial cingulid that does not extend along the buccal or lingual sides.

This cingulid is distally bounded by the curved protoprecristid and the similarly curved but much shorter metaectocristid, which do not join but are interrupted by a groove that runs from the mesiolingual end of the cingulid into the profossid. The latter is mostly occupied by a short but very thick paraprecristid and is thus slit-like in morphology. The protoendocristid and metaendocristid partially merge with one another on their distal ends. The pentaconid is located on the distalmost end of the crown, which is slightly projected distally, defining very tiny foveae on either side. The m3 shows a similar occlusal configuration as the m2 except for the more distally extended talonid. As far as can be ascertained, the mesial cingulid appears to be as developed as in the preceding molars but extends slightly more distally on the buccal side, ending at about the level of the hypoectoconulid. Unlike in the m1–m2, this buccal ectoconulid appears double because it is split by the transverse groove that separates the mesial from the distal lobe. This groove is wider than in the preceding molars, and as a result the end of the similarly well-developed metaendocristid is more clearly separated from the hypoprecristid. Unlike in the preceding molars, in the m3 there is also a small entoectoconulid on the lingual side. The hypoconid and entoconid are closer to one another than in the m1-m2. Distally from these cusps, there is a well-developed pentapreconulid that is slightly more lingually located but only slightly smaller than the hypopreconulid. The pentaconid is centrally located on the distalmost end of the crown (better aligned with the hypopreconulid than with the pentapreconulid). The mesial end of the pentaconid base is adjacent to the distal aspect of the pentapreconulid without any intervening distinct pentaprecristid (which is slightly more distinct in the talonid fragment IPS126455; Figure 1h). Lingually from these cusps there is a beaded cingulid with cuspid-like protrusions of the enamel, whereas on the buccal side two larger and

more distinct pentaectoconulids define a narrow fossa located on the buccal side of the pentapreconulid.

Comparisons

Dental scatter plots comparing the Ca l'Almirall material with other tetraconodontines included in the comparative sample are reported in Figure 2. An attribution of the Ca l'Almirall tetraconodont to *C. simorreensis* (Ginsburg 1977: fig. 2; Kubiak 1981: Pl. 1 figs. 1–3, Pl. 2 fig. 6; Van der Made and Morales 2003: Pl. 1; Pickford 2013a: figs. 2–3, 5–6; Pickford and Laurent 2014: figs. 2–4, 23A, 24D, 26E; Pickford 2016: fig. 34B) can be ruled out based on multiple differences, particularly in the premolars. The P2 from Ca l'Almirall P2 is shorter and relatively broader than those of *C. simorreensis* (Figure 2a; BLI = 35–41%, N = 3), whereas the P4 displays similar size and proportions (Figure 2b; BLI = 123–137%, N = 3) but a less oval contour, with more angulated mesiobuccal and distobuccal corners, better defined paraectocrista and metapostocrista, and a longer protopostocrista that reaches the distal cingulum at the level of the protofossa.

Differences in the lower premolars are even more clear-cut: the p3 from Ca l'Almirall is much smaller and relatively narrower than those of *C. simorreensis* (Figure 2d; BLI = 59–70%, N = 6), while the p4 is similar in length but much less robust (Figure 2e; BLI = 69–86%, N = 12). Furthermore, besides being less distally expanded, the lower posterior premolars from Ca l'Almirall display a better-developed (more cuspid-like) prestylid, and the p3 is more sectorial and shows a less distally tilted protoconid. With regard to the lower molars, the m1 and m2 overlap in proportions with those of *C. simorreensis* (Figure 2f–g; m1 BLI = 73–82%, N = 8; m2 BLI = 68–84%, N = 11), but the m3 is slightly narrower (Figure 2h; BLI = 58–63%, N = 9), displays a larger pentapreconulid, and the pentaconid is less buccally tilted.

An attribution of the Ca l'Almirall material to the poorly known species *C. doati* (Azanza 1986: Pl. II fig. 1; Van der Made and Tuna 1999: fig. 3; Pickford and Laurent 2014: fig. 7; Pickford 2016: figs. 3–4) can also be discounted based on the same differences mentioned above regarding the p4 of *C. simorreensis* and especially the much larger size of *C. doati* (Figure 2b, d–h). The P4 from Nuri Yamut, Turkey, originally assigned to *Conohyus giganteus* by Van der Made and Tuna (1999) but later reassigned to *C. doati* by Pickford (2016), further shows multiple differences compared with the Ca l'Almirall specimen (which is longer on the lingual half of the crown and displays more developed protocone cristae and a better developed protofossa), thus more closely resembling that of *C. simorreensis*.

An assignment of the Ca l'Almirall specimens to *P. valentini* (Pickford 2014: figs. 9–18, 2016: figs. 7, 9A–C, 11, 13, 21–22, 26B–C), considered a large form of *C. simorreensis* by Van der Made (2020), can be ruled out on similar grounds. Although the P2 cannot be adequately compared because only a distal fragment has been reported for *P. valentini*, the Ca l'Almirall P2 clearly differs by displaying a less divergent distal root, broader occlusal proportions, a greater distolabial crown expansion with a secondary cuspule, and a much better developed distobuccal cingulum. The P4 also shows several differences despite possessing similar size and proportions to *P. valentini* (Figure 2b; BLI = 123–140%, N = 8), including the seemingly more closely packed paracone and metacone (although this is difficult to ascertain due to wear), the less oval and lingually tapering occlusal contour (which is more angulated in the Ca l'Almirall specimen, only tapering lingually from the protocone). The available molars from Ca l'Almirall display similar size and proportions to those of *P. valentini*, including not only the M1 (Figure 2c; BLI = 89–106%, N = 9) but also the m1 (Figure 2f; m1 BLI = 71–80%, N = 4), the m2 (Figure 2g; BLI = 68–76%, N = 7), and the m3 (Figure 2h; BLI

= 52–59%, N = 5), thus not differing once the variation in the *P. valentini* sample is taken into account. In contrast, the lower posterior premolars show additional differences. The p3 from Ca l'Almirall is more similar in occlusal contour to those of *P. valentini* than to those of *C. simorreensis*, but nevertheless differs from the former by displaying a better developed prestylid and by being much smaller (even if only slightly less robust) than those of *P. valentini* (Figure 2d; BLI = 53–59%, N = 5). In turn, the p4 from Ca l'Almirall is smaller and less inflated than many, but not all, of the specimens of *P. valentini* (Figure 2e; BLI = 62–79%, N = 6), and in particular more distally tapering on the distal third of the crown, further displaying a more distinct prestylid (as in the p3).

The material from Ca l'Almirall shows greater resemblances with the two species of *Versoporcus* recognised by Pickford (2014), including the type species *V. steinheimensis* (Fraas 1870: Pl. VIII figs. 1–3; Chen 1984: Pl. 1 figs. 1–2, Pl. 2 fig. 1, Pl. 4 fig. 2; Pickford 2016: fig. 15–18, 20) as well as the recently resurrected *V. grivensis* (Gaillard 1899: Pl. III figs. 6, 8–9; Van der Made et al. 2014: figs. 3–4; Pickford 2014: fig. 30–31, 33, 2016: figs. 6, 24). The P2 from Ca l'Almirall resembles the P2s of both species in proportions (Figure 2a; BLI = 43–46%, N = 3 in *V. grivensis*; BLI = 38–45%, N = 5 in *V. steinheimensis*) and general occlusal morphology—characterised by the presence of mesial and distal cingular swellings on both sides of the crown, but more marked lingually, and a buccally located distal cuspule—despite some minor differences at least compared to figured specimens (less bulging crown at the paracone level, and better-developed lingual than buccal cingula). The small prestyle with development of secondary crests and the distinct distobuccal cuspule on the buccal side of the parapostcrista more closely resemble the holotype of *V. grivensis* than the specimens of *V. steinheimensis*, but this might be variable within the species.

Nevertheless, based on size the Ca 1'Almirall P2 supports an assignment to *V. grivensis* instead of *V. steinheimensis*. The P4 from Ca 1'Almirall similarly resembles those of *Versoporcus* in the angulated occlusal contour, the closely-packed paracone and metacone, and the distally wide and deep profossa (which is distally enclosed by a cuspule located on the distal cingulum that originates from the end of the long protopostcrista). In terms of proportions, the P4 from Ca 1'Almirall overlaps with the two species (Figure 2b; BLI = 122–140%, N = 6 in *V. grivensis*; BLI = 123–140%, N = 7 in *V. steinheimensis*). Based on figured specimens, the apices of the protocone and paracone seem slightly less coalescent (more distinct) in *V. grivensis* than in *V. steinheimensis* and the Ca 1'Almirall specimen at comparable wear stages, but this might be variable and it is certainly difficult to evaluate due to wear. The occlusal profile of the P4 from Ca 1'Almirall is particularly similar to the holotype of *V. grivensis*, whereas the specimen of *V. grivensis* from Anwil more closely resembles *V. steinheimensis* in this regard, so this feature is probably too variable to be diagnostic. Therefore, the only clear indication of closer affinities with one of the two species is size: the Ca 1'Almirall P4 is larger than all specimens of *V. steinheimensis*, and only minimally wider than the largest specimen of *V. grivensis*, thereby further supporting an assignment to the latter species. The same applies to the Ca 1'Almirall M1 size and proportions (Figure 2c), which better fit those of *V. grivensis* (BLI = 86–103%, N = 7) than those of the generally smaller and somewhat narrower M1s of *V. steinheimensis* (BLI = 84–95%, N = 9).

The lower cheek teeth further favour an assignment of the Ca 1'Almirall material to *Versoporcus*. The morphology and proportions of the p3 from Ca 1'Almirall are compatible with both species (Figure 2d; BLI = 51–55%, N = 5 in *V. grivensis*; BLI = 51–56%, N = 9 in *V. steinheimensis*), except that the prestylid appears more marked

than in the figured specimens of *V. steinheimensis*, and hence more similar to the holotype and the figured specimen from Gratkorn of *V. grivensis*. Only in terms of absolute size the Ca l'Almirall p3 more closely matches the variation of *V. steinheimensis*, being smaller than previously reported specimens of *V. grivensis*, although there is considerable overlap between the two species. Similarly, the p4 from Ca l'Almirall resembles those of both species in occlusal contour and proportions (Figure 2e; BLI = 66–77%, N = 8 in *V. grivensis*; BLI = 66–75%, N = 13 in *V. steinheimensis*). Indeed, both species display considerable variation in p4 size and occlusal contour, with some specimens of *V. grivensis* being very stout and widest distally, whereas others more closely resemble *C. steinheimensis* and the Ca l'Almirall p4 in being more distally tapering and displaying a marked distobuccal angulation at about two-thirds of crown length. Nevertheless, the Ca l'Almirall p4 appears more similar to specimens of *V. grivensis* in displaying a well-developed prestylid (as in the p3), thus fitting better with this species once variation in p4 occlusal contour is taken into account. Finally, the proportions, occlusal contour, and marked development of Fürchen (with only minimal enamel wrinkling despite a slight degree of wear) in the Ca l'Almirall lower molars also closely resembles the condition of *Versoporcus*. In terms of size, the lower molars match both species, which display considerable overlap even though *V. grivensis* possesses larger molars on average. This further applies to the m3, since two specimens of *V. grivensis* from Gratkorn are not only much smaller than the rest of the sample of this species, but most similar in size to the smaller specimens of *V. steinheimensis*. In occlusal proportions, the lower molars from Ca l'Almirall (Figure 2f–h) also fit with both *V. grivensis* (m1 BLI 66–82%, N = 8; m2 BLI = 70–82%, N = 9; m3 BLI = 56–61%, N = 8) and *V. steinheimensis* (m1 BLI = 63–76%, N = 20; m2 BLI = 69–80%, N = 16; m3 BLI = 53–60%, N = 12). Their occlusal contour appears more

similar to that of the figured specimens of *V. grivensis*, whereas *V. steinheimensis* tends to display more marked constrictions between the mesial and the distal (m2) or the central (m3) lobe. However, this feature might be variable in both species and is hence of questionable diagnostic utility. The same applies to distal contour of the m3 talonid, which in the Ca l'Almirall material resembles that of *V. steinheimensis* and some specimens of *V. grivensis*, whereas other specimens of the latter species show a more compact talonid.

Discussion

Attribution to genus rank

Unfortunately, we were unable to locate one of the specimens mentioned by Golpe-Posse (1971, 1972) and Crusafont Pairó and Golpe Posse (1975) in the collections of the ICP. The remaining specimens are consistent with an attribution to a single tetraconodont species, except for a lower incisor germ fragment, which we attribute to a listriodont. Interestingly, this validates at the subfamily rank the previous citation of *Listriodon splendens* by Crusafont Pairó (1959), which Crusafont Pairó and Golpe Posse (1975) speculated might correspond to *L. lockharti* but were unable to substantiate based on any fossil from the site.

In turn, the descriptions and comparisons of the Ca l'Almirall tetraconodontine upper and lower permanent cheek teeth with the material of similarly-sized tetraconodontine species from the Middle to Late Miocene (MN6 to MN9) of Europe confirms that the former displays closer affinities with *Versoporcus* spp. (or *P. steinheimensis* sensu Van der Made 2020) than with either *Conohyus* or *P. valentini*. It is beyond the scope of this paper to critically evaluate whether *C. simorreensis*, *C. doati*, and *P. valentini* represent three distinct species from two different genera (as argued by Pickford and Laurent 2014; Pickford 2014, 2016) or a single species (*C. simorreensis*

sensu Van der Made 2020). However, the marked size differences between the two species of *Conohyus* suggest that, based on currently available material, they are best kept separate. In turn, the classification of *P. valentini* in *Parachleuastochoerus* instead of *Conohyus* would ideally require confirmation based on the find of lower male canine (which in *Conohyus* is very scrofic and uniquely characterised by a cementum ridge along the distal enamel-free face, whereas in *Parachleuastochoerus* it is verrucosic and lacks the cementum band; Pickford and Laurent 2014; Pickford 2016). This unsettled taxonomic debate, in any case, is rather irrelevant regarding the Ca l'Almirall material because the latter more closely resembles *Versoporcus* than any of the other taxa mentioned above. In contrast, the discussion as to whether the latter genus is distinct and polytypic (Pickford 2014, 2016) or whether it merely corresponds to a single species of *Parachleuastochoerus* (Van der Made 2020) is directly relevant for the described material and requires additional discussion.

According to Pickford's (2014) diagnoses of *Parachleuastochoerus* and *Versoporcus*, the latter genus would differ from the former (including *P. valentini*), among other features, by possessing a more anterior zygomatic root, more anteriorly placed posterior choanae, a scrofic (instead of verrucosic) male lower canine, and a different morphology of the anterior upper premolars (with mesial and distal cingular swellings and prominent mesial and distal cuspules that are slightly buccally positioned in *Versoporcus*, as opposed to more elongate premolars with a slightly swollen distal end in *Parachleuastochoerus*). The differences in cranial morphology rely on the inclusion of *P. valentini* in *Parachleuastochoerus*, which, as explained above, would need additional confirmation by the discovery of a lower male canine of this species. Nevertheless, these differences at least strongly support that *P. valentini* and *V. steinheimensis* belong to different genera—such that, if the former is included in

Parachleuastochoerus, then a distinct genus is warranted for the latter. This is the taxonomic opinion favoured in this paper until the purported synonymy between *P. valentini* and *C. simorreensis* advocated by Van der Made (2020)—or at least their potential congeneric status—are further clarified. Of the diagnostic features mentioned above, only the morphology of the P2 can be evaluated in the Ca l'Almirall material. This tooth displays the mesial and distal cingular swellings and the slightly buccally positioned distal cuspule that are diagnostic of *Versoporcus*. The mandibular fragment from Ca l'Almirall further fits with the diagnosis of *Versoporcus* in the possession of a p3 smaller than the p4 (albeit somewhat longer, as noted by Chen 1984), whereas other features considered diagnostic by Pickford (2014), such as the morphology of the P3 and the anterior lower premolars, cannot be evaluated with the available material. Our comparisons, in any case, show that the Ca l'Almirall material differs from both *P. valentini* and even more clearly from *Conohyus* spp. in dental proportions and occlusal morphology, particularly with regard to the premolars (including the P4).

Attribution to species rank

With regard to the taxonomic assignment of the Ca l'Almirall material to the species rank, the question arises as to whether the hypodigm of *V. grivensis* is sufficiently different from that of *V. steinheimensis* to warrant a distinct species, as argued by Pickford (2014, 2016). Before delving in this question, however, it is necessary to recapitulate first the nomenclatural issues related to the type species of the genus. Depéret (1887) originally assigned some tetraconodontine material from La Grive to *Sus* aff. *steinheimensis*, but a decade later the same author (Depéret 1892) assigned the same specimens to a new taxon (*Hyotherium soemmeringi* race *grivense*). According to the International Code of Zoological Nomenclature (ICZN 1999: Art. 45), the name established by Depéret (1892) would be nomenclaturally available if published before

1960 preceded by the terms ‘variety’ or ‘form’ and would be nomenclaturally unavailable if the author gave it an infrasubspecific rank or the work unambiguously reveals it was proposed for an infrasubspecific entity—except if adopted as a valid (sub)species name or treated as a senior homonym in a publication before 1985.

Although 'race' might appear infrasubspecific, in fact infrasubspecific entities refer to specimens that stand out due to intrapopulational variability. This does not apply to the taxon erected by Depéret (1892: p. 84), who considered it a ‘local race’ (i.e., differing due to interpopulational variability), thereby supporting Pickford's (2014) decision to treat it as available. This is even more conclusively supported by the fact—not explicitly mentioned by Pickford (2014)—that the name *H. soemmeringi grivense* was used as a valid subspecies by Trouessart (1898).

Notwithstanding the above, when describing additional tetraconodontine material from La Grive, Gaillard (1899) erected a new species (*Sus grivensis*) explicitly to replace Depéret's (1892) race, which was included in the synonymy. If the material described by the two authors were considered to belong to a single species, given that Depéret's (1892) taxon is nomenclaturally available, the authorship of the species should be attributed to Depéret (1892), while Gaillard's (1899) nominal species should be considered a junior synonym (and homonym). However, Pickford (2014) argued that the type series of Depéret's (1892) taxon was based on specimens attributable to two species from different genera—the M3 (Depéret 1887: Pl. XIII fig. 29) and the P4 (Depéret 1887: Pl. XIII fig. 28) being attributable to *C. simorreensis*, and the P3 and p4 (Depéret 1887: Pl. XIII figs. 26–27) to the same species (or at least genus) represented by the more complete remains subsequently described by Gaillard (1899). To solve this nomenclatural and taxonomic conundrum, Pickford (2014) designated the M3 figured by Depéret (1887) as the lectotype of *H. soemmeringi grivense* and considered it a

junior synonym of *C. simorreensis* (which was described by Lartet 1851, and hence has priority), thereby eliminating the synonymy and homonymy with Gaillard's (1899) species. At some point, Pickford (2014: p. 207) inadvertently asserted that 'The lectotype of *H. s. grivense*, belongs to the same species as the type material of *Sus grivensis*', but this must be a lapsus calami because he clearly stated that the lectotype was excluded from the synonymy and considered instead a synonym of *C. simorreensis* (e.g., Pickford 2014: table 9).

As the holotype of Gaillard's (1899) species includes associated maxillary and mandibular remains, Pickford's (2014) lectotype designation provides a much better basis for discussing the taxonomic validity of *V. grivensis* than had he chosen to designate instead one of the *Versoporcus* premolars described by Depéret (1887) as the lectotype of the homonymous species described by Depéret (1892). Pickford (2014) considered that the two species of *Versoporcus* are recorded at La Grive, with *V. grivensis* being slightly larger than *V. steinheimensis*. In the respective diagnoses of these species, Pickford (2014) reported lower molar row lengths of ca. 65 mm for *V. grivensis* and 63 mm for *V. steinheimensis*. He further noted that *V. grivensis* displays larger molars and anterior premolars than *V. steinheimensis* but third and fourth premolars of about the same size. These differences in dental size noted by Pickford (2014) based on the La Grive material are somewhat obscured when additional measurements reported by Pickford (2016) for *V. grivensis* from Anwil and Gratkorn as well as *V. steinheimensis* from Steinheim are included. Admittedly, *V. grivensis* is dentally larger on average than *V. steinheimensis*, but for many tooth loci both species considerably overlap, as shown in our dental plots based on Pickford's (2014, 2016) data. The m1–m3 series in the Ca l'Almirall mandible is 67 mm long, which is more consistent with *V. grivensis*—although given the considerable overlap in lower molar

size between the two species, a few millimetres difference in molar row length does not seem a very reliable diagnostic criterion. The P2 and P4 from Ca l'Almirall, in contrast, more closely resembles *V. grivensis* in terms of size and occlusal morphology, thereby supporting an assignment to this species. Larger samples would ideally be required to further evaluate variation in size and shape for these tooth positions, but coupled with the overall size of the Ca l'Almirall tooth sample, generally larger than in *V. steinheimensis* and more similar to that of *V. grivensis* (except for the p3), we tentatively support the taxonomic distinction of the two species and favour an assignment of the studied sample to the latter species.

Chronostratigraphic distribution

The distinction between the two species of *Versoporcus* would be better substantiated if their respective chronostratigraphic ranges were clarified further. The fact that the two species are morphologically very similar and mostly differ in size might suggest that they constitute two chrono(sub)species of a single evolving lineage, but this is contradicted by the sites in which each species has been identified (Pickford 2014, 2016; this paper), despite some age uncertainties. In the discussion below, we exclude the taxon from Lučane (Croatia) originally described as *Conohyus olujici* by Bernor et al. (2004), and subsequently considered a subspecies of *P. steinheimensis* (Van der Made et al. 2014; Van der Made 2020), because Pickford (2014, 2016) alternatively synonymized it with *Parachleuastochoerus huenermanni*. The Lučane tetraconodont is dated to ~15.0 Ma (MN5; de Leeuw et al., 2010), and hence older than both *Versoporcus* spp. and *P. huenermanni* as recorded elsewhere, so that more detailed comparisons would be required to better ascertain its systematic affinities.

According to Pickford (2016), *V. steinheimensis* would be present at Steinheim (type locality), La Grive, and several localities from the Vallès-Penedès Basin,

including Ca l'Almirall as well as Can Feliu, Hostalets de Pierola, and Castell de Barberà. Pickford (2016) distinguished between MN7 and MN8 (which are here informally referred to as early and late MN7+8, respectively) and correlated Steinheim with early MN7, La Grive with MN7+8 as a whole, and all the Vallès-Penedès sites to late MN7+8. However, Ca l'Almirall is best correlated with MN6 (as discussed in this paper, see above), Can Feliu is currently considered likely MN9 (Casanovas-Vilar et al. 2016a), Hostalets de Pierola encompasses both pre-Vallesian and Vallesian levels (from MN6 to MN9; Alba et al. 2006, 2017; Casanovas-Vilar et al. 2016a, 2016b), and Castell de Barberà is securely dated to the earliest MN9 (11.2 Ma; Alba et al. 2019). The fact that the material from Ca l'Almirall is attributable to *V. grivensis* instead of *V. steinheimensis* suggests that the Vallès-Penedès material—formerly assigned to *P. steinheimensis* by Van der Made (1997) and *V. steinheimensis* by Pickford (2016), but not described in some detail since Golpe-Posse (1971, 1972)—needs to be revised in the light of Pickford's (2014) resurrection of *V. grivensis*. Until then, any of the citations from the Vallès-Penedès should not be taken as prima facie evidence indicating that *V. steinheimensis* survived until the early Vallesian.

In turn, the age of the karstic fissure fillings from La Grive—where according to Pickford (2014) both species of *Versoporcus* are recorded—is not accurately known, although it is certain that different quarries cover different time spans (Mein and Ginsburg, 2002). Unfortunately, Pickford (2014) did not report the quarry provenance of the material from La Grive assigned to either species. However, Mein and Ginsburg (2002) reported *P. steinheimensis* (i.e., *Versoporcus* sp.) from the early MN7+8 Lechartier Quarry 7 (L7), as well as from the late MN7+8 Peyre et Beau Quarry fissure A (PBA) and Lechartier Quarries 3 (L3) and 5 (L5)—respectively corresponding to approximate age intervals of 12.4–11.9 Ma and 11.9–11.2 Ma (Casanovas-Vilar et al.

2011b, 2016b). Without further details on the provenance of the material, it is impossible to know whether the two species overlapped in time and space at La Grive (but see below regarding the holotype of *V. grivensis*). In any case, the type locality of *V. steinheimensis* (Steinheim) dates back to at least 13.5 Ma, as the Steinheim Basin was formed by a meteoritic impact 14.3 ± 0.2 Ma that led to the establishment of an endorheic freshwater lake that lasted at least several thousand years until 13.5 Ma (Tütken et al. 2006). It is thus possible that the Steinheim remains encompass a time interval of several thousand years, with 13.8 Ma sometimes taken as a very approximate dating (Hilgen et al. 2012: fig. 29.9). This would imply a chronostratigraphic range for *V. steinheimensis* of more than 1 Myr, from about 13.8 Ma (and no less than 13.5 Ma) to sometime between 12.4–11.9 Ma or even younger.

With regard to *V. grivensis*, according to Pickford (2016) it would be present at La Grive (type locality), Anwil, Gratkorn, and Kaisersteinbruch. Pickford (2016) correlated La Grive with MN7+8, Anwil with late MN7+8, Gratkorn with late MN7+8 or MN9, and Kaisersteinbruch with either MN6 or MN7+8. As discussed above, the La Grive quarries vary in age, but it is known that the material described by Depéret (1887) came from La Grive PBA, whereas that from L3, L5, and L7 was collected during the 20th century (Mein and Ginsburg 2002). This suggests that the holotype of *V. grivensis* described by Gaillard (1899) also came from PBA and is thus late MN7+8 in age (11.9–11.2 Ma). In contrast, Gratkorn has been dated to 12.2–12.0 (Gross et al. 2014)—i.e., early MN7+8 instead of late MN7+8 or even MN9 as indicated by Pickford (2016)—whereas Anwil, despite being the former reference locality of MN8, is even older with an approximate age of ~13.3 Ma (Kälin and Kempf 2009; Hilgen et al. 2012: fig. 29.9). Previously published evidence would therefore imply that the chronostratigraphic range of *V. grivensis* would extend from ~13.3 Ma to at least 11.9 Ma, thereby substantially

overlapping (at least between 13.3 and 12.4 Ma, probably more) with that of *V. steinheimensis* (see above).

The composition of the hypodigms of both *Versoporcus* species as conceived by Pickford (2014, 2016) therefore argues against the hypothesis that they constitute a single evolving lineage and imply a cladogenetic event well before 13 Ma, the uncertainties about the provenance from La Grive karstic fissures notwithstanding. In any case, the chronostratigraphic range inferred for *V. grivensis* is consistent with our identification of the species at the early MN6 site of Ca l'Almirall. Although Steinheim and Anwil were formerly considered to be the reference localities for MN7 and MN8 (Fahlbusch 1976), respectively, they were subsequently subsumed into a single zone (with La Grive M as reference locality) because they were considered to be too close in time (de Bruijn et al. 1992), not only relative to one another but also compared with Sansan (Kälin and Kempf, 2009), which is the reference locality for MN6. Admittedly, the dating of MN6 lower boundary has long been controversial—with proposals by different authors ranging from 13.8 Ma to as much as 16.5 Ma (see discussion in Bernor et al. 1996 and Steininger et al. 1996)—to a large extent due to uncertainties about the age of Sansan.

Controversies about the dating of Sansan stem from different interpretations of the magnetostratigraphic data. Thus, Sansan was initially correlated by Sen (1997) and Sen and Ginsburg (2000) to C5Bn.2n (15.160–15.032 Ma; chron boundaries after Ogg 2020). However, Daams et al. (1999a) favoured an alternative correlation to C5Abn (13.608–13.363 Ma) based on the (incorrect) assumption that, in the Montalbán-Daroca Basin, *M. gersii* was present in zones F and G1 (13.8–13.3 Ma; Daams et al. 1999b). As remarked by Pickford (1998), a dating of Sansan based exclusively on the local magnetostratigraphy is not reliable, as it could even be correlated to C5Ar.2n (12.887–

12.829 Ma). Nevertheless, if one accepts the definition of the MN6 lower boundary based on *M. gersii* as proposed by Hilgen et al. (2012), and given the recognition that *M. gersii* is indeed recorded in the Montalbán-Daroca Basin between 14.4 and 13.8 Ma in the preceding zones Dd and E (Oliver Pérez 2015; contra Daams et al. 1999a, 1999b), a correlation of Sansan to C5ADn (14.609–14.163 Ma) seems more likely. Taken together, biostratigraphic and magnetostratigraphic data would thus indicate an estimated age of ~14.4–14.2 Ma for Sansan, consistent with the generalized view that this site is slightly older than 14 Ma (Kälin and Kempf 2009; Maridet and Sen 2012; Hilgen et al. 2012: fig. 29.9; Van der Meulen et al. 2012).

This would indicate that Sansan is only slightly older than Central European sites customarily correlated with MN7+8, such as Steinheim and Anwil, which indeed predate the MN6/MN7+8 boundary, at least as defined on biochronological grounds in Western Europe (Hilgen et al., 2012; Casanovas-Vilar et al., 2016b). In this regard, it should be taken into account that the bioevents involved in the definition of MN units are patently diachronous among different regions (Bernor et al. 1996; Van der Meulen et al., 2011, 2012; Casanovas-Vilar et al., 2016b). Moreover, further discrepancies arise as a result of two competing concepts of MN units (Van Dam, 2003; Hilgen et al. 2012)—the classic faunal concept based on reference localities (de Bruijn et al. 1992) vs. a biostratigraphic concept based on biochronological events (Agustí et al. 2001; Hilgen et al. 2012; Casanovas-Vilar et al. 2016b). This leads to the apparent paradox that the former reference localities for MN7 (Steinheim) and MN8 (Anwil) should be correlated in fact with MN6 as currently conceived in Western Europe, where the MN6/MN7+8 boundary is dated to ~12.4 Ma (Casanovas-Vilar et al., 2016b) instead of at ~13.9 Ma (Kälin and Kempf, 2009)—in the same way that Can Llobateres 1 (9.76 Ma), the reference locality of MN9, does indeed correlate with MN10 (Casanovas-Vilar

et al. 2016b; Alba et al., 2018). As such, our preferred correlation of Ca l'Almirall to early MN6 (as defined in Western Europe based on biostratigraphic criteria) implies an age that is roughly coeval with the previously known first appearance datums of both *V. steinheimensis* and *V. grivensis* in Central Europe.

Conclusions

We describe the scarce dentognathic suid remains recorded at the Middle Miocene site of Ca l'Almirall, based on currently available material housed in the ICP, which includes both upper and lower permanent teeth. A lower incisor fragment is attributed to an indeterminate listriodont, whereas the rest of the available material seems to belong to a single tetraconodont species. Based on dental size and shape, we conclude that the described material differs from *Conohyus* spp. and *P. valentini*, and more closely resembles *Versoporcus*, in agreement with previous authors, who assigned the material to *V. steinheimensis* (the type species of the genus). However, mostly on the basis of dental size we favour an alternative attribution to *V. grivensis*, which considerably overlaps with *V. steinheimensis* in chronostratigraphic range. The site of Ca l'Almirall is certainly older than 12.4 Ma (the dating of the MN6/MN7+8 boundary as defined in Western Europe) and tentatively correlated here with early MN6 with an age of ~14.0–13.5 Ma, slightly younger than Sansan but roughly coeval with Steinheim. Although such correlation must be considered tentative, it strengthens the view that, as indicated by the previous citation of *V. grivensis* from Anwil, both species overlapped in time well before their potential co-occurrence at the La Grive fissure fillings.

It is noteworthy that *V. grivensis* has been sometimes considered a junior subjective synonym of the type species of the genus (Van der Made 2020). However, based on size differences, we tentatively favour their distinctiveness, while recognizing that additional samples should be investigated to more clearly delimit the variation

range as well as the chronostratigraphic and geographic distribution of both species. The future revision of previously published tetraconodontine material from various sites of the Vallès-Penedès Basin (e.g., Can Feliu) and, especially, the description of unpublished remains from Abocador de Can Mata and Creu de Conill—which are currently under study—offer interesting prospects in this regard. In the meantime, previous citations of *P. steinheimensis* s.l. (Van der Made 1990, 1997) or *V. steinheimensis* s.s. (Pickford 2014) from Vallès-Penedès localities should be taken with great caution, given the potential confusion with *V. grivensis* and other tetraconodontines such as *P. valentini* (as exemplified by Pickford 2014 in the case of Sant Quirze).

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Disclosure statement

The authors report there are no competing interests to declare.

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Table 1. Suid material from Ca l’Almirall previously reported in the literature and studied in this paper. Previously published catalogue numbers are provided within brackets. Abbreviations: w/n, without number; GP, Golpe-Posse (1971); CPGP, Crusafont Pairó and Golpe Posse (1975).

Catalogue No.	Old catalogue No.	Anatomical identification	Assignment	Previous reports	Figure
IPS31238	[IPS1514]	Left mandibular fragment with p3–m3	<i>V. grivensis</i>	GP, CPGP	1f
IPS3612	[IPS1798]	Left p3	<i>V. grivensis</i>	GP, CPGP	1g
—	[IPS1447]	Left M1–M2	Not found	GP, CPGP	—
IPS1733	[IPS1515]	Right maxillary fragment with P4–M1	<i>V. grivensis</i>	GP, CPGP	1c
IPS126486	[IPS1799]	P1 mesial fragment (originally reported as P2)	<i>V. grivensis</i>	GP, CPGP	1a
IPS118131	w/n	Left P2 (originally reported as P1 or P2)	<i>V. grivensis</i>	CPGP	1b
IPS126409	w/n	i1 germ fragment (originally reported as left)	Listriodontinae indet.	CPGP	1e
IPS31237	w/n	Right M2 mesiobuccal crown fragment (originally reported as m1 or m2?)	cf. <i>V. grivensis</i>	CPGP	1d
IPS126455	w/n	m3 germ distal fragment	<i>V. grivensis</i>	CPGP	1h

Table 2. Measurements (in mm) of the suid material from Ca l’Almirall except for [IPS1799] (not found) and IPS126455 (too fragmentary to provide a meaningful measurement). Previously published measurements are reported but were not used in the comparisons. Previously published catalogue numbers are provided within brackets. Specimens without current catalogue number could not be located in the ICP collections. Abbreviations: L, mesiodistal length; B, labiolingual/buccolingual breadth (maximum); Bm = B at the mesial lobe; Ld = B at the distal lobe; GP, Golpe-Posse (1971); CPGP, Crusafont Pairó and Golpe Posse (1975).

Catalogue No.	Old catalogue No.	Tooth locus	GP and CPGP		This study			
			L	B	L	B	Bm	Bd
IPS31238	[IPS1514]	p3	19.5	9.8	19.3	10.0		
IPS31238	[IPS1514]	p4	17.4	12.3	18.3	12.3		
IPS31238	[IPS1514]	m1	17.7	13.0	17.4	13.1	12.9	13.1
IPS31238	[IPS1514]	m2	20.7	13.9	20.6	14.4	14.4	13.7
IPS31238	[IPS1514]	m3	27.3	15.3	27.6	15.2	15.2	13.1
IPS3612	[IPS1798]	p3	18.1	8.6	>17.9	8.8		
—	[IPS1447]	M1	19.1	16.8				
—	[IPS1447]	M2	21.8	18.0				
IPS126486	[IPS1799]	P1	—	—	>9.0	5.9		
IPS1733	[IPS1515]	P4	14.7	17.4	14.0	18.8		
IPS1733	[IPS1515]	M1	18.2	16.7	18.0	17.4	17.0	17.4
IPS118131	w/n	P2	—	—	17.8	8.0		
IPS126409	w/n	i1	—	—	>6.5	≥8.1		
IPS31237	w/n	M2	>14.0	—	—	>15.8	—	

Figure captions

Figure 1. Suid remains from Ca l'Almirall described in this paper: a, left P1 mesial fragment (IPS126486), in buccal (a1), lingual (a2), and occlusal (a3) views; b, left P2 (IPS118131), in buccal (b1), lingual (b2), and occlusal (b3) views; c, right maxillary fragment with P4–M1 (IPS1733), in buccal (c1), lingual (c2), and occlusal (c3) views; d, right M2 mesiobuccal crown fragment (IPS31237) in occlusal view; e, i1 germ fragment (IPS126409), in labial (e1), mesial or distal (e2), and lingual (e3) views; f, left mandibular fragment with p3–m3 (IPS31238), in occlusal (f1), buccal (f2), and lingual (f3) views; g, left p3 (IPS3612), in occlusal (g1), buccal (g2), and lingual (g3) views; h, m3 germ distal fragment (IPS126455) in occlusal view. All specimens are attributed to *Versoporcus grivensis* (tentatively in the case of IPS31237) and IPS126409 (*Listriodontinae* indet.). In occlusal views mesial is on top.

Alt Text: Photographs of the suid dentognathic remains from Ca l'Almirall. Most specimens are depicted in several views.

Figure 2. Scatter plots of mesiodistal length (L) vs. buccolingual breadth (B) of upper and lower cheek teeth preserved at Ca l'Almirall: a, P2; b, P4; c, M1; d, p3; e, p4; f, m1; g, m2; h, m3. For data sources of the comparative sample, see Materials and methods.

Alt Text: Seven diagrams depicting length against breadth for each of the cheek tooth positions recorded in the Ca l'Almirall material compared with other tetracodonontine species (*Versoporcus steinheimensis*, *Versoporcus grivensis*, *Conohyus simorreensis*, *Conohyus doati*, and *Parachleuastochoerus valentini*), each depicted with a different symbol. The plots indicate more or less overlap among species depending on the tooth, but overall indicate that the Ca l'Almirall material most closely resembles *Versoporcus* species (this is particularly clear-cut for the third and fourth lower premolars).

