

Research Article

The suid assemblage from the Vallesian locality of Can Llobateres 1 (Vallès-Penedès Basin, NE Iberian Peninsula) revisited

Sara G. Arranz¹, Souzanna Siarabi¹, Sharrah McKenzie^{1,2}, Isaac Casanovas-Vilar¹, David M. Alba¹

¹ Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain

² Department of Anthropology, Washington State University, PO Box 644910, Pullman, WA 99164–4910, USA

<https://zoobank.org/E65B4CD1-F9CD-473F-932A-AF8759A72C31>

Corresponding authors: Sara G. Arranz (sara.arranz@icp.cat); David M. Alba (david.alba@icp.cat)

Academic editor: G. Aguirre-Fernández ♦ Received 18 October 2025 ♦ Accepted 6 February 2026 ♦ Published 24 February 2026

Abstract

The suid assemblages from Europe experienced considerable turnover during the Vallesian (MN9–MN10, early Late Miocene), ultimately leading to a marked decline in diversity during the Turolian. To provide further insight into the timing and paleoecological context of this Vallesian turnover in the suid assemblages, here we revisit the taxonomic composition of the suids from the Late Miocene (9.8 Ma) fossil locality of Can Llobateres 1 (CLL1; Vallès-Penedès Basin, NE Iberian Peninsula), with emphasis on species other than the small tetraconodontine *Parachleuastochoerus crusafonti* (for which CLL1 is the type locality). Although CLL1 is one of the most thoroughly sampled Vallesian sites from Europe, a recent revision of the faunal list evinced that the occurrence of multiple large mammals is based on fossil remains that were described many decades ago or that have never been published, leading to potentially misleading or, at least, insufficiently substantiated attributions. According to published accounts, three additional suid species are recorded at CLL1, being much scarcer than *Pa. crusafonti*: the listriodontine *Listriodon splendens*, the suine *Propotamochoerus palaeochoerus*, and a large tetraconodontine variously assigned to *Versoporcus steinheimensis* or ‘*Parachleuastochoerus*’ *valentini*. Our revision of the available remains, including unpublished material recovered from the 1980s onward, confirms the presence of the two former species and the assignment of the large tetraconodontine to ‘*Pa.*’ *valentini*. On biochronological grounds, the association of these taxa is characteristic of the early Vallesian, with the record of *L. splendens* representing the last well-dated occurrence of this species. From a paleoenvironmental viewpoint, the suid assemblage from CLL1 is consistent with previous inferences indicating the presence of a densely forested and humid environment with more open habitats nearby.

Keywords

Dental morphology, Europe, evolution, Miocene, Spain, suids, systematics, taxonomy

Introduction

Suid assemblages were more diverse (both at the species and subfamily rank) during the Middle than the Late Miocene (Fortelius et al. 1996; Van der Made 2022). However, during the early Late Miocene (i.e., the Vallesian, MN9–MN10) they still maintained a higher diversity than in the Turolian, owing to the survival of some Aragonian elements (such as listriodontines) and

the appearance of new taxa (particularly, suines). Recent work on Miocene suids from Europe has supported the co-occurrence of several suid species during the earliest Vallesian (McKenzie et al. 2023a, 2024; Alba et al. 2024), but this remains to be better ascertained in younger Vallesian localities. Furthermore, as a result of taxonomic revisions and controversies about the taxonomy of European tetraconodontines during the last couple of decades, previously published taxonomic identifications

provided in faunal lists (without detailed descriptions and iconography) are impossible to corroborate without inspecting the original material. Here we focus on the suid assemblage from the Late Miocene locality of Can Llobateres 1 (CLL1; Vallès-Penedès Basin, NE Iberian Peninsula; see review in Alba et al. 2011a; Fig. 1), which is renowned for yielding fossil remains of the extinct great ape *Hispanopithecus laietanus* (see Alba et al. 2012, and references therein) and has also figured prominently in the study of Miocene mammal assemblages from Europe (Mein 1975, 1990, 1999; de Bruijn et al. 1992).

Taxonomic controversies about European tetraconodontines

To better understand some current uncertainties about the composition of the Can Llobateres 1 suid assemblage, it is necessary to briefly review some recent taxonomic debates about Miocene tetraconodontines of Europe. Such controversies stem from the work by Pickford and colleagues (Pickford 2014, 2016; Pickford and Laurent 2014), which included multiple taxonomic opinions and nomenclatural acts. These have been subsequently disputed by Van der Made (2020), questioned by Iannucci and Begun (2022), and either accepted, rejected, or modulated in several recent papers focused on Late Miocene material from the Vallès-Penedès Basin (McKenzie et al. 2024, 2025; Alba et al. 2025). The most relevant taxonomic controversies for the revision of the Can Llobateres 1 suid assemblage are briefly introduced below.

The genus *Versoporcus* Pickford, 2014 was erected based on *Versoporcus steinheimensis* (Fraas, 1870)—previously included in either *Parachleuastochoerus* (Fortelius et al. 1996; Van der Made 1999) or *Conohyus* (Chen 1984; Bernor et al. 2004)—as its type species. Furthermore, Pickford (2014) further distinguished a second species of this genus, *Versoporcus grivensis* (Gaillard, 1899). This was not supported by Van der Made (2020: supplementary information), who synonymized the two species and further considered that *Versoporcus* is a junior subjective synonym of *Parachleuastochoerus* Golpe-Posse, 1972 without further justification. Initially, McKenzie et al. (2023a) tentatively accepted the distinction of both species within *Versoporcus*. However, soon thereafter McKenzie et al. (2024) showed, based on material from Castell de Barberà, that the purported differences in dental size and proportions alluded by Pickford (2014, 2016) are best interpreted as intraspecific variation, therefore concluding that *V. grivensis* is a junior subjective synonym of *V. steinheimensis*. This is further supported by the fact that Pickford (2014, 2016) considered both species to be present at La Grive but included in one or the other species different cheek teeth from the same mandibular fragment (the m2–m3 of MDC LGR 640bis, the p2–p4 of MDC LG648, and the m2–m3 of MDC LGR 669; see Pickford 2014: tables 7 and 8). The examination of this material by one of us (S.S.) confirms that these specimens were attributed to

both species simultaneously, which most clearly shows that their distinction was arbitrary.

The distinction of *Versoporcus* from *Parachleuastochoerus*, in contrast, is a more complex question. A definitive conclusion in this regard is hindered by the lack of cranial remains of *Parachleuastochoerus crusafonti* Golpe-Posse, 1972, which is the type of the genus. Pickford (2014) justified the generic distinctiveness of *Versoporcus* based on cranial differences compared with a snout from Valentine (Saint-Gaudens), which he considered the holotype of *Parachleuastochoerus valentini* (Filhol, 1882). This species had been resurrected by Pickford and Laurent (2014)—who further designated a lectotype for *Conohyus simorrensis* (Lartet, 1851) and provided an emended diagnosis of the genus *Conohyus* Pilgrim, 1925. This supported the distinction of *Pa. valentini*, which was described in greater detail by Pickford (2014, 2016). According to the latter author, this large tetraconodontine would have remained unnoticed in multiple MN7+8 and MN9 sites because its remains were misidentified as *Versoporcus* or even *Propotamochoerus*. This was taken with much skepticism by Van der Made (2020), who questioned the provenance of the aforementioned snout, considered it was merely a large individual of *C. simorrensis*, and ultimately concluded (without much discussion) that *Pa. valentini* is just a junior subjective synonym of *C. simorrensis*. In contrast, subsequent authors (McKenzie et al. 2023b, 2024; Alba et al. 2024, 2025) considered the species resurrected by Pickford and Laurent (2014) to be distinct and attributed to it multiple remains from various localities of the Vallès-Penedès Basin. At the same time, these authors substantially modified Pickford's (2014, 2016) hypodigm composition. In particular, McKenzie et al. (2023b) concluded that *Conohyus melendezi* is a synonym of *C. simorrensis* (Van der Made 2020) instead of *Pa. valentini* (Pickford 2014, 2016), while McKenzie et al. (2024) concluded that *Conohyus doati* (Lartet, 1851) is a nomen dubium and that most of the material attributed to the latter by Pickford (2014, 2016) belongs in fact to *Pa. valentini*. The most complete account of the latter species is Alba et al.'s (2025) description of the Sant Quirze sample (only partially described by Pickford 2014), which confirms that the species may be distinguished in multiple dental features from *C. simorrensis* and is, thus, distinct at least to the species rank. This is further supported by the lower male canine morphology of *Pa. valentini* (first described by Alba et al. 2025), which lacks the distal cementum band that, according to Pickford and colleagues (Pickford 2014, 2016; Pickford and Laurent 2014), is diagnostic of both *C. simorrensis* and *Conohyus* s.s.

Despite supporting the validity of the species, Alba et al. (2025) used open nomenclature (i.e., '*Pa.*' *valentini*, with the genus name within quotes) to reflect the current uncertainty about its genus ascription. While the lack of the aforementioned enamel band in the c1m and the reduced premolar-to-molar proportions differ from the condition of *C. simorrensis*, these features might have evolved in parallel and are compatible with both *Pa. crusafonti* and *V. steinheimensis*. In turn, the cranial differences between '*Pa.*' *valentini* and *V. steinheimensis*

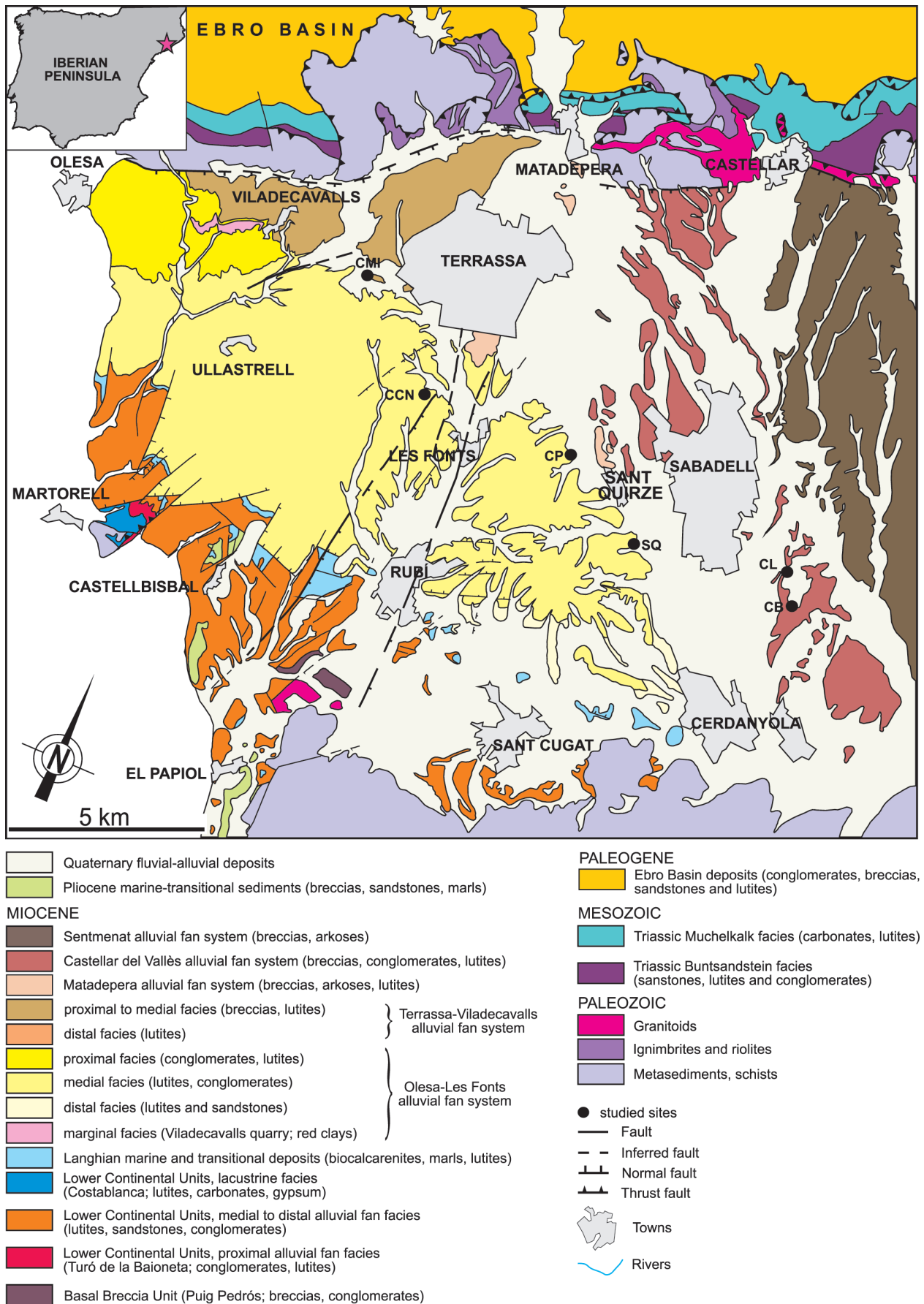


Figure 1. Geological map of the Vallès Sector of the Vallès-Penedès Basin, and location of the basin within the Iberian Peninsula (inset), showing the location of Can Llobateres (CL) and other late Aragonian and Vallesian major suid-bearing sites: CB, Castell de Barberà; CCN, Creu de Conill; CMI, Can Missert; CP, Can Poncic; SQ, Sant Quirze. Modified from Casanovas-Vilar et al. (2016a: fig. 2).

noted by Pickford (2014) support their generic distinction but must not necessarily imply that the former belongs to *Parachleuastochoerus*, as they could be interpreted as supporting a closer relationship with *Conohyus* (Iannucci and Begun 2022). Indeed, a cladistic analysis performed by Alba et al. (2025) did not support close phylogenetic relationships between either '*Pa.* *valentini*' or *V. steinheimensis* and *Pa. crusafonti*. This issue cannot be conclusively resolved without an in-depth revision of the type species of *Parachleuastochoerus*, which is a work in progress by several authors of this paper. In the meantime, we consider it necessary to reflect with open nomenclature the uncertainty in the genus ascription of '*Pa.* *valentini*', as well as to provisionally retain *V. steinheimensis* within a different genus from *Pa. crusafonti*—in the hope that future analyses outside the scope of this paper will clarify further the systematic arrangement of the aforementioned species at the genus rank.

The suid assemblage from Can Llobateres 1

The locality of Can Llobateres 1 is particularly interesting for investigating the timing and paleoecological context of the suid faunal turnover during the Vallesian because (1) it is particularly well investigated from a paleoenvironmental viewpoint (e.g., Marmi et al. 2012; Arranz et al. 2023); and (2) it is also accurately dated, slightly preceding the disappearance of multiple forest-adapted mammals during the extinction event known as the Mid-Vallesian Crisis (Casanovas-Vilar et al. 2014, and references therein). On biostratigraphic grounds, CLL1 is correlated to the *Cricetulodon hartenbergeri* – *Progonomys hispanicus* interval subzone of the local Vallès-Penedès Basin biozonation (Casanovas-Vilar et al. 2016a, 2016b), while on magnetostratigraphic grounds it is correlated to chron C4Ar.3r (Agustí et al. 1996, 1997; Garcés et al. 1996), with an interpolated age of 9.76 Ma (Casanovas-Vilar et al. 2016a). Under a strictly biostratigraphic (rather than faunal) approach to MN units (Hilgen et al. 2012), CLL1 may be correlated to early MN10 instead of late MN9, because it postdates the appearance of *Progonomys* elsewhere at ~10.0 Ma (Van Dam et al. 2014; Casanovas-Vilar et al. 2016a; Alba et al. 2018; Pandolfi et al. 2025).

The restricted faunal list initially reported for CLL1 (Villalta-Comella and Crusafont-Pairó 1943) was much refined in later decades, once the first systematic excavations took place (Crusafont Pairó 1964). Further faunal lists were subsequently published as the study of various groups progressed (e.g., Crusafont-Pairó and Golpe-Posse 1973; Golpe-Posse 1974; de Bruijn et al. 1992; Alba et al. 2011a), the most recent one corresponding to that of Arranz et al. (2023). According to the latter authors, up to 78 mammalian species would be recorded from CLL1, including 39 small and 39 large mammals. However, it should be taken into account that, even if CLL1 was not excavated during most of the 1970s, additional excavations

took place there in 1981, 1990, and 2010–2015 (Alba et al. 2011a, 2011b, 2012; Alba 2025). With the exception of the primate (Begun et al. 1990; Golpe-Posse 1993; Alba et al. 2012) and plant (Marmi et al. 2012) remains recovered during these campaigns, very few taxa from CLL1 have been described and/or revised in print during the last couple of decades (but see Robles et al. 2010, 2013; Madurell-Malapeira et al. 2014; Casanovas-Vilar et al. 2015; Escanero Aguilar and Casanovas-Vilar 2015; Furió et al. 2015; Villa et al. 2019; Pandolfi et al. 2025). As a result, unpublished fossil remains of multiple taxa (particularly, artiodactyls and perissodactyls) from CLL1 that might potentially refine their taxonomic ascription remain to be studied in detail among the collections of the Institut Català de Paleontologia Miquel Crusafont (ICP; Sabadell, Spain). With this aim in mind, here we critically revisit the composition of the suid assemblage from CLL1, to support the most updated identifications provided by Arranz et al. (2023). Particularly, we describe all the identifiable remains (mostly found decades ago but unpublished until now) attributable to suid species other than *Parachleuastochoerus crusafonti* Golpe-Posse, 1972, for which CLL1 is the type locality and which deserves an in-depth systematic review of its own (Alba et al. 2025), which is outside the scope of this paper.

In her PhD dissertation, Golpe-Posse (1971, 1972) studied the then available suid fossil remains from CLL1 and described the small tetraconodontine suid *Pa. crusafonti*, placing it in a by then monotypic genus of its own. Remains of this species from CLL1 were subsequently described by Pickford (1981, 2014) and the validity of the species is not questioned (Pickford 2016; Van der Made 2020; Alba et al. 2025). Nevertheless, Golpe-Posse (1971, 1972) also reported three additional suid species from CLL1, based on a handful of teeth (see Materials and methods): *Listriodon splendens* Von Meyer, 1846, *Hyotherium soemmeringi* Von Meyer, 1834, and ?*Hyotherium* sp. One of the specimens was seemingly identified as both *L. splendens* and ?*Hyotherium* sp. (see below). The same identifications were provided by Golpe-Posse (1974), except that the question mark of *Hyotherium* sp. was removed. In contrast, de Bruijn et al. (1992) only reported the presence of *Pa. crusafonti* and the suine *Korynochoerus palaeochoerus* (Kaup, 1833)—currently in *Propotamochoerus*, following Fortelius et al. (1996) and Van der Made et al. (1999). Most likely, de Bruijn et al. (1992) just followed Van der Made (1990), who did not report *L. splendens* or a larger-bodied tetraconodontine from the site. Indeed, Van der Made (1990) noted that most of the citations of *H. soemmeringi* by Golpe-Posse (1971, 1972) belonged to *Conohyus steinheimensis* (Fraas, 1870)—currently in *Parachleuastochoerus* (e.g., Van der Made 2020) or *Versoporcus* (Pickford 2014, 2016; McKenzie et al. 2023a, 2024)—but omitted CLL1 from the list of localities that yielded remains of this species. It is uncertain whether these omissions were inadvertent or implicitly implied that Van der Made (1990) assimilated previous

citations of *Hyotherium* by Golpe-Posse (1971, 1972) to *Propotamochoerus palaeochoerus*. However, in a monograph on listriodontines, Van der Made (1996) listed CLL1 as having yielded remains of *L. splendens* (see also Van der Made et al. 2022), while Van der Made (1997) reported again four different suid species from CLL1 (including not only *Pa. crusafonti* and *Pr. palaeochoerus*, but also *L. splendens* and *Pa. steinheimensis*). The same taxa were included by Alba et al. (2011a) in the faunal list from CLL1, except that *Pa. steinheimensis* was included in *Conohyus*, implicitly following Bernor et al. (2004). More recently, Pickford (2014, 2016) reported *L. splendens* and *Pr. palaeochoerus* but no tetraconodontine other than *Pa. crusafonti* from CLL1, whereas Arranz et al. (2023) added *Parachleuastochoerus valentini* to the list.

Given the paucity of the suid material from CLL1 attributed to taxa other than *Pa. crusafonti* in the literature (Golpe-Posse 1971, 1972)—see Materials and methods for further details—the presence of *Pr. palaeochoerus* and, especially, *L. splendens* and *V. steinheimensis* remains doubtful. The former is currently considered a typically Vallesian element, mostly present in MN9 and a few MN10 sites (Pickford 2013; Alba et al. 2022, 2024; McKenzie et al. 2023b, 2024; Siarabi et al. 2024), and hence its presence at CLL1 is to be expected. However, Golpe-Posse (1971, 1972) did not cite *Hyotherium palaeochoerus* (as the species was known by then), but merely *?Hyotherium* sp., based on a single purported P3 that was further identified by her as a p2 of *L. splendens*. Therefore, the presence of *Pr. palaeochoerus* at CLL1 remains to be substantiated with descriptions, measurements, and/or pictures in print. The same applies to *L. splendens*, which was more abundant during MN6 and MN7+8 but persisted into MN9 in Western Europe (Van der Made 1996; Pickford and Morales 2003), with CLL1 apparently representing its latest occurrence (Van der Made 1996; Van der Made et al. 2022). Given the biochronological importance of the CLL1 record of *L. splendens*, it is thus surprising that the few fossils reported in the literature were not described nor figured. Besides the aforementioned premolar attributed to both *L. splendens* and *?Hyotherium* sp., Golpe-Posse (1971, 1972) further attributed to *L. splendens* a lower molar from CLL1 that Pandolfi et al. (2025) recently assigned to *Tapirus priscus*, thereby casting further doubts on the presence of the species. Van der Made (1996) reported measurements for additional specimens of *L. splendens* from CLL1 but he did not figure them, and his identifications cannot be checked because of missing and incorrect catalog numbers. However, among the CLL1 collections we found previously unpublished suid remains that confirm the presence of *L. splendens* in this locality, which are first described herein.

Finally, even if frequently omitted from the faunal lists of CLL1, a second tetraconodontine (larger than *Pa. crusafonti*) is conclusively documented based on the

lower premolar assigned to *H. soemmeringi* by Golpe-Posse (1971, 1972)—the latter author also attributed a talus to this species, but we have been unable to locate the specimen. Determining the taxonomic identity of this tetraconodontine was hindered by the fact that Golpe-Posse (1971, 1972) provided measurements but did not figure or describe the specimen, and is further complicated by the aforementioned controversies and uncertainties about European tetraconodontines. Most recently, the large tetraconodont from CLL1 was attributed to *Pa. valentini* by Arranz et al. (2023) without supporting such an assignment with descriptions, comparisons or figures, which are first provided here. In summary, based on previously published specimens, the presence of *L. splendens*, *Pr. palaeochoerus*, and ‘*Pa.*’ *valentini* is not well supported. Here we figure and describe the meager sample of suid remains from CLL1 attributed by Golpe-Posse (1971, 1972) to taxa other than *Pa. crusafonti* and we further describe additional remains from this locality that do not belong to the latter taxon and were not described by that author because they were presumably recovered more recently.

Materials and methods

Studied sample

The catalog numbers used by Golpe-Posse (1971, 1972), preceded by the acronym IPS (for ‘Institut de Paleontologia de Sabadell’, the former name of the ICP), are not the same as those currently in use at the ICP (despite being preceded by the same acronym). Nevertheless, Golpe-Posse’s (1971, 1972) catalog numbers are generally preserved in the museum labels/record and/or the fossils themselves, which in this case enabled us to identify the fossil teeth from CLL1 assigned by this author to suids other than *Pa. crusafonti*. When reporting such specimens, we have used the current catalog numbers as well as the old numbers within brackets. The complete list of specimens, including also those first reported here, is provided in Table 1. Note that Golpe-Posse (1971, 1972) reported a left P3 of *?Hyotherium* sp. and a right p2 of *L. splendens* from CLL1 with the same catalog number. Given that the measurements provided for both taxa are the same and that we found a single specimen with this number in the ICP collections, we conclude that Golpe-Posse (1971, 1972) inadvertently provided two identifications for the very same specimen.

Comparative sample

Comparative measurements and iconography were taken from the literature, including *L. splendens* (Van der Made 1996; Pickford 2012; Van der Made et al. 2014), *Pr. palaeochoerus* (Mottl 1966; Hellmund 1995; Van

Table 1. List of suid teeth from CLL1 belonging to taxa other than *Parachleuastochoerus crusafonti*

Catalog No.	Tooth locus	Assignment	Figure
IPS1684	R DI1	<i>L. splendens</i>	Fig. 2b
IPS1686	L di1	<i>L. splendens</i>	Fig. 2d
IPS1687	L di2	<i>L. splendens</i>	Fig. 2e
IPS1688	L dp3	<i>L. splendens</i>	Fig. 2g
IPS1689	L dp2	<i>L. splendens</i>	Fig. 2f
IPS1700 ^a	L dp3	<i>P. palaeochoerus</i>	Fig. 4l
IPS27111	R C1f	<i>L. splendens</i>	Fig. 2a
IPS28145a–i	Tooth series: R DI1 (a) + L DI1 (b) + R DP2 (c) + R DP3 (d) + L DP3 (e) + R DP4 (f) + L DP4 (g) + R M1 germ (h) + L M1 germ (i)	<i>P. palaeochoerus</i>	Fig. 4a–i
IPS28164 [IPS1880] ^b	L p1	' <i>Pa.</i> ' <i>valentini</i>	Fig. 2i
IPS28171 [IPS1760] ^c	R dp2	<i>P. palaeochoerus</i>	Fig. 4j
IPS39504a–b	R mandibular fragment with dp3–dp4 + m1 germ (a) + L mandibular fragment with dp4–m1 (b)	<i>P. palaeochoerus</i>	Fig. 4m–o
IPS39508	R DP2	<i>L. splendens</i>	Fig. 2c
IPS39523	R p2	<i>P. palaeochoerus</i>	Fig. 4p
IPS39525	L DI1	' <i>Pa.</i> ' <i>valentini</i>	Fig. 2j
IPS39526 [IPS1987] ^d	L i3	' <i>Pa.</i> ' <i>valentini</i>	Fig. 2h
IPS39527	L di1	' <i>Pa.</i> ' <i>valentini</i>	Fig. 2k
IPS39538	L dp2	<i>P. palaeochoerus</i>	Fig. 4k

Old catalog numbers are provided within brackets.

^a Also recorded as IPS39540, it might be the same individual as IPS39504.

^b Tentatively identified by Golpe-Posse (1971, 1972) a left p2? of *H. soemmeringi* (MD = 17.6 mm, BL = 5.2 mm).

^c Tentatively identified by Golpe-Posse (1971, 1972) a right p2? of *Pa. crusafonti* (MD = 11.4, BL = 4.2 mm).

^d Not reported by Golpe-Posse (1971, 1972) despite having an old collection number.

der Made et al. 1999; Fortelius et al. 2005; Pickford 2013, 2015; Iannucci and Begun 2022; McKenzie et al. 2023b, 2024), '*Pa.*' *valentini* (Pickford 2014, 2016; McKenzie et al. 2023b, 2024; Alba et al. 2024, 2025), and *V. steinheimensis* (Pickford 2014, 2016; McKenzie et al. 2023a, 2024). Given the potential confusion between *Pr. palaeochoerus* and '*Pa.*' *valentini* (Pickford 2014, 2016), the comparative sample of the former species does not include material from other localities of the Vallès-Penedès Basin published by Golpe-Posse (1972), which is currently under study and will be described in further detail elsewhere. It is also noteworthy that, following McKenzie et al. (2024) and Alba et al. (2024, 2025), we exclude the material from Mira (Mira Basin, central Spain), originally described as *Conohyus melendezi* Golpe-Posse, 1972, from the hypodigm of *Pa. valentini* (contra Pickford 2014, 2016; Pickford and Laurent 2014). This locality was correlated to MN9 by Pickford (2014, 2016), but the rodent assemblage indicates a correlation with late MN5 (Agustí et al. 1988; Oliver Pérez 2015) and on morphological grounds we further concur with Van der Made (2020) that the material is best included in *C. simorreensis*—see discussion in McKenzie et al. (2024) and Alba et al. (2024, 2025).

Dental terminology and measurements

Dental axes follow the recommendations by Smith and Dodson (2003: fig. 7) except that 'buccal' instead of 'labial' is used for cheek teeth. Occlusal features are named after Van der Made (1996: figs 1–15) with modifications (see

McKenzie et al. 2023b, 2024), so that the 'paraconid' of lower premolars is termed 'prestylid' and that the 'tetracone' and 'tetrapreconule' of upper molars are referred to as 'hypocone' and 'hypopreconule', respectively.

Dental measurements of maximum mesiodistal length (**MD**) and labiolingual/buccolingual breadth (**BL**) were taken with a digital caliper to the nearest 0.1 mm. For deciduous fourth premolars and permanent molars, BL was taken both at the mesial (**BLm**) and the distal/central (**BLd**) lobes. Crown proportions were measured using a breadth/length index ($BLI = BL / MD \times 100$). Dental dimensions and proportions were visually assessed by means of bivariate plots of BL vs. MD.

Abbreviations

Anatomical abbreviations. **D/d**, deciduous; **C/c**, canine; **f/m**, female/male; **I/i**, incisor; **L**, left; **M/m**, molar; **P/p**, premolar; **R**, right.

Measurement abbreviations. **BL**, maximum labiolingual or buccolingual breadth; **BLd**, BL of molars at the distal lobe (or central in the case of third molars); **BLI**, breadth/length index; **BLm**, BL of molars at the mesial lobe; **Max**, maximum; **Min**, minimum; **SD**, standard deviation.

Locality abbreviations. **CLL1**, Can Llobateres 1.

Institutional abbreviations. **ICP**, Institut Català de Paleontologia Miquel Crusafont, Sabadell, Barcelona, Spain; **IPS**, acronym of the ICP collections (following the former informal name of this institution, 'Institut de Paleontologia de Sabadell').

Systematic Paleontology

Order Artiodactyla Owen, 1848

Superfamily Suoidea Gray, 1821

Family Suidae Gray, 1821

Subfamily Listriodontinae Gervais, 1859

Subfamily Listriodontini Gervais, 1859

Genus *Listriodon* Von Meyer, 1846*Listriodon splendens* Von Meyer, 1846

Fig. 2a–g

Referred material. See Table 1 for a list of material and Table 2 for measurements.

Description. Permanent teeth. A complete right C1f (Fig. 2a) with a worn and damaged crown (with enamel only preserved distally and slightly labially) is the only permanent tooth of a listriodontine among the CLL1 sample. The crown appears slightly longer than broad and is distolabially curved from cervix to apex. The root is much larger (longer, broader and, especially, higher) than the crown, reaching its maximum cross-sectional area (MD = 21.7 mm, BL = 18.0 mm) at about midheight and progressively tapering apically (slightly inclined distolabially). Both a

labial and a lingual sulcus are visible along the root, which displays a mildly bifurcated apex, evidencing that it is composed of two (mesial and distal) partially fused roots—the distal being broader than the mesial.

Deciduous teeth. Two upper and four lower deciduous teeth are available. The right DI1 (Fig. 2b) preserves the slightly worn crown and a large portion of the root. An interproximal wear facet against its antimeres is present on the mesial end of the crown, which is low and very labiolingually compressed (BLI = 34%). It displays two moderately distinct lobes, and multiple mamelons can be further distinguished along the incisal edge (except on its distal-most portion). The labial crown wall is markedly convex and lingually recurved from base to apex, whereas the lingual portion is concave and displays a distinct but low lingual cingulum, as well as minor corrugations of the enamel (i.e., there is no distinct endocrista). The crown markedly protrudes from the cervix mesially, where a moderately developed preanticleline can be discerned, and to a lesser extent distally, where it shapes a more indistinct endosyncline. The root is very compressed labiolingually and distally tilted.

The right DP2 (Fig. 2c) only preserves the crown, which is lightly worn (with dentine exposure only at the

Table 2. Measurements (in mm) of suid teeth from CLL1 belonging to taxa other than *Parachleuastochoerus crusafonti*

Catalog No.	Tooth locus	Assignment	MD.	BL	BLm	BLd	BLI
IPS1684	R DI1	<i>L. splendens</i>	16.4	5.6			34.1
IPS1686	L di1	<i>L. splendens</i>	8.6	5.6			65.1
IPS1687	L di2	<i>L. splendens</i>	10.2	6.8			66.7
IPS1688	L dp3	<i>L. splendens</i>	12.6	7.6			60.3
IPS1689	L dp2	<i>L. splendens</i>	11.3	5.8			51.3
IPS1700	L dp3	<i>P. palaeochoerus</i>	12.7	6.5			51.2
IPS27111	R C1f	<i>L. splendens</i>	>10.8	>10.5			—
IPS28145a	R DI1	<i>P. palaeochoerus</i>	>6.6	(5.1)			—
IPS28145b	L DI1	<i>P. palaeochoerus</i>	8.1	5.2			64.2
IPS28145c	R DP2	<i>P. palaeochoerus</i>	11.9	6.4			53.8
IPS28145d	R DP3	<i>P. palaeochoerus</i>	15.5	10.9			70.3
IPS28145e	L DP3	<i>P. palaeochoerus</i>	15.2	11.1			73.0
IPS28145f	R DP4	<i>P. palaeochoerus</i>	16.2	>12.8	>12.8	>11.6	—
IPS28145g	L DP4	<i>P. palaeochoerus</i>	16.5	13.4	13.4	12.8	81.2
IPS28145h	R M1	<i>P. palaeochoerus</i>	20.4	16.5	16.5	14.8	80.9
IPS28145i	L M1	<i>P. palaeochoerus</i>	20.2	(16.5)	(16.5)	(15.2)	(81.7)
IPS28164 [IPS1880]	L p1	' <i>Pa.</i> ' <i>valentini</i>	17.3	5.3			30.6
IPS28171	R dp2	<i>P. palaeochoerus</i>	11.4	4.2			36.8
IPS39504a	R dp3	<i>P. palaeochoerus</i>	12.9	6.5			50.4
IPS39504a	R dp4	<i>P. palaeochoerus</i>	22.0	10.6			48.2
IPS39504a	R m1	<i>P. palaeochoerus</i>	20.1	12.8	12.6	12.8	63.7
IPS39504b	L dp4	<i>P. palaeochoerus</i>	22.1	10.3			46.6
IPS39504b	L m1	<i>P. palaeochoerus</i>	20.0	>12.0	>12.0	>12.0	—
IPS39508	R DP2	<i>L. splendens</i>	14.3	9.0			53.8
IPS39523	R p2	<i>P. palaeochoerus</i>	15.1	6.4			42.4
IPS39525	L DI1	' <i>Pa.</i> ' <i>valentini</i>	6.8	5.0			73.5
IPS39526 [IPS1987]	L i3	' <i>Pa.</i> ' <i>valentini</i>	6.1	10.8			177.0
IPS39527	L di1	' <i>Pa.</i> ' <i>valentini</i>	5.1	5.8			113.7
IPS39538	L dp2	<i>P. palaeochoerus</i>	11.4	4.5			39.5

Em dashes denote that measurements are not available, greater than signs precede measurements smaller than the original value due to incomplete preservation, and estimates are provided within parentheses.

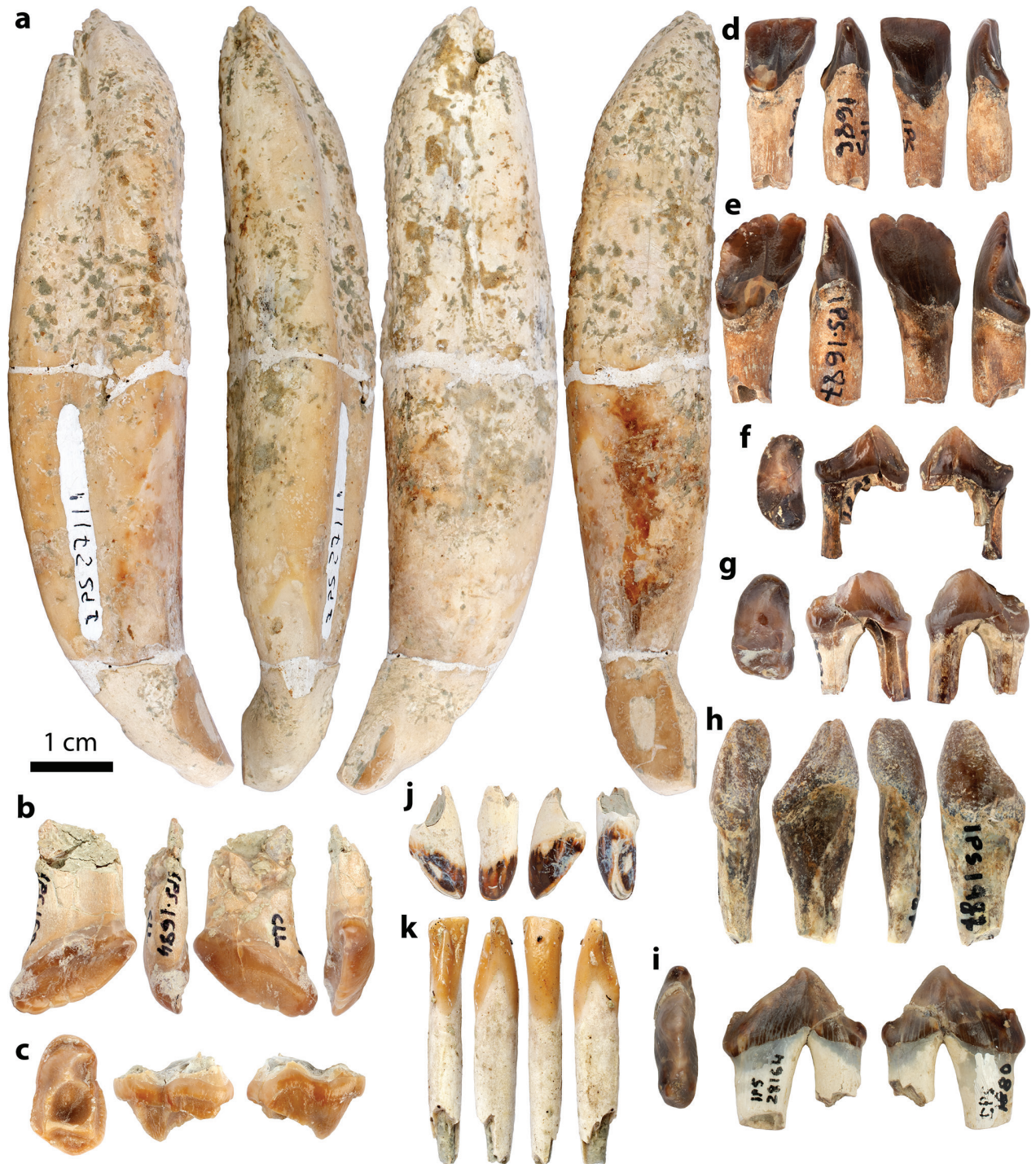


Figure 2. Dental remains of *Listriodon splendens* (a–g) and ‘*Parachleuastochoerus*’ *valentini* (h–j) from Can Llobateres 1: **a.** IPS27111, right C1f in lingual, mesial, labial, and distal views; **b.** IPS1684, right DI1 in lingual, mesial, labial, and distal views; **c.** IPS39508, right DP2 in occlusal, lingual, and buccal views; **d.** IPS1686, left di1 in lingual, mesial, labial, and distal views; **e.** IPS1687, left di2 in lingual, mesial, labial, and distal views; **f.** IPS1689, left dp2 in occlusal, lingual, and buccal views; **g.** IPS1688, left dp3 in occlusal, lingual, and buccal views; **h.** IPS39526 [IPS1987], left i3 in lingual, mesial, labial and distal views; **i.** IPS28164 [IPS1880], left p1 in occlusal, lingual and buccal views; **j.** IPS39525, left DI1 in lingual, mesial, labial and distal views; **k.** IPS39527, left di1 in lingual, mesial, labial and distal views.

metacone and metaendocrista). It displays an oval occlusal contour, being longer than broad (BLI = 63%) and broader distally than mesially, with a mild lingual constriction at the paracone level. The crown is relatively low and was originally two-rooted. The highest cusp is the paracone,

which is pointed and centrally located on the mesial half of the crown. The paraprecrista curves mesiolingually until merging with the cingulum, separating the convex and bulging mesiobuccal crown wall from the concave lingual wall of the paracone. The parapostcrista and

paraendocrista further curve distally from the paracone apex in opposite directions, merging with the mesiodistally aligned metapreocrista and hypopreocrista, respectively. The metacone and hypocone are lower and more crestiform than the paracone. These distal cusps are almost transversely aligned and connected with one another by a distinct metaendocrista. All the aforementioned cusps and crests, except for the parapreocrista, encircle a deep and rather round protofossa. The crown base displays an almost continuous cingulum, which is particularly developed mesially, distolingually and, especially, distally (where it becomes ledge-like and distally protruding), and much narrower and poorly defined buccally. The cervix displays moderately developed ectoanticline and endoanticline, and a more marked distal postanticline.

The remaining four lower deciduous teeth probably belong to a single individual but there is no spatial information to confirm this. The left di1 (Fig. 2d) preserves the slightly worn crown and most of the root. The crown is spatulate, bilobed (not clearly visible due to wear), and labiolingually compressed (BLI = 65%), progressively tapering toward the incisal edge, where several mamelons can still be discerned despite of wear. Interproximal wear facets can be discerned both mesially and distally. The labial crown wall is moderately convex, whereas the lingual is concave and more asymmetrical. The verticalized poststylid and the more inclined prestylid merge with the subtle but thicker lingual cingulid. A moderately developed and slightly mesially tilted endocristid originates from the junction of the lingual cingulid and the prestylid, and progressively tapers apically before reaching the incisal edge, separating the triangular prefossid from the subequal but squarer endofossid. The cervix displays a well-developed postanticlinid and a deeper preanticlinid, as well as a marked and distally tilted endosynclinid and a more symmetrical ectosynclinid. The root is waisted just below the cervix and progressively tapers apically; it is vertically oriented and much less labiolingually compressed than the crown. The left di2 (Fig. 2e) similarly preserves the crown and most of the root, but the former is almost unworn, except for a mesial interproximal wear facet. Like that of the di1, the di2 crown is spatulate and labiolingually compressed (BLI = 67%), but larger, higher, and clearly more asymmetrical. The incisal edge displays a bilobed shape, with the protopreconulid being separated from the protoconid by a deep notch; additional but less marked mamelons can be distinguished along the incisal edge. The labial wall is moderately convex, while the lingual is concave (especially in the half distal portion). The lingual morphology is similar to that of the di1, but in the di2 it can be appreciated that the poststylid is serrated. Furthermore, the distal portion of the lingual cingulid is more bulging and rootwardly extended than in the di1, resulting in a more asymmetrical endosynclinid. In turn, the ectosynclinid and, especially, the postanticlinid are much shallower than in the di1, contrasting with the similar development of the preanticlinid. The root is less waisted below the cervix and more mesially curved than in the di1.

The left dp2 (Fig. 2f) preserves the crown and a large portion of the distal root. The former is only slightly worn and, overall, well preserved despite some cracks. It displays a subelliptical, kidney-shaped occlusal contour that is longer than wide (BLI = 51%) and convex on all sides except the lingual one. The only well-developed cuspid is the protoconid, which is pointed and centrally located slightly toward the mesial half of the crown. The preprotocristid displays a convex profile in buccal/lingual views and curves mesiolingually from the protoconid apex until bifurcating close to the mesial end of the crown. A short protoposteristid descends in distobuccal direction from the protoconid apex, whereas a poorly distinct metaconid is located distolingually from the latter. Two longer cristids progressively diverge in distobuccal and distolingual direction distally from the metaconid, delimiting a shallow fossid. The cingulids are restricted to the mesial and distal crown portions, but poorly developed. The buccal crown wall is mesially convex and distally concave, whereas the lingual is concave except at the level of the protoconid. The crown markedly protrudes distally from the cervix, which displays a greater rootward extension distally than mesially.

The dp3 (Fig. 2g), in turn, preserves the moderately worn and well-preserved crown (despite a conspicuous crack), as well as most of the mesial and distal roots. The crown is larger (particularly stouter; BLI = 60%) than that of the dp2, and displays a suboval occlusal contour, which is broader distally than mesially and less asymmetrical than that of the dp2. The occlusal pattern is similar to that of the dp2, except that the metaconid is better developed and a single crest (metaposteristid) originates from it, terminating in a much lower cuspid on the distolingual corner of the crown. Furthermore, a short transverse cristid originates from this cuspid, curving until merging with the middle portion of the distal cingulid, forming a tiny and shallow fossid. The crown walls are convex on the mesiobuccal and lingual aspects of the protoconid, and otherwise rather concave. The cingulids are similarly restricted to the mesial and distal crown portions, but slightly better developed than in the dp2. The distal root is slightly stouter and more verticalized than the mesial, which is slightly tilted mesially.

Comparisons. Permanent teeth. As far as it can be ascertained (given its incomplete preservation), the C1f from CLL1 differs from the C1f attributed to *L. splendens* from Arroyo del Val IV (Van der Made 1996: pl. 38, fig. 13) in displaying a smaller and slenderer crown relative to the root as well as two partially fused roots that are broadest around midheight and taper both apically and cervically (instead of a single root that is broader near the cervix and progressively narrows toward the apex). In contrast, the CLL1 specimen seemingly resembles in crown shape a specimen from Gratkorn (Van der Made et al. 2014: fig. 2h) that similarly displays two fused roots, albeit smaller than in the CLL1 specimen. The CLL1 specimen also closely resembles the unpublished C1fs of *L. splendens* from Abocador de Can Mata in both size and shape (S.G.A.

and D.M.A., pers. obs.), although metrical comparisons are precluded by the poor preservation of the CLL1 specimen.

Deciduous teeth. The DI1 from CLL1 falls in the size range of those of *L. splendens* from various sites (MD = 13.7–22.0 mm; BL = 5.0–9.7 mm; BLI = 29–44%; $n = 7$; Van der Made 1996). The described specimen resembles in shape a figured specimen from Paşalar (Van der Made 1996: pl. 35, fig. 16), despite exhibiting some minor differences (lower and less distally protruding crown, with a less developed lingual cingulum). The DP2 from CLL1, in turn, falls in the size range reported for *L. splendens* (MD = 11.6–14.4 mm; BL = 6.8–9.4 mm; BLI = 56–70%; $n = 11$; Golpe-Posse 1971; Van der Made 1996) and closely resembles in occlusal shape of the figured specimens from Paşalar (Van der Made 1996: pl. 35, figs 6, 10), although it differs from others (Van der Made 1996: pl. 35, fig. 9) as well as that from Manchones I (Van der Made 1996: pl. 39, fig. 7) in several aspects (more mesially located paracone, more buccally placed paraposterista and metacone, and more centrally located protofossa).

The di1 from CLL1 similarly falls within the size range of *L. splendens* (MD = 6.3–14.4 mm; BL = 3.9–5.6 mm; BLI = 39–65%; $n = 7$; Van der Made 1996). Although we have been unable to find figured di1s of this species, its similarities to the i1 (Van der Made 1996: pl. 35, figs 4, 8, 13, 14, pl. 36, fig. 4), coupled with the much smaller size, support our tooth locus attribution to *L. splendens*. The di2 from CLL1 also falls within the size range of *L. splendens* (MD = 9.5–11 mm; BL = 3.6–6.9 mm; BLI = 32–72%; $n = 4$; Van der Made 1996), and displays a similar shape to a figured di2 from Paşalar (Van der Made 1996: pl. 35, fig. 15). The dp2 from CLL1 similarly falls within the size range of *L. splendens* (MD = 11.7–13.6 mm; BL = 6.6–7.0 mm; BLI = 50–57%; $n = 3$; Van der Made 1996); although we found no figured dp2s in the literature, the similarities in occlusal morphology between the described specimen and the p2s of this species (Van der Made 1996: pl. 38,

figs 5, 15, pl. 42, fig. 2; Pickford 2012: fig. 24), coupled with the smaller and lower crown, support its identification as a dp2. Finally, the dp3 from CLL1 also falls within the size range of *L. splendens* (MD = 12.0–16.9 mm; BL = 6.0–12.9 mm; BLI = 47–77%; $n = 17$; Golpe-Posse 1971; Van der Made 1996, 2003) and displays a similar occlusal shape to the figured dp3s of *L. splendens* from Paşalar and Murrero (Van der Made 1996: pl. 35, fig. 12, pl. 38, fig. 14), with only minor differences (more convex buccal contour, more convex protoprecrestid and protoposteristid in buccal/lingual views).

Remarks. The premolar IPS39506 [IPS1062] from CLL1, which Golpe-Posse (1971, 1972) identified both as a left ?P3 of ?*Hyotherium* sp. and as a right p2 of *L. splendens*, is here identified as a left P3 of *Pa. crusafonti* (Fig. 3a). In turn, the lower cheek tooth IPS28172 [IPS1061], identified by Golpe-Posse (1971, 1972) as a left m1 of *L. splendens*, is in fact a right molar (m2?) of *T. priscus*—see Pandolfi et al. (2025: fig. 5o)—a perissodactyl otherwise recorded from CLL1 by a few dentognathic remains (Golpe-Posse and Crusafont-Pairó 1982; Pandolfi et al. 2025). Van der Made (1996) ignored these specimens but reported measurements for two additional ones: a right DP4 with IPS acronym but without catalog number; and a left DP2–DP4 series with old number [IPS1092]. The latter number is, however, incorrect, corresponding in fact to a worn right P3 of *L. splendens* from Hostalets according to both Golpe-Posse (1971) and Van der Made (1996), and currently cataloged as IPS16808. As a result, we were unable to find the specimens of *L. splendens* from CLL1 reported by Van der Made (1996) among the ICP collections and have serious doubts about their provenance. They might indeed come from CLL1 and have been mislabeled during the last couple of decades as coming from a different site; or, alternatively, they might have been mislabeled as coming from CLL1 during the 1970s—as was the case with the remains

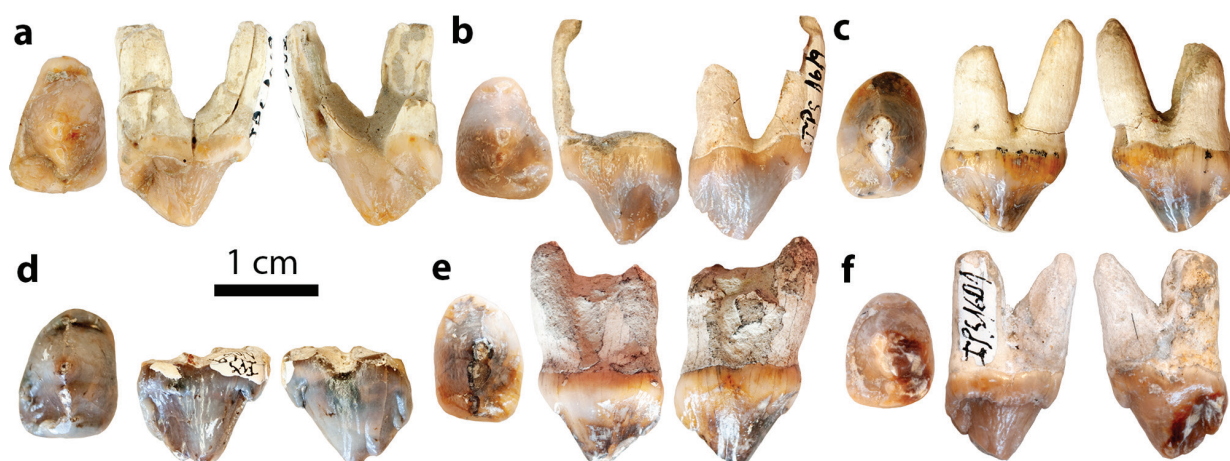


Figure 3. Left P3 of *Parachleuastochoerus crusafonti* from CLL1 (a), previously misidentified by Golpe-Posse (1971, 1972) as a left ?P3 of ?*Hyotherium* sp. and as a right p2 of *L. splendens*, as compared with other P3s of the same species from the same locality (b–f): a. IPS39506 [IPS1062], left P3; b. IPS94988 [IPS1619] right P3; c. IPS28157q [RCB9603] left P3; d. IPS94950 [IPS1669] left P3; e. IPS39510l [RCB9601] right P3; f. IPS1699 [IPS1601]. All specimens are depicted (from left to right) in occlusal, lingual, and labial views. Despite noticeable variation in size, occlusal contour, and the development of the protocone, all specimens share a similar crown shape that differs from the other suid taxa recorded at CLL1.

of *Parachleuastochoerus huenermanni* (Heissig, 1989) from Can Poncic 1, which were misreported as coming from Sant Quirze (Pickford 1981, 2014; Van der Made 1990) until Alba et al. (2025) clarified their provenance based on old catalog numbers used by Golpe-Posse (1971, 1972). In contrast, the presence of *L. splendens* at CLL1 can be unambiguously confirmed based on the five deciduous teeth first described here, which might potentially belong to a single individual. The fact that Golpe-Posse (1971, 1972) did not describe them suggests that they were not recovered until later, either 1981 or 1990, when the locality was briefly excavated again (Alba 2025). The fact that one of the fossils has the ‘CLL’ acronym written on the specimen, while others have quite low IPS numbers that do not coincide with those given by Golpe-Posse (1971, 1972), strongly suggests that these remains were recovered in 1981, in which case they would undoubtedly come from the hominoid-bearing levels of CLL1 (Begun et al. 1990; Alba et al. 2012).

Despite corresponding to deciduous teeth, the morphology of the deciduous incisors and premolars is so characteristic that no misassignment is possible to any of the other taxa recorded from CLL1. Given that *L. splendens* is the only listriodontine species generally recognized in the European Vallesian (Van der Made 1996), an attribution to this species is straightforward, at least given the state of the art of listriodontine systematics. Ginsburg (1980) recognized two subspecies of *L. splendens*, the Aragonian nominotypical subspecies and the Vallesian *L. splendens major* Roman, 1907, based on the purportedly larger size of the latter. Subsequent studies did not support differences in size but noted differences in dental proportions (Fortelius et al. 1996), while Van der Made (1996) recognized yet a third subspecies, *L. splendens tapirotherium* (de Blainville, 1847). These subspecies were considered chronosubspecies of a single lineage by Van der Made (1996), who attributed the remains from CLL1 to *L. splendens major*, which he considered to be recorded from late MN7+8 to MN9. However, Pickford and Morales (2003) and Pickford (2012) considered that most of the features used to diagnose these subspecies are too variable, and that only *L. s. major* warrants distinction as a geographic subspecies, recorded from MN6 to MN9 in the Iberian Peninsula, based on the presence of P2 and P3 metacones. While we tend to concur with the latter view, as in Alba et al. (2024), here we refrain from distinguishing subspecies of *L. splendens* because the Iberian material does not seem homogeneous enough and might include additional taxa. As noted by Van der Made (1996), there is some evidence that a distinct (larger and rarer) species (potentially referable to *Listriodon mongoliensis* Colbert, 1934) might be present during the Miocene, both in Europe and Asia. The coexistence of various morphotypes in Europe during MN7+8 is tentatively supported by our own observations on the unpublished material from the late Aragonian Abocador de Can Mata (S.G.A. and D.M.A., pers. obs.). This is the reason why describing the CLL1 material in detail is important, despite the common

assumption that a single subspecies is recorded in Iberia. Therefore, pending an in-depth taxonomic revision of the abundant material of *Listriodon* from Abocador de Can Mata recovered during the last two decades (covering the late MN6 and the whole MN7+8 up to the earliest MN9; Alba et al. 2022), here we provisionally refrain from providing a subspecies attribution for the CLL1 material.

Subfamily Tetraconodontinae Lydekker, 1876 Genus *Parachleuastochoerus* Golpe-Posse, 1972

‘*Parachleuastochoerus*’ *valentini* (Filhol, 1882)

Fig. 2h–j

Referred material. See Table 1 for a list of material and Table 2 for measurements.

Description. Permanent teeth. Only two permanent teeth are available, a left i3 and a left p1. The i3 (Fig. 2h) is almost complete, merely lacking the tip of the root and a chip of enamel on the incisal edge; the specimen is otherwise well preserved except from some superficial etching of the enamel. The crown is much broader than long (177%) and somewhat asymmetrical (distolingually bulging and mesially tilted). The crown walls are markedly convex except at the lingual side, which is concave and displays a marked endocristid. The latter stretches from the crown base, just above the cervix, to the merging of the poststyloid with the incisal edge. Thereby, the endocristid completely separates the more spacious prefossid from the groove-like and more basally located endofossid. The cervix displays a marked preanticiplinid mesiolingually. The root is verticalized, moderately waisted below the cervix, very mesiodistally compressed, and markedly tapering toward the apex (especially in labiolingual diameter).

The left p1 (Fig. 2i), in turn, preserves the very slightly worn crown (which displays a conspicuous crack on its mesial portion) and a large portion of the two roots. The crown has a trenchant morphology and displays a very buccolingually compressed (BLI = 31%) and subelliptical occlusal contour, which more markedly tapers mesially than distally and displays mild constrictions lingually and distobuccally. The protoconid is centrally located on the mesial half of the crown, distally tilted, and not particularly bulging. The mesially oriented protopreacristid is steep and displays a convex profile on buccal/lingual views, which progressively becomes concave basally toward the distinct but small prestyloid. The protopostcristid is sharper but somewhat shorter, more sinuous, and less steeply inclined than the protopreacristid. The former ends in a poorly distinct metaconid, from which two short and thin cristids diverge, delimiting a very small distal fossid. The lingual metaendocristid ends before reaching the distal end of the crown, whereas the metapostcristid ends in a small but distinct hypoconid. The latter is distobuccally located, lower than the other main cuspids, but higher than the prestyloid. A subvertical and denticulated hypopostcristid connects the hypoconid with the distal end of the

crown. The crown walls are moderately concave, except around the protoconid. There are no distinct cingulids except around the prestylid and the cervix extends farther rootward distally than mesially. The distal root is more verticalized and stouter than the mesial one.

Deciduous teeth. Two (upper and lower) incisors are assigned to this taxon. The left DI1 (Fig. 2j) preserves the moderately worn crown (with dentine exposure along the incisal edge and part of the lingual side) and part of the root. The crown is somewhat labiolingually compressed (BLI = 74%) and possesses convex walls except for the concave lingual aspect. Due to wear, the lingual morphology cannot be adequately ascertained. The endocrista is very worn and appears slightly mesially tilted from base to apex, separating the prefossa from the more restricted (almost groove-like) endofossa. The cervix displays a shallow mesiolingual preanticleline, while the root is somewhat labiolingually compressed.

In turn, the left di1 (Fig. 2k) preserves the lightly worn crown and most of the root. The crown is labiolingually broader than mesiodistally long (BLI = 114%) but progressively becomes longer and more labiolingually compressed toward the incisal edge, which is slightly tilted (the crown is slightly higher mesially than distally). The labial wall is convex, while the lingual is concave except for a thick endocristid that originates from a basal swelling and progressively tapers apically before reaching the incisal edge. The endocristid separates two similarly-sized and triangular fossids, which become groove-like toward the cervix (the prefossid extending farther rootward than the endofossid). The poststylid and prestylid are moderately developed on the apical half of the crown and become more indistinct toward the basal swelling. The cervix exhibits very deep and V-shaped anticlinids, and the ectosynclinid extends slightly more onto the root than the endosynclinid. The root is minimally waisted at the cervix, verticalized, and somewhat labiolingually compressed.

Comparisons. Permanent teeth. The described i3 from CLL1 differs markedly from the i3s of *Pr. palaeochoerus* in size and proportions, being less mesiodistally elongated (MD = 9.4–14.1 mm; BL = 4.9–7.6 mm; BLI = 48–72%; n = 11; Van der Made et al. 1999; Fortelius et al. 2005; McKenzie et al. 2023b). The CLL1 i3 also differs in shape from those of *Pr. palaeochoerus* (Van der Made et al. 1999: pl. 2, fig. 6; McKenzie et al. 2023b: fig. 7p–t), displaying a less asymmetric crown, a more centrally (instead of distolingually) located endocristid, a better defined prefossid, and a more extensive endofossid. In contrast, the described specimen overlaps in size and proportions with some specimens attributed to *‘Pa.’ valentini* (MD = 6.0–7.1 mm; BL = 9.9–13.2 mm; BLI = 148–216%; n = 9; McKenzie et al. 2024; Alba et al. 2025). Its size and proportions also resemble those of *V. steinheimensis* (MD = 6.2–7.5 mm; BL = 9.4–10.6 mm; BLI = 125–193%; n = 5; Pickford 2014, 2016; McKenzie et al. 2024). However, in terms of shape, the i3 from CLL1 more closely resembles those of *‘Pa.’ valentini*

(McKenzie et al. 2024: fig. 8o–t; Alba et al. 2025: fig. 7K–O), which displays a higher and more slender crown, a less marked endocristid, a shorter and shallower endofossid, a lack of the labiolingual constriction at the cervix, and a more slender and more apically tapering root than the i3s of *V. steinheimensis* (Van der Made et al. 2014: fig. 4c; McKenzie et al. 2024: fig. 8u). An attribution to the small tetraconodontine *Pa. crusafonti* is also ruled out based on the smaller size and proportions of the latter species (MD = 3.0–3.6 mm; BL = 4.3–5.4 mm; BLI = 130–160%; n = 12; authors’ unpublished data).

In turn, the p1 from CLL1 differs markedly from those of *Pr. palaeochoerus* in both size and proportions (Fig. 5b; BLI = 42–52%; n = 11; Fortelius et al. 2005; Iannucci and Begun 2022; McKenzie et al. 2023b, 2024), being much longer and buccolingually compressed, as well as in shape (Iannucci and Begun 2022: fig. 2D; McKenzie et al. 2023b: fig. 9a–d, 2024: fig. 10a–c), displaying a more trenchant appearance, a more centrally located protoconid, a less distinct metaconid, more marked anticlinids, and two well distinct roots. The CLL1 premolar is larger than previously published p1s of *‘Pa.’ valentini* (Fig. 5b), but closely resembles them in proportions (BLI = 30–35%; n = 6; McKenzie et al. 2024; Alba et al. 2025) and occlusal shape—particularly those from Trinxera del Ferrocarril-Sant Quirze (Pickford 2014: fig. 14D; Alba et al. 2025: fig. 9A, B), whereas it differs from those of Castell de Barberà (McKenzie et al. 2024: fig. 10d–h) in some minor occlusal details (less elliptical and more constricted occlusal contour). An alternative identification as a p2 of *‘Pa.’ valentini* can be discounted given the slightly smaller size, narrower shape (Fig. 5c; BLI = 31–36%; n = 3; Alba et al. 2025), and the greater occlusal similarities with the published p1s (the p2s display a less elliptical and more constricted contour, a less protruding prestylid, and a more marked hypoconid; Alba et al. 2025: fig. 9C–F). In turn, an alternative attribution to *V. steinheimensis* may be also ruled out, despite similarities in crown shape (Chen 1984: pl. 2, fig. 2; Pickford 2016: figs 16, 17; McKenzie et al. 2024: fig. 10i, j). The p1s of this species are generally smaller and relatively stouter than those of *‘Pa.’ valentini* (Fig. 5b; BLI = 31–41%; n = 11; Pickford 2014, 2016; McKenzie et al. 2024), whereas the p2s overlap in size but are generally stouter (Fig. 5c; BLI = 34–42%; n = 11; Pickford 2014, 2016; McKenzie et al. 2024) and display multiple differences in occlusal shape (less steep protopostcristid, complete lack of cingulids, and more marked rootward extension of the cervix on the distal half of the crown; Pickford 2014: fig. 33, 2016: figs 16, 17; Van der Made et al. 2014: fig. 3b; McKenzie et al. 2024: fig. 10m–p). An identification as a p1 or p2 of *Pa. crusafonti* is clearly discounted based on the size of both p1 (MD = 7.4–9.0 mm; BL = 2.4–3.7 mm; n = 3; Pickford 1981) and p2 (MD = 10.2–11.4 mm; BL = 3.7–4.3 mm; n = 3; Pickford 1981).

Deciduous teeth. The DI1 from CLL1 is smaller and less labiolingually compressed than those of *Pr. palaeochoerus* (MD = 8.0–13.2 mm; BL = 5.0–13.6 mm; BLI = 44–103%; n = 12; Fortelius et al. 2005; McKenzie

et al. 2023b, 2024). It also differs in shape from the DI1s of *Pr. palaeochoerus* (Fig. 4a, b; McKenzie et al. 2023b: fig. 10a–d, 2024: fig. 12a, b) by displaying a lower and less asymmetric crown, a better defined endocrista, and a less marked preanticle. The CLL1 specimen is slightly smaller than those attributed to '*Pa.*' *valentini* from elsewhere (MD = 7.1–9.6 mm; BL = 4.9–7.0 mm; BLI = 66–85%; n = 11; McKenzie et al. 2024; Alba et al. 2025), but closely resembles them in shape (McKenzie et al. 2024: figs 3i, j, 12c–f; Alba et al. 2025: fig. 11A–F). No DI1s of *V. steinheimensis* have been published yet, although the smallest tetraconodontine DI1s from Castell de Barberà attributed to '*Pa.*' *valentini* by McKenzie et al. (2024) might alternatively belong to *V. steinheimensis* according to Alba et al. (2025). An alternative attribution to *Pa. crusafonti* can be discounted, because the specimen is too large for a DI1 (MD = 3.2–3.4 mm; BL = 4.3–4.7 mm; BLI = 127–144%; n = 3; Pickford 1981) and too small and relatively broad for an I1 (MD = 6.0–6.5 mm; BL = 8.4–9.8 mm; BLI = 133–157%; n = 5; Pickford 1981) of this species.

With regard to the lower deciduous teeth, the di1 from CLL1 falls in the range of the di1s of *Pr. palaeochoerus* (MD = 4.1–5.2 mm; BL = 5.3–6.1 mm; BLI = 115–142%; n = 9; McKenzie et al. 2023b, 2024) but differs from them in the broader endocristid, deeper prefossid and endofossid, and better developed prestylid and poststylid (McKenzie et al. 2023b: fig. 11a–e, 2024: fig. 13a–d). In contrast, it resembles those of '*Pa.*' *valentini* in size and proportions (MD = 4.5–5.3 mm; BL = 5.5–6.4 mm; BLI = 115–133%; n = 6; McKenzie et al. 2023b, 2024; Alba et al. 2025), as well as shape (McKenzie et al. 2023b: fig. 11f, g, 2024: figs 13e, f; Alba et al. 2025: fig. 11P–R), despite some minor differences (deeper and more V-shaped anticlinids). It also falls in the metrical range of the di1s of *V. steinheimensis* (MD = 4.9 mm; BL = 6.0 mm; BLI = 122%; McKenzie et al. 2024) but differs in occlusal shape (a less labiolingually compressed apical crown half; McKenzie et al. 2024: fig. 13g, h).

Remarks. The lower premolar IPS28164 was tentatively identified as a possible left p2 of *H. soemmeringi* by Golpe-Posse (1971, 1972), an attribution that is at odds with current systematics of European suids. As noted in the Introduction, Van der Made (1990) attributed most of Golpe-Posse's (1972) identifications of *H. soemmeringi* to the tetraconodontine *V. steinheimensis* (then in *Conohyus*) but did not report a large tetraconodontine from CLL1, and the same applies to Pickford's (2016) most recent work. However, our comparisons above unambiguously show that a large-bodied tetraconodontine is recorded from CLL1, even if represented by a small sample. An alternative attribution to the small-bodied tetraconodontine from CLL1 (*Pa. crusafonti*) is completely out of question due to the small size of the latter, while an assignment to the similarly sized suine *Pr. palaeochoerus* is further ruled out by the tetraconodontine affinities of the material described above, most clearly evidenced by the p1. Our morphological comparisons further favor an identification of this large tetraconodontine as '*Pa.*' *valentini*

(as previously reported by Arranz et al. 2023) instead of *V. steinheimensis*—especially based on the resemblances between the p1 from CLL1 and previously published material from other sites such as Sant Quirze (Alba et al. 2025), even though other tooth loci are also consistent with such an assessment.

Subfamily Suinae Gray, 1821

Tribe Dicoryphochoerini Schmidt-Kittler, 1971

Genus *Propotamochoerus* Pilgrim, 1925

Propotamochoerus palaeochoerus (Kaup, 1833)

Fig. 4

Referred material. See Table 1 for a list of material and Table 2 for measurements. This species is represented by multiple teeth and dentognathic fragments that might belong to a single juvenile individual (Fig. 4a–i, l, m), although this cannot be conclusively ascertained because they were labeled with five different catalog numbers and there are no field records to confirm they were in close spatial association at the site. These include: IPS28145a–i (Fig. 4a–i), which consist of the right and left DI1s, the right DP2, and the right and left DP3s, DP4s, and M1 germs; IPS39504a–b (Fig. 4m–o), including a right mandibular fragment with dp3–dp4, the isolated right m1 germ, and a left mandibular fragment with dp4 and m1 germ; and two isolated, right (IPS28171; Fig. 4j) and left (IPS39538; Fig. 4k) dp2s and an isolated left dp3 IPS1700 (=IPS39540; Fig. 4l), the latter being in all probability the antimer of the dp3 in the IPS39504a mandibular fragment. The M1 germs are unfinished and must have been inside their crypts at the time of death, which is even more clear in the case of the m1. The degree of wear in the deciduous premolars is fully comparable between the upper and the lower ones, with only minimal dentine exposure at the apices of a few teeth, further supporting that all these specimens belong to a single individual. The isolated right p2 (IPS39523; Fig. 4p) attests to the presence of at least an additional individual.

Description. Permanent teeth. The upper permanent teeth are only represented by a right (Fig. 4h) and a left (Fig. 4i) M1 unworn germs, the right one being slightly broken at the crown base both buccally and lingually. They display a subrectangular occlusal contour, somewhat longer than broad (BLI = 81–82%) and broader mesially than distally. The crown exhibits two distinct lobes (mesial and distal) of convex contour, separated by a transverse groove and both buccal and lingual constrictions; the distal lobe is more elongate than the mesial one. The mesial contour is almost straight, while the distal is convex and distally protruding. There are four main cusps of similar size, with the lingual ones being located more distally than the corresponding buccal cusps. The hypopreconule is centrally located and much smaller than the main cusps, being similar in size to the slightly more buccally located protopreconule, which is connected to the protopreocrista.

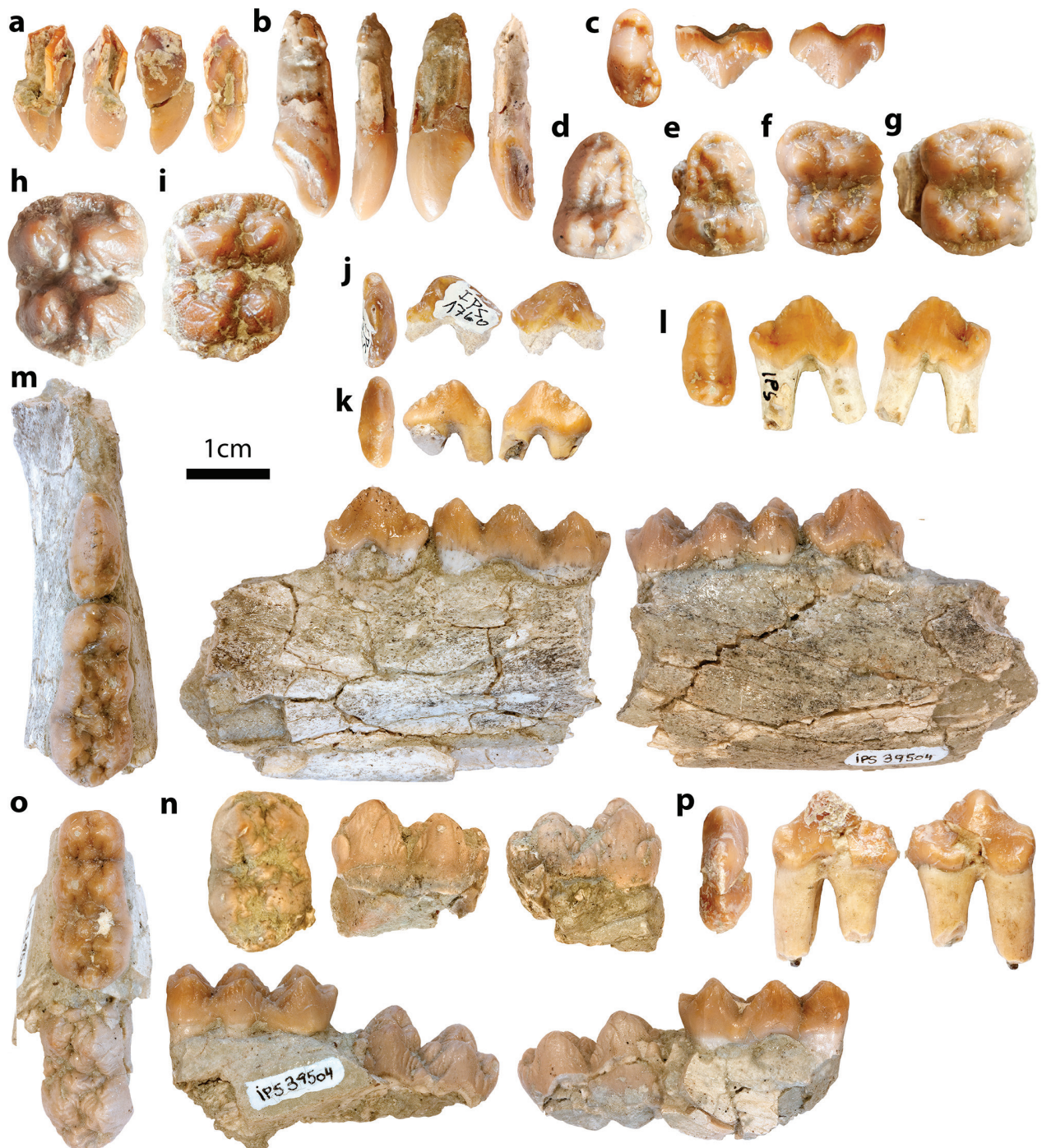


Figure 4. Dental remains of *Propotamochoerus palaeochoerus* from Can Llobateres 1: **a.** IPS28145a, damaged right DI1 crown in lingual, mesial, labial, and distal views; **b.** IPS28145b, left DI1 in lingual, mesial, labial, and distal views; **c.** IPS28145c, right DP2 in occlusal, lingual and buccal views; **d.** IPS28145d, right DP3 in occlusal view; **e.** IPS28145e, left DP3 in occlusal view; **f.** IPS28145f, right DP4 in occlusal view; **g.** IPS28145g, left DP4 in occlusal view; **h.** IPS28145h, right M1 germ in occlusal view; **i.** IPS28145i, left M1 germ in occlusal view; **j.** IPS28171, right dp2 in occlusal, lingual and buccal views; **k.** IPS39538, left dp2 in occlusal, lingual and buccal views; **l.** IPS1700, left dp3 in occlusal, lingual and buccal views; **m.** IPS39504a, right mandibular fragment with dp3–dp4 in occlusal, lingual, and buccal views; **n.** IPS39504a, right m1 germ in occlusal, lingual, and buccal views; **o.** IPS39504b, left mandibular fragment with dp4–m1 (in crypt, emerging) in occlusal, lingual, and buccal views; **p.** IPS39523, right p2 in occlusal, lingual and buccal views.

A distinct labial ectoconule is present at the end of the hypoectocrista, while a smaller one encloses the transverse valley buccally. The mesial and distal cingula are well-developed and display a beaded appearance due to the

abundant enamel folds, but do not extend either lingually or buccally. The mesial cingulum is partly interrupted by the protopreconule, while the distal one is buccolingually more restricted but distally projected. The cusps display

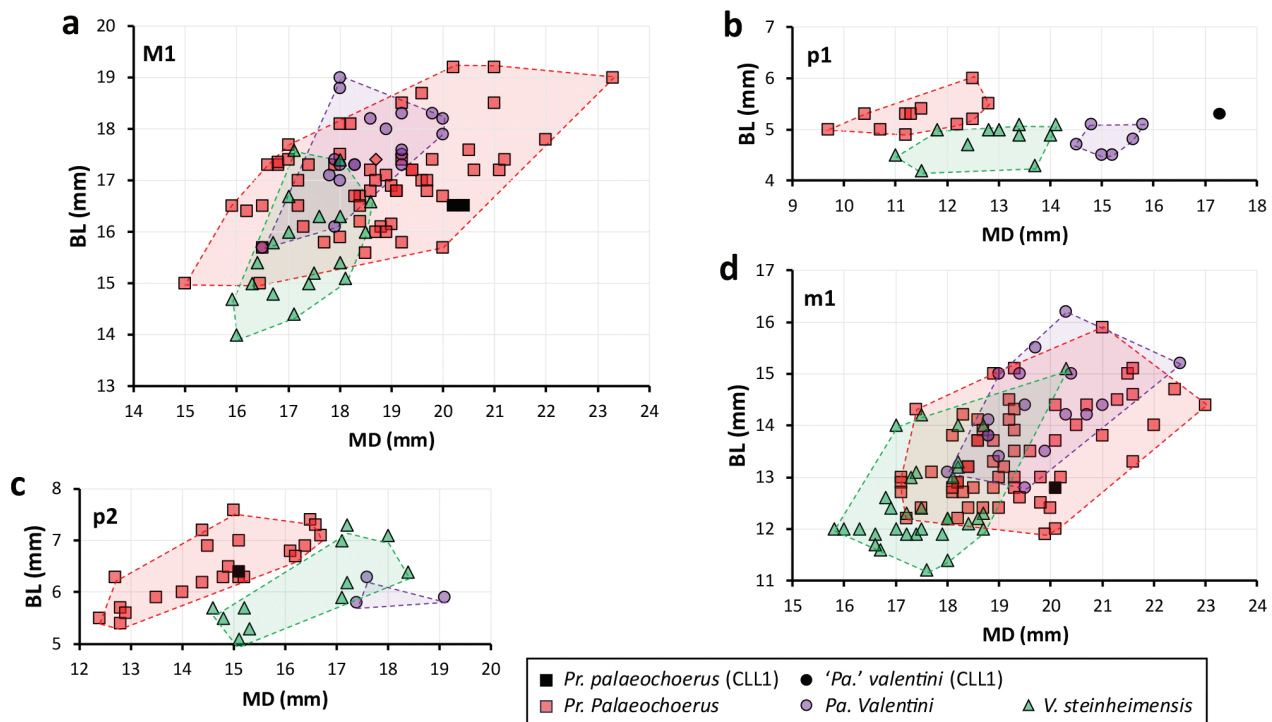


Figure 5. Bivariate plots of BL vs. MD in the permanent cheek teeth of *Propotamochoerus palaeochoerus* and ‘*Parachleuastochoerus*’ *valentini* from CLL1 as compared with *Pr. palaeochoerus* and selected tetraconodontines (‘*Pa.*’ *valentini* and *Versoporus steinheimensis*) from elsewhere: **a.** M1; **b.** p1; **c.** p2; **d.** m1. Metrical data for the CLL1 remains are reported in Table 2, while those for the comparative sample have been taken from the literature (see Material and methods for details on the published sources). Convex hulls outlining the variation of each species (without considering the remains from CLL1) are depicted.

marked Furchen and the rest of the occlusal surface further displays relatively abundant enamel wrinkling.

The lower permanent teeth are represented by a right p2 (Fig. 4p) and two m1 germs from a single individual (Fig. 4n, o). The p2 preserves most of the crown and the two roots, albeit the former is somewhat damaged and corroded. It displays an elliptical and very buccolingually compressed (BLI = 42%) occlusal contour, slightly convex buccally and straighter lingually. The crown walls are concave except at the level of the main cuspid (protoconid), which is centrally located toward the mesial half of the crown and mesially tilted in buccal/lingual profile. The thin protoprecristid that descends from the protoconid apex displays a concave profile in buccal/lingual views and slightly curves mesiolingually until reaching the weak prestylid. The shorter protoposteristid ends in a poorly-developed and buccolingually compressed (crestiform) metaconid, which is lower than and mesiodistally aligned with the protoconid. A similarly developed but even lower hypoconid is present distobuccally from the metaconid, being separated by shallow buccal and lingual notches on the crown wall. A poorly developed cingulid can only be discerned around the prestylid and along the distobuccal base of the crown. The mesial root is slightly tilted mesially and slightly stouter than the more verticalized distal root. In turn, the m1s display a subrectangular occlusal contour that is longer than wide (BLI = 64%), with two lobes separated by shallow buccal and lingual constrictions—the distal lobe being longer

and wider than the mesial, as well as markedly protruding distally. There are four main cuspids, the buccal ones being slightly higher and more mesially located than the corresponding lingual ones. The occlusal surface exhibits marked Furchen as well as abundant enamel wrinkling on the thick cristids and the cingulids. The mesial and distal cingulids are well-developed but do not extend lingually/buccally. A small protopreconulid, not merged with the mesial cingulid, is present at the end of the protoprecristid. The hypopreconulid is larger and more centrally located than the protopreconulid, but much lower and smaller than the four main cuspids. A twinned hypoecconulid buccally encloses the transverse valley. A distinct pentaconid, similar in size to the hypopreconulid, is centrally located on the distal end of the crown, encircled by the distal cingulid.

Deciduous teeth. The DI1 morphology can be only adequately ascertained on the left antimere (Fig. 4b), which preserves the lightly worn crown and part of the root, whereas the right antimere (Fig. 4a) is very damaged and only partially preserved. The crown is moderately high and quite labiolingually compressed (BLI = 64%), markedly convex mesiolabially and concave distolingually. There is a distinct but narrow lingual cingulum slightly above the cervix, and a thin and slightly obliquely inclined endocrista that originates from the cingulum and ends before reaching the incisal edge, separating the small prefossa from the better-developed endofossa. The cervix shapes a marked mesiolingual preanticle and a

more moderate distal endosyncline. The root appears quite verticalized and somewhat labiolingually compressed, and only slightly waisted below the cervix on the distal side.

The single available DP2 (Fig. 4c) is unworn. It displays an elongate (BLI = 54%) and asymmetrical (kidney-shaped) occlusal contour, which is buccally convex and lingually concave, and slightly broader distally than mesially due to the distolingual expansion of the crown base. The main cusp (paracone) is pointed and centrally located. The paraprecrista and parapostricrista are similarly long and steep, and both are serrated and slightly curved lingually along their course. The paraprecrista reaches a very well-developed prestyle that is flanked by conspicuous cingular developments. A poorly developed metacone, indistinguishable from the parapostricrista serrations, is located at the distal end of the crown. A much larger and bulging protocone, somewhat lower than the prestyle, is located on the distolingual extension of the crown, being separated from the parapostricrista by a deep and basin-like groove. The buccal cingulum is only well-developed at the prestyle level and totally interrupted along the mesiobuccal aspect of the paracone. In contrast, the lingual cingulum is continuous and much better developed, becoming ledge-like around the protocone and further displaying secondary cuspules distolingually from the paracone. The crown walls are bulging mesially the protocone, and concave distally. The cervix displays well-developed anticlines both buccally and lingually.

The DP3s (Fig. 4d, e) are well preserved, including the three (one mesial and two distal) roots as well as the crown, which is only moderately worn (with restricted dentine exposure at the apices of the three main cusps, particularly the protocone). The DP3s are larger than the DP2 and display a subtriangular occlusal contour, which is longer than wide (BLI = 70–73%) and broader distally than mesially, and displays moderately marked buccal and lingual constrictions at the level of the transverse valley that separates the mesial from the distal lobe. The paracone is centrally located on the mesial lobe. The mesially directed paraectocrista and the similarly short but thicker and mesiolingually oriented paraprecrista enclose a small and triangular basin against the mesial cingulum. The long and thick parapostricrista is distobuccally oriented and aligned with the metaectocrista on the distal lobe, whereas the distolingually oriented paraendocrista bifurcates, originating a secondary crista that resembles the parapostricrista in thickness and orientation. The metacone and protocone are transversely aligned on the distal lobe and display two mesial cristae each that end at the transverse valley. A short protopostcrista is also present, giving rise to a secondary cuspule where it merges with the distal cingulum. The well-developed mesial cingulum is prolonged lingually until about the level of the transverse valley (i.e., the end of the protoectocrista), displaying a beaded appearance and contrasting with the much more diffuse buccal cingulum. There is also a moderately developed but buccolingually restricted distal cingulum. The occlusal surface is characterized by profuse enamel wrinkling.

Finally, both the right and left DP4s are preserved (Fig. 4f, g), although the right one is missing the lingual-most portion of the crown, whereas the left is socketed and completely preserved. They only display slight wear (with some dentine exposure at the protocone apices), a subrectangular contour that is somewhat longer than broad (BLI = 81%), and a similar occlusal morphology to that of the M1s. The DP4 can be distinguished from the latter by being smaller and lower-crowned, and by displaying an obliquely oriented (mesiobuccally protruding) contour. Furthermore, unlike in the M1s, the hypoectoconule is double.

Regarding the lower deciduous dentition, the two dp2s preserve the complete crown and the basal part of the roots; the left dp2 (Fig. 4k) is almost unworn, whereas the right one (Fig. 4j) shows moderate dentine exposure but is otherwise comparable in shape. They display an elongate (BLI = 37–40%) and slightly asymmetrical occlusal contour, somewhat convex buccally and straighter lingually. The single main cuspid (protoconid) is centrally located, slightly toward the mesial half of the crown. The protoprecristid is steep, mesiodistally aligned, and slightly convex in buccal/lingual profile, ending in the weakly developed prestylid. The protopostcristid is longer and less steep than the protoprecristid, further displaying a serrated morphology when unworn and being slightly tilted distobuccally, terminating in a low hypoconid that can barely be distinguished from the preceding serrations. The lingual and buccal crown walls are concave, particularly distally from the protoconid, which is apically rounded but not basally bulging. No cingulids are present. The mesial root appears more mesially tilted and slenderer than the distal one.

The dp3 is similarly represented by two specimens (Fig. 4l, m), which are very lightly worn; the roots are almost completely preserved in the isolated (non-socketed) specimen. The dp3 is similar to the dp2, but larger and stouter (BLI = 50–51%), further displaying a suboval occlusal contour that is clearly broader distally than mesially. Other differences include the thicker protoprecristid and protopostcristid, the slightly more serrated and more lingually tilted protoprecristid, the better-developed prestylid flanked by cingular developments, the steeper and more convex protopostcristid in buccal/lingual views, the larger hypoconid higher than the prestylid, the deeper lingual and buccal notches at the level of the protopostcristid (connected with one another by a transverse groove that separates the end of the protopostcristid from the hypoconid), and the presence of a cingulid surrounding the distal half of the crown.

Finally, the dp4 is represented by two moderately worn antimeres (Fig. 4m, o) with minimal dentine exposure at the apex of some cuspid. They display an elongate (BLI = 47–48%) occlusal contour with three distinct lobes (increasingly broader from mesial to distal) that is characteristic of this tooth locus. There are six main cuspid of similar size, more or less transversely aligned in pairs. The occlusal surface displays marked Fürchen and thick cristids, which display abundant enamel crenulations.

The precristid of the primonid ends in a small but distinct primopreconulid, located on the lingual half of the crown, whereas the paraendocristid terminates in a similarly sized and centrally located paraendoconulid. Distally from the latter, on the opposite side of the transverse valley separating the mesial and the central lobes, there is a similarly sized protopreconulid. Between the central and the distal lobes, the protoendoconulid and hypopreconulid show a similar arrangement but are slightly larger. A distinct pentaconid, smaller than the main cuspids but larger than the endo- and preconulids, is centrally located on the projecting distal end of the crown (partly fused with the distal cingulid). There is an irregular and discontinuous buccal cingulid but no lingual cingulid.

Comparisons. Permanent teeth. The M1s from CLL1 fall within the size range of *Pr. palaeochoerus* (Fig. 5a) and their proportions also fit well (BLI = 79–104%; $n = 61$; Mottl 1966; Hellmund 1995; Van der Made et al. 1999; Fortelius et al. 2005; Pickford 2013, 2015; Iannucci and Begun 2022; McKenzie et al. 2023b, 2024). In terms of occlusal shape, the CLL1 specimens further resemble those of *Pr. palaeochoerus* figured in the literature (Stromer 1928: pl. II, fig. 20; Mottl 1955: fig. 1, 1966: pl. IV; Hünemann 1968: pl. 1, figs 2, 3; Van der Made et al. 1999: pl. 2, fig. 1; Fortelius et al. 2005: fig. 5; Iannucci and Begun 2022: fig. 2A; McKenzie et al. 2023b: fig. 4n–t, 2024: fig. 6a–f) but differ from those of ‘*Pa.*’ *valentini* in size (Fig. 5a) and shape (Pickford 2014: figs 9, 14E, 15B, 2016: figs 7A, 22C; McKenzie et al. 2023b: fig. 4u, 2024: fig. 6g–o; Alba et al. 2025: fig. 5A–L), especially the less transversely aligned main cusps (the buccal ones being more mesially located than their lingual counterparts) and the better developed ectoconule. The described M1s also differ from those of *V. steinheimensis* in size (Fig. 5a) and shape (Pickford 2014: fig. 29B, 2016: figs 6, 15, 24C, D; McKenzie et al. 2023a: fig. 1c, 2024: fig. 6p, q), displaying a longer and more asymmetric crown, with the main cusps less transversely aligned in pairs.

The p2 from CLL1 falls well within the range of size variation for *Pr. palaeochoerus* (Fig. 5c) and exhibits similar proportions (BLI = 41–51%; $n = 21$; Van der Made et al. 1999; Fortelius et al. 2005; Pickford 2013; Iannucci and Begun 2022; McKenzie et al. 2023b, 2024). Its occlusal shape closely resembles that of published specimens of *Pr. palaeochoerus* (Hünemann 1968: pl. 1, fig. 6; Van der Made et al. 1999: pl. 1, figs 1, 4, 5, pl. 2, fig. 3; Iannucci and Begun 2022: fig. 2D; McKenzie et al. 2023b: fig. 9f–i, 2024: fig. 10k, l), taking into account minor variation in the development of the prestylid and mesial cingulids, as well as in crown height. An alternative attribution to a tetraconodontine can be discounted, as the p2 from CLL1 is less elongate (relatively broader; Fig. 5c) than those of ‘*Pa.*’ *valentini* (BLI = 31–36%; $n = 3$; Alba et al. 2025) and *V. steinheimensis* (BLI = 34–42%; $n = 11$, Pickford 2014, 2016; McKenzie et al. 2024). In terms of shape, it differs from the p2s of ‘*Pa.*’ *valentini* in the less steep protopre-cristid and smaller prestylid (Alba et al. 2025: fig. 9C–F), and from those of *V. steinheimensis* in the less distally

expanded crown, the more centrally located protoconid, and the smaller prestylid (Pickford 2014: figs 31, 33, 2016: fig. 16, 17; McKenzie et al. 2024: fig. 10o).

The m1s from CLL1 agree well in size (Fig. 5d), proportions (BLI = 60–82%; $n = 61$; Hellmund 1995; Van der Made et al. 1999; Fortelius et al. 2005; Pickford 2013; Iannucci and Begun 2022; McKenzie et al. 2023b, 2024; Alba et al. 2024), and occlusal shape (Van der Made et al. 1999: pl. 1, figs 1, 4; Iannucci and Begun 2022: fig. 2D; McKenzie et al. 2023b: fig. 9r–w, 2024: fig. 11a–c) with those of *Pr. palaeochoerus* from elsewhere. In contrast, they differ from the m1s of ‘*Pa.*’ *valentini* (Pickford 2014: fig. 12A, 2016: figs 3A–C, 4A, B, 9C; McKenzie et al. 2024: fig. 11d, e; Alba et al. 2025: fig. 10A–I) and *V. steinheimensis* (Chen 1984: pl. 1, fig. 11, pl. 2, fig. 1, pl. 4, fig. 2; Pickford 2014: figs 31, 33, 2016: figs 6, 24F; Van der Made et al. 2014: figs 3a, 4a; McKenzie et al. 2023a: fig. 1f, 2024: fig. 11f–j) in displaying more abundant enamel wrinkling (when unworn or slightly worn), a more marked lingual constriction between the mesial and distal lobe, and generally a more distally protruding pentaconid.

Deciduous teeth. The DI1s from CLL1 generally resemble to those of *Pr. palaeochoerus* from elsewhere, both in size and proportions (MD = 5.7–13.6 mm; BL = 5.0–13.2 mm; BLI = 58–167%; $n = 12$; Fortelius et al. 2005; McKenzie et al. 2023b, 2024), as well as occlusal shape (McKenzie et al. 2023b: fig. 10a–d, 2024: fig. 12a, b)—differing from those of ‘*Pa.*’ *valentini* in the features noted above in the comparisons for this species.

In turn, the DP2 from CLL1 fits with the metrical variation of *Pr. palaeochoerus* in the comparative sample (Fig. 6a; BLI = 32–56%; $n = 9$; Fortelius et al. 2005; McKenzie et al. 2023b, 2024; Alba et al. 2024), further displaying a similar occlusal pattern with only minor differences (McKenzie et al. 2023b: fig. 10i–m, 2024: fig. 12m–o)—more buccally convex, lingually constricted, and distolingually expanded occlusal contour and better developed secondary cuspules in the distolingual crown expansion. The DP2 from CLL1 most clearly differs in the shorter length (Fig. 6a) and stouter proportions from those of ‘*Pa.*’ *valentini* (BLI = 34–37%; $n = 4$; McKenzie et al. 2024; Alba et al. 2025) and *V. steinheimensis* (BLI = 42–44%; $n = 3$; McKenzie et al. 2024). It further differs in occlusal shape from both ‘*Pa.*’ *valentini* (McKenzie et al. 2024: fig. 12p, q; Alba et al. 2025: fig. 11H, I) and *V. steinheimensis* (Chen 1984: pl. 4, fig. 1; McKenzie et al. 2024: fig. 12r–t), displaying a less elongate and distolingually tilted crown, a more protruding protocone, and a much less developed metacone.

The DP3s from CLL1 fall within the metrical range of *Pr. palaeochoerus* in both size (Fig. 6b) and proportions (BLI = 66–79%; $n = 14$; Van der Made et al. 1999; Fortelius et al. 2005; McKenzie et al. 2023b, 2024), and they further closely resemble in occlusal shape the DP3s of this species (McKenzie et al. 2023b: fig. 10n, 2024: fig. 12u–y). The CLL1 DP3s also resemble in size (Fig. 6b) and proportions those of both ‘*Pa.*’ *valentini*

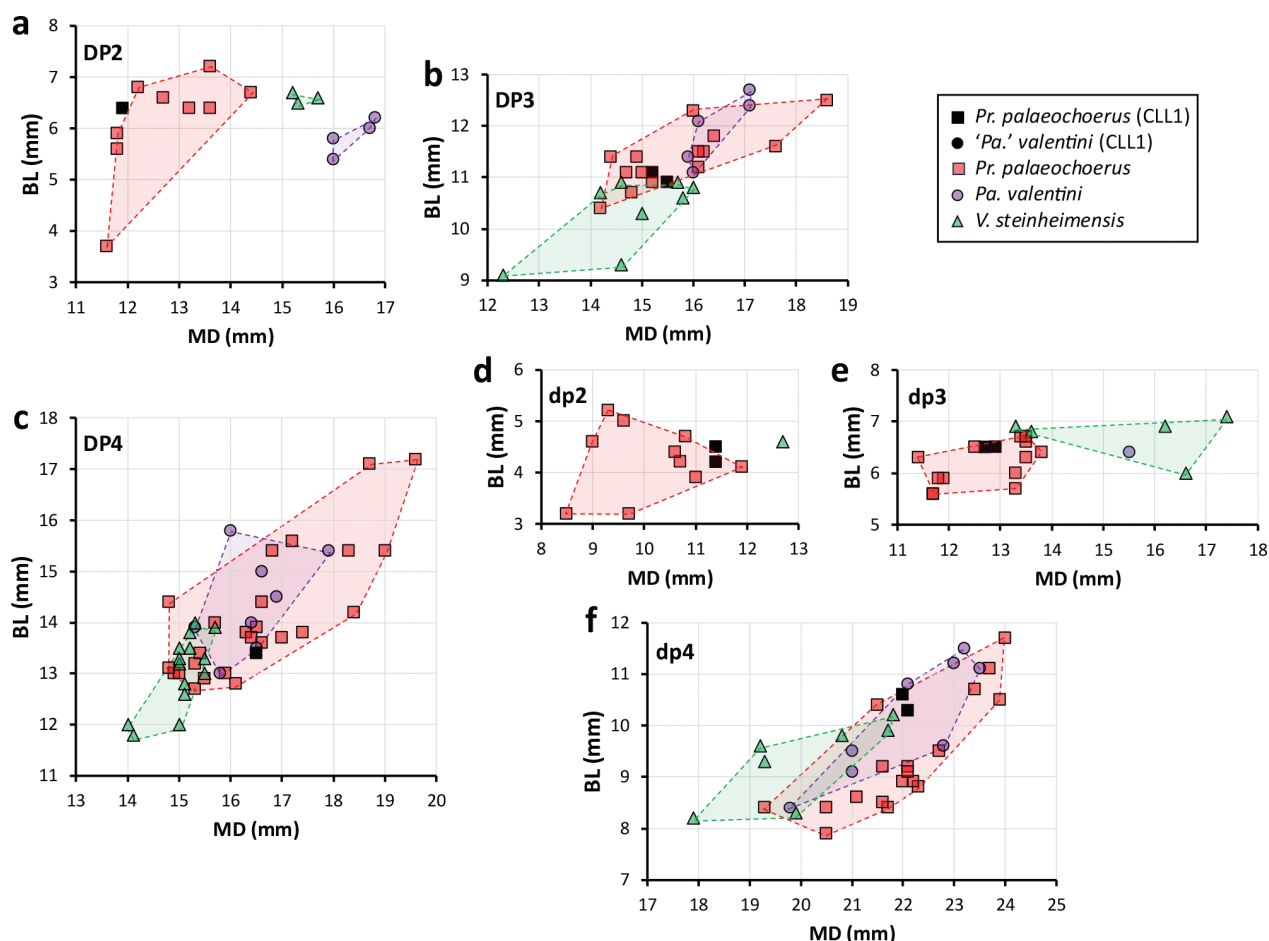


Figure 6. Bivariate plots of BL vs. MD in the deciduous premolars of *Propotamochoerus palaeochoerus* from CLL1 as compared with *Pr. palaeochoerus* and selected tetraconodontines (*'Pa.'* *valentini* and *Versoporcus steinheimensis*) from elsewhere: **a.** DP2; **b.** DP3; **c.** DP4; **d.** dp2; **e.** dp3; **f.** dp4. Metrical data for the CLL1 remains are reported in Table 2, while those for the comparative sample have been taken from the literature (see Material and methods for details on the published sources). Convex hulls outlining the variation of each species (without considering the remains from CLL1) are depicted.

(BLI = 69–75%; $n = 5$; McKenzie et al. 2023b, 2024; Alba et al. 2025) and *V. steinheimensis* (BLI = 64–75%; $n = 8$; Pickford 2016; McKenzie et al. 2024). However, an attribution to either *'Pa.'* *valentini* (McKenzie et al. 2023b: fig. 10r–t, 2024: fig. 12a'–g'; Alba et al. 2025: fig. 11J, K) or *V. steinheimensis* (Chen 1984: pl. 4, fig. 1; McKenzie et al. 2024: fig. 12h'–l') can be discounted based on occlusal shape, as the CLL1 specimens display a less asymmetrical distal lobe and lack a pronounced constriction between the mesial and distal lobes.

The DP4s from CLL1 fall within the metrical variation of *Pr. palaeochoerus* (Fig. 6c; BLI = 77–97%; $n = 25$; Fortelius et al. 2005; Pickford 2013; McKenzie et al. 2023b, 2024). Their occlusal shape is also consistent with previously published DP4s of this species (Hünemann 1968: pl. 1, fig. 17; McKenzie et al. 2023b: fig. 10u–w; McKenzie et al. 2024: fig. 12m'–s'). The CLL1 DP4s are similar in size to the DP4s of *'Pa.'* *valentini* (Fig. 6c; BLI = 82–99%; $n = 8$; McKenzie et al. 2023b, 2024; Alba et al. 2025) and only slightly longer than those of *V. steinheimensis* (Fig. 6c; BLI = 80–92%; $n = 13$; Pickford 2014, 2016; McKenzie et al. 2024). However, the former differ from those of *'Pa.'* *valentini* (Pickford 2014: fig. 16A;

McKenzie et al. 2023b: fig. 10 c'–y, 2024: fig. 12t'–v'; Alba et al. 2024: fig. 6z, 2025: fig. 11L–O) and *V. steinheimensis* (Chen 1984: pl. 4, fig. 1; McKenzie et al. 2024: fig. 12w'–y') in the better developed enamel wrinkling and cingula, and the more distinct protopreconule.

The dp2s from CLL1 fall in the upper size range of *Pr. palaeochoerus* (Fig. 6d) and also fit with this species in proportions (BLI = 33–56%; $n = 10$; Fortelius et al. 2005; McKenzie et al. 2023b, 2024) and shape (McKenzie et al. 2023b: fig. 11n, p, 2024: fig. 13p; Fig. 6d), with minor variation (straighter lingual contour and more mesially inclined mesial root). The CLL1 dp2 also displays similar proportions to the single available dp2 of *V. steinheimensis* (BLI = 36%; Pickford 2016), but is shorter (Fig. 6d) and an alternative attribution to a tetraconodontine can also be discounted based on occlusal shape. Thus, the dp2s from CLL1 differ from those of *'Pa.'* *valentini* (Alba et al. 2025: fig. 11U) by displaying a lower and narrower crown with a smaller prestylid and a serrated protopostcrisid, and without metaconid, and from those of *V. steinheimensis* (McKenzie et al. 2024: fig. 13q) in the higher but blunter crown with a serrated protopostcrisid and a single (instead of bifurcated) distal cristid. The specimen

is also similar in size and proportions to the p2s of *Pa. crusafonti* (MD = 10.2–11.4 mm; BL = 3.7–4.3 mm; MD = 35–39%; n = 3; Pickford 1981), but differs in occlusal shape, displaying a much lower crown, with a less rounded occlusal contour (Pickford 2014: fig. 3D).

The dp3s from CLL1 fall within the size range (Fig. 6e) and proportions (BLI = 43–55%; n = 13; Fortelius et al. 2005; McKenzie et al. 2023b, 2024) of *Pr. palaeochoerus* from elsewhere, and further resemble them in occlusal shape (McKenzie et al. 2023b: fig. 11q–u, 2024: fig. 13r), with minor differences in occlusal contour (mesially rounded instead of pointed). In contrast, the CLL1 dp3s are shorter and stouter than the single complete dp3 of '*Pa.*' *valentini* (Fig. 6e; BLI = 41%; Pickford 2016), and further differ from those of the latter species in the lower crown with a better developed hypoconid and a serrated protoposteristid (McKenzie et al. 2024: fig. 13s; Alba et al. 2025: fig. 11V). The CLL1 dp3s are also smaller than those of *V. steinheimensis* (Fig. 6e) while displaying similar proportions (BLI = 36–52%; n = 5; Pickford 2016), and further differ by displaying a convex buccal contour (lacking a marked buccal constriction and a distobuccal protrusion) and a single (instead of bifurcated) distal cristid (McKenzie et al. 2024: fig. 13t–v).

The dp4s from CLL1 fit well in size (Fig. 6f), proportions (BLI = 39–49%; n = 19; Fortelius et al. 2005; McKenzie et al. 2023b, 2024), and occlusal shape (McKenzie et al. 2023b: fig. 11b'–v, 2024: fig. 13w–z) with those of *Pr. palaeochoerus* from other sites. The CLL1 dp4s overlap in size with '*Pa.*' *valentini* and are only slightly larger than those of *V. steinheimensis* (Fig. 6f), further fitting in proportions with both '*Pa.*' *valentini* (BLI = 42–50%; n = 8; Pickford 2016; McKenzie et al. 2024; Alba et al. 2024, 2025) and *V. steinheimensis* (BLI = 42–50%; n = 7; Pickford 2016; McKenzie et al. 2024). However, the dp4s from CLL1 differ from those of '*Pa.*' *valentini* (Pickford 2014: fig. 16C, D; McKenzie et al. 2024: fig. 13a'; Alba et al. 2025: fig. 11 B'–W) and *V. steinheimensis* (Pickford 2016: fig. 24H; McKenzie et al. 2024: fig. 13b'–e') in several occlusal details, including the thicker cristids with more abundant wrinkling, the better-developed and more distally protruding pentaconid, the larger endo- and preconulids, and the more lingually convex contour of the lobes.

Remarks. The lower premolar IPS28171 [IPS1760] was tentatively identified as a p2 of *Pa. crusafonti* by Golpe-Posse (1971), but our comparisons support its identification as a dp2 of *Pr. palaeochoerus*. We further report unpublished associated deciduous and permanent teeth that most likely belong to a single individual. This material—which in all probability was not available to Golpe-Posse (1971, 1972) because it was not excavated until later—most conclusively records the presence of *Pr. palaeochoerus* at CLL1. This confirms previous reports of the species at CLL1 (Van der Made 1990; de Bruijn et al. 1992; Alba et al. 2011a; Pickford 2016; Arranz et al. 2023), which had never been supported by descriptions or iconography.

Discussion and conclusions

The material from CLL1 described in this paper includes previously unpublished material that supports the presence of three suid species in addition to the small-bodied tetraconodontine *Pa. crusafonti*. The latter is clearly the most abundant suid at CLL1, which is its type locality. Although the remains of *Pa. crusafonti* have been previously described (Golpe-Posse 1972; Pickford 1981), a more in-depth taxonomic revision is pending given its key role for clarifying the systematics of European tetraconodontines—particularly, the genus ascription of '*Pa.*' *valentini*, considering that *Pa. crusafonti* is the type species of *Parachleuastochoerus* (see discussion in Alba et al. 2025). Our comparisons with material from elsewhere confirm and further substantiate the taxonomic identity of the CLL1 suids as reported in the most updated faunal list of the site (Arranz et al. 2023), namely: the listriodontine *L. splendens*, based on different material from that reported by Van der Made (1996) and other unpublished remains; the large tetraconodontine '*Pa.*' *valentini*, based on material previously misidentified by Golpe-Posse (1971, 1972) and a few additional unpublished remains; and the suine *Pr. palaeochoerus*, including a premolar previously assigned to *Pa. crusafonti* by Golpe-Posse (1971, 1972) and more abundant and diagnostic unpublished material. The presence of the large tetraconodontine might have been previously overlooked because of the paucity of the material.

The presence of these suids at CLL1 has some biochronological implications. In the case of *L. splendens*, it represents the last appearance datum of listriodontines in Europe, as already noted by Van der Made et al. (2022), given that *L. splendens* became locally extinct in China (east Asia) and eastern Europe during MN7+8 but persisted in western Europe (including Iberia) until MN9 (Pickford and Morales 2003). This is also the case of '*Pa.*' *valentini*, which is recorded from both MN7+8 and MN9 localities (Pickford 2014, 2016; McKenzie et al. 2023b, 2024; Alba et al. 2024, 2025) but not conclusively recorded after the earliest Vallesian. The chronostratigraphic range of '*Pa.*' *valentini* largely overlaps with that of *V. steinheimensis* (Pickford 2016; McKenzie et al. 2023a, 2024), which further extends into the earliest Vallesian, but the record of the former from CLL1 indicates that this species outlived *V. steinheimensis* and, like *L. splendens*, survived throughout the whole early Vallesian. In contrast, the record of *Pr. palaeochoerus* from CLL1 agrees well with the previously known chronostratigraphic range of this species, which is currently considered to be restricted to the Vallesian—as previous citations of this taxon from MN7+8 (Ginsburg 1974, 1980; Van der Made and Moyà-Solà 1989; Van der Made 1990, 1997; Van der Made et al. 1999; Fortelius et al. 2005; Alba et al. 2006) are attributable to confusion with *Pa. valentini* (Pickford 2014, 2016; Alba et al. 2022, 2025) and to the incorrect correlation of some MN9 sites to MN7+8 (Alba et al. 2019, 2022). The same applies to *Pa. crusafonti*, which is recorded from

MN9 and some MN10 sites (Van der Made 1997, 1999; Pickford 2014, 2016).

It is remarkable that the suid assemblage from CLL1 is overwhelmingly dominated by the small tetraconodontine *Pa. crusafonti*, which is represented by 86.2% (206/239) of the suid teeth from this locality (authors' unpublished data), whereas the remaining three species identified here—*Pr. palaeochoerus* (7.5%, 18 teeth), *L. splendens* (4.6%, 11 teeth, including those reported by Van der Made 1996), and '*Pa.*' *valentini* (1.7%, only four teeth)—are only recorded by a few specimens. The suid composition agrees well with the paleoenvironmental reconstruction of CLL1 based on other taxa, fossil plant remains, and dental ecometrics. In particular, the large and small mammals from CLL1 and nearby areas are indicative of a subtropical to warm-temperate humid and closed forested paleoenvironment at the depositional area but further hint at the existence of relatively more open woodlands nearby (Köhler 1993; Andrews 1996; Costeur 2005; Marmi et al. 2012). Taxa such as the hominoid *H. laietanus*, tragulids, tapirids, chalicotheriids, moschids, cervids, rhinocerotids, arboreal dormice, and flying squirrels are consistent with the presence of dense riparian forests. The occurrence of the alytid amphibian *Latonia*, castorids, tragulids, tapirids, and the bovid *Miotragocerus pannoniae* points to freshwater courses or swampy areas, whereas the presence of giraffids, the cricetid *Hispanomys thaleri*, and ground squirrels is suggestive of open woodland habitats in the surroundings (Marmi et al. 2012; Andrews 2015; Villa et al. 2019; Arranz et al. 2023; Pandolfi et al. 2025). Macrofloral remains from CLL1 (representative of the local vegetation) confirm the presence of a dense wetland/riparian forest in the depositional area, surrounding a very humid marshy zone with reeds, palms, evergreen laurels, and fig trees (Marmi et al. 2012). The presence of mega-mesothermal taxa and the absence of deciduous taxa point to a subtropical to warm-temperate climate characterized by high mean annual temperatures (MAT) and low temperature seasonality. However, paleobotanical evidence from other nearby localities suggests that, at a regional scale, the zonal vegetation included a higher proportion of deciduous taxa in the forested areas, as well as more open woodlands far from the wetlands (Marmi et al. 2012). This interpretation is consistent with paleoclimatic estimates based on herbivore mammal dental ecometrics, although these provide relatively high MAT estimates of 25 °C, higher than expected for the Late Miocene, which place CLL1 within tropical climates (Arranz et al. 2023). The same methods estimate mean annual precipitation (MAP) at 881 mm with notable seasonality and consistent with a tropical seasonal forest with a marked, monsoon-like, rainy season. Nevertheless, the estimated precipitation of the driest month (>60 mm) suggests an intermediate environment between evergreen tropical forests and tropical deciduous forests, again supporting the presence of nearby open woodlands with deciduous vegetation (Arranz et al. 2023). Recent precipitation estimates based on the composition of the

small mammal faunas for the 9.8–9.7 Ma interval in the Vallès-Penedès (which includes CLL1) results in somewhat higher MAP estimates slightly above 1,000 mm and a far less marked precipitation seasonality (Casanovas-Vilar et al. 2026). Even though these results are more consistent with a humid subtropical climate than a tropical one with marked rainfall seasonality, they are also perfectly consistent with the presence of densely forested environments in the wetlands and more open woodlands far from them. Ongoing studies based on stable isotopes of the CLL1 mammals will certainly help to refine the associated paleoenvironment and paleoclimate.

No isotopic or dental wear analyses have been thus far published for *Pa. crusafonti*, but small suoids are generally interpreted as forest-adapted forms (Fortelius et al. 1996), suggesting that it may have exhibited a frugivorous feeding strategy on the ground, likely including figs and other fallen fruits. However, the morphology and wear of its lower incisors—high-crowned i1 and i2, very worn apically but also lingually (Pickford 1981)—is indicative of rooting behaviors (Van der Made et al. 2014), which would have allowed *Pa. crusafonti* to exploit alternative food resources. Isotopic evidence from the slightly larger but closely related *Parachleuastochoerus kretzoi* from Rudabánya shows depleted $\delta^{18}\text{O}$ values, interpreted as evidence of high dependence on drinking water, as well as rooting behaviors, thus including roots and tubers in its diet (Eastham et al. 2016). The high abundance of *Pa. crusafonti* at CLL1 further suggests that it inhabited the locally humid habitat at the deposition environment throughout the year, probably thanks to the possession of rooting behaviors. The latter would have enabled it to cope with periods of fruit scarcity, documented by the frequent enamel hypoplasias displayed by *Hispanopithecus* (see discussion in Marmi et al. 2012, and references cited therein). Both the suine *Pr. palaeochoerus* (Van der Made et al. 2014; Eastham et al. 2016, 2017; Iannucci and Begun 2022; McKenzie et al. 2023b, 2025) and the large tetraconodontine '*Pa.*' *valentini* (McKenzie et al. 2023b, 2025) are also considered to have had rooting behaviors. Dental topographic analyses classify *Pr. palaeochoerus* as an omnivorous or mixed feeder and '*Pa.*' *valentini* as a mixed feeder, indicating a high degree of trophic flexibility, with *Pr. palaeochoerus* being best interpreted as a generalist and opportunistic feeder (McKenzie et al. 2025). Coupled with their low abundance at CLL1, this suggests that none of these species preferentially inhabited the depositional environment and likely exploited trophic resources from more open habitats nearby. The survival and coexistence of '*Pa.*' *valentini* and *Pr. palaeochoerus* throughout MN9—following the dispersal of the latter species during the earliest Vallesian (Alba et al. 2022 and references therein)—suggests some degree of niche partitioning between the two species, although both would have inhabited more seasonal and open environments than *Pa. crusafonti*.

Finally, while some studies suggest that *L. splendens* thrived in relatively open environments (Fortelius et al.

1996; Van der Made et al. 2014, 2022), this species is also frequently recorded in relatively humid and densely forested environments from the Vallès-Penedès Basin, such as those from Abocador de Can Mata and particularly Castell de Barberà (Casanovas-Vilar et al. 2008; McKenzie et al. 2024), while being absent from Creu de Conill 20, generally interpreted as a more open and arid environment (Casanovas-Vilar et al. 2006; Alba et al. 2019; McKenzie et al. 2023b; but see Pandolfi et al. 2025). Therefore, the closed and humid environment inferred for CLL1 cannot explain the rarity of *L. splendens*. This species is generally considered a folivorous browser that specialized on low vegetation (Hunter and Fortelius 1994; Van der Made 1996), probably consuming not only leaves but also a significant proportion of fruits (Aiglstorfer et al. 2014; Van der Made et al. 2014, 2022). Dental topographic analyses have classified *L. splendens* as a mixed feeder (McKenzie et al. 2025), as previously suggested by Aiglstorfer et al. (2014), indicating a flexible diet (including not only leaves and grasses, but also herbs, sedges, forbs, and fruits) and suggesting the exploitation of a wide range of habitats. Nevertheless, *L. splendens* lacked rooting behaviors, as evidenced by cranial morphology and incisor shape and wear (Van der Made 1996; Fortelius et al. 1996; Aiglstorfer et al. 2014; Van der Made et al. 2014, 2022), which would have made it more vulnerable to resource scarcity during the unfavorable season as compared to both suines and tetraconodontines. The progressive decline and eventual extinction of listriodontines throughout MN9 (Van der Made et al. 2022) might thus have been driven by paleo-environmental factors (such as increased seasonality) coupled with competition with other suid species, such as *Pa. crusafonti*, which likely exploited similar resources in addition to roots and rhizomes.

Acknowledgments

We thank J.M. Robles and P. Logrosán-Soriano for collection assistance, as well as F. Carrasco and J. Barrull (Museu Geològic del Seminari de Barcelona), M. Gross (Universalmuseum Joanneum in Graz), and D. Berthet (Musée des Confluences in Lyon), for access to comparative fossil suid material. We also thank the editor (Gabriel Aguirre Fernández) and two anonymous reviewers for helpful and constructive comments on a previous version

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- Additional information**
- Conflict of interest**
- The authors have declared that no competing interests exist.
- Ethical statement**
- No ethical statement was reported.
- Use of AI**
- No use of AI was reported.
- Funding**
- This work is part of R+D+I project PID2024-159434NB-I00, funded by the Agencia Estatal de Investigación of the Spanish Ministry of Science and Innovation. Research has also been supported by the Generalitat de Catalunya/CERCA Programme; the Agència de Gestió d'Ajuts Universitaris i de Recerca (AGAUR) of the Generalitat de Catalunya (consolidated research group 2017 SGR 116 GR); the Departament de Cultura of the Generalitat de Catalunya (CLT0009_22_000018); and two predoctoral Joan Oró-FI fellowships (2024 FI-2 00112 to S.G.A. and 2023 FI-3 00396 to S.S.), co-funded by the AGAUR and the European Social Fund Plus (FSE+).
- Author contributions**
- SGA and DMA designed the research; SGA, SS, SM, and DMA collected data (measurements and/or photographs); SGA, SS, and DMA analyzed metrical data and identified the specimens; SGA and DMA prepared the figures; ICV and DMA raised funds and supervised research; SGA and DMA wrote the manuscript with input from the remaining authors.
- Author ORCIDs**
- Sara G. Arranz  <https://orcid.org/0000-0003-4249-6289>
- Souzanna Siarabi  <https://orcid.org/0000-0002-3928-224X>
- Sharrah McKenzie  <https://orcid.org/0000-0002-8259-3756>
- Isaac Casanovas-Vilar  <https://orcid.org/0000-0001-7092-9622>
- David M. Alba  <https://orcid.org/0000-0002-8886-5580>
- Data availability**
- All data supporting the findings of this study are available within the paper and its additional files. The original fossils described herein are available for study at the ICP, which is a registered museum recognized by the Generalitat de Catalunya.
- Paleomagnetic calibration and correlation with global events. *Palaeogeography, Palaeoclimatology, Palaeoecology* 133: 149–180. [https://doi.org/10.1016/s0031-0182\(97\)00084-9](https://doi.org/10.1016/s0031-0182(97)00084-9)
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Supplementary material 1

Supplementary Information

Authors: Sara G. Arranz, Souzanna Siarabi, Sharrah McKenzie, Isaac Casanovas-Vilar, David M. Alba

Data type: zip

Explanation note: Contains additional files with comparative measurements (in mm) in CSV and PDF format.

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