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EARLY PLIOCENE BARB (TELEOSTEI, CYPRINIDAE, BARBINAE) FROM THE CAMP DELS NINOTS SITE (SPAIN)

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Abstract. The Pliocene site of Camp dels Ninots (Caldes de Malavella, NE Spain) is considered a Konservat-Lagerstätte due to the remarkable preservation of its macro and microvertebrate record, along with floral remains such as leaf imprints and seeds. Its lacustrine deposits, dated to the Early Pliocene, have provided a number of semi-articulated and isolated remains of middle to large sized cyprinid fish, apparently belonging to subfamily Barbinae. These specimens allow recognize a number of skeletal characters, including specific morphology of the pharyngeal dentition and denticulation at the posterior side of the last unbranched dorsal fin ray. The latter character is well discernable in smaller individuals, while in the larger specimens the denticulation is lost. These features, together with general osteological characterization, allow to classify the specimens under consideration to the species *Luciobarbus graellsii* (Steindachner, 1866b), or to a closely related form morphologically non discernable from the latter. Fish of the *Luciobarbus graellsii* species is typical native barb inhabitant of today North-Eastern Iberian Peninsula. The specimens excavated in the Camp dels Ninots documents its earliest and first known fossil record. Inferences for the Pliocene palaeogeography of the region as well as the palaeoecology of the species is discussed. This new fossil record enlarges the known environmental requirements of the species (as it manage to survive from the warmest period of the Pliocene to the coldest period of the Pleistocene) and documents its early abilities to disperse in peculiar aquatic environment (i.e., maars). A brief overview of the fossil record barbs from Central, Western and Southern Europe is provided.

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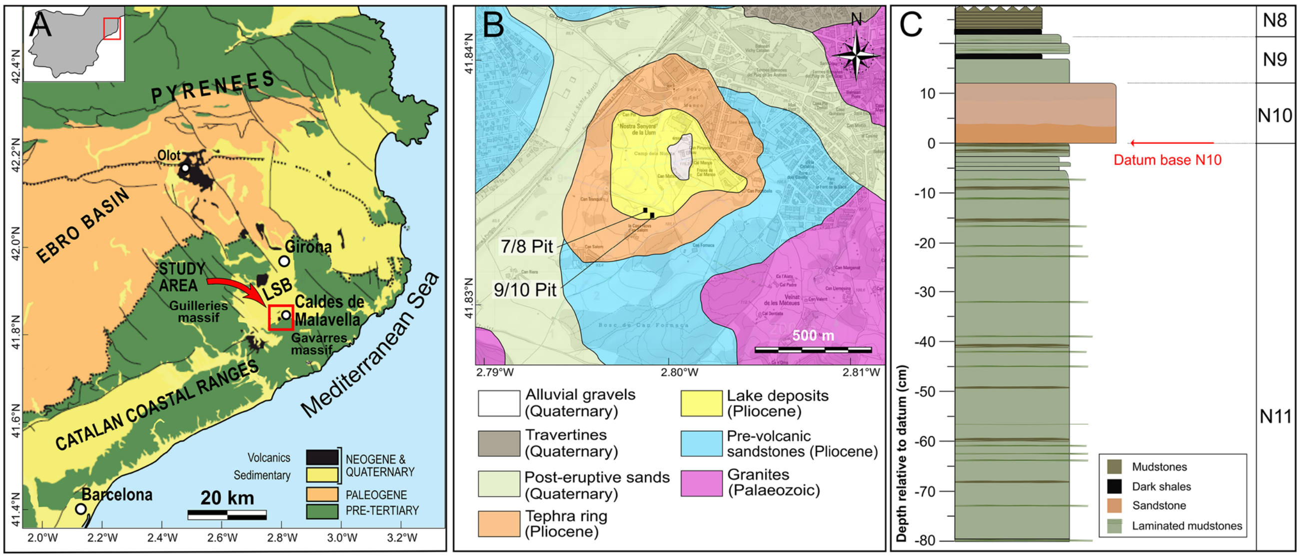

Fig. 1 - Geographical position of Camp dels Ninots locality (Caldes de Malavella, Girona, Spain). A) General geographical context of the site; B) a geological map of the site, and C) is the synthetic stratigraphic log. Adapted from Goméz de Soler et al. (2012). Articulated or semi-articulated specimens of *Luciobarbus graellsii* studied here come from levels 9 and 11, while level 10 only provided isolated bones.

INTRODUCTION

The family Cyprinidae is the largest freshwater fish family in the world with more than 3000 species organized within 367 genera (Nelson et al. 2016). Its fossil record is extensive (e.g. Cavender 1991; Chang & Chen 2008; Murray 2020), but many are represented by isolated pharyngeal teeth and/or bones only. Consequently, comparison and phylogenetic evaluation is frequently avoided and a comprehensive understanding of the evolutionary history of this group is far from to be complete. Even well palaeontologically explored regions provide just fragmentary information regarding quite usual taxa. This is true also for barb fishes of the genera *Barbus* Daudin, 1805 *in* Cuvier 1816 and *Luciobarbus* Heckel, 1843, preserving handful fossil specimens in various stages of preservation within Europe (for more information see the overview below). The Iberian Peninsula is inhabited nowadays by eight to ten species of the *Barbus*—*Luciobarbus* lineages (Almaça 1967; Miranda & Escala 2003; Kottelat & Freyhof 2007) and the fossil record is practically limited to isolated pharyngeal teeth, with single known exception, represented by specimens from the Camp dels Ninots.

The Lower Pliocene Camp dels Ninots site (Caldes de Malavella, Girona, Catalonia, Spain) provided large number of disarticulated, semi-articulated and articulated specimens of large mammals, rodents, birds, chelonians, amphibians, fish, and numerous plant remains (Gómez de Soler et al. 2012; Claude et al. 2014; Přikryl et al. 2016; Grandi et al. 2022; Blain et al. 2024a; Pandolfi et al. 2023). The fish preserved at the locality are represented by two cyprinid taxa only, including remains of the barb fish, previously classified as *Barbus* (*'Luciobarbus'*) sp., and a species of Leuciscinae fish (Přikryl et al. 2016). A number of well-preserved specimens were obtained from multiple excavation allowing a detailed examination of their anatomy. This fact, together with access to extant comparative specimens, provided enough information to describe, interpret and classify the specimens properly. This paper presents a description and interpretation of the single articulated and semi-articulated fossil record of the barb fish from the Iberian Peninsula known up to date.

GEOLOGICAL SETTING

The Camp dels Ninots site is located in the NE Spain within Girona province (Fig. 1) and it is interpreted to be a mixed hard-soft maar-diatreme originated as part the Catalan Volcanic Complex (Oms et al. 2015; Bolós et al. 2021). The site is located within a Pliocene sedimentary and volcano-sedimentary lacustrine infill of a maar lake (Gómez de Soler et al. 2012) containing exceptionally well-pre-

Tab. 1 - List of the studied specimens and related acronyms used within the text. Abbreviations: CN: Camp dels Ninots; No: number of registers inside the square; Zinf: Height in meters above the mean sea level; Fig: Figure in the manuscript.

Acronym	Year	Sector	Pit	Layer	Square	No	Zinf	Fig
CN-1	2013	Can Argilera	9/10	11	Y50	3	101,54	2A, 3C
CN-2	2012	Comercial			AM0	1	97,14	2B
CN-3	2013	Can Argilera	9/10	11	X47	3	100,48	3A
CN-4	2013	Can Argilera		11	AB52	1	101,52	3B, D
CN-5	2007	Can Argilera	7/8	10		screening	98,75	4A
CN-6	2021	Can Argilera	9/10	11	AC52	7	101,59	4B, C, E, F, G, I, M, N, O, P
CN-7	2011	Can Argilera	9/10	10	L18			4D
CN-8	2013	Can Argilera		11	AC54	1	101,75	4H, L, Q
CN-9	2005	Can Argilera	7/8	10	M23	1	98,74	4J
CN-10	2013	Can Argilera	9/10	11	AB55		102,48	4K
CN-11	2021	Can Argilera	9/10	10	AD55	1	101,92	5A
CN-12	2023	Can Argilera	9/10	9	AB44	1	100,92	5B
CN-13	2008	Can Argilera	7/8	10		screening	98,75	5C
CN-14	2008	Can Argilera	7/8	10		screening	98,75	5D
CN-15	2013	Can Argilera	9/10	11	AA51		101,25	5E
CN-16	2008	Can Argilera	7/8	10		screening	98,75	5F
CN-17	2008	Can Argilera	7/8	10		screening	98,75	5G
CN-18	2008	Can Argilera	7/8	10		screening	98,75	5H
CN-19	2008	Can Argilera	7/8	10		screening	98,75	5I
CN-20	2008	Can Argilera	7/8	10		screening	98,75	5J
CN-21	2008	Can Argilera	7/8	10		screening	98,75	5K
CN-22	2013	Can Argilera		11	AB52		101,70	5L
CN-23	2008	Can Argilera	7/8	10		screening	98,75	5M
CN-24	2008	Can Argilera	7/8	10		screening	98,75	5N
CN-25	2008	Can Argilera	7/8	10		screening	98,75	5O
CN-26	2008	Can Argilera	7/8	10		screening	98,75	5P
CN-27	2013	Can Argilera	9/10	11	AA51		101,25	5Q
CN-28	2008	Can Argilera	7/8	10		screening	98,75	5R
CN-29	2013	Can Argilera	9/10	11	AA51		101,25	5S
CN-30	2008	Can Argilera	7/8	10		screening	98,75	5T
CN-31	2013	Can Argilera	9/10	11	AA51		101,25	5U
CN-32	2008	Can Argilera	7/8	10		screening	98,75	5V
CN-33	2008	Can Argilera	7/8	10		screening	98,75	5W
CN-34	2008	Can Argilera	7/8	10		screening	98,75	5X
CN-36	2013	Can Argilera	9/10	11	AB50	Level bag	101,50	6A
CN-37	2008	Can Argilera	7/8	10	J19	2	109,00	6B
CN-38	2021	Can Argilera	9/10	11	AC52	5	101,57	6C, D
CN-39	2005	Can Argilera	7/8	10	M23	10	98,77	6E

served biotic remains (e.g., Grandi et al. 2022; Blain et al. 2024a). Since 2003, the lacustrine infill has been investigated through systematic excavations. The well-preserved palaeontological record has allowed to describe the site as a *Konservat-Lagerstätte* of Pliocene age (Gómez de Soler et al. 2012; Campeny et al. 2015). Such palaeontological record describes a palaeo-ecosystem characterized by large vertebrates including bovids, rhinoceros and tapirs (Gómez de Soler et al. 2012; Campeny et al. 2015), fish (Přikryl et al. 2016), turtles (Claude et al. 2014), amphibians (Blain et al. 2024a) and squamate reptiles and macrobotanical remains (Robles et al. 2013). Additional studies based on core data drilled in the center of the lake have allowed to constrain the palaeoenvironmental conditions (Jiménez-Moreno et al. 2013; Rodríguez-Salgado et al. 2021) and assigned an age range between 3.3 and 3.1 Ma for the complete lacustrine infill based on magnetostratigraphic data (Carrancho et al. 2012; Jiménez-Moreno et al. 2013). More recently, new numerical age determinations suggest an Early Pliocene age (Bolós et al., personal comm.).

The studied semi-articulated and isolated fish remains were collected in two areas 30 m apart (Pit 7/8 and Pit 9/10), located in Can Argilera sector (Fig. 1; Table 1). The excavated succession at Can Argilera comprises a >2-m-thick stratigraphic sequence of laminated clay deposits intercalated by silt and sand-rich layers interpreted as mass flow deposits. A total of 12 units (labelled N1-N12) can be differentiated.

All the studied specimens were recovered from the N9, N10 and N11 units which in Can Argilera sector contains most of the fossiliferous material excavated to date. The N11 consists of 0.8-m-thick succession dominated by dark brown claystones intercalated with mm-scale green clay stringers (Fig. 1C). The uppermost part of this unit consists of a 3-cm-thick dark interval rich in opal melinites. This interval transitions upwards into a 2-cm-thick level dominated by leaf imprints. Overall, this level is rich in fish scales and, within the studied sector, fish and turtle remains are common. This unit is bioturbation free and displays no evidence of subaerial exposure (i.e. no mudcracks nor paedogenesis). In addition, the lack of ripples suggests suspension as mechanism for deposition. The top of the unit sharply transitions into the N10 unit which consists of a 12-cm-thick sequence of poorly cemented medium to fine grained sandstones and siltstones. This unit is interpreted as a result of a mass flow event, and it is found in different pits excavated at Can Argilera sector. This explains why the recovered fish remains are isolated and were obtained following the screening process. For this reason, the basal part of this unit is used as a datum to correlate the fossiliferous levels found in the N11. Lastly, the N9 consists of 15-cm-thick unit of heterogeneous texture. The lowermost part is formed by a light green silt with abundant charcoal fragments, followed by a 3-cm-thick black clays with abundant leaf imprints and on the top a 3-cm-thick of dark brown and green laminated clays.

The stratigraphy at the Pit 7/8 and Pit 9/10 corresponds to the greenish-greyish laminated and greyish green claystones with sand (GCS) lithological group (Rodríguez-Salgado et al. 2021). This facies type is poor in carbonates, and it is dominated by detrital quartz and feldspars. Quartz grains are fine to coarse and angular to subangular in roundness. The interval is composed of sub-centimetric laminae indicating a relatively steady sediment accumulation. Whereas diatoms are very common in these levels, no skeletal carbonates are found. In the center of the lake accumulation rates of 0.19 mm· year^{-1} are estimated (Jiménez-Moreno et al. 2013). Since no information is available on the sedimentation rate at the lake margin (i.e., pit 7/8), it is expected to be lower than that estimated at the center of the maar, as the stratigraphy become condensed at the margins.

MATERIAL AND METHODS

The specimens were excavated from the shale deposits of the locality. Part of the specimens were preserved at the surface of the sediment; other specimens were extracted from the sediment entirely. The fossils are housed in the IPHES-CERCA (the Catalan Institute of Human Paleoecology and Social Evolution, Tarragona, Spain). List of the studied material and used acronyms is presented in the Table 1. The specimens were compared with data in literature and dried comparative skeletons of *Barbus* and *Luciobarbus* species from Iberian Peninsula kept in the Department of Biodiversity and Evolutionary Biology of the Museo Nacional de Ciencias Naturales (MNCN), Madrid.

The detailed osteological understanding of Barbinae is limited to a relatively few publications (especially Obrhelová 1967; Vandewalle 1977; Howes 1987; Rojo 1987; Doadrio 1990; Miranda & Escala 2003; Murray 2019; and Vasilyan et al. 2019). The nomenclature of the pharyngeal bone and teeth follow Obrhelová (1967), Nakajima (1984), and Böhme (2002); other osteological element nomenclature follows Obrhelová (1967), Howes (1987) and Doadrio (1990).

The abbreviation SL (= standard length) is used elsewhere. Measurements were taken from the tip of snout to the end of the caudal peduncle by caliper or from the photos using ImageJ software.

SYSTEMATIC PALAEONTOLOGY

Order **Cypriniformes** Bleeker, 1860
Family Cyprinidae Bonaparte, 1840
Subfamily Barbinae Bleeker, 1859
Genus *Luciobarbus* Heckel, 1843

Luciobarbus graellsii (Steindachner, 1866b)

Figs. 2-6

2016 *Barbus* (‘*Luciobarbus*’) sp. – Přikryl et al.: Fish fauna… 350; figs 3–6.

Description. The specimens are represented by middle to large sized fish with SL up to 420 mm (the largest specimen with this size was included into the study and it is figured in the Fig. 2A). The body is spindle shaped, tapering posteriorly. The head length represents about 30 % of the SL. The dorsal fin starts at the half of the body length. The anal fin is located in half-length between the end of dorsal and start of caudal fins. The pectoral fin inserts on the body close to the ventral margin of the body. The pelvic fins insert to the body at the level of the start of the dorsal fin or very slightly poste-

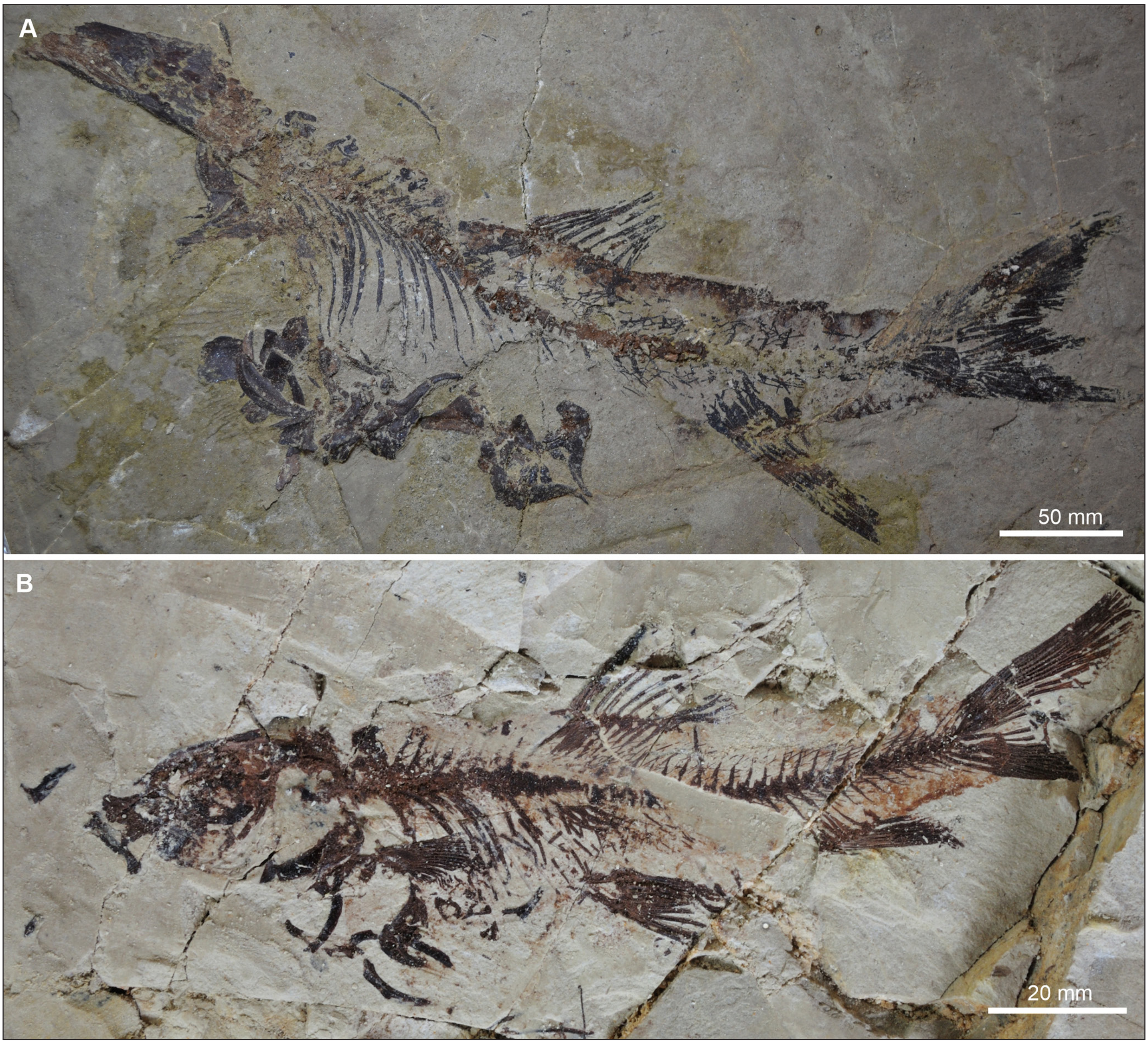

Fig. 2 - *Luciobarbus graellsii*, Camp dels Ninots locality, Pliocene. General view of a relatively complete semi-articulated large and middle-sized specimens: A) CN-1; B) CN-2.

riorly. Measurements were presented by Přikryl et al. (2016).

Neurocranium. The neurocranium in the dorsal and ventral views is elongated in the shape of an isosceles trapezoid. In the lateral view, it has straight ventral and slightly convex dorsal margins (Fig 3A–C). The frontals are articulated in the midline by a more or less wavy suture, and covers anteriorly mesethmoid, postero-laterally sphenotics and pterotics and posteriorly are in contact with parietals. The frontals are widest just posteriorly to orbital margin, in front of the fossa musculi dilatoris operculi, and this maximal width is contained slightly more than twice in the frontal length (Fig. 4A1, 2). The frontal bears ventral lamina at the level of the articulation with the autosphenotic and prootic. This ventral lamina is perforated by large foramen, well visible from the lateral side of the bone (see arrow at the Fig. 4A3). The parietals are sub-square shaped and articulate each with other medially, with frontals anteriorly, with the pterotics laterally and the supraoccipital posteriorly (Fig. 3A, C). Details of the ethmoid and occipital section of the skull are not entirely clear, although general position and general shape of the mesethmoid, prootic and pterotics are recognizable (Fig 3A, B). The prootic bears well-recognizable hyomandibular-jugular foramen (marked by arrow at the Fig. 3B). The parasphenoid is straight in the

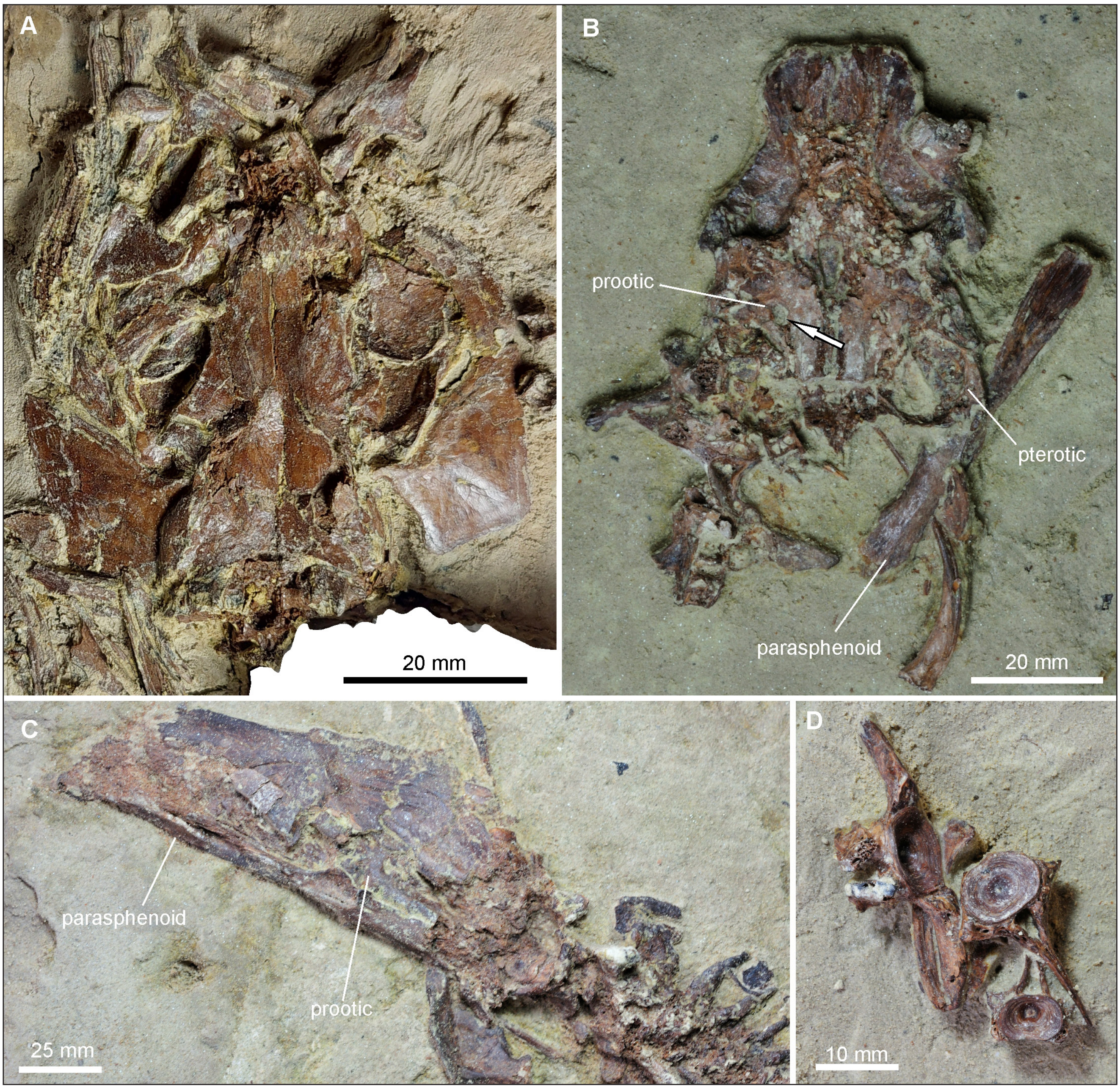

Fig. 3 - *Luciobarbus graellsii*, Camp dels Ninots locality, Pliocene. Articulated skull remains and anterior part of the vertebral column. A) Dorsal view of the neurocranium and associated parts of viscerocranial elements CN-3; B) ventral view of the neurocranium CN-4; C) lateral view of the skull CN-1; D) anteriormost vertebral centra preserved at the CN-4.

lateral view, with anterior and posterior extremities slightly enlarged in the dorso-ventral view (Fig. 3B, C). There is developed paired articular facet in the posterior-most quarter of the bone.

Jaws. The jaw bones (maxilla, premaxilla, dentary) are toothless. The premaxilla is in the general shape of elongated triangle with elevated ascending process. The maxilla (Fig. 4D) bears well developed processus postmaxillaris at the dorsal margin of the bone and postero-ventrally enlarged processus dentalis. The caput maxillaris is well separated from the main shaft, robust and reaching same depth as processus postmaxillaris. The processus intermaxillaris is flat, low, but well-pronounced and heading anteriorly. The processus ligamenti palato-maxillaris is relatively short and blunt. The lower jaw consists of dentary and angulo-articular; a presence and shape of the retroarticular is not clear. The dentary bears well developed coronoid process declined posteriorly (Fig. 4E). The antero-dorsal surface of the dentary is reinforced and flattened and from the coronoid process separated by well-developed concavity;

along ventral margin of the bone is recognizable neural canal. The angulo-articular bears well-separated articular facet for quadrate; the corpus of the bone is anteriorly tapered, with convex dorsal margin of the bone (Fig. 4F, G).

Suspensorium. The hyomandibula is shortened, with more or less straight posterior edge and elevated opercular facet (Fig. 4B, C). The prootic and sphenotic articular heads are antero-ventrally declined. The hyomandibular shaft is straight, short and foramen for nervus facialis is shifted slightly dorsally (marked at the Fig. 4C). The quadrate is roughly triangularly shaped, with massive posterior edge ventrally terminate in the articular head (Fig. 4H). The head for articulation of lower jaw is separated from the anterior margin of the bone by a notch (see arrow at the Fig. 4H, I). The fossa symplectica is narrow and short (reaching approximately half of the bone depth). Number of quadrates are secondarily broken anteriorly (Fig. 4I) and give impression of the relatively narrow structure, but this condition is the result of an inadequate preservation. The meta-, ento-, and ectopterygoids are flat, slightly arched elements, but their state of preservation prevents a more detailed description of their morphology.

Opercular series. The opercle (Fig. 4J, K, L) is more or less diamond shaped, with well-developed, antero-dorsally oriented processus supraglenoidalis and triangular dorsal process (see arrow in the Fig. 4K). Many specimens lack these processes due to their broke-off (Fig. 4J). The preopercle is slightly bent, but relatively widely open antero-dorsally.

Hyoid apparatus and branchial skeleton. The anterior ceratohyal (Fig. 4M, N) is about twice deeper in the posterior margin than in the anterior part, with maximum depth contains about twice in the length of the bone. The dorsal margin of the bone is straight; the ventral margin is concave. The anterior ceratohyal articulates posteriorly with posterior ceratohyal (Fig. 4O, P) that forms almost a triangular shape. Its postero-ventral part is flattened; the dorsal margin is straight. There is shallow socket developed at the antero-dorsal surface, originally served for articulation with interhyal. There are three branchiostegal rays. The fifth ceratobranchial (pharyngeal bone) is sigmoidal-shaped, in the central part bearing toothed area (Fig. 5A, B). The teeth are antero-dorsally oriented and set in the three rows, with the adult pharyngeal formula 4.3.2/4.3.2. The A1 tooth is the most robust tooth of the mammiliform type (molariform in some cases), with recognizable spike and wide basis. The A2 to A4 teeth are spatulate, crown is medially elongated and medial tip of individual tooth bears more or less distinctive spike. The B1 and B2 teeth are similar to A3 type, but significantly smaller and crown is spatulate, with more or less distinctive sharp edge at the antero-medial chawing margin. The B3 is slender, with flat spatulate crown. The C row contains two teeth generally similar to these preserved in the B row. Number of the excavated specimens show slight morphological differences (such as shape of crown and basis, and size of spike at the crown), reflecting its individual age, topographical position within the pharyngeal bone and abrasion ratio. The teeth functionally act against to the masticatory triangular process of the basioccipital (Fig. 4Q).

Vertebral column and intermuscular bones. The vertebral column is composed by of about 42 vertebrae. The anterior 27 to 28 vertebrae are located in the abdominal section of the vertebral column, with four anterior-most ones included in the Weberian apparatus. Details of the Weberian apparatus are not clear in any of the studied specimens – some elements are exceptionally preserved, like second centrum with elongated lateral processes (Fig. 3D). The caudal portion is composed by 14 or 15 vertebrae. The neural arches and/or spines of several abdominal vertebrae are supported by praezygapophysis of the following vertebrae. The epineurals and epipleurals are presented.

Caudal skeleton and fin. The caudal skeleton shows general cyprinid condition, with parhypural, five separated hypurals (hypural six was not recognizable neither fusion of any of them with compound caudal centrum), and most probably single epural. The ventral lobe of the fin is furthermore supported by distal part of the haemal spines of the first and second preural vertebrae. The caudal fin is deeply forked, with 7 or 8 procurrent rays, single unbranched and 7 or 8 main rays in the dorsal lobe, while ventral part of the fin is composed by 8 or 9 main rays, single unbranched ray and about 5 procurrent rays.

Median fins and supports. In front of the dorsal fin are recognizable numerous flat, plate like predorsal bones in several specimens, but details of their morphology, exact number and distribution are unclear due to insufficient preservation. The dorsal fin is located in the half of the body, and consists of three single rays and about nine branched and segmented rays. The first unsegmented ray is very short. The last unbranched ray of the dorsal fin is the longest one and in smaller individuals bears pronounced denticulation (Fig. 6), that seems to be completely lost in the larger specimens. The serration is not located at the absolute base of the ray, but starts slightly distally and orientation of the serration is postero-dorsal one. The last segmented and branched ray is split up to its base. The pterygiophores of the dorsal fin are simple and relatively thin, except the first one, that seems to be complex one (= fused) creating wide plate. The anal fin consists of about five segmented and branched rays precede by probably three simple unbranched rays. The anal fin does not reach the base of the caudal fin. There are eight anal fin pterygiophores, their shape is narrow and straight.

Paired fins and girdles. The pectoral fin is trapezoid shaped, inserts to the body relatively ventrally and consist of one or two unbranched and 16 or 17 rays. Details of the pectoral girdle are almost entirely missing. The pelvic fins insert to the body below start of the dorsal fin (or very slightly posteriorly) and consist of 5 or 6 rays. The pelvic girdle seems to be fused in midline, with well-developed posterior process and anteriorly bifurcated anterior process.

Scales and soft tissues. Scales, preserved as individual elements or *in situ* at the body are not recognizable. Several specimens show partially preserved dark spots and pigment remains, that are best visible immediately after its excavation. As sediment moisture decreases, the pigment remains become gradually less recognizable. These pigments are tentatively classified as soft tissue remains.

Other skeletal elements are not sufficiently preserved to be described.

Remarks. The order Cypriniformes is monophyletic group (e.g., He et al. 2008; Wiley & Johnson 2010) characterized by 9 or up to 13 characters (Fink & Fink 1981, 1996; Wiley & Johnson 2010; Nelson et al. 2016), of which only several can be traced in the fossil record due to their fossiliferous potential, namely presence of a kinethmoid; fifth ceratobranchial enlarged with teeth ankylosed to the bone; pharyngeal teeth opposed to enlarged posterior process of the basioccipital bone; elongation of the lateral process of the second vertebral centrum, projecting into somatic musculature; ascending process of the premaxillae; upper jaw protractile; jaws and palate are toothless; three branchiostegal rays; and presence of spine like ray in the dorsal fin. The presence of pharyngeal teeth opposed to enlarged posterior process of the basioccipital bone and elongation of the lateral process of the second vertebral centrum set clearly specimens under consideration to this order. The pharyngeal bone morphology, with arrangement of the teeth in three rows with less than 8 teeth in any row clearly indicates that the affiliation of the specimens pertains to the Cyprinidae family (Nelson et al. 2016).

The Cyprinidae family is distributed mainly in a freshwater environment (although some taxa are adapted to brackish waters too) of North America, Africa and Eurasia (Nelson et al. 2016). Various approaches based on morphology or molecular analyses were used to establish interrelationships of the Cyprinidae (see e.g. Chen et al. 1984; Howes 1991;

Fig. 4 - *Luciobarbus graellsii*, Camp dels Ninots locality, Pliocene. Isolated cranial elements (except fifth pharyngobranchyal and associated teeth that are presented at the Figure 5). A) Right frontal of CN-5 in ventral (A1), dorsal (A2), and lateral (A3) views. The arrow marks foramen within ventral lamina; B) right hyomandibula of CN-6 in lateral (B1), and medial (B2) views; C) left hyomandibula of CN-6 in medial (C1), and lateral (C2) views; D) left maxilla of CN-7 in lateral (D1), medial (D2), and dorsal (D3, D4) views. The dorsal views present posterior and anterior extremities, respectively, only. E) Left dentary of CN-6 in lateral (E1), and medial (E2) views; F) left articulare of CN-6 in lateral (F1), and medial (F2) views; G) right articulare of CN-6 in lateral (G1), and medial (G2) views; H) right quadrate of CN-8 in lateral (H1), and medial (H2) views. The arrow marks supraarticular notch. I) Left quadrate missing antero-dorsal part of the bone of CN-6 in medial (I1), and lateral (I2) views; J) left opercle of CN-9 in lateral (J1), and medial (J2) views.; K) right opercle of CN-10 in lateral (K1), and medial (K2) views. The arrow marks well developed dorsal process. L) Right opercle of CN-8 in lateral (L1), and medial (L2) views; M) right anterior ceratohyal of CN-6 in medial (M1), and lateral (M2) views; N) left anterior ceratohyal of CN-6 in lateral (N1), and medial (N2) views; O) left posterior ceratohyal of CN-6 in medial (O1), and lateral (O2) views; P) right posterior ceratohyal of CN-6 in lateral (P1), and medial (P2) views; Q) basioccipital masticatory facet of CN-8 in ventral (Q1), and dorsal (Q2) views.

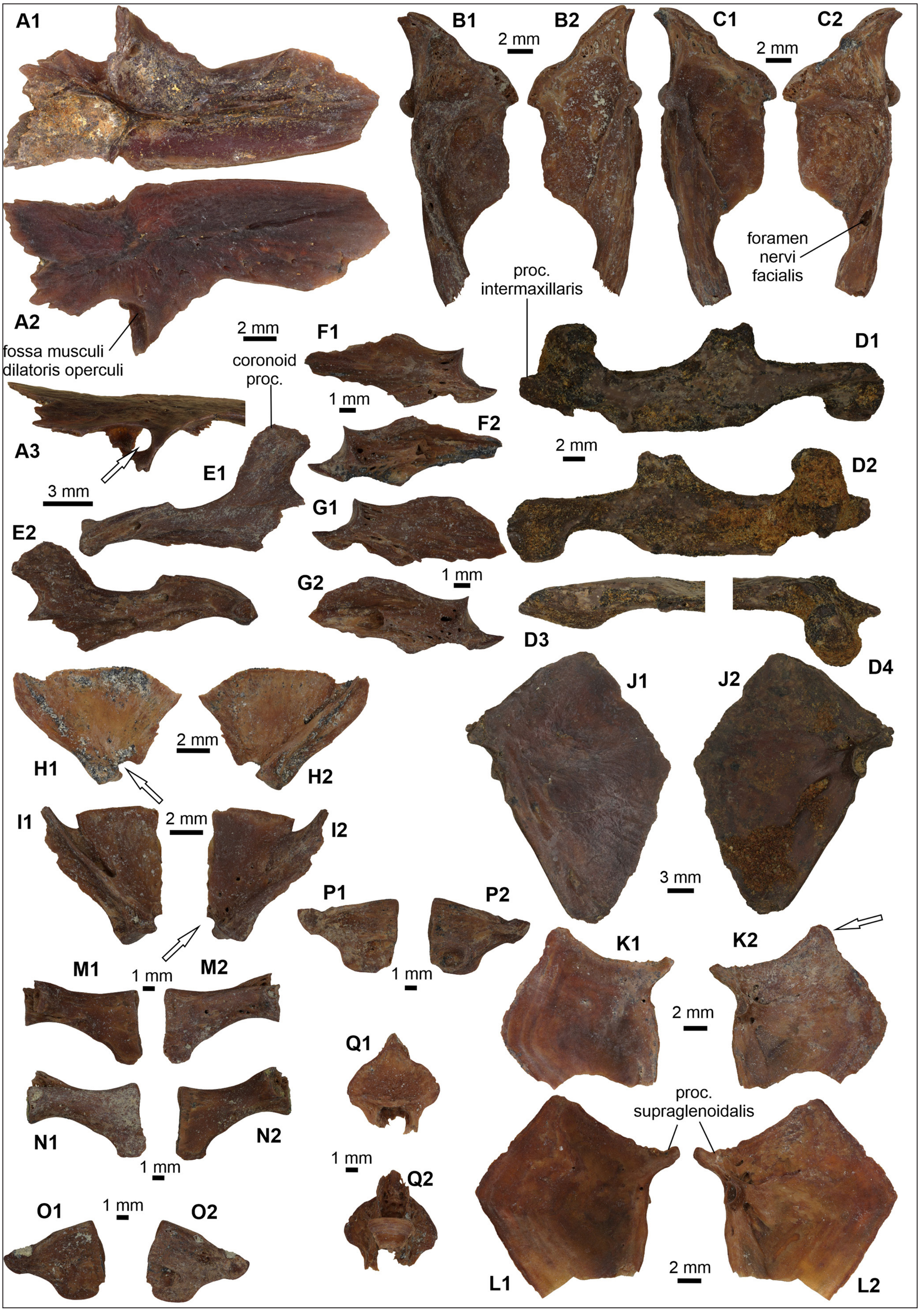
A1
A2
fossa musculi dilatoris operculi
A3
3 mm
2 mm
B1
B2
2 mm
C1
C2
2 mm
foramen nervi facialis
proc. intermaxillaris
D1
2 mm
D2
D3
D4
coronoid proc.
E1
E2
F1
1 mm
F2
G1
1 mm
G2
H1
2 mm
H2
I1
2 mm
I2
J1
J2
3 mm
K1
K2
2 mm
proc. supraglenoidalis
L1
L2
2 mm
M1
1 mm
M2
N1
1 mm
N2
O1
1 mm
O2
P1
1 mm
P2
Q1
1 mm
Q2

Figure 4

Kong et al. 2007; He et al. 2008; Levin et al. 2012; Wang et al. 2012; Yang et al. 2015 and references herein). Generally, the family can be divided into up to 12 subfamilies (He et al. 2008; Yang et al. 2015; Nelson et al. 2016 and references herein). Due to morphology of teeth (see description above), and typical pharyngeal formula (4.3.2/4.3.2 in adults and probably 5.3.2/5.3.2 in juveniles, although this condition was not documented directly in any of the available specimens), the specimens can be unquestionably placed into the genus *Luciobarbus* (Doadrio 1990, 2002 and supported by personal observation), therefore member of the Barbinae subfamily.

The Iberian Peninsula is inhabited by several *Barbus* and *Luciobarbus* species that differ (aside of molecular characters that are practically indistinct in the fossil record) by the number of morphological characters, especially proportions, scale patterns and morphology of spinous dorsal fin ray – the data and key references can be found in the Doadrio (2002), Kottelat & Freyhof (2007) and Doadrio et al. (2011). It is also necessary to stress out that *Luciobarbus*, *Barbus* and *Capoeta* Valenciennes in Cuvier & Valenciennes, 1842 are considered as separate genera within the clade Barbinae (see Machordom & Doadrio 2001; Tsigenopoulos et al. 2003; Kottelat & Freyhof 2007; Levin et al. 2012; Yang et al. 2015). It is also necessary to stress out that the genus *Luciobarbus* has been recognized for long time as a subgenus of the genus *Barbus*, but we consider it as a separate taxon in the generic level (see Machordom & Doadrio 2001; Tsigenopoulos et al. 2003; Kottelat & Freyhof 2007).

As mentioned above, spinous dorsal fin ray and its morphology may be used as distinctive species character in Iberian Peninsula barbs (Table 2; for references see above). Most of the fossil specimens under consideration show distinctive serration in the posterior side of last unbranched dorsal fin ray with various extents of this serration (Fig. 6). The serration does not start in the most proximal section of the ray, but somehow distally and in the larger specimens (Fig. 6E) the serration is significantly reduced and shifted to more distal part of the ray. In the largest articulated specimens (with SL more than 400 mm) the serration was not observed at all. Due to this fact it is reasonable to assume that serration of the dorsal fin ray change during ontogeny until complete loss of this character in large specimens, same as in *Luciobarbus graellsii* (see Table 2). Attribution of the fossil specimens to this species is also supported by the overall morphology of the opercle with large and blunt dorsal protrusion, shape of hyomandibula, etc. The morphology of complete pharyngeal dentition is fully comparable with that species too (Fig. 7), but some individual teeth show resemblance also with *Luciobarbus bocagei* (Steindachner, 1864) and *L. guiraonis* (Steindachner, 1866a). *L. bocagei* inhabiting Atlantic slope of Iberian Peninsula (Kottelat & Freyhof 2007) and due to this biogeographic distribution, we consider such determination of studied fossils improbable – the partial similarity of the pharyngeal dentition was most probably independently produced as a result of adaptation for same feeding with no systematic meaning. The classification of studied specimens to *L. guiraonis* based on partial similarity suggests plausible explanation from the point of the biogeography within the Iberian Peninsula, but morphology of antero-ventral limb of the pharyngeal bone exclude such alternative – the antero-ventral limb is robust in *L. guiraonis*, while subtle, but with well-developed spike-like process in *L. graellsii* (Doadrio 1990: fig. P2; Miranda & Escala 2003: fig. 5 – compare with Figure 5B; the spike-like process marked by arrow).

Fig. 5 - *Luciobarbus graellsii*, Camp dels Ninots locality, Pliocene. The fifth ceratohyal and associated teeth. A) almost complete central part of the right pharyngeal bone of CN-11 with teeth articulated *in situ* in dorso-lateral (A1), and medial (A2) views. The most posterior teeth of the second and third rows are missing and their basis are marked by dotted lines. B) Complete left pharyngeal bone of CN-12 in medial view; C–D) mammiliform teeth, (C) right tooth of CN-13; D) left tooth of CN-14; E) right tooth of CN-15; F) right tooth of CN-16; G) left tooth of CN-17; H) left molariform tooth of CN-18. I–M) spatulate teeth, (I) right tooth of CN-19; J) left tooth of CN-20; K) left tooth of CN-21; L) right tooth of CN-22; M) left tooth of CN-23; N) left mammiliform tooth of CN-24; O–X) spatulate teeth, (O) left tooth of CN-25; P) left tooth of CN-26; Q) right tooth of CN-27; R) right tooth of CN-28; S) left tooth of CN-29; T) left tooth of CN-30; U) left tooth of CN-31; V) right tooth of CN-32; W) left tooth of CN-33; X) right tooth of CN-34; (N, U–X) deeply abraded teeth.

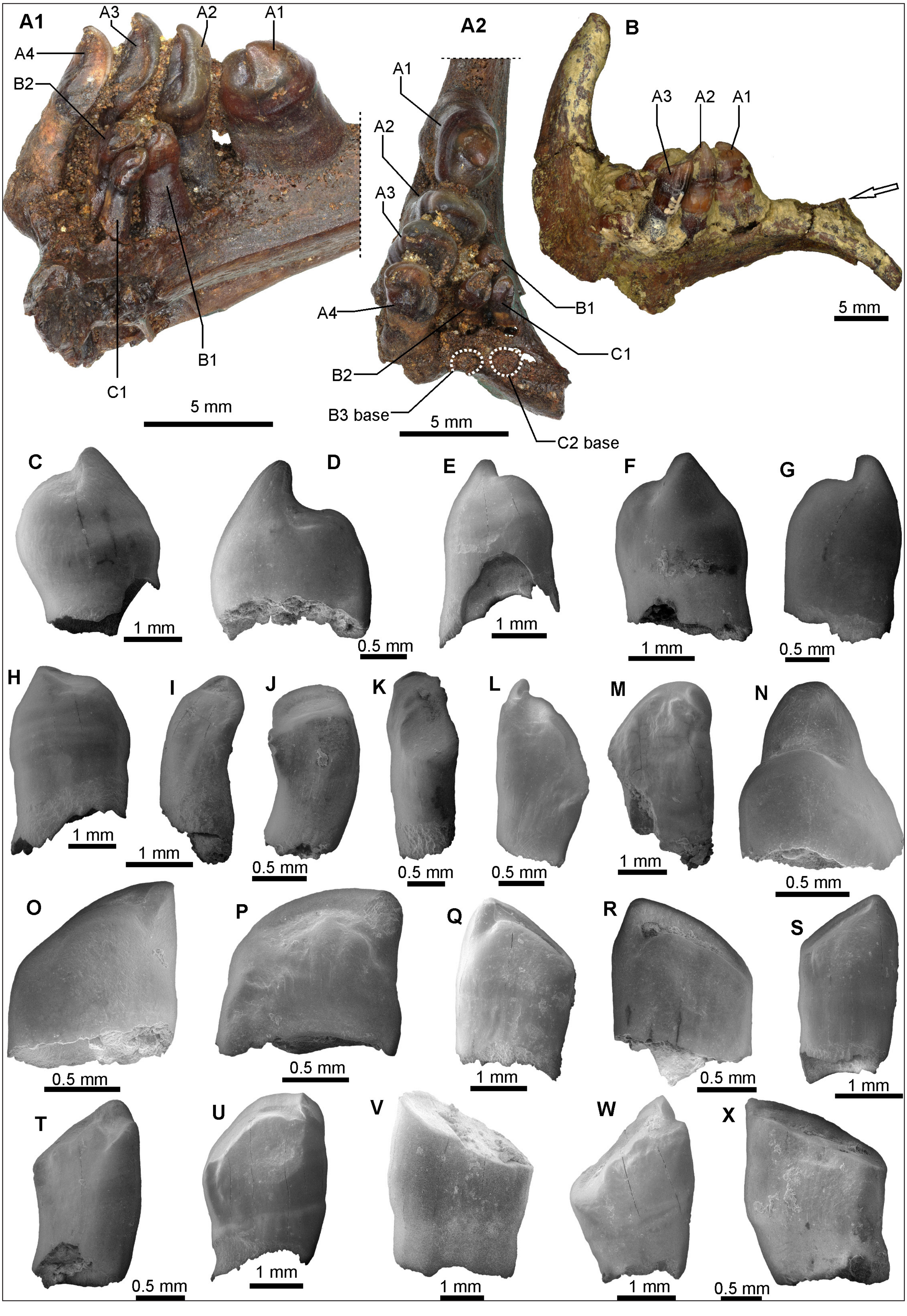
A1
A3
A2
A1
A4
B2
C1
B1
5 mm
A2
A1
A2
A3
A4
B1
C1
B2
B3 base
C2 base
5 mm
B
A3
A2
A1
5 mm
C
1 mm
D
0.5 mm
E
1 mm
F
1 mm
G
0.5 mm
H
1 mm
I
1 mm
J
0.5 mm
K
0.5 mm
L
0.5 mm
M
1 mm
N
0.5 mm
O
0.5 mm
P
0.5 mm
Q
1 mm
R
0.5 mm
S
1 mm
T
0.5 mm
U
1 mm
V
1 mm
W
1 mm
X
0.5 mm

Figure 5

Taxa	Pharyngeal formula	Dorsal fin	Anal fin	Pectoral fin	Ventral fin	Last unsegmented dorsal fin ray
Luciobarbus graellsii (Steindachner, 1866b) - studied specimens	4.3.2/4.3.2	III/9?	III/5?	I–II/16–17	5 or 6	denticulation lost in adults
Barbus haasi Mertens, 1925	5.3.2/5.3.2	III-IV/7-9	III/5	I/18	I/8	denticulated in most specimens
Barbus meridionalis Risso, 1827	5.3.2/5.3.2	III-IV/8	III/5	I/18	II/7-8	denticulation absent
Luciobarbus bocagei (Steindachner, 1864)	5.3.2/5.3.2	III-IV/(7)8(9)	III/5	I/16-18	II/8	denticulation presented in adults only in short area just below middle of it
Luciobarbus comizo (Steindachner, 1864)	4.3.2/4.3.2 (5.3.2/5.3.2 in juveniles)	IV/8(9)	III/5	II/16-17	II/7-8	very stout and strongly serrated
Luciobarbus graellsii (Steindachner, 1866b)	4.3.2/4.3.2 (5.3.2/5.3.2 in juveniles)	IV/8	III/5	II/16-18	II/7-8	denticulation lost in adults
Luciobarbus guiraonis (Steindachner, 1866a)	4.3.2/4.3.2 (5.3.2/5.3.2 in juveniles)	III-IV/8(9)	III/5	I/17	I/7	without denticulation or very weak in adult specimens
Luciobarbus microcephalus (Almaça, 1967)	4.3.2/4.3.2 (5.3.2/5.3.2 in juveniles)	IV/8	III/5	I/16-17	II/8	very robust and strongly serrated
Luciobarbus sclateri (Günther, 1868)	4.3.2/4.3.2 (5.3.2/5.3.2 in juveniles)	IV/(7)8	III/5	II/16-17	II/8	medium sized denticulation in almost all of its extension, but smaller than in *L. comizo* and *L. microcephalus*

Tab. 2 - Selected characters of the studied specimens and their comparison with Iberian barbs (according to Doadrio 1990, 2002, and Doadrio et al. 2011).

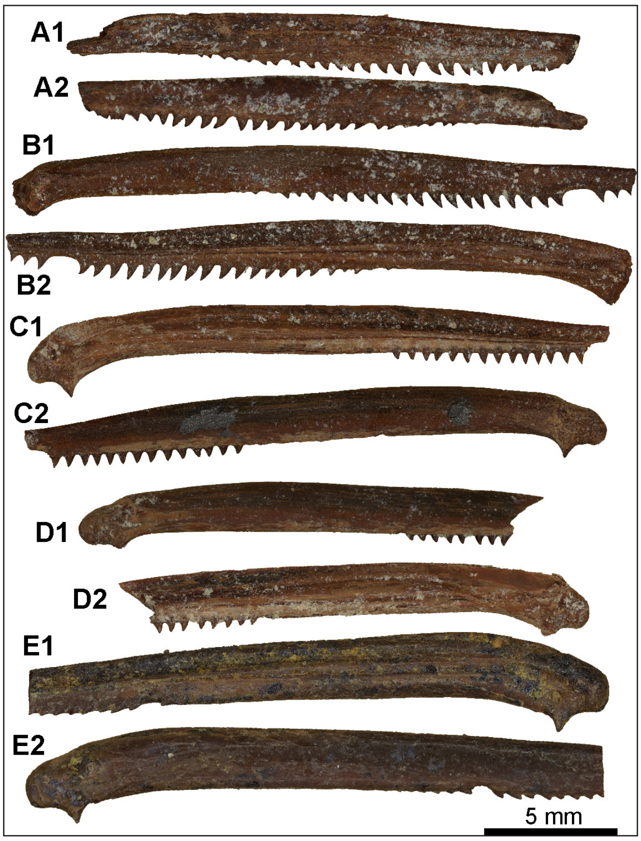

Fig. 6 - *Luciobarbus graellsii*, Camp dels Ninots locality, Early Pliocene. Last unbranched dorsal fin ray and variously developed serration of its posterior margin. A) Specimen CN-36 in lateral (A1), and medial (A2) views; B) specimen CN-37 in medial (B1), and lateral (B2) views; C, D) left and right part, respectively, of specimen CN 38 in lateral (C1, D2), and medial (C2, D1) views; E) specimen CN-39 in lateral (E1), and medial (E2) views.

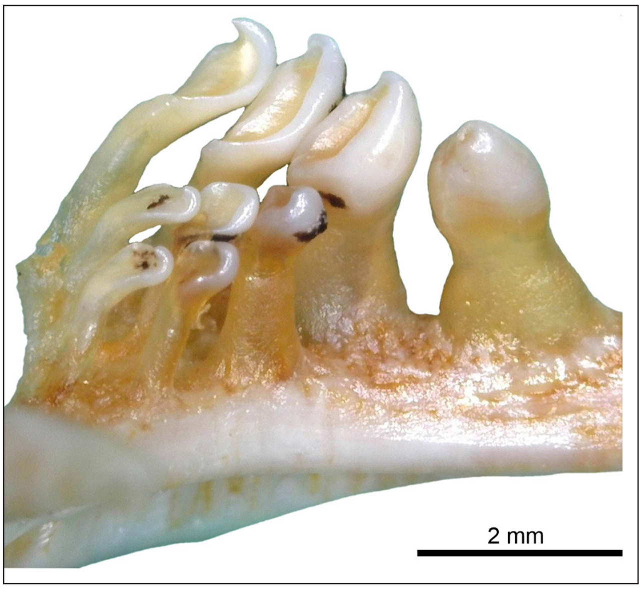

Fig. 7 - *Luciobarbus graellsii*, Matarranya river, Teruel, Spain, Recent. Dentition of the right fifth ceratohyal of the MNCN 021508.

Palaeogeography and palaeoecology

Today, *Luciobarbus graellsii* is a gregarious species that live in groups, often with other cyprinid taxa (Doadrio 2002). It is a native inhabitant of Mediterranean drainages from Ebro to Ter and Ason drainage of the Atlantic slope (Kottelat & Freyhof 2007; Doadrio et al. 2011; Fig. 8). As visible on Fig. 8, the modern range of the species is discontinuous between the Ter River drainage system and the Llobregat and Ebro River drainage system. The Camp dels Ninots site probably documenting the aquatic ecosystems related with the modern Ter River drainage system. Doadrio (2002) mentioned the ability of this species to colonize all types of environments, but it prefers lower and middle sections of rivers and natural lagoons with slow currents (see also Doadrio et al. 2011). They search for quiet environment with water plants and roots, while during reproduction season they look for environments with sand and gravel (Doadrio 2002; Kottelat & Freyhof 2007). Species distribution models and consensus models have also been used to reconstruct the potential distribution of the species in the Ebro basin. The most important predictor variables for *L. graellsii* are distance to the sea, catchment altitude and valley floor width (González-Ferreras et al. 2016). These authors predicted the presence of this fish in almost all of the Ebro Basin and in some northern areas belonging to the Atlantic basins. *L. graellsii* could be present in areas with the distance to the sea of up to 935 km. In connection with the two other predictor variables, the higher occurrence probability is in river reaches located at ranges from 70 to 2000 m and with a valley floor width from 30 m to almost 9400 m.

La Selva depression (Fig. 9), where Camp dels Ninots is located, is a Neogene basin that is bounded by several faults oriented N-NE and S-SW. These faults co-create several basin depocentres that were infilled with fluvio-alluvial and lacustrine sediments having a thickness that range between 60 and 300 meters as known by geoelectric data (Pous et al. 1990). Interstratified with the sedimentary succession, several volcanic deposits were emplaced at the edges of the depression (mainly lava flows) that are dated as Late Miocene to Early Pliocene (see compilation in Miranda-Muruzábal et al. 2024). An Early Pliocene age is also established for the Camp dels Ninots volcano (Bolós et al., personal comm.).

The sedimentary infill of la Selva depression (Cabrera 1992) is terrestrial and is characterized by the occurrence of alluvial systems in the southern portion of the depression that were sourced from the nearby igneous rocks, mainly represented by granites. These alluvial systems (Fig. 9) are composed of gravels and arkosic sands organized in channelized bodies, and mudstones. These systems evolved northwards to finer materials (mudstones) where both aquatic and terrestrial malacofauna is found (Cabrera 1992). Among them, limnic gastropods record the presence of lakes in the northern edge of the depression. The occurrence of wetlands that persisted until present day together with the weakly incised river valleys suggest the drainage of the depression towards the Mediterranean is Pleistocene in age (or post-Early Pliocene, in any case). We can thus hypothetically presume that the species colonized the Camp dels Ninots maar lake via the Ter River drainage system (Fig. 9), but details are for the moment unclear. Direction and timing of dispersal(s) between the different river drainage systems in NE Spain will require a larger fossil database. Even if out of the potential distribution map elaborated by González-Ferreras et al. (2016), the Selva depression and its palaeogeographical reconstruction during the Early Pliocene (Fig. 9) is concordant with the predictor variables of the modern distribution of the species *L. graellsii.*

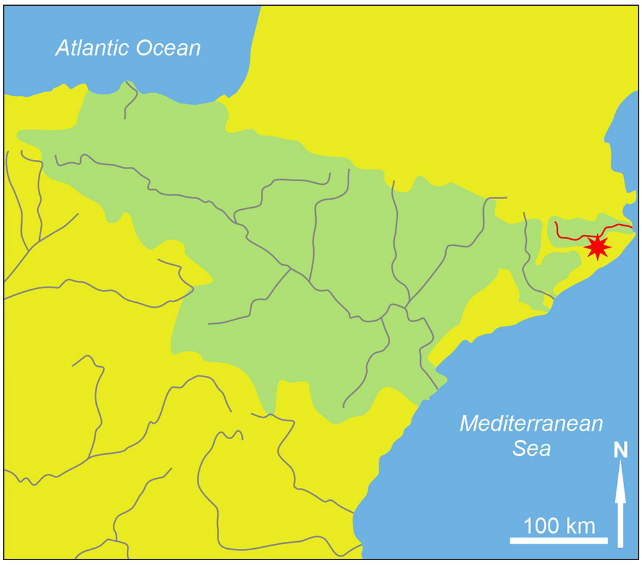

Fig. 8 - Distribution of the contemporary *Luciobarbus graellsii* and marking of the Camp dels Ninots site (red asterisk). Based on the data presented by Doadrio et al. (2011).

From a palaeoecological point of view, the recovered Early Pliocene palaeobotanical taxa at Camp del Ninots point to very different palaeoclimatic and palaeoenvironmental conditions when compared to present ones. They document a 'subtropical type of flora with lauroid leaves of evergreen trees' under warm and humid conditions, which is in accordance with the presence of tapirs

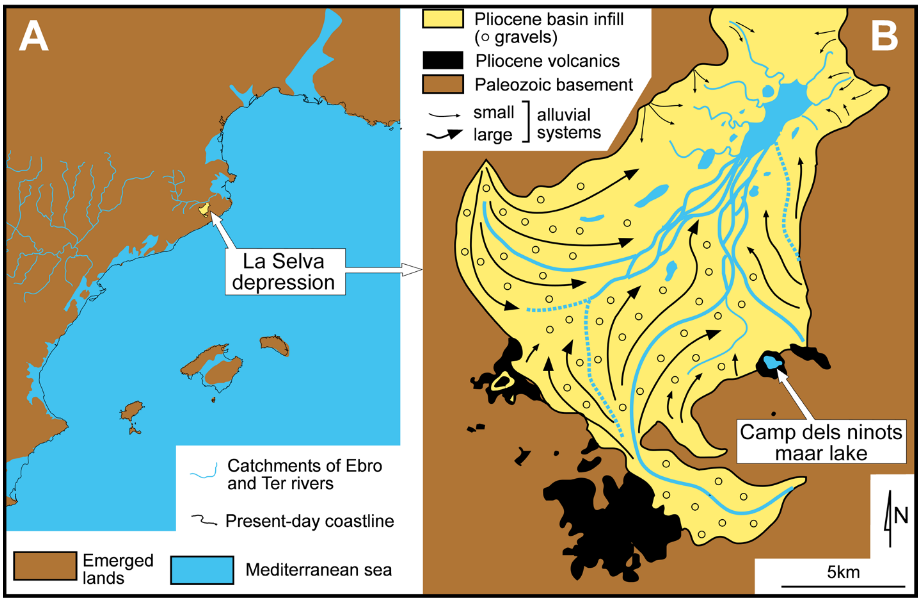

Fig. 9 - A) Palaeogeography of NW Iberia during the Early Pliocene (including data from Jiménez-Moreno et al. 2010), location of la Selva depression and present-day catchment of the Ebro and Ter rivers; B) palaeogeography of the La Selva depression with information from Cabrera (1992), IGC (2006) and IGC-ICC (2008, 2009).

(*Tapirus arvernensis* Croizet & Jobert, 1828) that may be further indicative of a close humid environment (Gómez de Soler et al. 2012; Jiménez-Moreno et al. 2013). The botanical macroremains (leaves, wood and seeds) suggest that the vegetation in the vicinity of the maar lake was characteristic of a broadleaved riparian forest and laurel forest together with the aquatic plants from the lake edge. Such a botanical association is indicative of a pre-Mediterranean context (Robles et al. 2013). Similar vegetal association can be found nowadays at the Canary Islands and in the humid subtropical forest of central Asia (Robles et al. 2013), environments displaying today a high biodiversity. The eco-climate values obtained using OLS regression models and compared with previous palaeoclimate reconstructions suggest an original palaeotemperature of 14.3 ± 2.6°C and a palaeoprecipitation rate of 846.8 ± 165.4 mm (Martínez-Monzón et al. 2023). These data thus expand the known chorological range of the species, and show that *Luciobarbus graellsii* was able to disperse and adapt to the peculiar conditions of a maar lake. Moreover, the new dating of Camp dels Ninots place it at the onset of the Early Pliocene Warmth, with global average temperatures around 4°C higher than preindustrial times (Fedorov et al. 2013), suggesting that it was able to adapt from the warmest period of the Pliocene to the coldest period of the Pleistocene.

As shown by sedimentology and preliminary taphonomic studies, unit N11 is bioturbation free and displays no evidence of subaerial exposure (i.e. no mudcracks nor paedogenesis). Bathymetry of the excavated area is still under investigation, but the lack of bioturbation indicates possible anoxic conditions in the lake, probably below 10 m depth (Håkanson & Jansson 1983). In such environments, strong currents are not frequent, in accordance with the modern requirements of the species.

TEMPORAL DISTRIBUTION OF CENTRAL, WESTERN AND SOUTHERN EUROPEAN FOSSIL BARBINAE

The fossil record of the Barbinae within Europe is relatively poor, represented mostly by isolated pharyngeal teeth (rarely by other skeletal elements), with several articulated and semi-articulated more complete specimens. Many of them were classified within the open nomenclature. The following overview is restricted to Central, Western, and Southern Europe (mentioned as "area of interest" below; Fig. 10), while Eastern and South-Eastern Europe and Turkey is not particularly commented, mainly due to separate phylogenetic character of Middle East *Luciobarbus* clade (Tsigenopoulos et al. 2003) and relatively poor publication record there. The following list of fossil records requires revision and therefore it is important to understand these interpretations as preliminary.

Two fossil species of the genus *Barbus,* based on articulated specimens, have been described from the area of interest: *Barbus bohemicus* Obrhelová, 1967 from the Early Miocene of the Czech Republic (Burdigalian deposits of North Bohemian locali-

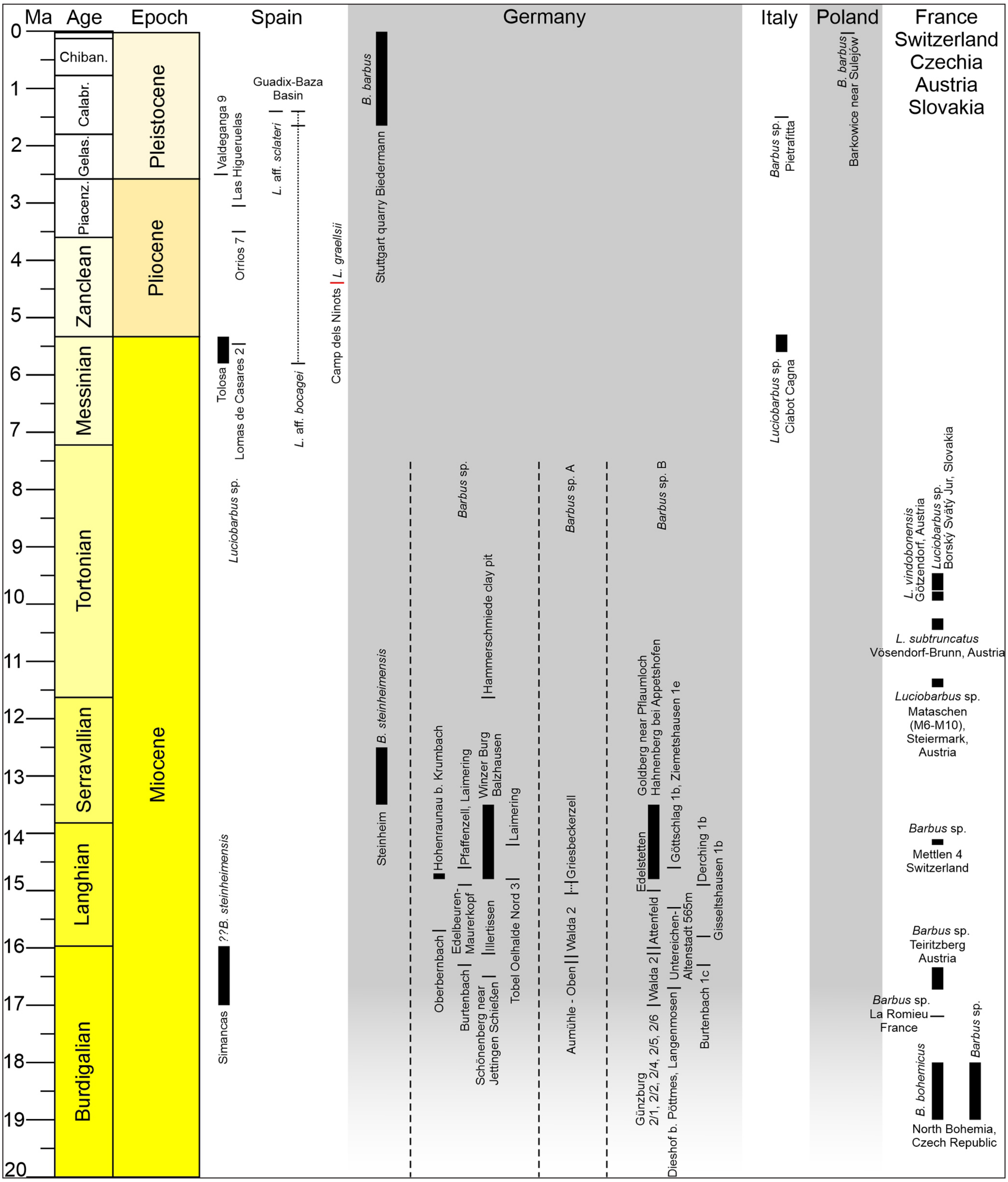

Fig. 10 - Schematic presentation of the stratigraphic range of central, western and southern European barbinae fossils.

ties; Obrhelová 1967, 1990) and *Barbus steinheimensis* (Quenstedt, 1852) from the Middle Miocene of Germany (Serravallian deposits of Steinheim am Albuch; for details see Gaudant 1989). Doadrio (1990) mentioned the latter species also from Late Miocene of the Duero basin, but real affinity of these specimens may be different (see de la Peña 1995). Isolated remains of the genus are often preserved in a number of localities—the species *Barbus barbus* (Linnaeus, 1758) in the Upper Pleistocene deposits of Germany and Poland (Pawłowska 1963; Böhme & Ilg 2003), and three forms classified as *Barbus* sp. Two different species (*Barbus* sp. A and *Barbus* sp. B) were recognized in the Early and Middle Miocene of Germany (recorded in the Burdigalian, Langhian, and Serravallian deposits; Böhme & Ilg 2003) and another one from the Early to Late Miocene of Austria, Czech Republic, France, Germany, and Switzerland (recorded in the Burdigalian, Langhian, Serravallian, and Tortonian deposits; Böhme & Ilg 2003; Ekrt et al. 2022) and Pleistocene of Italy (recorded in the Calabrian deposits; Böhme & Ilg 2003).

Fossil record of the *Luciobarbus* species is restricted to isolated skeletal remains from the Miocene to Pleistocene deposits. The specimens in this study, originally classified as *Barbus* (*'Luciobarbus'*) sp. by Přikryl et al. (2016), represent the only known articulated finds within the area of interest. Böhme (2002) described *Luciobarbus subtruncatus* (Münster, 1842) from the Late Miocene of Austria (Tortonian deposits of Vösendorf-Brunn near Vienna) and *Luciobarbus vindobonensis* (under generic name *Bertinius* that in now considered junior synonym of the *Luciobarbus*) from other Austrian locality (Götzendorf) of coeval age. Isolated teeth of *Luciobarbus* aff. *bocagei* (Steindachner, 1864) were recorded in the Miocene deposits of Spain (Guadix-Baza Basin; Doadrio & Casado 1989). *Luciobarbus* sp. has been recorded in the Late Miocene of Austria (Tortonian deposits of Mataschen; Böhme & Ilg 2003), Late Miocene of Italy (Messinian deposits of Ciabot Cagna; Böhme & Ilg 2003), Late Miocene of Slovakia (Tortonian deposits of Borský Svätý Jur; Böhme & Ilg 2003), and Late Miocene, Pliocene and Pleistocene of Spain (Messinian deposits of Lomas de Casares and Tolosa, Zanclean deposits of Orrios, Piacenzian deposits of Las Higueruelas, and Gelasian deposits of Valdeganga; Böhme & Ilg 2003; Blain et al. 2024b).

The appearance of the genus *Luciobarbus* in the Iberian Peninsula has been explained by two main hypotheses (see especially Tsigenopoulos et al. 2003 and Casal-López et al. 2018): the first hypothesis supposes that *Luciobarbus* reached the Iberian Peninsula from Middle East via North Africa (Kosswig 1973; Doadrio 1990). The second hypothesis proposed dispersion across the present day Mediterranean Sea during the Lago Mare event (e.g. Casal-López & Doadrio 2018) that is still intensively debated terminal stage of the Messinian Salinity Crisis (see e.g. Caruso et al. 2020).

The overview listed several *Luciobarbus* specimens discovered in Austria and Slovakia, that verify the presence of this genus in the Central Europe during the Tortonian (Late Miocene). Interestingly, these occurrences have the same timing as the presence of genus *Heterobranchus* Geoffroy Saint-Hilaire, 1809 in the same region, plus Eastern Europe (Thenius 1952; Weinfurter 1953; Böhme 2002; Kovalchuk & Ferraris 2016). This catfish is considered to be a typical African element, and consequently, similar immigrations of other African elements can be reasonably expected (Gaudant 2015; Kovachuk & Ferraris 2016), and most probably including also members of genus *Luciobarbus*. Reasons that lead to these events are not understood, but we can speculate, that such migratory events were not obviously restricted to the Late Miocene, especially to Lago Mare events, as usually presented (Casal-López & Doadrio 2018). Finally, it is not clear, if the following dispersal activity of *Luciobarbus* within the Eurasian continent may have reached the Iberian Peninsula, or if these regions were colonized by separate (later) impulses with different spatio-temporal connections and migratory courses.

CONCLUSIONS

The direct comparison of the studied specimens with comparative specimens and data from the literature shows that studied fossil Barbinae fish from the Camp dels Ninots site belong to the modern species *Luciobarbus graellsii* and prove its occurence in the North-Eastern Iberian Peninsula at least since Early Pliocene times. This is the first report of the species in the fossil record. A brief overview of the fossil record of the genus *Luciobarbus* shows its presence in Central Europe during the Late Miocene (Tortonian), although relation of these specimens to the younger record from the Iberian Peninsula is not clear. The fossil record from Camp dels Ninots thus enlarges the known climatic requirements of the species (as it manage to survive from the warmest period of the Pliocene to the coldest period of the Pleistocene) and documents its early abilities to disperse in specific aquatic environments (i.e., maar lakes).

Author's contributions

The study is based on fieldwork directed by BGS, GC, and JA. EMR oversaw the preparation and preservation of the fossil specimens. The systematic study was carried out by TP; OO and PRS contributed to the geological and palaeogeographical context; and TP and HAB contributed to the palaeoecological interpretation. The manuscript was prepared by TP and HAB with contributions from all co-authors.

Data Availability Statement

The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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