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First record of *Latonia gigantea* (Anura, Alytidae) from the Iberian Peninsula

Andrea Villa[a]*, Massimo Delfino[a,b], Àngel H. Luján[c,b], Sergio Almécija[d,b], David M. Alba[b]

[a]*Dipartimento di Scienze della Terra, Università degli Studi di Torino, via Valperga Caluso 35, 10125 Torino, Italy.*

[b]*Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, Carrer de les Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallès, Barcelona, Spain.*

[c]*Masaryk University, Faculty of Sciences, Department of Geological Sciences, Kotlářská 2, 611 37 Brno, Czech Republic.*

[d]*Center for Advanced Study of Human Paleobiology, Department of Anthropology, The George Washington University, Washington, District of Columbia.*

*Corresponding author: a.villa@unito.it

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The single extant species of the anuran genus *Latonia* lives in Israel, but in the fossil record the genus is known mainly from Europe, spanning from the Oligocene to the early Pleistocene. Here we describe new remains of *Latonia* from the early to late Miocene of the Vallès-Penedès Basin (NE Iberian Peninsula), coming from the following localities: Sant Mamet (MN4), Sant Quirze, Trinxera del Ferrocarril (MN7+8), Castell de Barberà, Can Poncic 1 and Can Llobateres 1 (MN9). Fossils from the late Aragonian and early Vallesian are attributed to *Latonia gigantea* mainly because of the morphology of the ornamentation that covers the maxillae. In turn, an ilium from Sant Mamet is not diagnostic at the specific level and is assigned only to the genus *Latonia*. The newly reported remains represent the first record of *L. gigantea* in the Iberian Peninsula, where *Latonia* was previously known by a single report of *Latonia* cf. *ragei* from Navarrete del Río (MN2) and remains from other localities unassigned to species. Moreover, the Vallès-Penedès remains represent one of the southernmost records of the species known thus far. The presence of *Latonia* in these

localities confirms the humid and warm environment suggested by the recorded mammal fauna.

Keywords: Palaeoherpetofauna, fossil anurans, Discoglossinae, Miocene, Vallès-Penedès Basin.

Introduction

The genus Latonia

The genus *Latonia* v. Meyer, 1843 includes medium to large-sized frogs of subfamily Discoglossinae (Alytidae). This genus was originally erected by v. Meyer (1843) based on fossil remains from the middle Miocene (MN7+8) of Öhningen (Germany) and considered extinct for 170 years. However, most recently, Biton et al. (2013) referred to this genus an extant species from Israel, *Latonia nigriventer* (Mendelssohn and Steinitz, 1943), previously included in *Discoglossus* Otth, 1837. Currently, four extinct species of *Latonia* are known, mainly from Europe (Roček 1994; Böhme and Ilg 2003): *Latonia gigantea* (Lartet, 1851), *Latonia seyfriedi* v. Meyer, 1843 (the type species), *Latonia ragei* Hossini, 1993 and *Latonia vertaizoni* (Friant, 1944).

The oldest certain record of *Latonia* is known from the late Oligocene (Chattian, MP30) of France (Coderet and Vertaizon; Roček 1994, 2013; Böhme and Ilg 2003). However, older remains possibly belonging to *Latonia* have also been reported from various middle to late Oligocene French localities as *Discoglossus giganteus* or *Discoglossus* cf. *giganteus* (Crochet 1971; de Bonis et al. 1973; Rage 1984; but see Roček, 1994, who treated these reports with caution), as well as from the middle and late Oligocene of Germany and the middle Oligocene of Switzerland (Böhme and Ilg 2003; although these reports are based on unpublished remains and cannot be verified based on the

available literature). Rage (2006) further mentioned *Latonia* aff. *vertaizoni* from the early to middle Oligocene (Rupelian, MP22-23) of Phosphorites du Quercy, but no specimens were figured or described, and this record was not included in Roček's (2013) summary of Mesozoic and Tertiary anurans from Laurasia.

During the Miocene, *Latonia* spread out all over Europe, being recorded from Austria, Czech Republic, France, Germany, Greece, Hungary, Italy, Poland, Romania, Russia, Slovakia, Spain and Ukraine (Roček 1994, 2013, and references therein; Delfino 2002; Böhme and Ilg 2003; Rage and Roček 2003). During this period, *Latonia* was the most common alytid in Europe, with very few remains being attributed to other genera (Roček 1994, 2005, 2013; Böhme and Ilg 2003; Rage and Roček 2003; Venczel 2004; Venczel and Sanchiz 2006; Bastir et al. 2014). The predominance of *Latonia* in the European Miocene has led to the conclusion that other (smaller) discoglossines (and maybe alytids in general) were unable to outcompete the species of this genus (Roček 1994). However, there are a few localities, such as Mátraszőlős (MN6) and Rudabánya (MN9) in Hungary in which sympatry occurs (Venczel 2004; Roček 2005).

The Pliocene record of *Latonia* marks a decrease in the presence of the genus in Europe and a constriction of its range towards the southern part of the continent (Roček 1994, 2013; Böhme and Ilg 2003; Rage and Roček 2003). The youngest European remains, which come from the early Pleistocene (late Villafranchian) of Pietrafitta (Italy; Delfino 2002; Delfino et al. 2004), were long thought to be the last known occurrence of the genus prior to its presumed extinction. The disappearance of *Latonia* from Europe, possibly due to a climate deterioration, was followed by a wider distribution of other discoglossines (i.e., *Discoglossus*) in that continent (Roček 1994, 2013; Böhme and Ilg 2003). Roček (1994) hypothesized that this replacement might be linked to an evolutionary transition from *Latonia* to *Discoglossus* due to paedomorphosis. However, the discovery of fossil remains of *Discoglossus* from the Oligocene and Miocene (Boulenger 1891; Böhme and Ilg 2003; Venczel 2004; Venczel and Sanchiz 2006; Roček 2013) is at odds with this

hypothesis. The alternative hypothesis put forward by Roček (1994), namely, that *Latonia* and *Discoglossus* are sister taxa that diverged from a common ancestor, may thus be favored.

Outside Europe, undisputed remains of *Latonia* have been reported from the early Pleistocene of Turkey (Vasilyan et al. 2014) and the early to late Pleistocene of Israel (Biton et al. 2013, 2016). Even though the latter fossils are attributable to the extant species, *L. nigriventer*, Vasilyan et al. (2014) assigned the Turkish remains to a different, maybe new, species. A number of other possible occurrences of *Latonia* or related forms come from the Oligocene, Miocene and Pliocene of Turkey and from the Miocene of Morocco (Roček 1994, 2013; Böhme and Ilg 2003; Gardner and Rage 2016; Bailon et al. 2017). However, these records are still unpublished or based on remains that lack clear diagnostic features of the genus and must be treated with caution.

Here we provide the first description of *Latonia* fossils from the Iberian Peninsula, based on unpublished remains from the Miocene of the Vallès-Penedès Basin, which represent the first Iberian record of *L. gigantea*.

Age and geological background

The fossil material described in this paper comes from several localities of the Vallès-Penedès Basin (Fig. 1), which is located close to Barcelona in NE Iberian Peninsula, between the Catalan Coastal (Littoral and Prelittoral) Ranges and roughly parallel to the coastline. This basin is a Neogene elongated half-graben originated by the rifting of the NW Mediterranean (Cabrera et al. 2004; de Gibert and Casanovas-Vilar 2011) and it has a rich fossil record of terrestrial vertebrates from the early to the late Miocene (Casanovas-Vilar, Alba, Robles et al. 2011; Casanovas-Vilar, Madern et al. 2016). Among the localities included in this paper, only the classical site of Sant Mamet (Rubí) is early Miocene in age. It corresponds to alluvial fan deposits in the upper portion of the Upper Detritic Unit, Lower Continental Complexes of the Vallès-Penedès Basin. These deposits

are located just below the marine and transitional sediments of the Marine and Transitional Complexes of the basin (Casanovas-Vilar, DeMiguel et al. 2011). Based on biostratigraphic data, Sant Mamet is correlated to MN4 (early Aragonian; Casanovas-Vilar, DeMiguel et al. 2011; Casanovas-Vilar, Madern et al. 2016), and probably to local zone C of the Calatayud-Montalbán Basin (Casanovas-Vilar, Madern et al. 2016), with an estimated age of ca. 16.6–16.0 Ma (after van der Meulen et al., 2012). In contrast, the remaining localities covered in this paper belong to the Upper Continental Complexes of the basin, being dominated by alluvial fan deposits and correlated to the late Aragonian (MN7+8) or the early Vallesian (MN9), depending on the site. Sant Quirze is not a single locality, but a set of classical large mammal sites (of which Trinxera del Ferrocarril is the one that has delivered most abundant remains) together with three microvertebrate sites (Casanovas-Vilar, Madern et al. 2016). On biostratigraphic grounds, all the Sant Quirze sites are correlated to the *Democricetodon crusafonti – Hippotherium* interval subzone of the Vallès-Penedès Basin (Casanovas-Vilar, Alba, Garcés et al. 2011; Casanovas-Vilar, Garcés et al. 2016; Casanovas-Vilar, Madern et al. 2016), with an estimated age of 11.9–11.2 Ma (MN7+8). In the past, Castell de Barberà (Barberà del Vallès) was similarly correlated to MN7+8 (e.g., Casanovas-Vilar, Alba, Garcés et al. 2011), albeit being considered somewhat younger than Sant Quirze. However, a correlation with the earliest MN9 (*Hippotherium – Cricetulodon hartenbergeri* interval subzone), with an age probably close to (or only slightly younger than) 11.2 Ma, has been subsequently favored for Castell de Barberà (Alba and Moyà-Solà 2012; Casanovas-Vilar, Garcés et al. 2016; Casanovas-Vilar, Madern et al. 2016), given the presence of some scarce hipparionin remains (Rotgers and Alba 2011). In turn, the site of Can Poncic 1 (Sant Quirze del Vallès) is younger that the localities mentioned above, being correlated to the *Cricetulodon hartenbergeri* range subzone (MN9), with an estimated age of 10.3–10.0 Ma (Casanovas-Vilar, Alba, Garcés et al. 2011; Casanovas-Vilar, Garcés et al. 2016; Casanovas-Vilar, Madern et al. 2016). Finally, Can Llobateres 1 (Sabadell) is the youngest locality considered in this work, being correlated to the upper-most portion of MN9 (*Cricetulodon hartenbergeri – Progonomys hispanicus* interval subzone) and with

a magnetostratigraphically well-constrained interpolated age of 9.76 Ma (Casanovas-Vilar, Alba, Garcés et al. 2011; Casanovas-Vilar, Garcés et al. 2016; Casanovas-Vilar, Madern et al. 2016).

Materials and methods

The material described in this paper includes up to 99 fossil remains from several localities of the Vallès-Penedès Basin. Most of these remains are housed at the Institut Català de Paleontologia Miquel Crusafont (IPS), Universitat Autònoma de Barcelona, Spain (acronym 'IPS', following the former name of this institution, 'Institut de Paleontologia de Sabadell'), except for a few housed at the Museu Geològic del Seminari de Barcelona (MGSB). Most of the ICP material was found among the classical collections of the various reported sites housed in the institution, although some remains were recovered during the 2015 fieldwork campaign performed at Castell de Barberà (level D, which corresponds to the classical layer that delivered most of the Castell de Barberà remains; SA, unpublished data). Anatomical terminology follows Sanchiz (1998a) and Roček (1994). Selected specimens were photographed with a Leica MZ16 stereomicroscope equipped with a camera Leica IC 3D and the software Leica Application Suite version 2.8.1.

Systematic palaeontology

Order **Anura** Fischer von Waldheim, 1813

Superfamily **Discoglossoidea** Günther, 1858

Family **Alytidae** Fitzinger, 1843

Subfamily **Discoglossinae** Günther, 1858

Genus ***Latonia*** v. Meyer, 1843

Latonia gigantea (Lartet, 1851) (Figs. 2, 3, 4, 5A-F')

Studied material:

Sant Quirze: three maxillae (IPS19112, IPS95022, IPS95023), and three trunk vertebrae (MGSB31638a, MGSB31638.15, MGSB31638.16).

Trinxera del Ferrocarril: a frontoparietal (IPS9636), two fragments of frontoparietal (IPS95016, IPS95017), five maxillae (IPS83607, IPS83610, IPS95018, IPS95019, IPS95020), a trunk vertebra (IPS83609), a sacral vertebra (IPS95021), and a humerus (IPS83608).

Castell de Barberà: eleven maxillae (IPS95024, IPS95030, IPS95037, IPS95041, IPS95044, IPS95046, IPS95049, IPS95050, IPS95052, IPS95055, IPS95075), 20 trunk vertebrae (IPS95028, IPS95031, IPS95033, IPS95035, IPS95036, IPS95040, IPS95045, IPS95047, IPS95048, IPS95051, IPS95053, IPS95056, IPS95057, IPS95058, IPS95059, IPS95060, IPS95061, IPS95062, IPS95063, IPS95064, IPS95076), a sacral vertebra (IPS95029), four urostyles (IPS95039, IPS95042, IPS95070, IPS95071), a scapula (IPS95068), four humeri (IPS91814, IPS92052, IPS95027, IPS95066), twelve ilia (IPS95025, IPS95026, IPS95032, IPS95034, IPS95038, IPS95054, IPS95065, IPS95067, IPS95069, IPS95072, IPS95073, IPS95074).

Can Poncic 1: a maxilla (IPS83612), a trunk vertebra (IPS83611), an urostyle (IPS83613), a humerus (IPS9367), a femur (IPS95015), two tibiofibulae (IPS95013, IPS95014).

Can Llobateres 1: a sphenethmoid (IPS9213i), a maxilla (IPS9213a), a pterygoid (IPS95009), four prearticulars (IPS28999a, IPS87410, IPS9213p–q), a trunk vertebra (IPS9213j), four urostyles (IPS9326a, IPS28979, IPS87409, IPS87411), a coracoid (IPS9213l), a scapula (IPS9213m), two

humeri (IPS9213n–o), three radioulnae (IPS87408, IPS9326c, IPS9213k), an ilium (IPS11607), a tibiofibula (IPS9326b).

Description:

All bones can reach a very large size, even if they are often fragmentary. Small specimens are also present, interpreted as young individuals.

The sphenethmoid (IPS9213i; Fig. 2A–B) is very poorly preserved, only including part of its posterior half. It shows a wide antrum pro lobo olfactorio. On the right side, a small portion of the dorsal surface of the bone is visible: it is flat and displays very light striae, being the articulation surface with the frontoparietal. A small preserved portion of the right lamina supraorbitalis projects laterally. The ventral surface of the bone, contacting the parasphenoid in the living animal, bears a distinct longitudinal striation, whereas its lateral surfaces are smooth.

The most completely preserved frontoparietal (IPS9636; Fig. 4A–B) is very fragmentary, only preserving the right portion of its anterior half. It was unpaired in origin. The dorsal surface is covered by a dense and well-developed dermal ornamentation, mainly consisting of small tubercles that, toward the anterior end of the bone, fuse with one another forming anterolaterally directed ridges. A small smooth surface is present on the anterolateral corner, apparently representing the remaining part of the broken right anterior horn. A sharp and moderately low pars contacta (contact surface for the sphenethmoid) is visible on the ventral surface of the frontoparietal, crossing obliquely the entire fragment and anteriorly giving rise to the anterior horn. Medial to the pars contacta, there is a small remnant of the anterior portion of the incrassatio frontoparietalis, which is marked laterally by a very low ridge. A rough surface is present between the pars contacta and the incrassatio. Lateral to the pars contacta, there is a wide tectum supraorbitale. The two fragments of frontoparietal (IPS95016, IPS95017) are very poorly preserved, but their dorsal surface shows an ornamentation similar to that more clearly visible in IPS9636.

Most of the maxillary specimens are fragmentary (except for IPS9213a, which is almost complete; Fig. 2C–D) and preserve the middle part of the maxilla, although both anterior (IPS95019, IPS95046 and IPS95049) and posterior (IPS19112, IPS83607 and IPS95044) fragments are also present. The morphology of the fragmentary specimens (Figs. 3K–L, 4C–H, S-B', 5A–F) is consistent with that of IPS9213a. The latter is 41 mm in length and has more than 60 tooth positions, some of which still bear partially-preserved teeth; these are pleurodont, cylindrical and closely packed. The lamina horizontalis is very narrow and high, and the crista dentalis continues beyond the posterior end of the former. A thick base for a robust but broken processus pterygoideus is present by the posterior end. The posterior end of the maxilla is subrectangular in medial or lateral views. The processus posterior is broken in all specimens, which nonetheless allow to ascertain that it was originally longer than the processus zygomaticomaxillaris. A wide posterior depression, marked anteriorly by a low ridge is also recognizable on the medial surface of the posterior end of the maxilla. Because of an incomplete preservation in IPS9213a, the base of the processus pterygoideus and/or the above-mentioned ridge, are more clearly visible in other specimens (IPS19112, IPS83607, IPS95044 and IPS95044). The margo orbitalis is rather straight. The processus palatinus is partially preserved in IPS9213a, as well as in IPS83610 and IPS95463, even though it lacks its dorsal tip. This process is anteriorly inclined and gutter-shaped, because of the presence of a posterodorsally concave edge running towards the lamina horizontalis on its medial surface. The concavity of this edge defines the narrow sulcus nasolacrimalis, which is continued posteriorly, on the dorsal side of the lamina horizontalis, by the narrow and moderately deep groove for palatoquadrate bar. Anterior to the processus, in IPS9213a there is a very long and high lamina anterior, also preserved in IPS95019, IPS95046 and IPS95049. The dorsal margin of this lamina is roughly straight. Under the processus palatinus, there is a deep and very narrow fossa maxillaris. The anterior end of the maxilla does not show a rostellum. The lateral surface of the bone bears an ornamentation made up by tubercles and parallel ridges, but it covers only the dorsal half of the two posterior thirds of the bone. Both the ventral margin and the whole anterior portion

of the bone are smooth. Anteriorly, the ornamentation is made up only by tubercles, which fuse to form parallel ridges in the posterior third. A thin layer of spongy tissue separates the ornamentation from the underlying bone.

The fragment of pterygoid (IPS95009; Fig. 2E-F) only includes the ramus maxillaris, lacking its anterior tip. The margo orbitalis is straight, whereas the margo mandibularis is strongly convex because of the presence of a well-developed ventral flange (sensu Biton et al. 2016). The ventral surface of the pterygoid is smooth, whereas the dorsal side shows a very narrow sulcus pterygoideus.

The best preserved prearticular (IPS9213p; Fig. 2G–I) bears both a processus paracoronoideus (anteriorly) and a processus coronoideus (posteriorly). Whereas the latter is broken, the former displays a flat dorsal surface and a sharp margin. There are no foramina located posteriorly to the processus coronoideus on the medial surface. A low crista paracoronoidea passes by the lateral side of the two processes, marking the medial wall of the narrow sulcus cartilagine Meckeli. The sulcus is very deep at the level of the processus coronoideus, but shallower anteriorly. Posteriorly, it widens to form the extremitas spatulata, whose posterior end is missing. The lateral surface of the bone presents a well-distinct and sharp crista mandibulae externa, which ventrally marks a wide and deep depressed area that is further marked dorsally by a lower ridge. The remaining prearticulars (Fig. 2J–P) are more fragmentary, but their morphology is comparable to that of IPS9213p. The processus coronoideus is preserved in IPS28999a, being slender, flat and dorsally bent.

Trunk vertebrae are in most instances represented only by the vertebral centrum (Figs. 2Q–R, 3M–N, 4I–J, C’–D’, 5G–L), which is robust and cylindrical. In lateral view, a shallow ventral concavity is visible at about centrum mid-length. A hint of condylar neck (a typical feature of opisthocoelous vertebrae) seems to be recognizable, even when the condyle is particularly eroded. The left processus transversus is preserved in IPS9213j (Fig. 2Q–R). It is robust and cylindrical, being laterally directed and slightly widening towards its distal end. The proximal end of the robust fused

rib is also visible. Only IPS95036 and MGSB31638a preserve the dorsal part of a long neural arch (Fig. 4E'). Its dorsal surface is flat and bears a well-developed carina neuralis, strongly projecting posteriorly with a robust point. Prezygapophyses are missing, whereas the postzygapophyses are subelliptical and dorsally tilted about 45°.

The sacral vertebrae (Fig. 4K–P) have an anterior condyle and two posterior condyles. The former is circular in anterior view, whereas the latter are slightly broader mediolaterally. In lateral view, the centrum shows a shallow ventral convexity, as in the trunk vertebrae. The neural arch, preserved only in IPS95021, is short and has robust walls, which define a subelliptical and dorsoventrally compressed neural canal. The dorsal surface of the neural arch is flat and displays a moderately low but distinct carina neuralis. The prezygapophyses are wide, subcircular and dorsally tilted about 45°. The sacral diapophyses are mostly broken, but their preserved bases are robust and moderately craniocaudally elongated.

Urostyles (Figs. 2S–Y, 3O–P, 5M–N) have a straight and long shaft, which displays a very slightly concave ventral profile in lateral view. Two fossae condyloideae are present anteriorly, being subcircular (only very slightly broader mediolaterally). The neural arch is often missing, but, when preserved, it has two small transverse processes on its anterior end, as well as a suboval canalis coccygeus. In IPS28979, a low and short horizontal lamina is present behind each transverse process (Fig. 2W). Less developed laminae are also present in IPS9326a (Fig. 2U) and IPS87409 (Fig. 2S). Along the crista dorsalis of IPS9326a, IPS28979 and IPS87409, there is a very narrow dorsal fissure, which appears larger in IPS28979 merely due to preservational reasons.

The coracoid (Fig. 2Z–A') is long, slender and straight, provided with a very constricted middle portion. It has a large and robust pars glenoidalis and a moderately wide and laminar pars epicoracoidalis. The proximal margin of the latter is slightly eroded, but originally its proximal end appears to have been slightly narrower than the distal. In dorsal view, the margo posterior is straight, whereas the margo anterior is concave.

The scapulae (Figs. 2B'–C', 5O–P) are very short and wide. They bear a well-developed crista anterior (tenuitas cranialis sensu Roček 1994), whose anterior margin is broken in the two available specimens. The posterior margin of the scapula is distinctly concave. The pars suprascapularis is wide. The pars glenoidalis is broken off in all specimens, such that only the medially-directed cavitas glenoidalis is preserved. The pars acromialis, preserved only in IPS95068, is short and does not participate in the articulation with the humerus. In origin, a deep and narrow sinus interglenoidalis separated the two portions of the medial end of the bone. Both the internal and external surfaces of the scapula are smooth.

IPS9213n (Fig. 2D'–E') is the best preserved humerus, being almost complete. Most of the remaining specimens only preserve the distal epiphysis (Fig. 4Q–R), except for IPS83608, IPS9213o (Fig. 2F'–G'), IPS95027 (Fig. 5Q–R) and IPS95066 (Fig. 5S–T) (which preserves part of the shaft) and IPS9367 (which includes the proximal half of the bone; Fig. 3Q–R). The very large and spherical eminentia capitata is flanked by a very well-developed epicondylus ulnaris on the medial side and by a small epicondylus radialis on the lateral side. Because of incomplete preservation, it is often impossible to discern the developmental pattern of the proximal portion of the related cristae (medialis and lateralis), although in IPS9213n–o, IPS95027 and IPS95066 they are well developed. The crista medialis is much more marked than the crista lateralis, and the proximal part of the former further shows a steeply inclined margin. The eminentia capitata is shifted laterally compared to the main axis of the bone. This feature is less obvious when the diaphysis is lacking, although the lateral inclination of the wide and proximodistally long impronta olecranica is evident in all specimens. A shallow fossa cubitalis ventralis is present. The well-developed crista ventralis, preserved only in IPS9367 and IPS9213n, is flanked medially by a small crista paraventralis.

Radioulnae (Fig. 3A–F) are rather slender, despite the large size. The articulation surface with the humerus is large. In distal view, the radial component of the distal epiphysis is circular, whereas the

ulnar component is elliptical and distinctly compressed. On both the lateral and medial surface, the two components are separated by a wide sulcus longitudinalis.

Ilia (Figs. 3G–H, 5U–F') show a well-developed and laminar crista dorsalis, originating from an anteroposteriorly elongate tuber superior. However, most of the shaft is lacking in all the specimens. The tuber superior is inclined anteriorly, forming a markedly obtuse angle with the pars ascendens, and not being clearly distinguished from the crista. A wide and shallow fossula tuberis superioris is present ventral to the tuber, on the lateral surface of the crista dorsalis; it is pierced by small foramina in some specimens. Both the pars ascendens and the pars descendens are well developed. A strong interiliac tubercle (ventrally) and a deep interiliac groove (dorsally) are present between these structures on the medial surface of the bone. The development of the interiliac tubercle increases with size. The pars descendens is not ventrally expanded. The acetabulum is wide and has a sharp margin, which is more developed anteroventrally. There are no supracetabular or preacetabular fossae.

Only the proximal epiphysis of the femur is preserved (Fig. 3S–T). It is moderately slender and displays the base of a robust crista femoris, which is otherwise broken away.

Tibiofibulae (Fig. 3I–J, U–X) lack the distal epiphysis and most of the diaphysis in all specimens. This bone is moderately slender, and has a sharp and distinct crista cruris on its dorsal surface. In proximal view, the two components of the proximal epiphysis are elliptical and similar in size. Their main axes form a very small angle, being subparallel.

Remarks: The opisthocoelous vertebrae, the moderately dilated sacral diapophyses, the bicondylar sacro-urostylar articulation, the small transverse processes of the urostyle, the short scapulae, the shallow fossa cubitalis ventralis and the subparallel components of the tibiofibula are all features of the subfamily Discoglossinae (Roček 1994, 2013; Bailon 1999). In particular, the fossils described herein are attributed to the genus *Latonia* based on the following characters (Roček 1994, 2013;

Biton et al. 2016): presence of striae at the contact surface between the sphenethmoid and the parasphenoid as well as between the sphenethmoid and the frontoparietal, unpaired frontoparietal, elongated anterior portion of the incrassatio frontoparietalis, presence of a wide posterior depression on the medial side of the maxilla, presence of a well-developed ventral flange on the pterygoid, presence of processus paracoronoideus on the prearticular, laterally-shifted eminentia capitata on the humerus, presence of a thin crista dorsalis on the ilium, and a very obtuse angle between the tuber superior and the pars ascendens of the ilium. An assignment of the described specimens to *L. ragei*, *L. nigriventer* and *L. vertaizoni* can be discounted based on the smooth lateral surface of their maxillae. In contrast, an ornamentation made of tubercles that form parallel ridges posteriorly is diagnostic of *L. gigantea* (Roček 1994, 2013; Biton et al. 2016). The condition of the maxillae of *L. seyfriedi* is unknown, since all known specimens of this species are preserved on slabs and only the medial surface of the maxillae is visible (Roček 1994). In any case, the ornamentation of the frontoparietal in the described specimens might further support an attribution to *L. gigantea*, because the presence of densely packed and small tubercles that fuse into ridges anteriorly is mentioned as a characteristic feature of adult individuals of this species by Roček (1994, 2013). It has to be noted, however, that Sanchiz (1998b) attributed to *L. ragei* similarly ornamented frontoparietals from the lower Miocene of Oberdorf (Austria), and therefore this feature might be shared by different species of *Latonia*. The maxilla from Can Poncic 1 (IPS83612; Fig. 3K–L) lacks any ornamentation on its lateral surface, but it is only a small fragment that might preserved an unornamented portion of an otherwise ornamented maxilla. All the remaining fossils from this locality are consistent in size and shape with those from similarly-aged Vallès-Penedès sites assigned to *L. gigantea*, and are thus formally attributed to the same species.

Latonia sp. (Fig. 5G'–H')

Studied material:

Sant Mamet: an ilium (IPS87368).

Description

IPS87368 (Fig. 5G'–H') is a fragmentary ilium, preserving only the body of the bone. The lateral surface is almost completely covered by the matrix, and so it is not possible to distinguish the presence or absence of features such as the fossula tuberis superioris, the supracetabular fossa or the preacetabular fossa. Nevertheless, in spite of being largely covered by the matrix, the large acetabulum displays a sharp and well-developed margin. The tuber superior is anteroposteriorly elongated and strongly inclined anteriorly. A thin crista dorsalis is present, but largely missing, because of the breakage of the shaft. The pars ascendens is well developed, even though its tip is missing. The angle between the pars ascendens and the tuber superior is distinctly obtuse. The pars descendens is well developed and not anteroventrally enlarged. The medial surface of the specimen displays a strong interiliac tubercle and a deep interiliac groove.

Remarks: The ilium from Sant Mamet is similar in morphology to those described above from younger Vallès-Penedès sites, being similarly attributed to *Latonia*. However, this bone is not informative enough to enable a conclusive assignment to the species rank, and the absence of other, more informative fossils from the same locality makes it preferable to leave this specimen unassigned to species. It might either belong to *L. gigantea* (like the remaining Vallès-Penedès specimens of *Latonia*) or to a different, non-ornamented species, as further supported by the report of *Latonia* cf. *ragei* from the early Miocene site of Navarrete del Río in the Iberian Peninsula (see Discussion).

Discussion

In their online database of fossil vertebrate occurrences, Böhme and Ilg (2003) reported *Latonia* from a number of Miocene localities in the Iberian Peninsula (Tab. 1). Most of these data are based on Böhme's personal observations and are still unpublished, although remains of *Latonia* from Can Llobateres, Cerro del Otero, Masía del Barbo and Navarrete del Río have also been mentioned in several other works (Sanchiz 1977, 1998a; Roček 1994, 2013). The report from Can Llobateres (Sanchiz 1977, 1998a; Roček 1994; Böhme and Ilg 2003) evidences that the presence of *Latonia* in the Vallès-Penedès Basin was already known, although no species assignment was provided before. In contrast, the maxillae described herein display unambiguous diagnostic features of *L. gigantea*, indicating that this species was present in the basin at least during the late Aragonian and early Vallesian (MN7+8 and MN9). These remains represent the first report of *L. gigantea* in the Iberian Peninsula, as well as one of its southernmost records, together with remains tentatively attributed to this species from Gargano (Italy; Delfino 2002) and some records from Turkey based on unpublished material (Böhme and Ilg 2003). During its evolutionary history spanning from the late Oligocene to the early Pleistocene, this species considerably spread throughout western, central and eastern Europe, although it seems to be less abundantly represented in Mediterranean countries (Roček 1994, 2013; Böhme and Ilg 2003). The latter fact might be an artifact due to misidentifications instead of an indication of the real absence of the species, because fossils attributed to *Latonia* but indeterminate at the species rank have also been reported from the Mediterranean area from Spain (Tab. 1; Sanchiz 1977, 1998a; Roček 1994, 2013; Böhme and Ilg 2003) to Greece (MD, unpublished data).

Previously-known Iberian remains of *Latonia* were unassigned to species (Böhme and Ilg 2003; Roček 2013), with the sole exception of *Latonia* cf. *ragei* from the early Miocene (MN2) of Navarrete del Río (Teruel; Sanchiz 1998a; Böhme and Ilg 2003; Roček 2013). The taxonomic distinction between the material of *Latonia* from the latter locality and that from the younger Iberian sites of Can Llobateres (MN9) and Masía del Barbo (MN10) was already noted by Sanchiz

(1977). Our study further confirms that at least two different species of *Latonia* were present in the northern Iberian Peninsula during the Miocene: *Latonia* cf. *ragei* in Navarrete del Río and *L. gigantea* in the late Aragonian and early Vallesian sites of the Vallès-Penedès Basin. A revision of the remains of *Latonia* from Masía del Barbo is needed to clarify whether they are conspecific with the remains from the Vallès-Penedès (as suggested by Sanchiz, 1977) or not. The presence of a second species of *Latonia* is uncertain for the Vallès-Penedès Basin, because the scarce material from the only early Miocene site in which *Latonia* is recorded, Sant Mamet (MN4), does not allow us to determine its taxonomic ascription. Although this site is much distinctly younger than the remaining Vallès-Penedès localities in which *L. gigantea* has been documented (MN7+8 to MN9), elsewhere in Europe both *L. gigantea* and *L. ragei* are known also from localities dating back to the MN4 (Roček 1994, 2013; Sanchiz 1998b; Böhme 2003; Böhme and Ilg 2003; Rage and Bailon 2005): the remains from Dolnice (Czech Republic) and Günzburg and Langenau (Germany) constitute the oldest records of *L. gigantea*, whereas *L. ragei* has been found also in Oberdorf (Austria), Béon 1 (France) and Petersbuch (Germany). Given the presence in Europe of two *Latonia* species during the MN4, and in the absence of diagnostic elements such as maxillae or frontoparietals, we prefer to leave the ilium from Sant Mamet unassigned to species.

Based on its postcranial anatomy, *Latonia* has been considered a frog adapted to jumping and swimming like brown frogs (genus *Rana*), which similarly possess an ilium provided with a high crista dorsalis and a well-developed tuber superior (Böhme 2002; Tempfer 2005). Thus, the presence of an anuran such as *Latonia* in the reported Vallès-Penedès localities indicates a generally moist palaeoenvironment. However, besides moisture, it is difficult to determine more ecological specifics because extant brown frogs live in a very wide array of different environments, and *Latonia* might have had similar poorly selective ecological requirements. Extant species of discoglossin alityds (i.e., *Discoglossus* spp. and *L. nigriventer*) inhabit a wide range of wet habitats in areas with a warm climate, including ponds, streams and even brackish waters (Tempfer 2005;

AmphibiaWeb 2016; Speybroeck et al. 2016). In turn, the extant *L. nigriventer* is found in the marshy environment of the Hula Valley, where the remnants of the swampy Hula Lake are surrounded by swamps, springs and streams (Biton et al. 2013, 2016; Perl et al. 2017). The climate in the Hula Valley is Mediterranean with hot dry summers and cool rainy winters (Biton et al. 2016). A similar environment, consisting in a permanent marshy area with surrounding wetland forests has been inferred for Can Llobateres 1 based on plant remains and in accordance to the mammal fauna (Marmi et al. 2012). The faunal composition of other *Latonia*-bearing localities of the Vallès-Penedès Basin is further indicative of humid conditions (Begun 1992; Casanovas-Vilar, Alba, Robles et al. 2011), as further confirmed here by the presence of *Latonia.* However, the presence of the latter taxon must not necessarily be an indicator of marshy conditions in all these localities, since the low environmental specificity of extant discoglossines other than *Latonia* as well as of its supposed ecological equivalent, the brown frogs, might have also been characteristic of extinct species of this genus. Anyway, *Latonia* supports the warm palaeoclimate inferred for some localities of the basin using different proxies (Marmi et al. 2012).

Conclusions

Our analysis of anuran fossil remains coming from the Vallès-Penedès Basin indicates that Latonia was present in north-eastern Iberian Peninsula from the early (MN4) to the late (MN9) Miocene. *Latonia gigantea* is recorded in four different late Aragonian to early Vallesian localities from the basin (from older to younger: Sant Quirze/Trinxera del Ferrocarril, Castell de Barberà, Can Poncic 1 and Can Llobateres), confirming the moist palaeoenvironment previously inferred for them. Together with reports from Italy and Turkey, the Vallès-Penedès Basin records of *L. gigantea* are among the southernmost occurrences of this species, even though *Latonia* remains unassigned to species (mostly unpublished) have been reported also from other parts of the Iberian Peninsula. In

the future, the revision of the latter fossils might result in a wider distribution for this anuran in Iberia. In the early Miocene, *Latonia* is only recorded in the Vallès-Penedès Basin by an isolated ilium from Sant Mamet. Although a species identification of this fossil is not possible, the possibility of it belonging to a different species of *Latonia* cannot be discounted, given the presence of *Latonia* cf. *ragei* in another early Miocene locality from Spain.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Figure captions

Figure 1. Geological map of the Vallès-Penedès Basin, with the locations of the sites of Can Llobateres 1 (CLL), Can Poncic 1 (CP), Castell de Barberà (CB), Sant Mamet (SM), Sant Quirze (SQ) and Trinxera del Ferrocarril (TF). Map modified from Casanovas-Vilar, Madern et al. (2016).

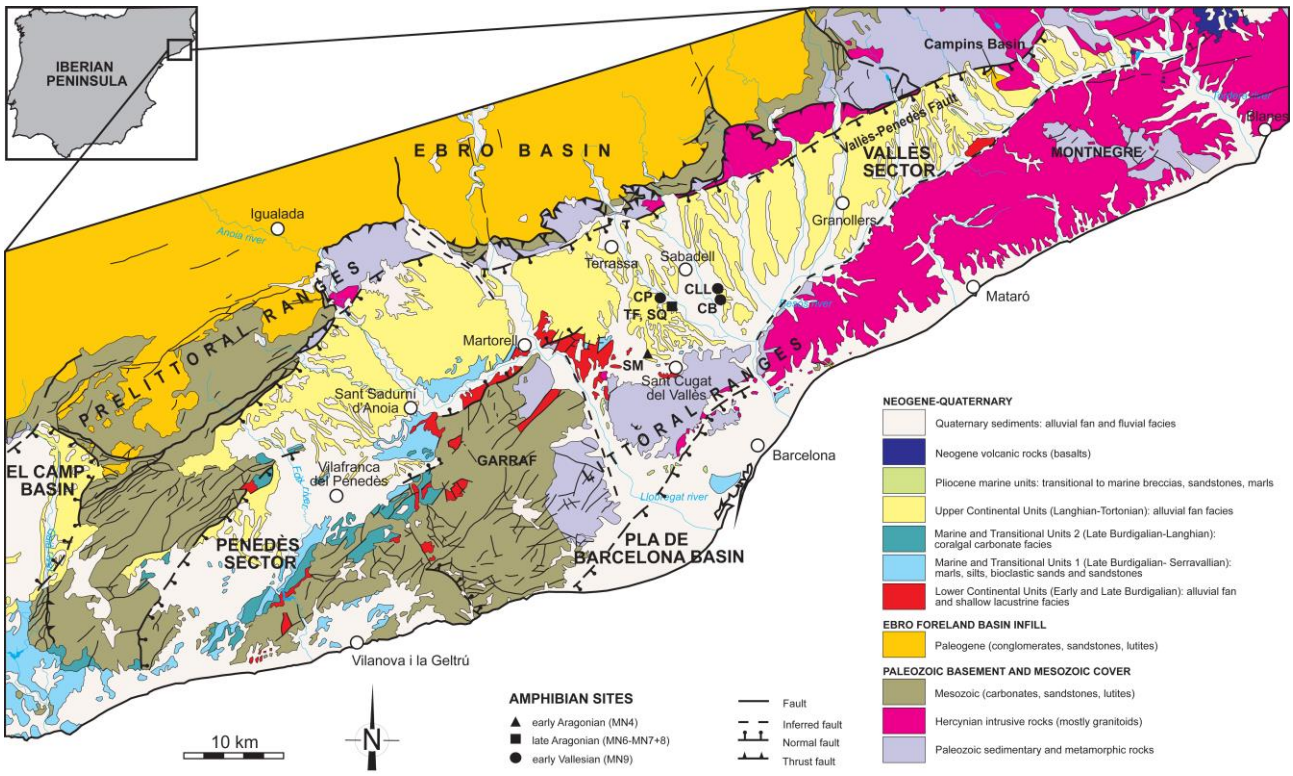

Figure 2. Remains of *Latonia gigantea* from Can Llobateres 1. A–B: sphenetmoid (IPS9213i) in ventral (A) and dorsal (F) views. C–D: right maxilla (IPS9213a) in lateral (C) and medial (D) views. E–F: left pterygoid (IPS95009) in ventral (E) and dorsal (F) views. G–I: left prearticular (IPS9213p) in dorsolateral (G), medial (H) and ventral (I) views. J–L: right prearticular (IPS9213q) in dorsal (J), lateral (K) and medial (L) views. M–N: left prearticular (IPS28999) in medial (M) and dorsal (N) views. O–P: left prearticular (IPS87410) in dorsal (O) and medial (P) views. Q–R: trunk vertebra (IPS9213j) in dorsal (Q) and ventral (R) views. S–T: urostyle (IPS87409) in dorsal (S) and ventral (T) views. U–V: urostyle (IPS9326a) in dorsal (U) and ventral (V) views. W–X: urostyle (IPS28979) in dorsal (W) and ventral (X) views. Y: urostyle (IPS87411) in ventral view. Z–A': right coracoid (IPS9213l) in ventral (Z) and dorsal (A') views. B'–C': right scapula (IPS9213m) in dorsal (B') and ventral (C') views. D'–E': left humerus (IPS9213n) in dorsal (D') and ventral (E') views. F'–G': right humerus (IPS9213o) in dorsal (F') and ventral (G') views.

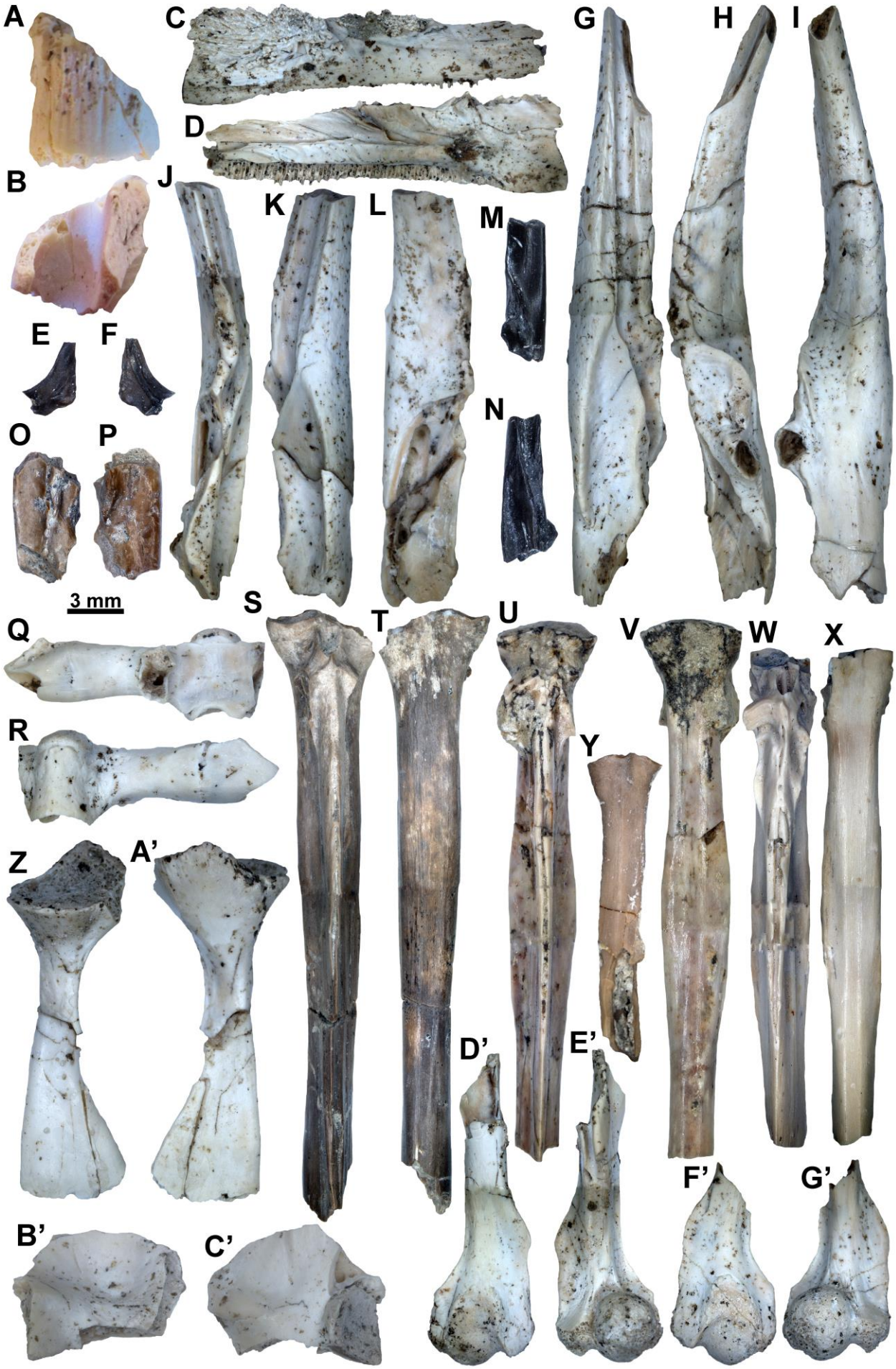
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Figure 3. Remains of *Latonia gigantea* from Can Llobateres 1 (A–I) and Can Poncic 1 (K–X). A–B: left radioulna (IPS9326c) in lateral (A) and medial (B) views. C–D: right radioulna (IPS87408) in lateral (C) and medial (D) views. E–F: left radioulna (IPS9213k) in medial (E) and lateral (F) views. G–H: right ilium (IPS11607a) in lateral (G) and medial (H) views. I–J: left tibiofibula (IPS9326c) in dorsal (I) and ventral (J) views. K–L: right maxilla (IPS83612) in lateral (K) and medial (L) views. M–N: trunk vertebra (IPS83611) in ventral (M) and dorsal (N) views. O–P: urostyle (IPS83613) in dorsal (O) and ventral (P). Q–R: right humerus (IPS9367) in lateral (Q) and medial (R) views. S–T: right femur (IPS95015) in dorsal (S) and ventral (T) views. U–V: left tibiofibula (IPS95013) in dorsal (U) and ventral (V) views. W–X: right tibiofibula (IPS95014) in dorsal (W) and ventral (X) views.

Figure 4. Remains of *Latonia gigantea* from Trinxera del Ferrocarril (A–R) and Sant Quirze (S–E'). A–B: frontoparietal (IPS9636) in dorsal (A) and ventral (B) views. C–D: left maxilla (IPS95020) in lateral (C) and medial (D) views. E–F: right maxilla (IPS95019) in lateral (E) and medial (F) views. G–H: left maxilla (IPS95018) in lateral (G) and medial (H) views. I–J: trunk vertebra (IPS83609) in dorsal (I) and ventral (J) views. K–P: sacral vertebra (IPS95021) in dorsal (K), ventral (L), right lateral (M), left lateral (N), anterior (O) and posterior (P) views. Q–R: left humerus (IPS83608) in dorsal (Q) and ventral (R) views. S–T: right maxilla (IPS83610) in lateral (S) and medial (T) views.

U–V: right maxilla (IPS83607) in lateral (U) and medial (V) views. W–X: left maxilla (IPS19112) in lateral (W) and medial (X) views. Y–Z: left maxilla (IPS95023) in lateral (Y) and medial (Z) views. A’–B’: left maxilla (IPS95022) in lateral (A’) and medial (B’) views. C’: trunk vertebra (MGSB31638.15) in ventral view. D’: trunk vertebra (MGSB31638.14) in ventral view. E’: trunk vertebra (MGSB31638.06) in dorsal view.

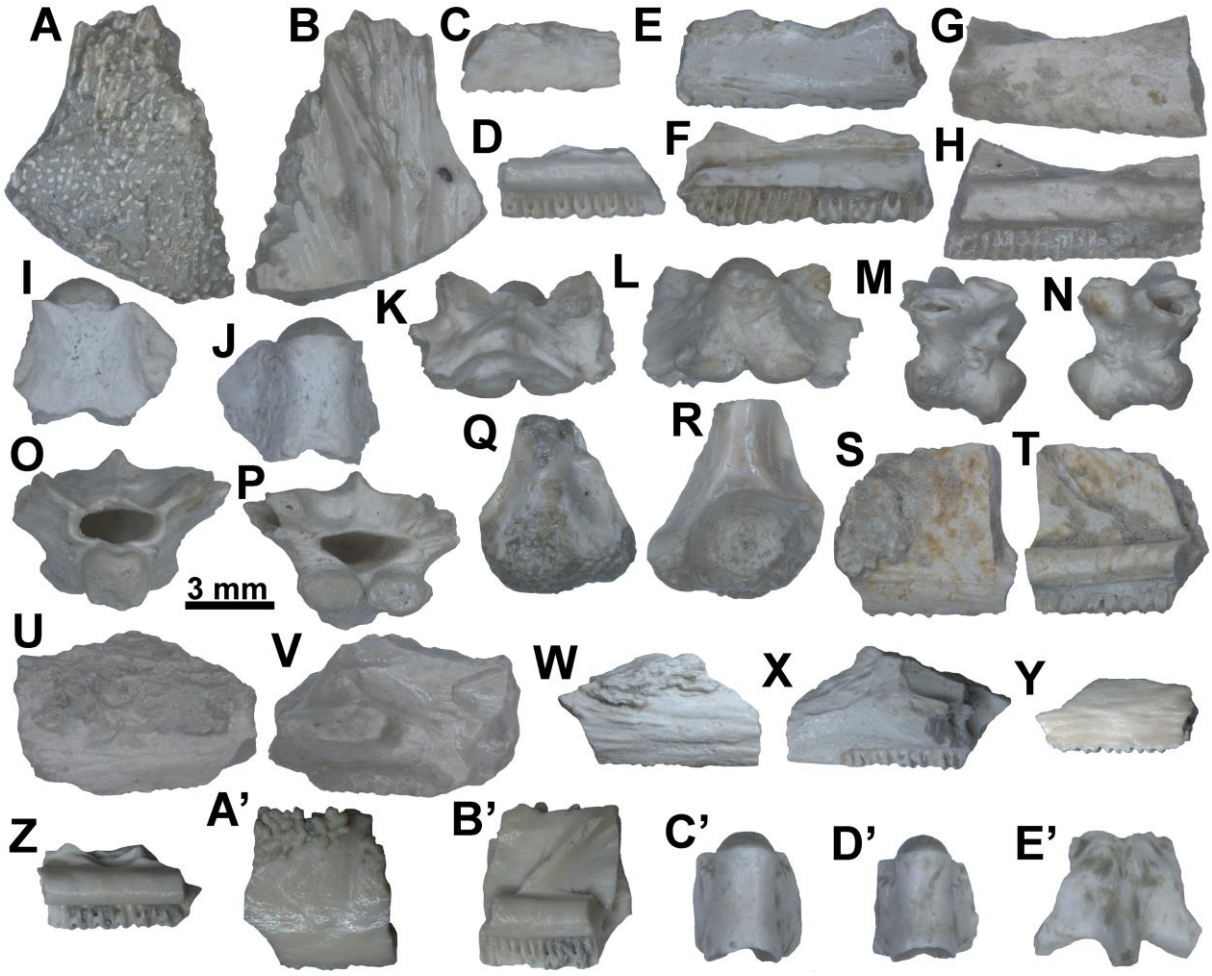

Figure 5. Remains of *Latonia gigantea* from Castell de Barberà (A–F) and remains of *Latonia* sp. from Sant Mamet (G’–H’). A–B: left maxilla (IPS95046) in lateral (A) and medial (B) views. C–D: left maxilla (IPS95024) in lateral (C) and medial (D) views. E–F: left maxilla (IPS95044) in lateral (E) and medial (F) views. G–H: trunk vertebra (IPS95047) in dorsal (G) and ventral (H) views. I–J: trunk vertebra (IPS95045) in dorsal (I) and ventral (J) views. K–L: trunk vertebra (IPS95033) in dorsal (K) and ventral (L) views. M–N: urostyle (IPS95070) in dorsal (M) and ventral (N) views. O–P: left scapula (IPS95067) in dorsal (O) and ventral (P) views. Q–R: left humerus (IPS95027) in ventral (Q) and dorsal (R) views. S–T: right humerus (IPS95066) in ventral (S) and dorsal (T) views. U–V: right ilium (IPS95068) in lateral (U) and medial (V) views. W–X: right ilium (IPS95025) in lateral (W) and medial (X) views. Y–Z: right ilium (IPS95069) in lateral (Y) and

medial (Z) views. A’–B’: right ilium (IPS95026) in lateral (A’) and medial (B’) views. C’–D’: right ilium (IPS95065) in lateral (C’) and medial (D’) views. E’–F’: right ilium (IPS95034) in lateral (E’) and medial (F’) views. G’–H’: right ilium (IPS87368) in lateral (G’) and medial (H’) views. All specimens are at the same scale (3 mm) except for M–N and C'–F' (1.5 mm).

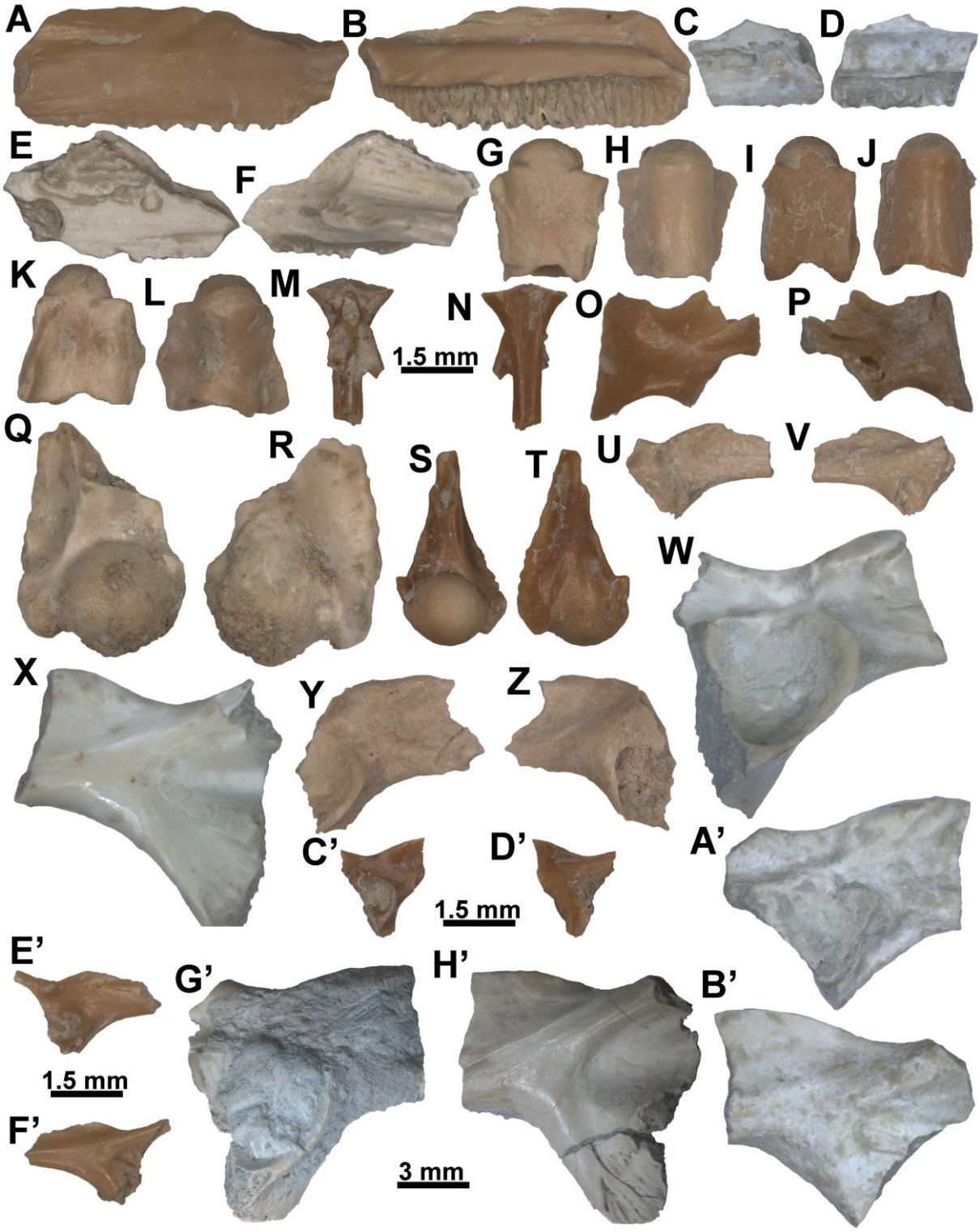

Table 1. Previous reports of *Latonia* from the Iberian Peninsula.

Locality	Identification	Age	References
Agramón	cf. *Latonia* sp.	early Miocene (MN3–MN4)	Böhme and Ilg (2003)
Ampudia 5	*Latonia* sp.	late Miocene (MN10)	Böhme and Ilg (2003)
Ampudia 6	*Latonia* sp.	late Miocene (MN10)	Böhme and Ilg (2003)
Ateca 3	aff. *Latonia* sp.	early Miocene (MN3)	Böhme and Ilg (2003)
Bañón 4	*Latonia* sp.	early Miocene (MN3)	Böhme and Ilg (2003)
Can Llobateres	*Latonia* sp./cf. *Latonia* sp.	late Miocene (MN9)	Sanchiz (1977, 1998a); Roček (1994); Böhme and Ilg (2003)
Casas Altas 75/76	*Latonia* sp.	late Miocene (MN9)	Böhme and Ilg (2003)
Cerro del Otero	*Latonia* sp.	middle to late Miocene (MN7+8)	Sanchiz (1998a); Roček (2013)
Duenas V.F.	*Latonia* sp.	middle Miocene (MN6)	Böhme and Ilg (2003)
Frausilla 2	*Latonia* sp.	middle Miocene (MN6)	Böhme and Ilg (2003)
La Col B (= La Col 2)	*Latonia* sp.	middle Miocene (MN5)	Böhme and Ilg (2003)
Las Planas 5H	*Latonia* sp.	middle to late Miocene (MN7+8)	Böhme and Ilg (2003)
Masía del Barbo	cf. *Latonia* sp.	late Miocene (MN10)	Sanchiz (1977); Roček (1994); Böhme and Ilg (2003)
Navarrete del Río	*Latonia* cf. *ragei*	early Miocene (MN2)	Sanchiz (1977, 1998a); Roček (1994, 2013); Böhme and Ilg (2003)
Olmo Redondo 4A	*Latonia* sp.	early Miocene (MN4)	Böhme and Ilg (2003)
Punta Nati, Menorca	*Latonia* sp.	early Pliocene (MN14–MN15)	Böhme and Ilg (2003)
Torremormojón 1	*Latonia* sp.	late Miocene (MN10)	Böhme and Ilg (2003)
Torremormojón 3	*Latonia* sp.	late Miocene (MN9)	Böhme and Ilg (2003)
Torremormojón 4	*Latonia* sp.	late Miocene (MN9)	Böhme and Ilg (2003)
Torremormojón 6B	*Latonia* sp.	middle Miocene (MN6)	Böhme and Ilg (2003)
Los Valles de Fuentidueña	*Latonia* sp.	late Miocene (MN9)	Böhme and Ilg (2003)