

Shifting shell morphology in a Late Miocene-Pliocene land snail species lineage (Gastropoda: Stylommatophora: Spiraxidae), with the description of a new species

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ABSTRACT

The genus *Palaeoglandina* Wenz, 1914 (Gastropoda: Stylommatophora: Spiraxidae) is a common member of land snail communities in the European Cenozoic. It has been reported from numerous stratigraphic horizons in the Iberian Peninsula ranging from the Middle Eocene (Lutetian) to the Early Pleistocene (Calabrian). Investigating Late Miocene to Early Pliocene communities in the Teruel Basin in eastern Spain, we found that previous species records proved to be misidentifications of a yet undescribed species. Based on a thorough review of contemporaneous European species of the genus we introduce a new species, *Palaeoglandina turolensis* n. sp. It is characterized by a large oval to fusiform, comparatively stout shell with moderately convex whorls, short spire and large last whorl, large, pyriform aperture, and a characteristic protoconch ornamentation, consisting of a deep spiral groove flanked by thick, short, prosocyrtr riblets. We applied geometric morphometric analyses to assess the species' morphological variability. Our results indicate differences in the species' morphospace occupation through time, which we interpret as a morphological shift from the Late Miocene to the Early Pliocene, from broad, short-spined shells to slender, long-spined shells.

KEY WORDS

Terrestrial molluscs,
Neogene,
Teruel Basin,
Iberian Peninsula,
geometric
morphometrics,
Palaeoglandina,
new species.

RÉSUMÉ

Changement de la morphologie de la coquille dans une lignée d'espèces de gastéropodes terrestres du Miocène supérieur et du Pliocène (Gastropoda: Stylommatophora: Spiraxidae), avec la description d'une nouvelle espèce. Le genre *Palaeoglandina* Wenz, 1914 (Gastropoda: Stylommatophora: Spiraxidae) est un membre commun des communautés de gastéropodes terrestres du Cénozoïque européen. Il a été signalé dans de nombreux horizons stratigraphiques de la péninsule ibérique allant de l'Éocène moyen (Lutétien) au Pléistocène précoce (Calabre). En étudiant les communautés du Miocène supérieur au Pliocène inférieur dans le bassin de Teruel, dans l'est de l'Espagne, nous avons constaté que les espèces précédemment signalées s'étaient révélées comme des erreurs d'identification, étant une espèce non décrite. Sur la base d'un examen approfondi des espèces européennes contemporaines du genre, nous présentons une nouvelle espèce, *Palaeoglandina turolensis* n. sp. Elle se caractérise par une grande coquille ovalé à fusiforme, relativement robuste, avec des verticilles modérément convexes, une courte spire et un grand dernier verticille, une grande ouverture piriforme et une ornementation caractéristique du protoconque, consistant en un profond sillon spiralé flanqué de riblets prosocyrts épais et courts. Nous avons appliqué des analyses morphométriques géométriques pour évaluer la variabilité morphologique de l'espèce. Nos résultats indiquent des différences dans l'occupation morphospatiale de l'espèce au fil du temps, que nous interprétons comme un changement morphologique entre le Miocène supérieur et le Pliocène inférieur, de coquilles larges et de spire courte à des coquilles élancées et de spire longues.

MOTS CLÉS

Mollusques terrestres,
Néogène,
Bassin de Teruel,
Péninsule Ibérique,
morphométrie
géométrique,
Palaeoglandina,
espèce nouvelle.

INTRODUCTION

The land snail superfamily Oleacinoidea is a diverse group today comprised of two families, 37 genera and 426 species distributed mainly in the tropical and subtropical regions of America (Zilch 1959-1960; Schileyko 2000; MolluscaBase 2023). Their centre of diversity is in the Caribbean islands, accommodating numerous species of the two families Oleacinidae and Spiraxidae (Schileyko 2000). Oleacinoids are mostly predatory gastropods that preferably prey on other snails and slugs, but also on small vertebrates, carrion and even members of their own species (Barker & Efford 2004; Rosenberg & Muratov 2006; González-Guillén & López-Silvero 2021).

In the Palaearctic region, the group is today represented by the family Spiraxidae (subfamily Euglandininae; e.g. Hausdorf & Solvery 2021). There, Oleacinoidea have a long-fossil record that dates back to the Late Paleocene (Thanetian) and is represented by five genera: three extinct genera, which are traditionally placed in Oleacinidae, i.e. *Palaeoglandina* Wenz, 1914, *Pseudoleacina* Wenz, 1914 and *Trachyglandina* Pfeffer, 1930, as well as the spiraxid genera *Spiraxis* C. B. Adams, 1850 and *Poiretia* P. Fischer, 1883 (Harzhauser & Neubauer 2021).

Considering only the fossil taxa, *Pseudoleacina* is with 26 species the most speciose genus. It is the oldest member and ranges from the Late Paleocene to the Early Pleistocene (Harzhauser & Neubauer 2021; MolluscaBase 2023). The genus has never been recorded from the Iberian Peninsula, although Matamales-Andreu *et al.* (2016) discussed the possibility of attributing some incomplete moulds from the Eocene (Lutetian) of Spain to the genus.

The monotypic genus *Trachyglandina* has only been recorded from the Late Eocene (Priabonian) of Germany (Pfeffer 1930; Harzhauser & Neubauer 2021). *Poiretia* has

a spotty fossil record with three species occurring from the Chattian to the Pliocene, and *Spiraxis* is known from a single fossil species in the Chattian/Aquitania (Harzhauser & Neubauer 2021).

The fossil record of the genus *Palaeoglandina* encompasses 23 species (Harzhauser & Neubauer 2021; MolluscaBase 2023). It starts in the Early Eocene (Ypresian) of France (Wenz 1923; Le Renard & Pacaud 1995) and extends to the Early Pleistocene (Calabrian) of Italy (Esu *et al.* 1993; Gliozzi *et al.* 1997) and Spain (Montenat & Truc 1971; Montoya *et al.* 1999a, b, 2001). In the Iberian Peninsula, the genus *Palaeoglandina* has been reported from several stratigraphic horizons ranging from the Middle Eocene (Lutetian) to the Early Pleistocene (Calabrian). The first records of species attributable to this genus are from the Late Miocene of the Teruel Basin, where Vilanova i Piera (1863) cited "*Glandina antiqua*? Kraus" [sic] from the site of Conclud. Later, Dereims (1898) mentioned "*Glandina inflata* Reuss, 1849" from Conclud and Santa Bárbara, and Schlosser (1907) recorded "*Glandina aquensis* Matheron, 1843" in the site of Cueva Rubia (note that the location of this site is uncertain, it is probably situated in the area of Conclud, according to the indications of Dereims (1898) and Royo Gómez (1922) and the current toponymy of the area in which the classic Conclud site is located). Royo Gómez (1922) revised the determinations of Vilanova i Piera (1863) and Dereims (1898) and referred material from Los Aljezares and Conclud to "*Glandina aquensis* (Matheron)" and "*G. aquensis* var. *obtusa* Depéret, 1890". Later, Royo Gómez (1928) recorded "*Poiretia* (*Palaeoglandina*) *gracilis aquensis* (Matheron)" from the Upper Miocene sites of Pozuelo del Rey and Colmenar de Oreja in the Madrid Basin. Truyols (1950) listed "*Glandina aquensis*" from several Miocene sites in the Vallés-Penedés Basin, and Bataller & de Larragán (1957) in the vicinity of the village of El Buste (Ebro Basin), probably from Middle Miocene strata (Azanza 1986). Montenat &

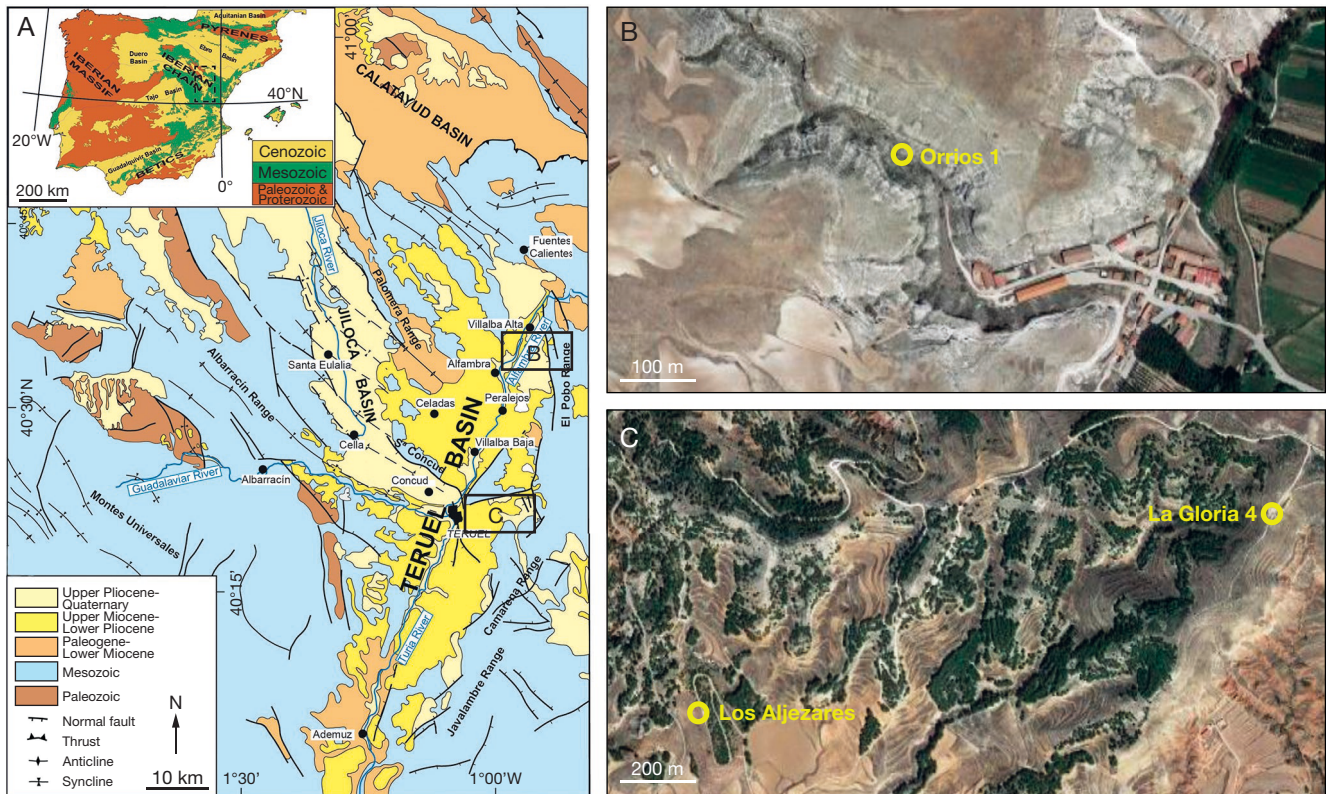


Fig. 1. — Geographical and geological overview of the studied sites in the Teruel Basin: **A**, schematic geological map of the Teruel Basin region indicating the areas in which the studied sites are located (modified after Ezquerro *et al.* 2022a); **B**, **C**, detailed locations of the Los Aljezares (AL), La Gloria 4 (LG4) and Orrios 1 (OR1) sites. Underlying images © Google Maps 2023, CNES/Airbus, Maxar Technologies.

Truc (1971) recorded in Pliocene strata of the Sierra de Santa Pola (Alicante) the new species *Palaeoglandina montenati* Truc, 1971, which was subsequently cited from the Lower Pleistocene site of Quibas (Montoya *et al.* 1999a,b, 2001). Albesa *et al.* (1991, 1997) listed the genus from the Upper Miocene deposits of Los Aljezares and Las Casiones and the Lower Pliocene site of La Gloria 4. Finally, Matamales-Andreu *et al.* (2016) documented *Palaeoglandina naudotii* (Michelin, 1832) at the Eocene site of Mas del Grau (Vallibona, Castellón).

Here, we present a revised taxonomy of the Late Miocene to Pliocene species of *Palaeoglandina* present in the Teruel Basin. Our study is based on specimens deposited in several Spanish museums and the assessment of photographs of those deposited in other European museums. We describe a new species and study its variability over time using geometric morphometric analyses. Moreover, the systematic position of the genus is discussed in broader context. This contribution constitutes a starting point to revise the fossil Iberian *Palaeoglandina* species group.

GEOLOGICAL SETTING

The Teruel Basin is an intramontane post-tectonic NNE-SSW trending depression located in the central part of the Iberian Chain (Spain). It is more than 100 km long and 15 km width (Fig. 1A). The infill of the basin consists of continental deposits

of Neogene and Quaternary age. Specifically in its northern part, a stratigraphic succession ranging from the Upper Miocene (*c.* 11.2 Ma) to the Lower Pleistocene (*c.* 1.8 Ma) crops out (Ezquerro *et al.* 2020). The sequence is composed of detrital, carbonate and evaporitic sediments reflecting deposition from alluvial fans fed from the two margins passing into freshwater or saline lakes towards the centre (Weerd 1976; Godoy *et al.* 1983a,b; Moissenet 1983; Alonso-Zarza *et al.* 2000; Ezquerro 2017; Ezquerro *et al.* 2020). The result is a continuous lacustrine-palustrine sequence, encompassing the early Vallesian (Neogene mammal zone MN9) to the late Villafranchian (MN17), that have yielded a plentiful fossil record across several sites (Ezquerro *et al.* 2022a, b). The studied specimens come from lacustrine deposits of three sites: Los Aljezares (40°20'30.2"N, 1°05'09.2"W), La Gloria 4 (40°20'48.5"N, 1°04'01.9"W) and Orrios 1 (40°35'29"N, 0°59'44"W), all located in the northern part of the basin (Fig. 1B, C). The strata at Los Aljezares are dominated by massive gypsum separated by clayey and siltstone levels (Godoy *et al.* 1983b). The studied shells derive from the gypsum layers, which belong to lithostratigraphic unit III of Alonso-Zarza & Calvo (2000) and were assigned to subchron C4n.2n, reflecting an estimated absolute age of *c.* 7.5 Ma (Ezquerro *et al.* 2022a; Dam *et al.* 2023), which corresponds to Neogene mammal zone MN12 on Iberian Peninsula (Gómez Cano *et al.* 2011). La Gloria 4 displays a succession of levels of clayey loams, carbonates and loams rich in organic matter (Albesa *et al.* 1997), which

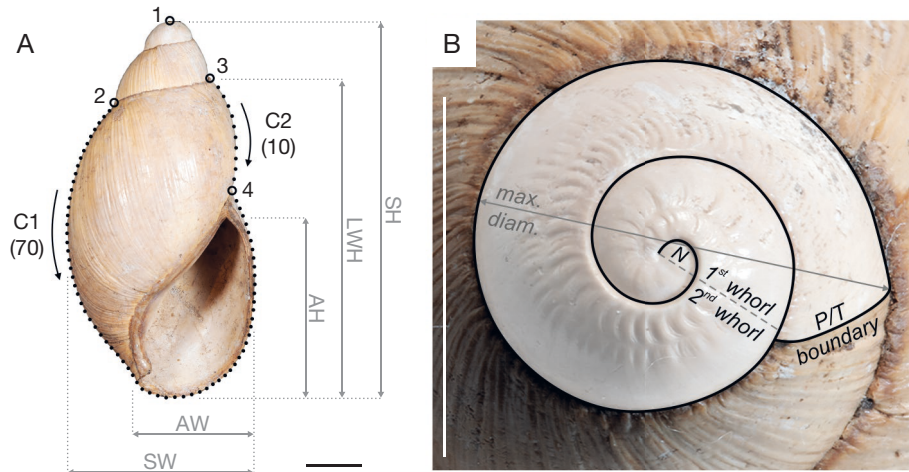


FIG. 2. — **A**, Shell measurements, following Solem & Climo (1985), and arrangement of landmarks (large circles) and semi-landmarks (small dots). The numbers in parentheses indicate the number of points for each of the two semi-landmark curves. See text for abbreviations. **B**, Protoconch measurements, following Verduin (1977). Abbreviations: **N**, nucleus; **P/T boundary**, protoconch/teleoconch boundary. Scale bar: A, 5 mm; B, 6 mm.

belong to lithostratigraphic unit IV of Alonso-Zarza & Calvo (2000) and were assigned to the subchron C3n.2n (c. 4.5 Ma, MN14; Ezquerro *et al.* 2022a). The material studied herein was collected from the loams rich in organic matter. The sequence at Orrios 1 contains levels of clayey, highly bioturbated limestones, with intercalations of shales and greyish or black marls (Godoy *et al.* 1983a) that contain the molluscs. The limestones also belong to lithostratigraphic unit IV and correlate with subchron C3n.1r (4.4 Ma, MN14; Ezquerro *et al.* 2022a).

MATERIAL AND METHODS

The specimens studied are deposited in several museums, corresponding both to historical collections (MHNM: Matheron collection; CERESE: Depéret collection; MGM and MNCN: Royo Gómez collection; MVHN: Robles collection; MRNS: Sacco collection) and to the results of more recent sampling carried in the years 1996, 1997 and 2022 out in the Teruel Basin (“Diputación General de Aragón”, files 028/96, 110/97 and 187/16-17-21-2022). All collected specimens have been stored in the MAP. Specimens deposited in the MGM, MNCN, MVHN and MAP have been directly analysed. Specimens of *Palaeoglandina aquensis*, *P. galloprovincialis*, *P. aquensis* var. *obtusata*, *P. gracilis* and *P. taurinensis* deposited in MHNM, CERESE, NHMW and MRSN have been studied from photographs. Photographs of specimens studied directly were taken using a Nikon D500 camera attached to a Sigma AF 105mm f/2.8 EX DG macro lens and using an image stacking procedure. The photographs of details were taken with the same stacking procedure and with a Hitachi H-4100 scanning electron microscope at the University of Valencia. Images were edited and assembled using the programmes Lighthouse CC v. 2015.0.0, Photoshop CC v. 2015.12 and CorelDRAW X8.

Shell dimensions were measured following the method proposed by Solem & Climo (1985) (Fig. 2A). The num-

ber of protoconch whorls was counted from the centre of the nucleus following the method used by Verduin (1977) (Fig. 2B).

We carried out a geometric morphometric analysis to quantify shell morphology and its variability across the three assemblages to assist taxonomic conclusions (compare Neubauer *et al.* 2021; Mihlbachler *et al.* 2023). We selected all complete, well-preserved, adult specimens available in museums and our own collections that have approximately the same number of whorls to avoid a bias from allometric growth. This amounts to a total of 27 specimens that cover the morphological range of the material. We defined four landmarks, all in frontal shell view (Fig. 2A): the apex (LM1), the left (LM2) and right (LM3) end points of the suture of the upper suture of the last whorl, the end point of the suture of the terminal part of the last whorl right behind the peristome (LM4). Two semi-landmark curves were defined to describe shell shape and outline between fixed landmarks: the curve connecting LM2 and LM4, including the last whorl and aperture (C1), and the curve between LM3 and LM4 (C2). We deliberately chose not to include the curvature of the inner lip, which is hard to delimit in most specimens or entirely missing in some. Images were processed using tpsDig v. 2.32 (Rohlf 2021; Appendix 1).

A Generalised Procrustes Analysis (Rohlf 1999) was performed on the (semi-) landmark configuration in R v. 4.1.2 (R Core Team 2021) using the package ‘geomorph’ v. 4.0.4 (Baken *et al.* 2021; D. Adams *et al.* 2022). Bending energy was estimated via approximate thin-plate spline mapping for the sliding semi-landmarks. Thin-plate spline deformation grids were generated with a magnification factor of 2 to visualize extreme axis values.

To test whether specimens deriving from the two biostratigraphic zones (MN12, MN14) form statistically different clusters, we ran a Procrustes ANOVA with the function ‘procD.lm’ of the ‘geomorph’ package, including residual randomisation with 1000 permutations.

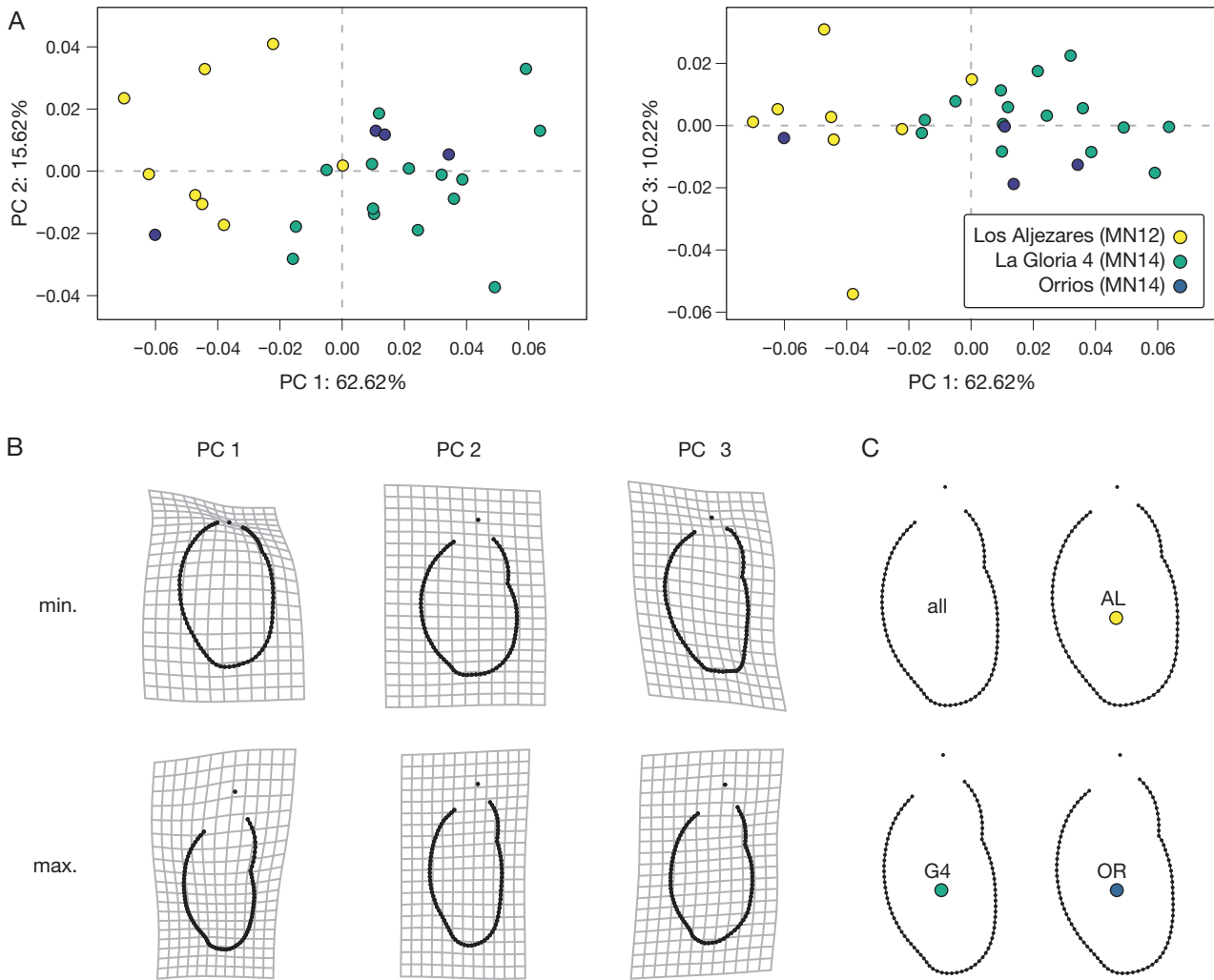


FIG. 3. — Results of the morphometric analyses: **A**, principal components analysis of the Procrustes shape coordinates; shown are the first three axes explaining 88.5% of the total variance; **B**, thin-plate spline deformation grid illustrating the extreme values for each principal component; deformations were magnified to a factor of 2 to highlight variation of distinct traits; **C**, reconstructed mean shapes for all material as well as across specimens for each locality.

ABBREVIATIONS

Institutions

MGM	Museo Geominero del Instituto Geológico y Minero de España, Madrid, Spain;
MNCN	Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain;
MVHN	Museu Valencià d'Història Natural, Alginet, Spain;
MAP	Museo Aragonés de Paleontología, Teruel, Spain;
MHNM	Musée d'Histoire naturelle de Marseille, Marseille, France;
CERESE	Centre de Ressources pour les Sciences de l'Évolution (Université Claude Bernard), Lyon, France;
NHMW	Natural History Museum Vienna, Vienna, Austria;
MRSN	Museo Regionale di Scienze Naturali, Torino, Italy.

Shell measurements

SH	shell height;
SW	shell width;
LWH	last whorl height;
AH	aperture height;
AW	aperture width.

RESULTS

The first three axes of the principal components analysis (PCA) of the Procrustes shape coordinates explain 88.5% of the total morphological variation described by the (semi-)landmark configuration (Fig. 3A). PC 1 (62.62%) corresponds to the variation of overall shape, specifically with respect to spire height and width of the base; negative values indicate bulbous morphologies with large last and broad whorl and low spire, while positive values signal elongate, high-spired shapes with narrow base (Fig. 3A, B). PC 2 (15.62%) parallels variation of shell width, without much variation in other features. PC 3 (10.22%) conforms to differences in aperture shape, with negative values corresponding to specimens with angular aperture, contrasting those with well-rounded aperture for positive values. Note that only a single specimen from Los Aljezales matches the angular morphology. Moreover, PC 3 covers slight variation in spire height.

Morphological variation differs among the assemblages of the three sites. Overall, specimens from the Late Miocene Los Aljezares tend to have broader shells with lower spires compared to the Early Pliocene shells from La Gloria 4 and Orrios 1, which are more slender and high-spired on average (Fig. 3A-C; see also Figs 4, 5). An exception is a specimen from Orrios 1 that falls well in the range of the Los Aljezares material (Figs 3A; 5A). Similarly, one of the shells from Los Aljezares clusters within the La Gloria 4-Orrios 1 group (Figs 3A; 5F). The differences between the localities of different age is also evident from the shell measurements. The average SH/SW ratio of the Los Aljezares specimens (MN12) is 1.78 compared to 1.96 of the La Gloria 4-Orrios 1 group (MN14). Similarly, the relative height of the last whorl (LWH/SH) is on average larger for MN12 specimens (91.56%) than for MN14 specimens (87.39%).

Finally, the differences of the morphospace occupied by specimens from the two biostratigraphic zones was also supported by the Procrustes ANOVA ($P = 0.001$).

SYSTEMATIC PALAEOLOGY

Class GASTROPODA Cuvier, 1795

Subclass HETEROBRANCHIA Burmeister, 1837

Superorder EUPULMONATA Haszprunar & Huber, 1990

Order STYLOMMATOPHORA Schmidt, 1855

Suborder HELICINA Rafinesque, 1815

Superfamily OLEACIONOIDEA H. Adams & A. Adams, 1855

Family SPIRAXIDAE Baker, 1939

Subfamily EUGLANDININAE Baker, 1941

REMARKS

The genera *Palaeoglandina*, *Pseudoleacina* and *Trachyglandina* are traditionally included in Oleacinidae (Wenz 1923; Nordsieck 2014; Harzhauser & Neubauer 2021). However, this systematic placement is based on an outdated concept that unites true oleacinids and European species presently considered to belong in Spiraxidae (compare e.g. Schileyko 2000 vs Hausdorf & Solvery 2021). Nordsieck (2014) considered the genera *Palaeoglandina* and *Pseudoleacina* to belong in Euglandininae, which is today ranked as a subfamily of Spiraxidae (see also Salvador 2013). We follow that concept, which is congruent with the similarity of the fossil species and modern representatives of the subfamily, such as *Euglandina* and *Poiretia* (Schileyko 2000). The monotypic genus *Trachyglandina* is here only tentatively referred to the Euglandininae, since it is based solely on a fragment; until further material of the type species, *Trachyglandina dietrichii* Pfeffer, 1930, is discovered both genus and type species should be considered *nomina dubia*.

The revised placement of the three genera is also supported by the geographic distribution of modern Euglandininae, some of which occur in the Mediterranean region and the Caucasus (e.g. Schileyko 2000; Welter-Schultes 2012; Hel-

werda 2015), while true Oleacinidae are restricted to the Americas (Schileyko 2000; Barker & Efford 2004) (note that some of these authors included the relevant genera in Oleacinidae).

Genus *Palaeoglandina* Wenz in K. Fischer & Wenz, 1914

TYPE SPECIES. — *Limnaea gracilis* Zieten, 1832; by original designation. Miocene, Germany.

Palaeoglandina turolensis n. sp.

(Figs 4A-O; 5A-O; 6G)

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Glandina antiqua – Vilanova I Piera 1863: pl. 2, fig. 26 [non Klein, 1852].

Glandina inflata – Dereims 1898: 175, 179 [non E. von Martens, 1891].

Glandina aquensis var. *obtusata* – Depéret & Sayn 1900: 108, pl. 1, fig. 77 [non Depéret, 1890]. — Royo Gómez 1922: 136-138, pl. 12, fig. 17a, b [non Depéret, 1890].

Glandina aquensis – Royo Gómez 1922: 136-138, pl. 12, fig. 16a, b [non Klein, 1852]. — Gómez Lluca 1931: 57, pl. 51, figs 14-17 [non Klein, 1852].

DIAGNOSIS. — Large oval to fusiform shell, with SH/SW ratio ranging between 1.63-2.05, and with up to 3.9 smoothly to moderately convex whorls separated by shallow sutures. Short spire constituting 10-15% of the total shell height. Protoconch up to 1.9 whorls, ornamented by deep spiral groove flanked by thick, short, prosocylindrical ribs towards the beginning of the shell. Large last whorl constituting about 85-90% of total shell height. Large, pyriform and often flattened aperture on palatal margin, corresponding to almost 60% of total shell height; outer lip thin, sharp, non-reflexed, mostly subvertical, angular at its adapical limit, strongly curved at base.

TYPE MATERIAL. — **Holotype**. MAP-8405: SH: 38.2 mm; SW: 19.1 mm. — **Paratypes**. MAP-8406: SH: 36.2 mm; SW: 18.0 mm. MAP-8407: SH: 39.5 mm; SW: 20.9 mm. MAP-8408: SH: 32.9 mm; SW: 16.7 mm. MAP-8409: SH: 33.9 mm; SW: 18.6 mm. MAP-8410: SH: 31.8 mm; SW: 15.5 mm. MAP-8411: SH: 31.0 mm; SW: 15.4 mm. MAP-8412: SH: 34.5 mm; SW: 17.2 mm. MAP-8413: SH: 32.2 mm; SW: 15.9 mm. MAP-8414: SH: 31.9 mm; SW: 16.0 mm.

ADDITIONAL MATERIAL. — MAP-8415: SH: 32.9 mm; SW: 16.4 mm. MAP-8416: SH: 33.0 mm; SW: 17.9 mm. MAP-8417: SH: 33.8 mm; SW: 17.3 mm. MAP-8418: SH: 31.2 mm; SW: 16.2 mm. MAP-8419: SH: 34.9 mm; SW: 16.6 mm. MAP-8421: SH: 45.6 mm; SW: 24.9 mm; MAP-8422: SH: 42.5 mm; SW: 21.3 mm. MAP-8423: SH: 40.1 mm; SW: 21.4 mm. MAP-8424: SH: 39.4 mm; SW: 20.8 mm; MNCNI-28900-A: SH: 40 mm; SW: 21.2 mm; MNCNI-28900-D: SH: 33.4 mm; SW: 20.5 mm. MNCNI-28900-E: SH: 44.4 mm; SW: 24.9 mm; MNCNI-11300-E: SH: 39.8 mm; SW: 23.8 mm; MVHN-040822JA01: SH: 37.4 mm; SW: 20.4 mm; MVHN-040822JA02: SH: 40.6 mm; SW: 21.7 mm; MGM118M: SH: 46.1 mm; SW: 24.8 mm. MGM3732M: SH: 33.1 mm; SW: 19.1 mm. MAP-8420: protoconch.

ETYMOLOGY. — In reference to the Teruel Basin, where the species is described from.



FIG. 4. — **A**, *Palaeoglandina turolensis* n. sp. from La Gloria 4 (Ruscian, Teruel Basin): **A1-A3**, MAP-8405, holotype; **B**, MAP-8406, paratype; **C**, MAP-8407, paratype; **D**, MAP-8408, paratype; **E**, MAP-8409, paratype; **F**, MAP-8410, paratype; **G**, MAP-8411, paratype; **H**, MAP-8412, paratype; **I**, MAP-8413, paratype; **J**, MAP-8414, paratype; **K**, MAP-8415; **L**, MAP-8416; **M**, MAP-8417; **N**, MAP-8418; **O**, MAP-8419. Scale bar: 10 mm.

TYPE HORIZON. — Marls of Lower Pliocene age (Zanclean, lower Ruscian, Neogene mammal zone MN14) rich in organic matter, with variable shades between grey-brown and purple and with frequent whitish carbonate nodulations, as well as local accumulations of iron oxides/carbonates (Albesa *et al.* 1997).

TYPE LOCALITY. — La Gloria 4 (Teruel, Spain) (40°20'48.5"N, 1°04'01.9"W).

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION. — This species is recorded from the late Tortonian (Turolian, MN12, 7.87 Ma) and Zanclean (Ruscian, MN14, 4.4–4.54 Ma) of the Teruel Basin (Royo Gómez 1922; Gómez Lluca 1931; this study).

DESCRIPTION

Large oval to fusiform shell with up to 3.9 smooth to moderately convex whorls separated by shallow, often slightly indented sutures. Short spire consisting of up to 2.9 whorls and accounting for 10–15% of total shell height; obtuse

apex. Shell shape, particularly spire height and SH/SW ratio, varies considerably among assemblages (Table 1; see also Fig. 3). Protoconch up to 1.9 whorls, with nucleus smooth and remaining portion ornamented by deep spiral groove located at approximately one third below upper suture and flanked by thick, short, prosocyrtr riblets, creating altogether a pattern remotely resembling a fern pinna with pinnules. Passage into teleoconch marked by irregularly shaped scar and onset of growth lines. Teleoconch formed by 2 whorls. Teleoconch ornamentation consists of strong and numerous growth lines, weakly prosocline to almost orthocline, crossed by fine, almost imperceptible spiral grooves, which give rise to weak reticulation. Large last whorl, about 85–90% of total shell height. Large aperture constituting almost 60% of total shell height; pyriform, acuminate at suture and rounded at base, often flattened at palatal edge and provided with well-marked notch at boundary between columellar and basal

edges; peristome simple with columellar edge arched and forming callosity which is obliquely truncated at base; outer lip thin, sharp, not reflexed, mostly subvertical, often adapically thickened and strongly curved at base. Not umbilicate.

REMARKS

Of the 23 species of *Palaeoglandina* currently recognized, the majority (18) come from Lower Eocene (Ypresian) to Middle Miocene (Langhian) deposits (e.g. Wenz 1923; Truc 1971; Le Renard & Pacaud 1995; Binder 2004; Harzhauser *et al.* 2014a,b; Höltnke & Rasser 2017; Höltnke *et al.* 2018; MolluscaBase 2023). Only five species have been recorded from the Late Miocene (Tortonian) to the Late Pliocene (Piacenzian)/Early Pleistocene (Calabrian) (e.g. Wenz 1923; Esu *et al.* 1993; Gliozzi *et al.* 1997; Montenat & Truc 1971; Montoya *et al.* 1999a, b, 2001; MolluscaBase 2023) and thus fall in a similar stratigraphic range as *Palaeoglandina turolensis* n. sp.

Two species have been located in supposedly Late Miocene sites, i.e. *Palaeoglandina aquensis* (Matheron, 1843), originally described from the Burdigalian of Aix-en-Provence (Bouches-du-Rhône, France; Esu 1999) but also cited from Tortonian strata (e.g. Schlosser 1907; Royo Gómez 1922), and *P. galloprovincialis* (Matheron, 1843), described from the Tortonian (?) of Peyrolles (Bouches-du-Rhône, France). (Note that the age of the deposits at Peyrolles is uncertain; it was indicated as “Pontien” by Wenz (1923), while species recorded from that site were attributed to both the Early Miocene (mammal stage MN4) and the Late Miocene (MN8) by Esu 1999). The possible syntype series of both species have been located in the MHNM. Since the entire Matheron collection is deposited in the MHNM (C. Borrelly pers. comm.), both the specimens of *P. aquensis* from Aix and those of *P. galloprovincialis* from Peyrolles could be the ones used by Matheron to describe the two species and thus belong to the type series. We examined two specimens whose measurements are similar to those given by Matheron (*P. aquensis*: MHNM 6034.9314.1, Fig. 6A; *P. galloprovincialis*: MHNM 6034.9317.1, Fig. 6B). However, none of the specimens match the figures of Matheron (1843: pl. 34, figs 8, 9; pl. 34, fig. 18), so we refrain from designating lectotypes until the material can be studied in greater detail. Among the above-mentioned records of *P. aquensis* in the Iberian Peninsula, only the specimens from the Teruel Basin have been located. *Palaeoglandina turolensis* n. sp., besides being much younger, clearly differs from *P. aquensis* in its shell morphology. *Palaeoglandina aquensis* has, according to the description, figures and measurements provided by Matheron (1843: 279, pl. 34, figs 8, 9), a SH/SW ratio greater than 2 (Fig. 6A; Table 1), as well as a less obtuse spire and a proportionally lower last whorl than the new species from Teruel, whose SH/SW ratio is on average less than 2 (Table 1) and has a more convex shell. Depéret (1890) described *P. aquensis* var. *obtusa* for specimens from the Pliocene of Roussillon with a slightly more obtuse spire and slightly more convex morphology. This author also indicated the possibility that the new variety is the same as *Palaeoglandina porrecta* (Gobanz, 1854) from the Miocene of the Styrian Basin (Austria). However, although we have not

been able to locate specimens from Roussillon and the work by Depéret (1890) does not contain associated figures, we think that *P. aquensis* var. *obtusa* is different from *P. porrecta*, a species found only in Middle Miocene sites (Harzhauser *et al.* 2014b; Höltnke & Rasser 2017). Besides the age difference, according to the description and figure of Gobanz (1854: 196, fig. 5), *P. porrecta* is characterised by a sharp ovate-elongate aperture that attains 70% of the total shell height according to the measurements indicated by Gobanz (1854), as well as an elongate, regularly convex last whorl. Note, however, that *P. porrecta* is currently considered a taxon inquirendum, since the type series is lost, and the limited available material is inconclusive (Harzhauser *et al.* 2014b). Depéret & Sayn (1900) listed the variety from Ratavoux (Cucuron, Vaucluse, France), dated, like Los Aljezares, to the Middle Turolian (MN12) (Ballesio *et al.* 1979; Esu 1999; Ménouret 2014). Our new species bears a strong resemblance to those from Ratavoux figured by Depéret & Sayn (1900: pl. 1, fig. 77) and those deposited at CERESÉ (UCBL-FSL 148027, Fig. 6D1-D2), all having a characteristic, convex shape. However, the degree of preservation of the French material makes a precise comparison difficult. *Palaeoglandina turolensis* n. sp. has a characteristic ornamentation on the protoconch not observed in any of the other European species we investigated, i.e. *Palaeoglandina gracilis* (Zieten, 1832) (Fig. 6H), *P. dactylina* Binder, 2004 (Binder 2004, Fig. 6b) and *P. taurinensis* (Sacco, 1886) (Fig. 6I). This ornamentation could be a diagnostic character, but the absence of an apex in the specimens of *P. aquensis* var. *obtusa* deposited at CERESÉ prevents us from studying it and comparing it with that of the new species. The strong resemblance between the Ratavoux and Los Aljezares specimens, supported by similar age, suggest that they may be conspecific taxa, but the state of preservation of the French specimens does not allow a final conclusion. If both taxa turn out to be synonymous, the name *turolensis* still has priority, since *Glandina aquensis* var. *obtusa* Depéret, 1890 is a junior homonym of *Glandina obtusa* Pfeiffer, 1845.

Regarding *P. galloprovincialis* (Fig. 6B), according to Matheron's description and the measurements he provided (Matheron 1843: 279, pl. 34, fig. 10), the species has, with a much higher SH/SW ratio than the new species, a more slender appearance.

Three species of the genus *Palaeoglandina* are currently recognised in the European Pliocene: *P. paladilhei* (Michaud, 1877), from the Early Pliocene (MN14) of Hauterives (France); *P. lunensis* (D'Ancona in Cocchi, 1867), from the Italian Late Pliocene to Early Pleistocene (MN16-MN17) (Esu 1999; Ciangherotti *et al.* 2007) and *P. montenati* Truc, 1971 from the Late Pliocene (MN16) and Early Pleistocene (MN17) of Alicante and Murcia (Montenat & Truc 1971; Montoya *et al.* 1999a,b, 2001).

Palaeoglandina paladilhei is a problematic species described from incomplete fragments of several specimens “three fragments, two of which show the last whorl and leave the opening fairly complete and the third comprising the apex” (Michaud 1877: 7), whose reconstruction was considered



FIG. 5. — A-D, O, *Palaeoglandina turolensis* n. sp. from Orrios 1 (Ruscinian, Teruel Basin): A, O, MAP-8421; B, MAP-8422; C, MAP-8423; D, MAP-8424; E-L, N, *P. turolensis* n. sp. from Los Aljezares (Turolian, Teruel Basin): E, 040822JA01; F, N, 040822JA02; G, MGM-3723; H, MNCNI-28900-D; I, MNCNI-28900-A; J, MGM-118M; K, MNCNI-28900-E; L, MNCNI-11300-E; M, *P. turolensis* n. sp. from La Gloria 4, MAP-8405. Scale bars: A-J, 10 mm; M-O, 6 mm.

“unsatisfactory” by Monténat & Truc (1971: 57). Although the reconstruction is indeed problematic and, in our opinion, shows one whorl too many, the fragments of the apical part of the shell and of the last whorl with the opening are drawn in great detail and are easily distinguishable from the inferred intermediate part. According to this information and the original description, *P. paladilhei* is very different from *P. turolensis* n. sp., easily distinguished by the shape of the first whorls, flat in the *Hauterivus* species and rounded in the new species, as well as by the shape of the last whorl and the aperture, narrower and more elongated in the French species.

Palaeoglandina lunensis, which has been figured and described in detail by De Stefani (1880), has a regularly fusiform shell with low-convex whorls and, with one more whorl, a slower growth. Moreover, the Italian species appears to have a very marked reticulate ornamentation of teleoconch (De Stefani 1880: pl. 2, fig. 13), which is not seen in *P. turolensis* n. sp. where the reticulation observed is very faint.

Palaeoglandina montenati, a large species with a total height of c. 60–70 mm (holotype, UCBL-FSL 98969: 59.5 mm; paratype, UCBL-FSL 98971: 69 mm, Monténat & Truc 1971: 57), has a more fusiform morphology (Monténat & Truc 1971: fig. 4a-c), with a SH/SW ratio of more than 2,

TABLE 1. — Shell measurements of several of the studied specimens. Data for species other than *P. turolensis* n. sp. derive from Matheron (1843) and Montenat & Truc (1971).

Register number	SH (cm)	SW (cm)	SH/SW	LWH (cm)	LWH/SH (%)	AH (cm)	AW (cm)
<i>P. turolensis</i> n. sp. from G4							
MAP-8405 (Holotype)	3.82	1.91	2.00	3.34	87.43	2.21	1.35
MAP-8406	3.62	1.80	2.01	3.08	85.08	1.94	1.33
MAP-8407	3.95	2.09	1.89	3.47	87.85	2.28	1.49
MAP-8408	3.29	1.67	1.97	2.80	85.11	1.84	1.12
MAP-8409	3.39	1.86	1.82	3.03	89.38	1.85	1.24
MAP-8410	3.18	1.55	2.05	2.78	87.42	1.80	0.97
MAP-8411	3.10	1.54	2.01	2.69	86.77	1.59	1.06
MAP-8412	3.45	1.72	2.01	2.90	84.06	1.77	1.15
MAP-8413	3.22	1.59	2.03	2.81	87.27	1.70	1.03
MAP-8414	3.19	1.60	1.99	2.78	87.15	1.79	1.10
MAP-8415	3.29	1.64	2.01	2.90	88.15	1.83	1.12
MAP-8416	3.30	1.79	1.84	2.87	86.97	1.85	1.18
MAP-8417	3.38	1.73	1.95	2.95	87.28	1.86	1.19
MAP-8418	3.12	1.62	1.93	2.74	87.82	1.74	1.10
MAP-8419	3.49	1.66	2.10	3.08	88.25	1.94	1.07
<i>P. turolensis</i> n. sp. from OR							
MAP-8421	4.56	2.49	1.83	4.21	92.32	2.91	1.67
MAP-8422	4.25	2.13	2.00	3.63	85.41	2.17	1.45
MAP-8423	4.01	2.14	1.87	3.51	87.53	2.35	1.36
MAP-8424	3.94	2.08	1.89	3.51	89.09	2.33	1.34
<i>P. turolensis</i> n. sp. MN14	–	–	1.96 ± 0.08	–	87.39 ± 1.76	–	–
<i>P. turolensis</i> n. sp. from AL							
MVHN-040822JA01	3.74	2.04	1.83	3.37	90.11	2.28	1.46
MVHN-040822JA02	4.06	2.17	1.87	3.62	89.16	2.35	1.45
MGM3732M	3.31	1.91	1.73	3.03	91.54	2.07	1.31
MGM118M	4.61	2.48	1.86	4.28	92.84	2.86	1.81
MNCNI-28900-A	4.00	2.12	1.89	3.61	90.25	2.45	1.49
MNCNI-28900-D	3.34	2.05	1.63	3.10	92.81	2.02	1.39
MNCNI-28900-E	4.44	2.49	1.78	4.12	92.79	2.86	1.45
MNCNI-11300-E	3.98	2.38	1.67	3.70	92.96	2.17	1.51
<i>P. turolensis</i> n. sp. MN12	–	–	1.78 ± 0.9	–	91.56 ± 1.43	–	–
<i>P. turolensis</i> n. sp. mean and standard deviation	3.67 ± 0.45	1.94 ± 0.30	1.91 ± 0.11	3.26 ± 0.46	88.62 ± 2.53	2.10 ± 0.36	1.30 ± 0.2
<i>P. aquensis</i>							
MHNM 6034.9314.1	4.80	2.30	2.09	–	–	–	–
<i>P. galloprovincialis</i>							
MHNM 6034.9317.1	4.60	1.90	2.42	–	–	–	–
<i>P. montenati</i>							
UCBL-FSL-98969	5.95	3.20	1.86	5.22	87.73	3.85	–
UCBL-FSL-98971	6.90	3.56	1.94	–	–	–	–
MVHN-180222GM05	5.79	3.20	1.81	5.31	91.71	3.72	2.35

a spire that attains about 10% of the total shell height and thus is proportionally shorter than that of the new species and a AH/SH ratio greater than in *P. turolensis* n. sp. (Table 1). The type specimens are moulds, but the specimens from Quibas are well preserved, showing a proportionally shorter spire with a flatter whorl profile, as well as a last whorl that is also proportionally wider and convex abapically. All this gives the shell a more fusiform morphology than the specimens from the Teruel Basin. On the other hand, the ornamentation of the protoconch is similar to that of *P. turolensis* n. sp., a circumstance that may indicate the possibility that they belong to the same evolutionary lineage. However, confirming this interpretation will require a more detailed assessment of well preserved specimens of other *Palaeoglandina* species.

DISCUSSION AND CONCLUSION

Although the genus *Palaeoglandina* has been reported from numerous stratigraphic horizons in the Iberian Peninsula, data are still scarce and identifications uncertain. The records are limited to a few Miocene sites in the Teruel, Madrid, Vallés-Penedés and Ebro basins (Royo Gómez 1922, 1928; Truyols 1950; Bataller & de Larragán 1957), as well as some isolated Eocene (Matamales-Andreu *et al.* 2016) and Plio-Pleistocene (Montenat & Truc 1971; Montoya *et al.* 1999a, b, 2001) outcrops in eastern Spain (provinces of Castellón, Alicante and Murcia). Except for the outcrops of the Spanish East, where specimens have been determined as *P. naudotii* (Eocene of Castellón; Matamales-Andreu *et al.* 2016) and *P. montenati* (Plio-Pleistocene of Alicante and



FIG. 6. — **A**, *Palaeoglandina aquensis* (Matheron, 1843) from Aix (Burdigalian, Aix Basin), MHNM 6034.9314.1; **B**, *P. galloprovincialis* (Matheron, 1843) from Peyrolles (Tortonian, Durance Basin), MHNM 6034.9317.1; **C1**, **C2**, *P. montenati* Truc, 1971 from Quibas (Calabrian, Quibas site), MVHN-180222GM05; **D1**, **D2**, *P. aquensis* var. *obtusata* (Depéret, 1890), UCBL-FSL 148027; **E1**, **E2**, *P. gracilis* (Zieten, 1832), NHMW 2013/0572/0040; **F1**, **F2**, *P. taurinensis* (Sacco, 1886), BS.093.02.001; **G**, *P. turoloensis* n. sp., MAP-8420, detail of protoconch; **H**, *P. gracilis* (Zieten, 1832), NHMW 2013/0572/0040, detail of protoconch; **I**, *P. taurinensis* (Sacco, 1886), BS.093.02.001, detail of protoconch; **J**, *P. montenati* Truc, 1971 from Quibas, MVHN-180222GM05, detail of protoconch. Scale bars: A-F, 10 mm; G, 1 mm; H-J, 2 mm.

Murcia; Montenat & Truc 1971; Montoya *et al.* 1999a, b, 2001), the rest of the Spanish specimens are as all lumped under the name *P. aquensis*.

Our study of specimens from the Teruel Basin revealed important differences from *P. aquensis*, differing for example in a stouter morphology. Moreover, *Palaeoglandina aquensis*

was originally described from Lower Miocene (Burdigalian) deposits (Esu 1999), which contrast the Late Miocene age of the Teruel material. Similarly, other Late Miocene (*P. galloprovincialis*) or Pliocene-Pleistocene (*P. paladilhei*, *P. lunensis* and *P. montenati*) species differ clearly from the Teruel species, which is consequently introduced here as a new species.

Palaeoglandina turolensis n. sp. is a morphologically highly variable species. The results of the geometric morphometric analysis indicate a general tendency for clustering between material from different time intervals (Fig. 3). Shells from the Late Miocene of Los Aljezares are on average broader, oval and have lower spires compared to those from the Early Pliocene of La Gloria 4 and Orrios 1 (Figs 3-5). However, the considerable overlap between the assemblages paired with a generally high morphological variability do not warrant a taxonomic distinction. Perhaps this is also due to the available material or the analysed morphological information. Rather than corresponding to distinct species, the differences in the occupied morphospace among assemblages may reflect a morphological shift within a single species through geological time. This view may be supported by the consistency of the peculiar ornamentation of the protoconch (Figs 5M-O, 6H), not observed in other species (with the exception of *P. montenati*). More material is required, however, to investigate this hypothesis in greater detail.

Additionally to the material investigated herein, we retrieved fragments from several sites with stratigraphic ages ranging from the late Vallesian (Tortonian, MN10) to Villanyan (Piacenzian, MN16), which show common characters with those of the specimens studied herein, including the ornamentation of the protoconch and teleoconch. These findings may indicate an even longer stratigraphic range for *Palaeoglandina turolensis* n. sp. or, alternatively, a more complex species lineage with more members that still await description.

The study of specimens attributed to *Palaeoglandina* and stored in museums has shown the need for a revision of the genus. *Palaeoglandina aquensis* and *P. galloprovincialis* could be synonymous, especially if it is confirmed that both are based on Burdigalian materials. *Palaeoglandina naudotii* from the Eocene of Spain has a different morphology than specimens from the Eocene of France deposited in the MNHN. *Palaeoglandina taurinensis*, with a very elongated morphology, could belong to the genus *Poiretia*, while *Poiretia senensis*, being more convex, could correspond to the genus *Palaeoglandina*. *Palaeoglandina paladilhei* is a problematic species that needs further study and more (and complete) material. Finally, the numerous determinations of Spanish *P. aquensis* are uncertain, as are those made by Truc (1971) for material from Ratavoux. The large amount of material missing, the dispersion of the existing material and, above all, the poor state of preservation complicate a final conclusion though.

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APPENDIX 1. — Landmark-semilandmark configurations for all 27 specimens analysed in this paper, generated with tpsDig v. 2.32: https://doi.org/10.5852/geodiversitas2023v45a21_s1