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Study of the morphological affinity between two species of benthic foraminifera from restricted environments: *Rosalina douvillei* (Cushman, 1928) and *Trichohyalus aguayoi* (Bermúdez, 1935)

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ABSTRACT

A biometric comparison is carried out on selected tests of the foraminiferal species *Rosalina douvillei* (Cushman, 1928) and *Trichohyalus aguayoi* (Bermúdez, 1935). The *Rosalina douvillei* specimens were recovered from the marginal marine Oligocene/Miocene site of Rüssingen (Mainz Basin, Germany), the lacustrine beds of the lower Miocene site of Buñol (Valencian Community, Spain) and the middle/upper Miocene site of Fuendetodos (Aragón, Spain). The *Trichohyalus aguayoi* tests were collected in the current coastal lagoon of Torreblanca and recovered from Holocene cores sampled in the Peñíscola marsh and in the coastal lagoon of l'Albufera de València, all them in the Valencian Community (Spain). In addition, the chronostratigraphic and geographical distribution of both species is also summarized. *Trichohyalus aguayoi* and *Rosalina douvillei* share many morphological characteristics but the measured specimens of *Trichohyalus aguayoi* are characterized by generally larger sizes, narrower and more elongate chambers and a higher number of chambers in the outer whorl. The *Rosalina douvillei* specimens from Fuendetodos are as large as *Trichohyalus aguayoi* and show particularly high chamber size increase rates but also few and less elongate chambers

RESUMEN

Se ha realizado un estudio biométrico de los caparazones de las especies de foraminíferos *Rosalina douvillei* (Cushman, 1928) y *Trichohyalus aguayoi* (Bermúdez, 1935). Los ejemplares de *Rosalina douvillei* fueron recuperados en los depósitos de ambiente costero marginal del yacimiento de Rüssingen (Oligoceno/Mioceno, cuenca de Maguncia, Alemania), de las capas lacustres del yacimiento de Buñol (Mioceno inferior, Comunidad Valenciana) y del yacimiento de Fuendetodos (Mioceno medio/superior, Aragón). Los ejemplares de *Trichohyalus aguayoi* fueron recolectados en la laguna costera actual de Torreblanca, en sondeos holocenos practicados en la marjal de Peñíscola y en la Albufera de Valencia (las tres localidades se hallan en la Comunidad Valenciana). Además, también se resume la distribución cronoestratigráfica y geográfica de ambas especies. *Trichohyalus aguayoi* y *Rosalina douvillei* comparten muchas características morfológicas pero los especímenes medidos de *Trichohyalus aguayoi* se caracterizan por tamaños en general más grandes, cámaras más alargadas y estrechas y un mayor número de cámaras en la última vuelta. Los ejemplares de *Rosalina douvillei* de Fuendetodos son tan grandes como *Trichohyalus aguayoi* y muestran tasas de incremento del tamaño de las

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in the last whorl. The number and shape of chambers in the last whorl seem thus to be controlled at least in part by hereditary factors. The morphological affinity between the two species probably constitute an example of convergence derived from similar environmental conditions but further research is required to discard phylogenetic proximity.

Keywords: *Rosalina douvillei*, *Trichohyalus aguayoi*, Foraminifera, morphological affinity.

cámaras particularmente altas pero también un bajo número de cámaras poco alargadas en la última vuelta. El número y forma de las cámaras en la última vuelta parece pues estar controlado, al menos en parte, por factores hereditarios. La afinidad morfológica entre las dos especies probablemente constituye un ejemplo de convergencia derivada de la similitud de condiciones ambientales pero son necesarios más estudios para poder descartar una proximidad filogenética.

Palabras clave: *Rosalina douvillei*, *Trichohyalus aguayoi*, foraminíferos, afinidad morfológica.

1. INTRODUCTION

The interpretation of skeletal structures in fossil species has been extensively developed by some authors (e.g., Raup & Stanley, 1971) and their functional significance has also been widely treated in foraminifera (e.g., Hottinger, 1978, 2000; Haynes, 1981; Hallock *et al*., 1991). When comparing phylogenetically closely related taxa it can be proposed that similar structures are homologous (i.e., they have identical ontogenetic origin) and have an equal function. However, if this phylogenetic relationship does not seem so clear, we can still argue that this structure could have the same or a similar function, an aspect that we call homoplasia.

Rosalina douvillei (Cushman, 1928) and *Trichohyalus aguayoi* (Bermúdez, 1935) are two species of benthic foraminifera with morphological similarity. Both are typical of restricted environments, but they are separated in time by about 5 million years. These species belong to different genera, so their similar form is possibly due to a process of convergence and adaptation to a particular environment. In both taxa the presence of a system of calcareous plates occupying the umbilical region is observed in the macrospheric form. In *R. douvillei* the macrospheric and the microspheric forms can be distinguished by the complexity in the secondary openings of the umbilical side. In *T. aguayoi* only the macrospheric form is known.

The aim of this study is to carry out a biometric comparison between the two species in order to quantify their morphological similarities and differences. This provides data to discern which characters can be considered of taxonomic significance and which ones might be attributed to other factors like habitat, environment or life style.

2. MATERIAL AND METHODS

A comparative biometric analysis was carried out on well-preserved tests of *T. aguayoi* and *R. douvillei* recovered from the > 125 µm size-fraction of samples collected in six different localities in western Europe, in Spain and Germany (Fig. 1) and available at the University of València. For each locality, 25 specimens of *T. aguayoi* or *R. douvillei* were randomly selected (e.g., by using random numbers to select files and rows of foraminifers fixed to storage slides, etc.) from samples rich in any one of the two species.

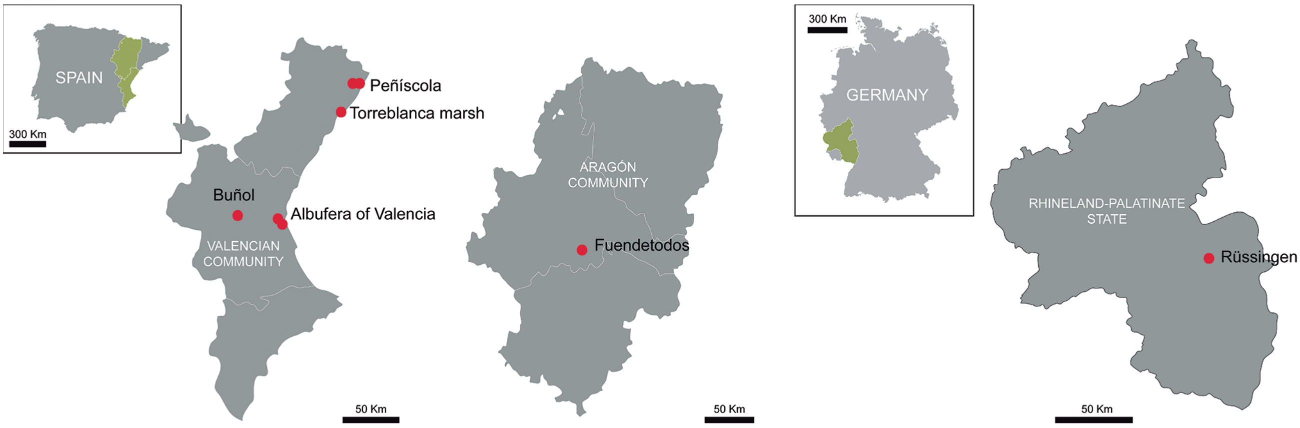

Figure 1. Geographic location of sampling sites.

The *R. douvillei* specimens were obtained from the following sites:

1) Rüssingen (Mainz, Germany). The specimens of *R. douvillei* were selected in samples (Gö-1, Gö-4, and Gö-10) recovered in the Rüssingen quarry, in the community of Göllheim (Mainz, Rheinland-Pfalz, Germany). Rüssingen (about 43 km SSW from Mainz, N 49º 37´ 22.4´´, E 8º 5´ 25.32´´) is located in the southwestern margin of the Mainz Basin, which constitutes one of the structural units of the Rhine rift-graben system that developed during the Palaeogene and connected the North Sea Basin with the Tethys area (Rothausen & Sonne, 1988). From the early Chattian (upper Oligocene) to the Aquitanian (lower Miocene) the Mainz Basin, together with other adjacent marginal marine areas, became increasingly isolated from both the north Germany and the western Paratethys basins (Gebhardt, 2003). The selected foraminifera were collected close to the Oligocene/Miocene boundary in the Rüssingen quarry (in the so-called Obere Cerithienschichten and *Corbicula*-Schichten Beds, see Kadolsky, 1988) and the assemblages show a progressive impoverishment in diversity, probably reflecting a gradual change from brackish to freshwater conditions (Bernabé *et al*., 1991).

2) Buñol (Valencia, Spain). The specimens of *R. douvillei* come from samples (BÑ-1, BÑ-2bis, and BÑ-5) collected in the Miocene athalassic lacustrine basin of Buñol (Valencia, Spain, N 39º 24’ 53.867”, W 0º 47’ 35.462”). The site of Buñol is known mainly for its numerous fossil vertebrate remains (Made *et al.*, 1998, and references therein) and has been dated as lower Aragonian, which is equivalent to the upper Burdigalian marine stage (Daams & Freudenthal, 1981). The composition and ecological characteristics of its foraminiferal assemblages have been studied by Márquez & Usera (1984, 1988).

3) Fuendetodos (Zaragoza, Spain). The lacustrine deposits of Fuendetodos are located in the central sector of the Iberian margin of the Ebro basin, south of the province of Zaragoza (Aragón, Spain). The stratigraphy of this site was studied by Pérez (1989), who differentiated three tectosedimentary units (Riba, 1989). It was in the upper unit TSU N3 (“Calcarenita de Fuendetodos”) where species of different groups of marine affinity (foraminifera, ostracoda and molluscs) were found (Anadón, 1989). The foraminifera found in this site were reported by Usera *et al.* (1991a). Observations on ostracods and isotope data were later carried out in order to determine the paleoenvironment in which this marine-like fauna developed (Anadón, 1992; Anadón *et al*., 1997). The *R. douvillei* specimens employed in this study were recovered from three selected samples (FT-108, FT-112 and FT-119) in the site of Fuendetodos (N 41º 16’ 2.597”, E 0º 52’ 3.928”).

The specimens of *T. aguayoi* were obtained in the following localities:

1) Torreblanca marsh (Castellón, Spain). The current Torreblanca marsh results from the infilling process of a Holocene coastal lagoon. The extraction of peat for its industrial exploitation has given place to a system of ponds-lagoons affected by sea water leaks and with salinity fluctuations throughout the year depending on the distance between each pond and the coastline. The annual salinity range recorded in several ponds, approximately 6-14‰ (Guillem, 2007), corresponds to mesohaline waters. The presence in these ponds-lagoons of *T. aguayoi* was detected by Usera *et al*. (1990b) and Arco *et al*. (1991). A taphonomic, taxonomic and ecologic study of the foraminiferal assemblages can be found in Guillem (2007). *Trichohyalus aguayoi* is abundant in most surface samples in the Torreblanca ponds, where it constitutes the dominant foramineral species. The selected specimens were recovered from sample TB 3.8.1. (N 40º 11’ 34.3”, E 0º 12’ 55.8”) near the bar separating the ancient coastal lagoon from the sea.

2) Albufera of Valencia (Valencia, Spain). The first data on the presence of *T. aguayoi* in the Albufera of Valencia come from the study of Robles *et al*. (1985), on the mollusc fauna of this natural site. Afterwards, surface sampling (Usera *et al*., 1990a) and surveys in different areas have been carried out, which have led to the study of different groups of organisms, including foraminifera (Usera *et al*., 2006a, 2007a, 2007b). No living foraminifera have been found in the current freshwater lagoon. The selected specimens of *T. aguayoi* were recovered from the upper section of two short cores, located close to each other (sample 66-65, core Centre: N 39º 20’ 12.85”, W 0º 21’ 13.66” and sample 56-55, core L’Antina: N 39º 19’ 58.78”W, 0º 22’ 1.13”), where this species was most abundant.

3) Peñíscola (Castellón, Spain). The Peñíscola marsh is located about 25 km north from Torreblanca and it constitutes another example of the final sedimentary infilling phase of an ancient coastal lagoon. The evolution of its foraminiferal assemblages during the Holocene was studied by Usera *et al*. (2003, 2006b). The selected specimens of *T. aguayoi* were picked from samples PÑ1-19 and PÑ2-43, in which this species was particularly abundant, and which belong to two cores (core S1: N 40º 21’ 52.58”, E 0º 23’ 59.69” and core S2: N 40º 22’ 5.44”, E 0º 24’ 6.32”) originally extracted by Usera *et al*. (2006b).

Although initially somewhat neglected (Scott, 1974), many biometrical studies of foraminiferal shells have already been developed, including those focused on particular species (e.g., only in small benthic foraminifera: Buzas, 1966; Corliss, 1979; Showers, 1980; Vénec-Peyré, 1983; Malmgren, 1984; Loubere *et al*., 1988; Gary *et al*., 1989; Collins, 1989; Caralp, 1989; Burgess & Schnitker, 1990; Usera *et al*., 1991b; Hayward *et al*., 2004; Lehmann *et al*., 2006; among others). Nevertheless, no specific biometrical analysis of *R. douvillei* is known to us. Arnold (1954), and particularly Tufesco (1969) have provided quantitative data about *T. aguayoi* dimensions but the most complete available biometrical study focused on this species is that from Foresi *et al*. (2004). Following in part the latter authors, six basic parameters were measured in each specimen with an ocular micrometre installed in a Wild M-10 binocular microscope: length (L) and breadth (B) of the whole test and length and height of the second (l_2, h_2) and third (l_3, h_3) last chambers (Fig. 2). Some specimens (particularly in *R. douvillei*) had to be constantly kept in wet conditions while being measured due to their partial opacity. The number of chambers in the last whorl was also noted for each test. A comparison between the two species was subsequently made, based on the biometric data. Additionally, a one-way analysis of variance (ANOVA) test was carried out in order to explore the significance of differences between localities. All statistical tests were done using the PAST software package (see Hammer & Harper, 2006 for procedures).

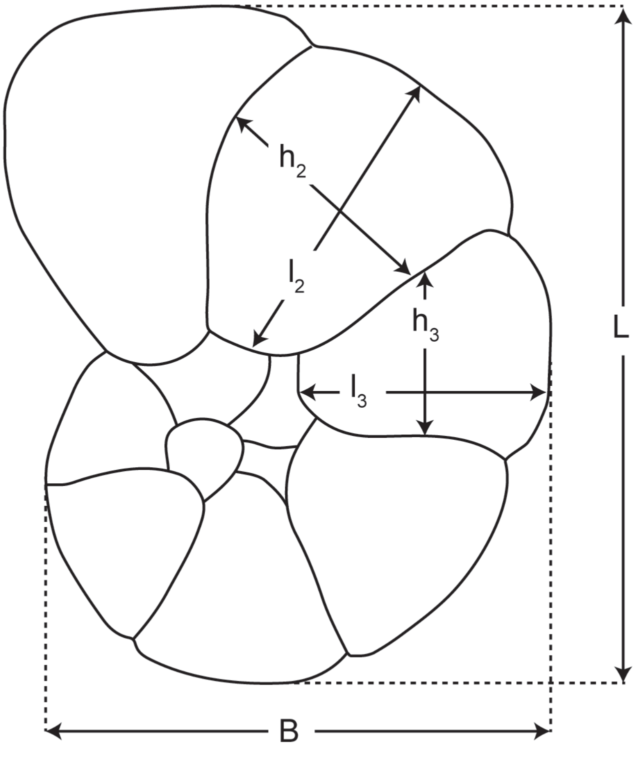

Figure 2. Biometrical parameters measured in *T. aguayoi* and *R. douvillei*. L: test length = largest diameter; B: test breadth (orthogonal to the largest diameter); l_2, l_3: length of the second and third last chambers; h_2, h_3: height of the second and third last chambers. Simplified from Foresi *et al*. (2004).

3. SYSTEMATIC PALAEONTOLOGY

Kingdom **CHROMISTA** Cavalier-Smith, 2010

Subkingdom **HAROSA** Burki *et al*., 2007

Infrakingdom **RHIZARIA** Cavalier-Smith, 2002

Phylum **FORAMINIFERA** d´Orbigny, 1826

Class **GLOBOTHALAMEA** Pawlowski, Holzmann & Tyszka, 2013

Order **ROTALIIDA** Delage & Hérouard, 1896

Superfamily **DISCORBOIDEA** Ehrenberg, 1838

Family **Rosalinidae** Reiss, 1963

Genus *Rosalina* d'Orbigny, 1826

Rosalina douvillei (Cushman, 1928)
(Figs. 3a-f)

1928 *Discorbis douvillei* Cushman, p. 54, Pl. 3, fig. 1.
1958 *Discorbis globularis* (d'Orbigny), Batjes, p. 145, Pl. 7, fig. 2.
1966 *Discorbis douvillei* Cushman, Le Calvez, p. 409, Pl. 2, figs. 3-7.
1970 *Rosalina douvillei* (Cushman), Le Calvez, p. 140-141, Pl. 29, figs. 3-5.
1983 *Rosalina douvillei* (Cushman), Setiawan, p. 115, Pl. VIII, fig. 2.
1984 *Rosalina douvillei* (Cushman), Odrzywolska-Bienkowa & Pozaryska, p. 133-134, Pl. 6, fig. 7.
1984 *Rosalina douvillei* (Cushman), Márquez & Usera, p. 226, Pl. 1, figs. 2 a-c, Pl. 2, figs. 1 a-c, 2 a-c.

Description. The original description of Cushman (1928) is as follows (translation from French is ours): "Test flat-convex; the dorsal side forms a wide and low spire. Ventral side flat or slightly concave, periphery rounded; chambers very differentiated, slightly inflated; dorsal sutures oblique, ventral sutures very shallow; wall smooth on the dorsal side, finely perforated on the ventral side with particular protuberances protruding towards the umbilical region; opening ventral with a broad border."

Occurrence. *Rosalina douvillei* is a brackish water species that has been found in the upper Eocene (Priabonian) of northern Italy (Setiawan, 1983; Barbin & Keller-Grünig, 1991) and Poland (Odrzywolska-Bienkowa & Pozaryska, 1984), in the lower Oligocene of the Paris Basin and in Belgium (Batjes, 1958; Le Calvez, 1966, 1970), in the upper Oligocene of Aquitaine (Andreieff *et al*., 1974), in the Oligocene-Miocene boundary of the Mainz Basin in Germany (Bernabé *et al*., 1991), in the lower Miocene of Buñol (Márquez & Usera, 1984, 1988) and finally in the

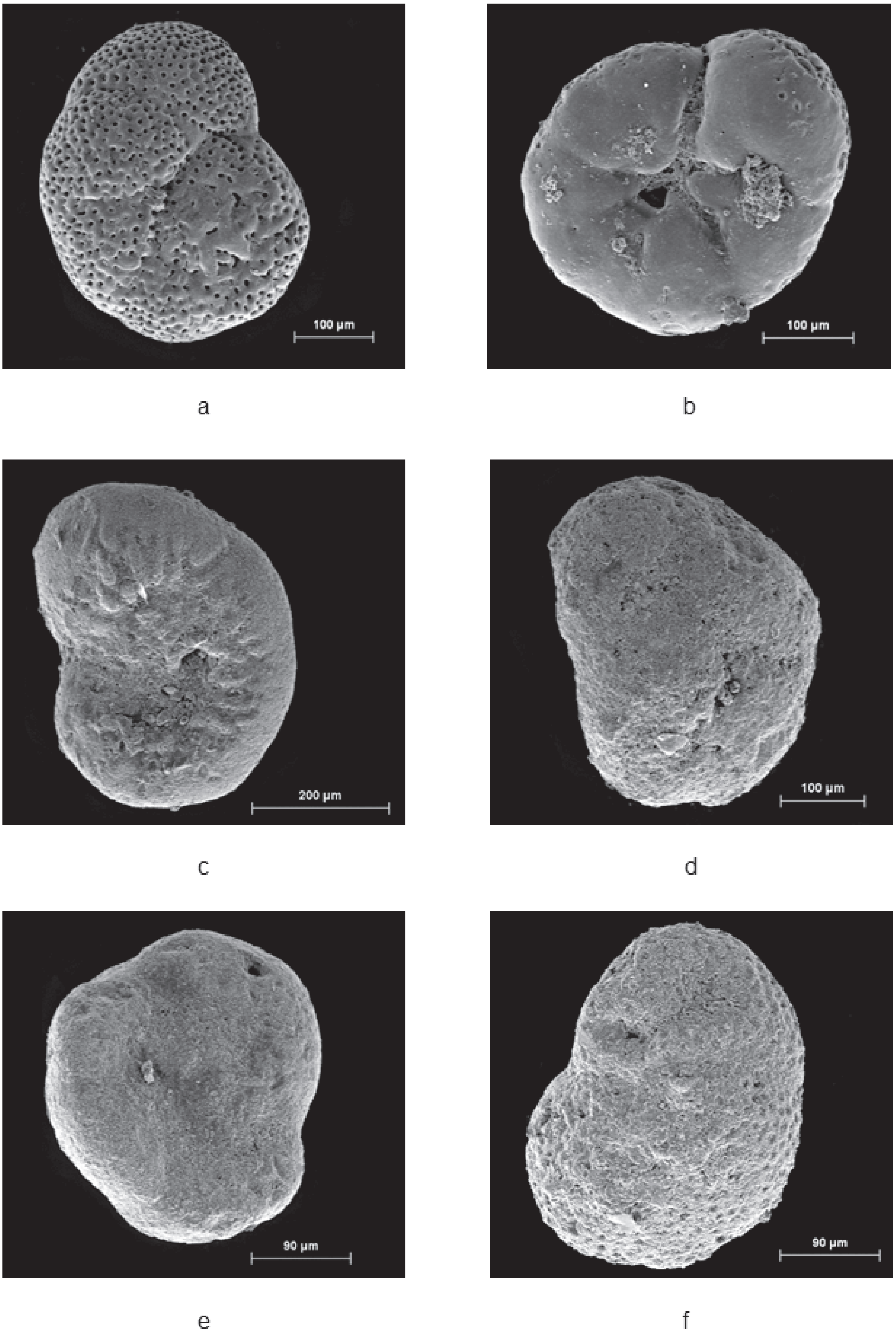

Figure 3. **a)** *Rosalina douvillei* (Cushman, 1928). Buñol. Spiral view. Microspheric form. Lower Miocene. **b)** *Rosalina douvillei*. Buñol. Umbilical view. Macrospheric form. Lower Miocene. **c)** *Rosalina douvillei*. Fuendetodos. Umbilical view. Macrospheric form. Middle/upper Miocene. **d)** *Rosalina douvillei*. Fuendetodos. Spiral view. Macrospheric form. Middle/upper Miocene. **e)** *Rosalina douvillei*. Rüssingen. Umbilical view. Macrospheric form. Upper Oligocene/lower Miocene. **f)** *Rosalina douvillei*. Rüssingen. Spiral view. Macrospheric form. Upper Oligocene/lower Miocene.

middle/upper Miocene of the Ebro Basin (Anadón, 1989, 1992; Usera *et al*., 1991a; Anadón *et al*., 1997).

Superfamily **CHILOSTOMELLOIDEA** Brady, 1881

Family **Trichohyalidae** Saidova, 1981

Genus *Trichohyalus* Loeblich & Tappan, 1953

Trichohyalus aguayoi (Bermúdez, 1935)
(Figs. 4a-f)

1935 *Discorbis aguayoi* Bermúdez, p. 204, Pl. 15, figs. 10-15.
1954 *Discorinopsis aguayoi* (Bermúdez), Arnold, p. 4-13, Pl. 1, figs. 2-10, Pl. 2, figs. 1-17.
1968 *Trichohyalus tropicus* (Bermúdez), Albani, p. 117, Pl. 10, figs. 13-14.
1969 *Trichohyalus aguayoi* (Bermúdez), Tufesco, p.47, figs. 1-2.
1974 *Lamellodiscorbis aguayoi* (Bermúdez), Resig, p. 75, Pl. 1, figs. 15-16.
1979 *Discorinopsis aguayoi* (Bermúdez), Scott *et al*., p. 257, Pl. 16, figs. 1-2.
1983 *Discorinopsis aguayoi* (Bermúdez), Boltovskoy & Hincapié de Martínez, p. 218, Pl. 2, figs. 8-9.
1990 *Discorinopsis aguayoi* (Bermúdez), Scott *et al*., p. 730, Pl. 1, figs. 6 a-b.
1991 *Discorinopsis aguayoi* (Bermúdez), Scott *et al*., p.385, Pl. 2, figs. 17-18.
1991 *Trichohyalus lacunae* (Silvestri), Albani *et al*., p. 34, Pl. 1, figs. 9-10.
1997 *Trichohyalus aguayoi* (Bermúdez), García-Forner, p. 108, Pl. 18, fig. 6, Pl. 19, fig. 1.
2003 *Discorinopsis aguayoi* (Bermúdez), Javaux & Scott, p. 14, figs 6-1, 6-2.
2004 *Discorinopsis aguayoi* (Bermúdez), Foresi *et al*., p. 326-329, Pl. 1, figs. 1-10, Pl. 2, figs. 1-11, Pl. 3, figs. 1-12, Pl. 4, figs. 1-13.
2005 *Trichohyalus aguayoi* (Bermúdez), Blázquez, p. 113, Pl. 10, fig. 6, Pl. 11, fig. 1.
2007 *Trichohyalus aguayoi* (Bermúdez), Guillem, p. 135-140, Pl. XVI, figs. 4-6, Pl. XVII, figs. 1-4, Pl. XXII, figs. 2, 4-6, Pl. XXIII, fig. 4, Pl. XXIV, figs. 3-4, Pl. XXV, figs. 1-2, Pl. XXVI, figs. 1-6, Pl. XXVIII, fig. 2, Pl. XXIX, figs. 4-6, Pl. XXX, figs. 5-6, Pl. XXXI, figs. 2-5.

Description. The original description of this species by Bermúdez (1935) is (translation from Spanish is ours): "Test vitreous, slightly trochoid, outline circular peripheral, smoothly lobed; margin rounded; dorsal side formed by numerous subglobular chambers; ten chambers in the last whorl, perforated by numerous remarkable holes; sutures limbate in the first whorls, depressed in the last whorl; all sutures limbate in some specimens; proloculus visible on the dorsal side: ventral side flat, with a large vitreous callus that occupies almost the entire surface; this callus is formed by a plate with radial riblets and rugosities, not reaching the lateral edge of the chambers; in specimens that have lost the last chamber wall it can be seen that this callus is partly free, forming a vitreous wall. Light brown coloured. Aperture a slit at the base of the last chamber, in contact with the whorl edge; broken specimens show inner chambers openings as a half-moon shape on the ventral edge of the whorl."

Occurrence. *Trichohyalus aguayoi* was originally described in littoral waters in Cuba (Bermúdez, 1935) and later reported in different brackish environments in the Caribbean and the Gulf of Mexico (Arnold, 1954; Boltovskoy & Hincapié de Martínez, 1983; Scott *et al*., 1991), in the Mediterranean and the Black Sea (Tufesco, 1969, 1973; Lévy, 1982; Albani *et al*., 1991; Zampi *et al*., 1996; Foresi *et al*., 2004), in the Atlantic (Javaux & Scott, 2003) and the Pacific coast of North America (Murray, 1991), in Hawaii (Resig, 1974), in South America (Boltovskoy & Vidarte, 1977; Scott *et al*., 1990) or even in Australia (Albani, 1968), where a very similar species, possibly co-specific with *T. aguayoi*, *Trichohyalus tropicus* (Collins, 1958), has also been found in non-marine saline lakes (Cann & De Dekker, 1981). In the Iberian Peninsula, this species is limited to the Mediterranean area and has been reported living in the Ebro Delta (Usera *et al*., 1989; Cearreta *et al*., 2016) in the Santa Pola Salinas (Zaninetti, 1984) or in the Torreblanca lagoon (Usera *et al*., 1990b; Arco *et al*., 1991; Guillem, 2007).

As a fossil, *T. aguayoi* has been detected as far back as in Messinian (upper Miocene) brackish lake deposits in Rosignano Marittimo by Foresi *et al*. (2004), who also report this species in Pliocene brackish lagoon sediments in Granaiolo (both localities in Tuscany, Italy). In the Iberian Peninsula it has been recorded in marsh or brackish lagoon Quaternary sediments, always in the Mediterranean area, in Catalonia (Calzada, 1970) or in the Valencian Community (Robles *et al*., 1985; Dupré *et al*., 1988; Mateu & Viñals, 1990; García-Forner *et al*., 1993; Viñals *et al*., 1993; López Buendía, 1995; Usera *et al*., 1996, 2001, 2003, 2006b, 2012; García-Forner, 1997; Blázquez & Ferrer, 2003; Usera, 2003; Blázquez & Usera, 2004, 2005; Blázquez, 2005; Ferrer *et al*., 2005; Carmona *et al*., 2016).

4. RESULTS

The basic results of the biometric analysis are shown in Table 1. As a whole, the *T. aguayoi* specimens are significantly longer (Mann-Whitney's U, $p = 0.001$ for

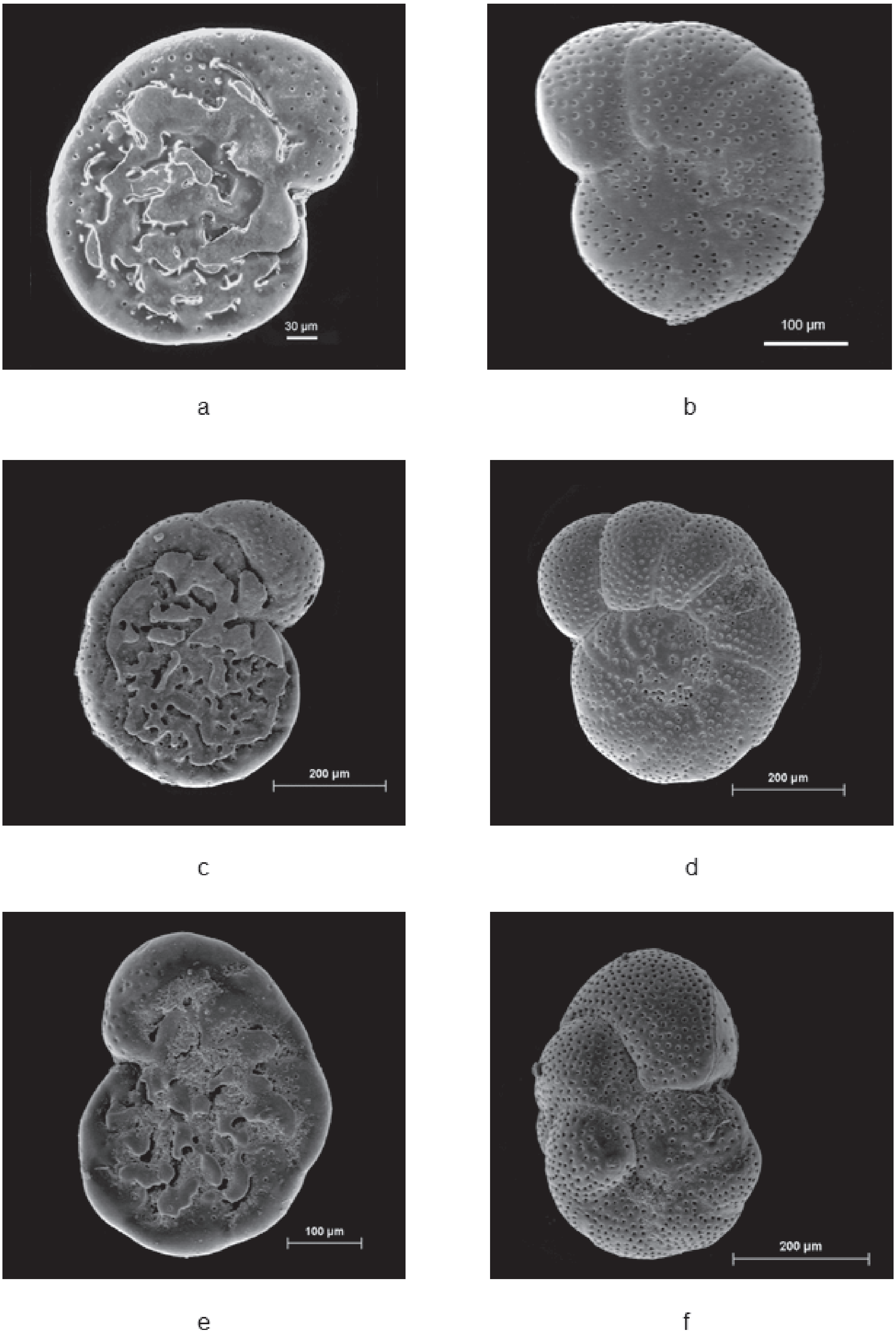

Figure 4. **a)** *Trichohyalus aguayoi* (Bermúdez, 1935). Peñíscola. Umbilical view. Macrospheric form. Holocene. **b)** *Trichohyalus aguayoi*. Torreblanca. Spiral view. Macrospheric form. Recent. **c)** *Trichohyalus aguayoi*. Torreblanca. Umbilical view. Macrospheric form. Recent. **d)** *Trichohyalus aguayoi*. Torreblanca. Spiral view. Macrospheric form. Recent. **e)** *Trichohyalus aguayoi*. Albufera of Valencia. Umbilical view. Macrospheric form. Holocene. **f)** *Trichohyalus aguayoi*. Albufera of Valencia. Spiral view. Macrospheric form. Holocene.

test length L) than the *R. douvillei* selected ones, and they are generally wider, although the difference in measured test breadth (B) is only significant at a 95% confidence level (Mann-Whitney's U, $p = 0.011$). Nevertheless, both parameters strongly co-vary in a very similar way in the two species ($r^2 = 0.970$ and 0.935 for *T. aguayoi* and *R. douvillei*, respectively, with a $p \approx 0$ in both cases) (Fig. 5). *Trichohyalus aguayoi* is also characterised by longer second and third last chambers (e.g., averages values $l_2 = 137$ and $l_3 = 121$ µm in *T. aguayoi vs.* $l_2 = 108$ and $l_3 = 84$ µm in *R. douvillei*; Mann-Whitney's U, $p = 2.05 \times 10^{-5}$ for l_2 and $p = 4.33 \times 10^{-8}$ for l_3) (Table 1). In contrast, the third last chamber height (h_3) is fairly equal in both species and the second last chamber is even slightly higher in *R. douvillei* (Mann-Whitney's U for h_2, $p = 0.045$), particularly in the specimens from Fuendetodos (Table 1; Figs. 6-7).

Therefore, *T. aguayoi* can be distinguished from *R. douvillei* by more elongate chambers and generally higher length: height (l_2/h_2 and l_3/h_3) ratios (Fig. 8). Average values are significantly higher for *T. aguayoi* ($l_2/h_2 = 1.682$ and $l_3/h_3 = 1.489$) than for *R. douvillei* ($l_2/h_2 = 1.177$ and $l_3/h_3 = 1.073$; Mann-Whitney's U, $p \approx 0$). Length and height exhibit a moderate but still significant positive correlation for both the second ($r^2 = 0.476$ for *T. aguayoi* and 0.629 for *R. douvillei*, $p = 8.35 \cdot 10^{-12}$) and the third ($r^2 = 0.744$ for *T. aguayoi* and 0.531 for *R. douvillei*, $p = 1.12 \times 10^{-13}$) last chambers.

The measured tests can also be distinguished by the number of chambers in the last whorl. In *T. aguayoi*, this parameter ranges from 5 to 10, although most individuals show 7-8 chambers. In *R. douvillei*, they vary between 4 and 8 but the large majority of tests exhibit 5-6 chambers (Fig. 9). The difference between the mean values in the two species (7.63 for *T. aguayoi* and 5.76 for *R. douvillei*) is again highly significant (Mann-Whitney's U, $p \approx 0$). This is clearly linked to the aforementioned difference in chamber shape (l_2/h_2 and l_3/h_3 ratios) since more chambers per whorl involve less space for each one of them.

Additional parameters were calculated basing on the metric measurements. The index of test curvature (L/B ratio), also represented in Figure 9, yields similar results for *T. aguayoi* (range = 1.11-1.49, average = 1.26) and *R. douvillei* (range = 0.90-1.38, average = 1.21) with slightly lower values for the latter. The chamber length and height increase rates (l_2/l_3 and h_2/h_3 ratios) are also comparable in both species, with strongly overlapping ranges (Fig. 10), although *R. douvillei* shows slightly higher average values ($l_2/l_3 = 1.32$ for *R. douvillei vs.* 1.16 for *T. aguayoi*; and $h_2/h_3 = 1.21$ for *R. douvillei vs.* 1.06 for *T. aguayoi*).

Table 1. Range (minimum and maximum) and average values of the seven basic parameters measured in *T. aguayoi* and *R. douvillei* tests recovered from the six selected localities. L: test length; B: test breadth; l_2: length of second last chamber; h_2: height of second last chamber; l_3 length of third last chamber; h_3: height of third last chamber; nc: number of chambers in the last whorl. All measures in µm except for nc.

		L	B	l2	h2	l3	h3	nc
Torreblanca	range	206-500	167-397	71-214	48-127	63-190	56-127	6-10
	average	312	249	129	80	112	80	7.72
L'Albufera	range	175-603	143-492	63-262	40-127	32-254	40-143	5-9
	average	331	264	137	80	123	77	7.48
Peñíscola	range	171-540	135-429	60-246	56-135	48-214	40-143	6-9
	average	350	278	146	87	127	85	7.68
Total	**range**	**171-603**	**135-492**	**60-262**	**40-135**	**32-254**	**40-143**	**5-10**
T. aguayoi	**average**	**331**	**264**	**137**	**82**	**121**	**80**	**7.63**
Rüssingen	range	183-444	159-333	56-183	48-127	48-183	48-167	4-7
	average	183	208	94	84	77	78	5.64
Buñol	range	175-333	143-325	56-135	40-127	32-135	48-95	6-8
	average	237	199	83	76	67	66	6.44
Fuendetodos	range	206-595	167-484	71-262	63-238	48-183	56-151	4-6
	average	362	297	148	122	109	96	5.20
Total	**range**	**175-595**	**143-484**	**56-262**	**40-238**	**32-183**	**48-167**	**4-8**
R. douvillei	**average**	**284**	**235**	**108**	**94**	**84**	**80**	**5.76**

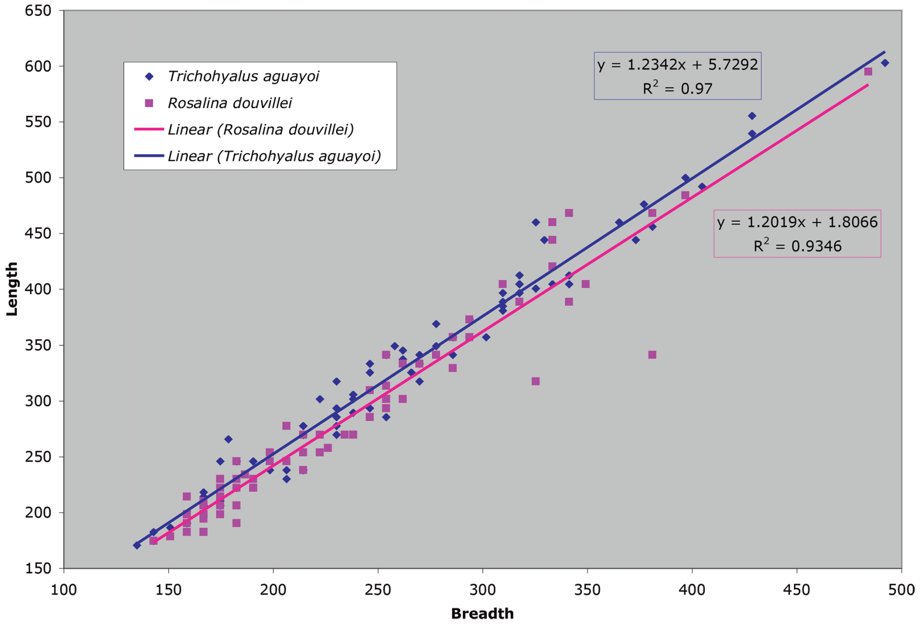

Figure 5. Test length (L) *versus* breadth (B) of *R. douvillei* (pink) and *T. aguayoi* (blue). All measures in µm. Regression lines and equations together with the r^2 coefficient are also shown.

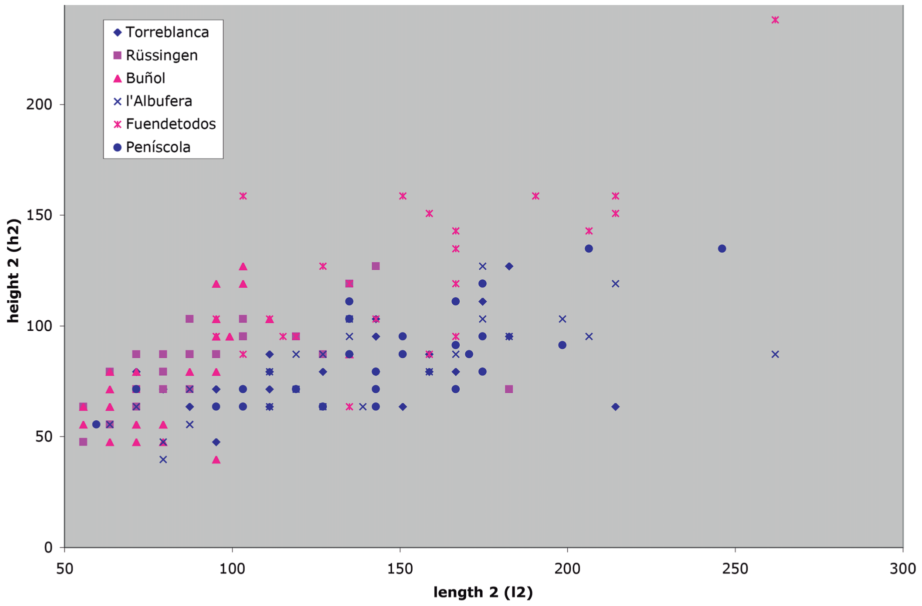

Figure 6. Height h_2 *versus* length l_2 (in µm) of the second last chamber of *R. douvillei* (pink) and *T. aguayoi* (blue).

The one-way ANOVA test reveals significant differences between the selected localities for every one of the parameters and ratios considered. Table 2 shows the results of a subsequent *post hoc* pairwise comparison between the localities employing the Tukey's HSD test (since the normality and equality of variances requirements for an ANOVA test were not always completely met, a Kruskal-Wallis test was carried out in each case to confirm results).

As expected, there are no relevant differences between the *T. aguayoi* localities, Torreblanca, l'Albufera and Peñíscola, in any of the measured parameters. And, with only one exception (number of chambers in the last whorl), this is also the case between two of the *R. douvillei* sites: Rüssingen and Buñol. There are generally significant differences between both groups (Torreblanca-Albufera-Peñíscola and Rüssingen-Buñol) in some parameters like length of the second and third last chambers (l_2 and l_3), number of chambers in the last whorl (nc) and second and third last chambers elongation (l_2/h_2 and l_3/h_3), always higher in the *T. aguayoi* specimens. To a lesser extent this is also the case for the whole test size (Table 2).

The *R. douvillei* specimens from Fuendetodos, however, remarkably differ in some parameters from their co-specific tests and are closer to *T. aguayoi*. Their tests are significantly larger (both length L and breadth B) than those from Rüssingen or Buñol and comparable to the *T. aguayoi* tests (Tables 1-2). The same result has been found for the lengths of the second and third last chambers (l_2 and l_3) (Tables 2B-2C). The specimens from Fuendetodos are even characterized by the largest heights of the second last chamber h_2, significantly above the other five localities, which explains the aforementioned higher average values of h_2 for *R. douvillei* (Tables 1, 2B; Fig. 6). They also show higher size increase rates from the third to second last chambers (h_2/h_3 and particularly l_2/l_3) (Table 2F; Fig. 10).

Three of the explored parameters establish a taxonomically coherent separation between *T. aguayoi* and *R. douvillei* among the six localities considered. These are: 1) the number of chambers in the last whorl, always higher in *T. aguayoi* as already seen, and with some differences between the three *R. douvillei* sites (Table 2D); and, 2) the l_2/h_2 and l_3/h_3 ratios, with more elongate chambers in *T. aguayoi* (Table 2E). The occurrence of a Fuendetodos specimen with an extremely elongate third last chamber (Fig. 8) probably results in a l_3/h_3 mean ratio not significantly different from the *T. aguayoi* from Torreblanca (Table 2E), but the Kruskal-Wallis test confirms the separation between the *T. aguayoi* and the *R. douvillei* localities also in this case.

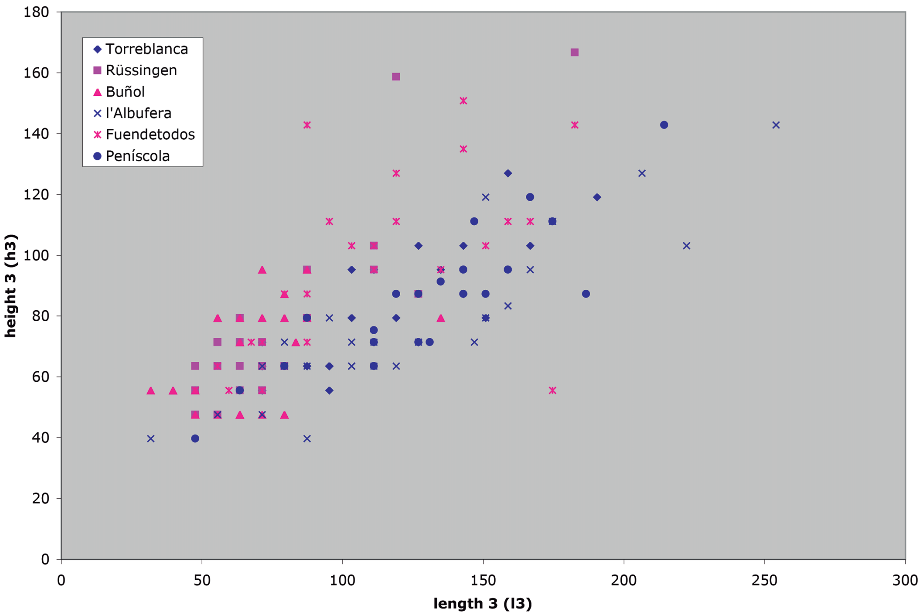

Figure 7. Height h_3 *versus* length l_3 (in µm) of the third last chamber of *R. douvillei* (pink) and *T. aguayoi* (blue).

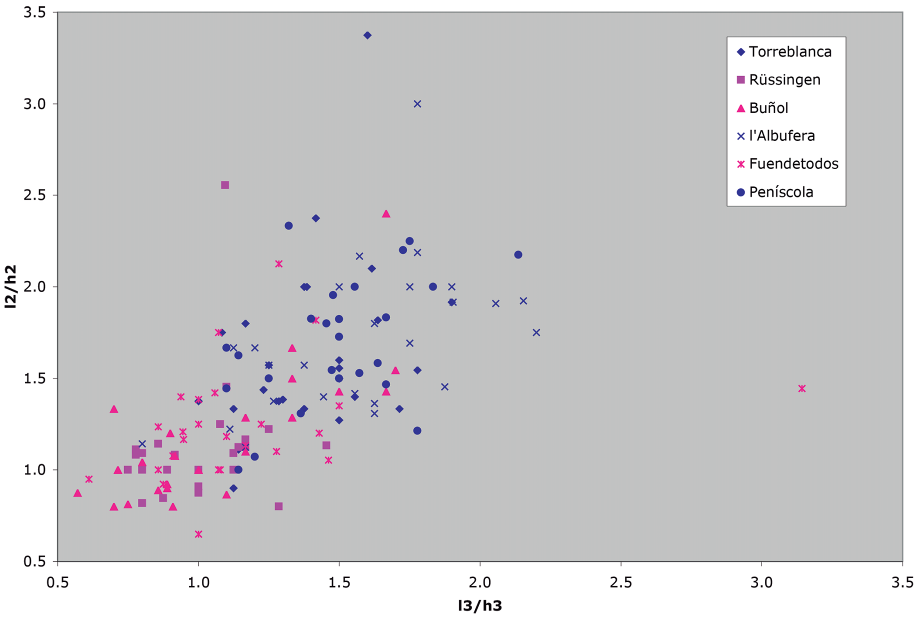

Figure 8. Length:height ratios of the second *versus* the third last chamber of *R. douvillei* (pink) and *T. aguayoi* (blue).

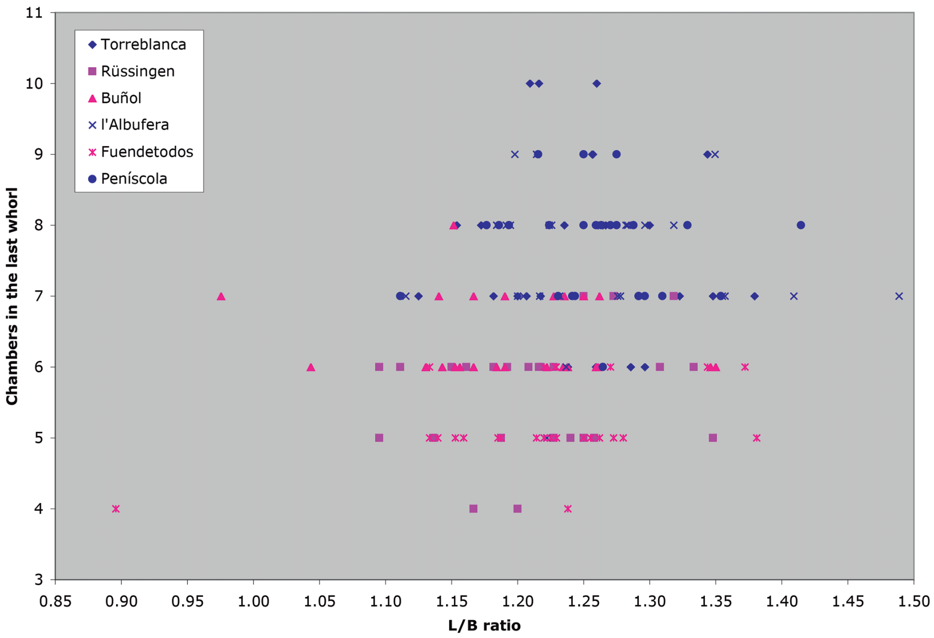

Figure 9. Number of chambers in the last whorl *versus* index of curvature (L/B ratio) in *R. douvillei* (pink) and *T. aguayoi* (blue).

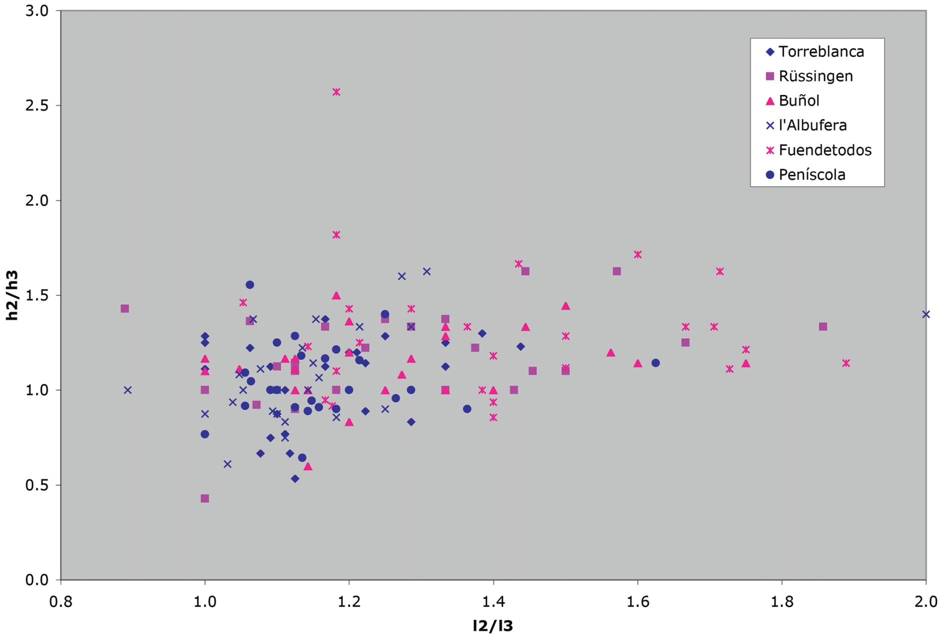

Figure 10. Increase rates in height (h_2/h_3) and length (l_2/l_3) of the second and third last chambers in *R. douvillei* (pink) and *T. aguayoi* (blue).

5. DISCUSSION

Rosalina douvillei and *Trichohyalus aguayoi* share many morphological characteristics. The results of the preliminary biometric analysis reveal that many parameters show similar ranges or average values in the two species, such as the height of the third last chamber and the index of test curvature (L/B ratio), or only slight differences, such as in the test breadth, the height of the penultimate chamber or the expansion rate (length and height) between the third and second last chambers. However, both species (at least the two sets of measured individuals) markedly differ in variables like the length and shape of the second and third last chambers and the number of chambers in the last whorl.

One of the main goals of the study by Foresi *et al.* (2004) was to distinguish between invariant (inherited) and ecophenotypic morphological features in *Discorinopsis aguayoi* (= *Trichohyalus aguayoi*) basing on the biometric study of four different brackish water populations (both fossil and recent) of this species in Tuscany (Italy). The measured *T. aguayoi* specimens in our selected localities (Table 1) do not reach the maximum test sizes of the Bermúdez (1935) syntypes (800 µm) but their length (L)

Table 2. Probabilities resulting from a Tukey's HSD pairwise comparison between localities subsequent to a one-way ANOVA for the parameters and ratios measured in *T. aguayoi* and *R. douvillei* tests. Asterisks show significant differences with * $p < 0.05$ and ** $p < 0.01$. **A)** Lower left: test length (L); upper right: test breadth (B). **B)** Lower left: second last chamber length (l_2); upper right: second last chamber height (h_2). **C)** Lower left: third last chamber length (l_3); upper right: third last chamber height (h_3). **D)** Lower left: test curvature ratio (L/B); upper right: number of chambers in the last whorl (nc). **E)** Lower left: length/height ratio for the second last chamber (l_2/h_2); upper right: length/height ratio for the third last chamber (l_3/h_3). **F)** Lower left: length increase rate (l_2/l_3); upper right: height increase rate (h_2/h_3).

A	Torreblanca	L'Albufera	Peñíscola	Rüssingen	Buñol	Fuendetodos
Torreblanca		0.976	0.677	0.267	0.105	0.130
L'Albufera	0.965		0.978	0.045*	0.012*	0.511
Peñíscola	0.609	0.973		0.004**	$7.75\cdot10^{-4}$**	0.918
Rüssingen	0.151	0.016*	$9\cdot10^{-4}$**		0.998	$7.40\cdot10^{-5}$**
Buñol	0.024*	0.001**	$6.03\cdot10^{-5}$**	0.984		$2.62\cdot10^{-5}$**
Fuendetodos	0.308	0.815	0.997	$1.28\cdot10^{-4}$**	$2.36\cdot10^{-5}$**	

B	Torreblanca	L'Albufera	Peñíscola	Rüssingen	Buñol	Fuendetodos
Torreblanca		1	0.904	0.985	0.994	$2.04\cdot10^{-5}$**
L'Albufera	0.986		0.926	0.991	0.990	$2.04\cdot10^{-5}$**
Peñíscola	0.630	0.950		0.999	0.608	$2.72\cdot10^{-5}$**
Rüssingen	0.016*	0.001**	$4.47\cdot10^{-5}$**		0.831	$2.12\cdot10^{-5}$**
Buñol	$3.77\cdot10^{-4}$**	$3.47\cdot10^{-5}$**	$2.04\cdot10^{-5}$**	0.922		$2.03\cdot10^{-5}$**
Fuendetodos	0.551	0.916	1	$3.35\cdot10^{-5}$**	$2.04\cdot10^{-5}$**	

C	Torreblanca	L'Albufera	Peñíscola	Rüssingen	Buñol	Fuendetodos
Torreblanca		0.998	0.977	1	0.380	0.169
L'Albufera	0.908		0.850	1	0.663	0.058
Peñíscola	0.677	0.998		0.931	0.080	0.583
Rüssingen	0.018*	$3.63\cdot10^{-4}$**	$6.14\cdot10^{-5}$**		0.521	0.102
Buñol	$4.73\cdot10^{-4}$**	$2.30\cdot10^{-5}$**	$2.05\cdot10^{-5}$**	0.929		$2.63\cdot10^{-4}$**
Fuendetodos	1	0.778	0.489	0.042*	0.002**	

D	Torreblanca	L'Albufera	Peñíscola	Rüssingen	Buñol	Fuendetodos
Torreblanca		0.916	1	$2.03\cdot10^{-5}$**	$2.13\cdot10^{-5}$**	$2.03\cdot10^{-5}$**
L'Albufera	0.994		0.960	$2.03\cdot10^{-5}$**	$2.07\cdot10^{-4}$**	$2.03\cdot10^{-5}$**
Peñíscola	0.997	1		$2.03\cdot10^{-5}$**	$2.29\cdot10^{-5}$**	$2.03\cdot10^{-5}$**
Rüssingen	0.544	0.224	0.263		0.010*	0.438
Buñol	0.133	0.030*	0.039*	0.9695		$2.29\cdot10^{-5}$**
Fuendetodos	0.701	0.348	0.398	1	0.908	

E	Torreblanca	L'Albufera	Peñíscola	Rüssingen	Buñol	Fuendetodos
Torreblanca		0.390	0.927	$1.29\cdot10^{-4}$**	0.001**	0.099
L'Albufera	0.994		0.934	$2.03\cdot10^{-5}$**	$2.04\cdot10^{-5}$**	$1.10\cdot10^{-4}$**
Peñíscola	0.998	1		$2.10\cdot10^{-5}$**	$3.54\cdot10^{-5}$**	0.005**
Rüssingen	$3.76\cdot10^{-5}$**	$2.12\cdot10^{-5}$**	$2.18\cdot10^{-5}$**		0.993	0.415
Buñol	$1.61\cdot10^{-4}$**	$2.98\cdot10^{-5}$**	$3.59\cdot10^{-5}$**	0.998		0.782
Fuendetodos	0.003**	$3.16\cdot10^{-4}$**	$4.68\cdot10^{-4}$**	0.869	0.982	

F	Torreblanca	L'Albufera	Peñíscola	Rüssingen	Buñol	Fuendetodos
Torreblanca		0.986	1	0.397	0.759	0.002**
L'Albufera	1		0.995	0.813	0.984	0.019*
Peñíscola	1	1		0.482	0.831	0.003**
Rüssingen	0.319	0.270	0.375		0.993	0.391
Buñol	0.396	0.340	0.457	1		0.130
Fuendetodos	$9.26\cdot10^{-5}$**	$6.62\cdot10^{-5}$**	$1.35\cdot10^{-4}$**	0.119	0.086	

Table 2. (Continued)

variation (171-603 µm) is totally within the range recorded by Arnold (1954) in laboratory specimens (60-750 µm, although these included also juvenile specimens). On the other hand, they encompass the limits observed by Tufesco (1969) in the Golovita lagoon in Romania (271-443 µm) and by Foresi *et al*. (2004) in their Italian localities (180-560 µm). The average length (331 µm) is almost identical to the one obtained by Foresi *et al.* (2004) in the locality of Montecatini (330 µm). The test breadth (B) range (135-492 µm) is also wider than the one observed in Golovita (200-343 µm) and somewhat lower, although with a strong overlap, than the variation (160-520 µm) recorded by Foresi *et al*. (2004). According to their study, size depends either on individual growth or on environmental conditions (salinity and others), as it has been established in foraminiferal ecological surveys (Boltovskoy & Wright, 1976). The size differences observed in general between *T. aguayoi* and *R. douvillei*, or between the *R. douvillei* specimens from Fuendetodos and those from Rüssingen or Buñol, might therefore be attributed to any of these two factors.

The curvature index (L/B) variation of the selected *T. aguayoi* specimens (1.11-1.49) is nearly identical to the one recorded by Tufesco (1969) in the Golovita lagoon (1.1-1.5) and reflects a more or less elongate test outline in this species. The *R. douvillei* specimens show a somewhat more circular outline (L/B range: 0.90-1.38) but without strong significant differences with the *T. aguayoi* localities (Table 2D). Foresi *et al*. (2004) report a high degree of variability in *T. aguayoi* and attribute the variation in this character to environmental conditions.

Chamber shape is less obviously related to external influences. The length:height ratios measured on the second and third last chambers in our *T. aguayoi* tests again yield mean values (l_2/h_2 = 1.65-1.71; l_3/h_3 = 1.40-1.58) well within the range observed in the Italian specimens (l_2/h_2 = 1.45-1.93; l_3/h_3 = 1.32-1.80 *sensu* Foresi *et al*., 2004), all of which still remain above those measured in the *R. douvillei* specimens (range of average l_2/h_2 = 1.12-1.24; l_3/h_3 = 1-1.17). So, *T. aguayoi* shows systematically narrower and more elongate second and third last chambers than *R. douvillei*. This pattern is persistent among the six studied localities, even taking into account the considerably higher second last chamber (high h_2) of the *R. douvillei* specimens from Fuendetodos. This is consistent with the attribution of the variation in this character to both environmental influences and heredity by Foresi *et al.* (2004).

As mentioned above, chamber shape cannot be considered as totally independent from the number of chambers in the last whorl. More chambers imply less space and consequently narrower and more elongate chambers. The *T. aguayoi* specimens show a range of 5-10, mainly 7-8 chambers in the outer whorl, nearly identical to that observed by Tufesco (1969) and by Foresi *et al.* (2004), who consider the maximum value as an invariant taxonomic character. This sets a marked difference, which is also constant in the studied six localities, with the specimens of *R. douvillei*, characterised by 4-8 (mainly 5-6) chambers in the last whorl. It is interesting to note that the Fuendetodos specimens show the lowest number of chambers (4-6), which is consistent with their higher second last chamber (Tables 1, 2B) and also with their larger chamber size increase (l_2/l_3 and h_2/h_3).

Finally, the complexity of the umbilical calcareous filling is attributed by Foresi *et al.* (2004) to the availability of $CaCO_3$. This structure is always present in *T. aguayoi* but in *R. douvillei* it is much reduced or absent in microspheric forms. Its function is unclear. Unfortunately, the number of macrospheric forms among the selected tests was too low to establish confident biometric comparisons. The relative scarcity of the macrospheric form was already recorded by Márquez & Usera (1988) in Buñol.

The absence of significant differences between the *T. aguayoi* specimens of the studied localities is not surprising. The three localities are closely related both geographically and ecologically. All correspond to Mediterranean coastal lagoons located in the Valencian Community and therefore they are/were presumably subject to very similar environmental conditions. Moreover, they are either Holocene or Recent in age, so there are no significant chronological gaps between them. In contrast, the *R. douvillei* sites are from different geographical areas that range from the Oligocene/Miocene to the middle/upper Miocene. In addition, they correspond to different environments from marginal marine-influenced areas (Rüssingen) to continental lakes (Buñol). Nevertheless, the specimens from Rüssingen and Buñol are relatively similar to each other (Table 2) and markedly different from the Fuendetodos tests. These differences, if confirmed by further research, might be explained by local environmental characteristics in a restricted area (the nature of the Fuendentodos palaeoenvironment is problematic, see Anadón *et al.*, 1997) or by the chronological interval separating Fuendetodos from the other sites (at least 4 Ma from Buñol and about 11 Ma from Rüssingen), but probably additional factors (e.g., evolutionary change) cannot be ruled out.

The morphological similarities between *T. aguayoi* and *R. douvillei* suggest a similar mode of life. *Trichohyalus aguayoi* is a euryhaline species living in shallow warm-temperate brackish waters. It has an epiphytic/epifaunal or shallow infaunal life style and thrives in fine grain sediments rich in organic matter and macrophyte remains (Tufesco, 1969). *Rosalina douvillei* has also been always found in brackish waters deposits (e.g., Le Calvez, 1970), either in marginal marine areas or in saline lakes. Little is known however about its life style. Like *T. aguayoi*, its low trochospiral test is coherent with an epiphytic or epifaunal life, with its aperture and its mainly imperforate umbilical side turned towards the substrate and its perforate spiral side exposed to the open water (Hottinger, 2000). Extant representatives of this genus, such as *Rosalina globularis* d'Orbigny, 1826, are indeed epiphytic, although they are strictly marine species (e.g., Colom, 1974; Martins & Dragao-Gomes, 2004).

As stated above, *R. douvillei* has a long stratigraphic range that lasts from the upper Eocene up to the Miocene. The last known occurrence of this species is dated as middle/upper Miocene (Anadón *et al.*, 1997) whereas the oldest known *T. aguayoi* are Messinian (upper Miocene) in age (Foresi *et al.*, 2004), which results in a cronostratigraphic separation of roughly 4-6 Ma between the two species. Despite their many similar morphological traits, including a calcareous umbilical filling, they are classified in different non-closely related taxonomic groups and the generic status of *T. aguayoi* in particular is problematic. Its classification in *Discorinopsis* (Scott *et al.*, 1990, 1991) would still place this species in the agglutinated order Textulariida (Hayward *et al.*, 2017). On the other hand, according to Le Calvez (1970), *R. douvillei* represents an intermediate evolutionary stage between the Eocene *Rosalina quadrata* Terquem, 1882 and the Miocene to Recent *R. globularis*. As far as it is known to us, no genetic foraminiferal study including *T. aguayoi* and any extant representative of *Rosalina* (e.g., *R. globularis*) has been carried out yet.

Thus, the question as to whether the observed similarities between *T. aguayoi* and *R. douvillei* constitute another case of morphological convergence, as it has been repeatedly the case in the evolution of foraminifera (Tappan & Loeblich, 1988), or they are the consequence of a close taxonomic proximity between the two species, cannot be elucidated here. A preliminary comparison between the upper Miocene (Messinian) specimens of *T. aguayoi* from Rosignano Marittimo studied by Foresi *et al.* (2004) and their chronostratigraphically closest *R. douvillei* tests from the middle/upper Miocene site of Fuendetodos still shows that the *T. aguayoi* tests are considerably larger, they have more chambers in the last whorl (6-10) and their second and third last chambers are clearly more elongate, which seems to point to different lineages with morphological affinities derived from their similar habitat. Further research to improve knowledge about the stratigraphic range of the two species and more complete biometric comparisons (including more specimens and additional biometric parameters) between their Miocene representatives may help to clarify their eventual relationship.

6. CONCLUSIONS

The biometric analysis of randomly selected tests from six Neogene and Quaternary localities reveals two taxonomically and morphologically coherent groups: the three *T. aguayoi* localities, Torreblanca, l'Albufera, and Peñíscola, and two of the *R. douvillei* sites, Rüssingen and Buñol. Both groups share some morphological characteristics such as the curvature ratio, the heights of the second and third last chambers and the chamber size increase and differ in others like size and chamber length.

Due probably to several factors (e.g., environmental conditions in a restricted basin, evolutionary change), the *R. douvillei* tests in Fuendetodos display peculiar characteristics: they are as large as *T. aguayoi* and show the highest second last chambers and the highest chamber size increase rates. Apart from this, *T. aguayoi* is always characterised by more chambers in the last whorl and more elongate second and third last chambers than *R. douvillei*, which confirms that chamber shape and the number of chambers in the last whorl are at least in part related to heredity factors. Further research is required to clarify if the affinities between the two species are due to phylogenetic proximity or, more probably, to morphological convergence between two non-related taxa, derived from a similar habitat.

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