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Recently isolated Atlantic neighbours: Insular populations of wall lizards (*Podarcis bocagei* and *Podarcis guadarramae*) across the Rías Baixas (Galicia, NW Spain)

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Lizards are probably one of the most resilient vertebrate groups of insular environments, as well as good colonisers via oversea dispersal events (i.e. rafting), and thus they became one of the most favourite taxonomic groups for island evolutionary studies. The most notorious case is the Caribbean *Anolis* group, which represents a textbook example of adaptive radiation in island ecosystems (Losos, 2011). Many of the present *Anolis* species evolved in sympatry (i.e. within an island) through niche shifts (e.g. trophic, habitat use, behaviour), and repeatedly across islands, leading to the classification of "ecomorphs" (Williams, 1983). However, phenotypic and genetic differentiation among insular populations also result from allopatric processes, where severe drift acted upon small insular populations. Thus, both neutral and adaptive forces accumulate genomewide variation and shape phenotypic patterns of insular lizard populations at different time scales. Land bridge insular populations that recently got isolated from the mainland constitute good natural laboratories to test predictions formulated with the theory of island biogeography (MacArthur and Wilson, 1967).

The *Rías Baixas* are five inlets of the Atlantic Ocean at the north-western corner of the Iberian Peninsula (Galicia): *Ría de Corcubión*, *Ría de Muros e Noia*, *Ría de Arousa*, *Ría de Pontevedra* and *Ría de Vigo* (Figure 1). These inlets originated with the sea-level rise after the last glaciation (ca. 14,000 years BP). As a result, coastal lowlands (i.e. river valleys) were flooded while mountain/hill tops along the former coastal line became islands and islets of different sizes, shapes and habitats (Figure 2). The age of these land bridge islands and islets also differ depending on their distance to the mainland and bathymetric levels, ranging from ca. 8,000 to hundreds of years BP (Pannekoek, 1966; Dias et al., 2000). During this process, some species persisted in these relatively recent insular environments, which led to vicariant events and morphological and genetic differentiation processes. For instance, insular populations of the fire salamander, *Salamandra salamandra*, diverged morphologically, behaviourally and genetically from their mainland counterparts, but also evolved from ancestral larviparity to viviparity (Velo-Antón et al., 2012; Velo-Antón and Cordero-Rivera 2017; Lourenço et al., 2018), which constitutes a remarkable example of reproductive shift at intra-specific level and a rapid evolution towards viviparity. Alike, the Bosca´s newt, *Lissotriton boscai*, fits into a vicariant biogeographic model that supports the reduction of genetic diversity and lack of contemporary gene flow in the two present insular populations (Lourenço et al., 2018). Other amphibians and reptiles occur in some of the islands scattered across the *Rías Baixas*, such as an anuran (*Discoglossus galganoi*), three snakes (*Zamenis scalaris*, *Natrix maura* and *Coronella girondica*), two skinks (*Chalcides striatus, Chalcides bedriagai*), a slowworm (*Anguis fragilis*) and three lacertids (*Timon lepidus*, *Podarcis guadarramae*, *Podarcis bocagei*) (see Galán, 2003), although the biogeographic histories of these species are largely unknown. Undoubtedly, wall lizards are the most successful group in these insular environments, occupying not only the large islands where other vertebrates co-occur, but also small islets dispersed across each of the five inlets (Galán, 1999), where no other non-volant vertebrates co-occur.

Podarcis guadarramae lusitanicus occurs in north-western Iberia (Geniez et al., 2014), and it is abundant along the western Galician coast. It is a typical wall lizard of flat appearance and a flat head, and of small size (adult snout-vent length: males 41.5 mm to 62.5 mm, mean 51.5, adult females 40 mm to 60 mm, mean 48.7;

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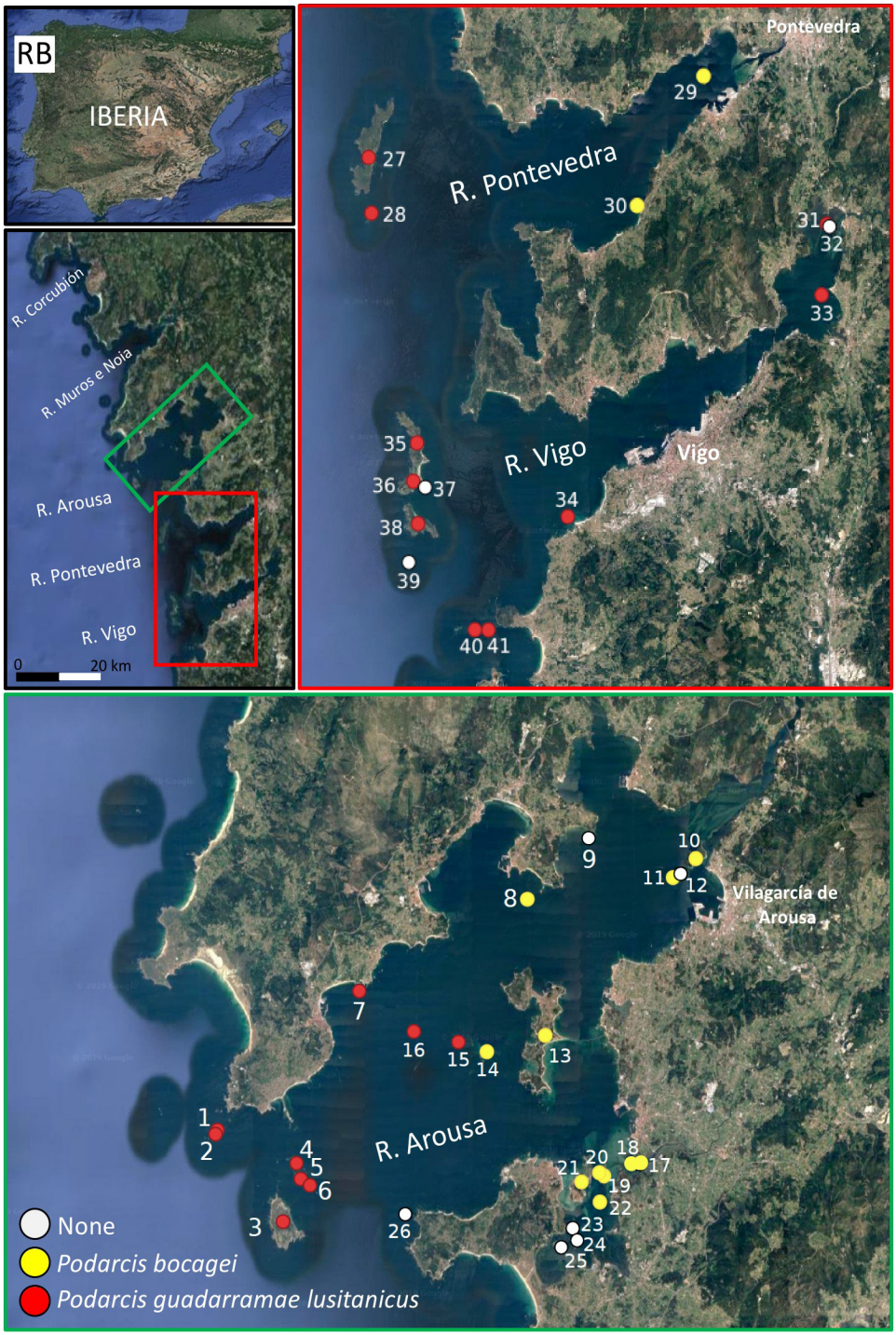

Figure 1. Location of the five inlets of the *Rias Baixas* (RB) (white inset in the Iberian map): *R. Corcubión, R. Muros e Noia*, *R. Arousa*, *R. Pontevedra* and *R. Vigo*. The studied islands and islets are represented in two detailed maps for *R. Arousa*, and *R. Pontevedra and R. Vigo*. *Podarcis bocagei* and *P. guadarramae lusitanicus* are represented in yellow and red circles, respectively. Islets where no wall lizards were observed are represented in white circles. Numbers correspond to each island ID reported in Table 1.

Table 1. List of the 41 islands and islets surveyed in the *Rías Baixas* (Arousa, Pontevedra and Vigo). For each island the location (in decimal degrees), the size (in hectares), and distance to the closest mainland (in km) are reported. The presence/non recorded of both *Podarcis guadarramae* and *P. bocagei* is indicated in each island based on this study and reviewed literature. References: [1]Mateo, 1997; [2]Galán, 1999; [3]Galán, 2003; [4]Arntzen and Sá-Sousa, 2002; [5]Băncilă and Arntzen, 2016; [6]Băncilă et al. 2010; [7]This study. *Populations of *P. g. lusitanicus* were wrongly reported as *P. bocagei* in these islands due to their phenotypic similarities (e.g. robust appearance).

ID	Ría	Lat.	Long.	Island	Area	Distance	Species	Reference
1	Arousa	42.51	-9.05	Sagres de Terra	1.9	0.8	*P. g. lusitanicus*	2*,3,7
2	Arousa	42.51	-9.05	Sagres de Fora	4.4	1	*P. g. lusitanicus*	2*,3,7
3	Arousa	42.47	-9.01	Sálvora	187,0	3.7	*P. g. lusitanicus*	2*,3,4,5,6,7
4	Arousa	42.50	-9.00	Vionta	11.3	2.6	*P. g. lusitanicus*	2*,3,4,5,6,7
5	Arousa	42.49	-9.00	Herbosa	1.5	3.1	*P. g. lusitanicus*	2*,3,6,7
6	Arousa	42.49	-9.00	Noro	3,0	3.5	*P. g. lusitanicus*	2*,3,4,5,6,7
7	Arousa	42.57	-8.97	Coroso	0.7	0.3	*P. g. lusitanicus*	4,5,6,7
8	Arousa	42.60	-8.88	Bensa	1.2	0.9	*P. bocagei*	1,2,4,6,7
9	Arousa	42.63	-8.84	Ostral	0.6	0.3	-	7
10	Arousa	42.62	-8.78	Cortegada	54,0	0.2	*P. bocagei*	2,3,4,6,7
11	Arousa	42.61	-8.80	Malveira grande	1.8	1.6	*P. bocagei*	2,3,4,6,7
12	Arousa	42.61	-8.79	Malveira pequena	0.6	1.2	-	3,7
13	Arousa	42.55	-8.87	Arousa	500,0	1.9	*P. bocagei*	2,4,6,7
14	Arousa	42.54	-8.90	Areoso	3.5	5.2	*P. bocagei*	2,4,6,7
15	Arousa	42.55	-8.92	Pedregoso	3,0	6.4	*P. g. lusitanicus*	2*,4,5,6,7
16	Arousa	42.55	-8.94	Rúa	3.5	2.7	*P. g. lusitanicus*	2,4,5,7
17	Arousa	42.50	-8.82	Illa do Este	0.9	0.1	*P. bocagei*	7
18	Arousa	42.50	-8.82	Illa do Oeste	1.2	0.35	*P. bocagei*	7
19	Arousa	42.49	-8.83	Toxa pequena	11,0	0.45	*P. bocagei*	1,2*,4,6,7
20	Arousa	42.49	-8.84	Ortigueira	0.4	0.8	*P. bocagei*	7
21	Arousa	42.49	-8.85	Toxa grande	99,0	0.35	*P. bocagei*	2*,7
22	Arousa	42.48	-8.84	Beiro	1.5	0.4	*P. bocagei*	1,2*,4,6,7
23	Arousa	42.47	-8.85	Loraña	0.8	0.3	-	7
24	Arousa	42.46	-8.86	Tourís novo	4,0	0.4	-	7
25	Arousa	42.47	-8.85	Marma N	0.6	0.6	-	7
26	Arousa	42.48	-8.94	Pombeiro	1.6	0.4	-	7
27	Pontevedra	42.37	-8.94	Ons	420,0	3.7	*P. g. lusitanicus*	1,2,3,7
28	Pontevedra	42.35	-8.94	Onza	26,0	7.5	*P. g. lusitanicus*	1,2,3,7
29	Pontevedra	42.41	-8.71	Tambo	27,0	0.9	*P. g. lusitanicus*	1,2,7
30	Pontevedra	42.35	-8.75	O Santo	0.9	0.1	*P. bocagei*	7
31	Vigo	42.34	-8.62	Alvedosa norte	0.5	0.5	*P. g. lusitanicus*	7
32	Vigo	42.34	-8.62	Alvedosa sur	0.4	0.6	-	7
33	Vigo	42.31	-8.63	San Simón	3.5	0.4	*P. g. lusitanicus*	1,2,7
34	Vigo	42.20	-8.80	Toralla	9,0	0.6	*P. g. lusitanicus*	1,2,7
35	Vigo	42.24	-8.90	Monteagudo	182,0	2.6	*P. g. lusitanicus*	1,2,3,7
36	Vigo	42.22	-8.91	Faro	106,0	4.2	*P. g. lusitanicus*	1,2,3,7
37	Vigo	42.21	-8.90	Viños	0.7	4.5	-	3,7
38	Vigo	42.20	-8.90	San Martiño	146,0	5.15	*P. g. lusitanicus*	1,2,3,7
39	Vigo	42.18	-8.91	Boeiro	0.5	5.5	-	3,7
40	Vigo	42.15	-8.86	Estela de fora	5,0	1.2	*P. g. lusitanicus*	1,2,7
41	Vigo	42.15	-8.86	Estela de dentro	6.7	0.5	*P. g. lusitanicus*	1,2,7

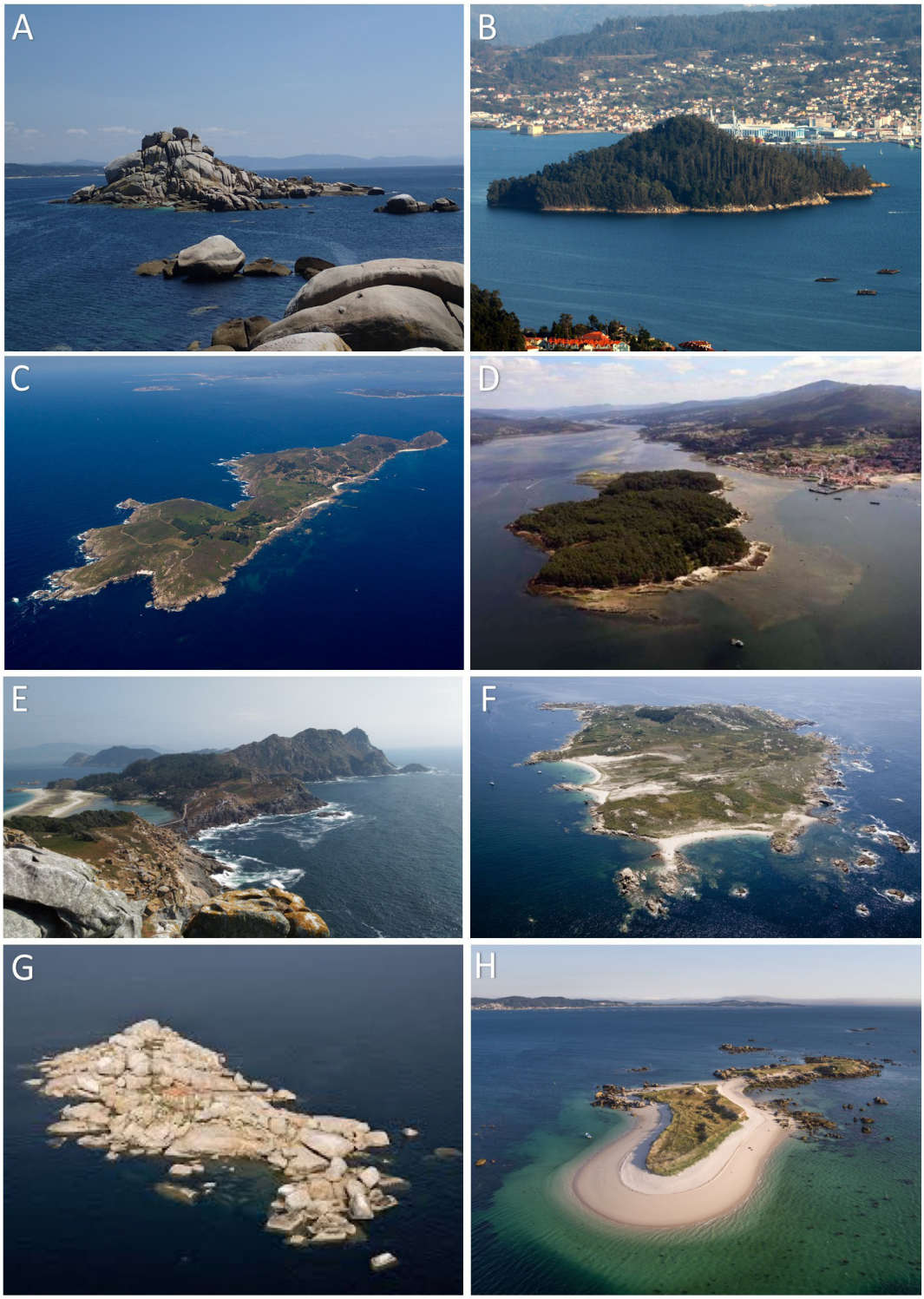

Figure 2. Images of some of the insular environments occupied by wall lizards: Noro (A), Tambo (B), Ons (C), Cortegada (D), Cíes arquipelago (E), Sálvora (F), Rúa (G), and Areoso (H). Some of these images (C, D, F, H) were obtained from the public portal of the Galician goverment (ww.turismo.gal).

Geniez et al., 2014), although insular populations in this study system show insular gigantism (Galán, 2003; data unpublished). *Podarcis bocagei* is also restricted to north-western Iberia and of similar body size as *P. guadarramae* (adult snout-vent length: males 43.3 mm to 64.9 mm, adult females 41.0 mm to 61.9 mm; Galán, 2009). The head of *P. bocagei* is higher than in *P. guadarramae* and the body has a robust appearance. Males of both species also differ in coloration, with *P. bocagei* showing yellow undersides (white in *P. guadarramae*) and green dorsal pattern (brownish in *P. guadarramae*) (Figure 3). Both species compete across their ranges, with *P. g. lusitanicus* restricted to natural rocky habitats (i.e. granite rock substrates) while *P. bocagei* is more ground-dwelling than the latter, and also occupies man-made structures such as stone walls (Galán, 2003; Geniez et al., 2014). In insular environments the two species usually exclude each other (Arntzen and Sá-Sousa, 2007), being *P. g. lusitanicus* the most common wall lizard across these inlets (Galán, 2003; Arntzen and Sá-Sousa, 2007; Băncilă et al., 2010; Băncilă and Arntzen, 2016).

Despite previous works reporting, and studying, some of the insular *Podarcis* populations across the *Rías Baixas* (Table 1), several small islets where wall lizards can occur have never been explored, or their presence never reported. Thus, I aim to provide an updated inventory of the presence of wall lizard populations (*P. bocagei* and *P. guadarramae*) in all islands and islets distributed in the three main inlets (hereafter Vigo, Pontevedra and Arousa). For this, I visited all of the 10 islands (> 25 hectares) and 31 islets (0.5-20 hectares) (Table 1). All islands and some islets were visited several times since 2004, while other islets were surveyed only once. Surveys were done during spring and summer when climatic conditions were appropriate for wall lizards' activity. The distances of these islands and islets to their closest mainland varies between 0.1 km and 7 km (Table 1). Small islets that re-connect to mainland during low tides where not included in this inventory. I also reviewed published information about insular populations of both species (Mateo, 1997; Galán, 1999; 2003; Arntzen and Sá-Sousa, 2007; Băncilă et al., 2010; Băncilă and Arntzen, 2016).

The number of islands is similar in the three inlets (three in Vigo and Pontevedra and four in Arousa), while the number of islets is disproportionally higher in Arousa, with up to 22 islets spread across this inlet, compared to one and eight islets present in Pontevedra and Vigo, respectively. I here report on twelve *P. bocagei* and 20 *P. g. lusitanicus* insular populations in the study area. All main islands harbour *Podarcis* populations, with the most inner islands (Arousa, Cortegada, Tambo, Toxa grande) are inhabited by *P. bocagei*, while islands located at the entrance of each inlet are occupied by *P. g. lusitanicus* (San Martiño, Faro, Monteagudo, Onza, Ons, Sálvora). Most of the surveyed islets contain *Podarcis* populations, with *P. bocagei* restricted to the inner islets of Arousa and the islet of Pontevedra (O Santo), while *P. g. lusitanicus* occupies outer islets of Arousa, and all the islets of Vigo (Table 1). Galán (1999) noted other insular populations of *P. bocagei* north of the *Ría de Arousa*.

Molecular data support the isolation of some of the insular populations from Arousa (Arntzen and Sá-Sousa, 2007; Băncilă and Arntzen, 2016), likely resulted from processes of population isolation and drift. However, oversea dispersal events between nearby islets with *P. bocagei* (Areoso) and *P. g. lusitanicus* (Pedregoso) were suggested to explain mitonuclear introgression and past hybridisation events between both species (Arntzen and Sá-Sousa, 2007). Băncilă and Arntzen (2016) also reported lower genetic diversity in insular populations of *P. g. lusitanicus* compared to mainland counterparts, with the islets showing lower genetic diversity. To investigate the biogeographic scenario of insular *Podarcis,* genetic analyses need to be extended to all the islands and islets where wall lizards occur. As it happened with other terrestrial species in this insular-mainland system (Velo-Antón et al., 2012; Lourenço et al., 2018), insular *Podarcis* populations from all *Rías Baixas* might have evolved independently from their mainland counterparts, constituting independent evolutionary units that persisted since their isolation. An independent evolutionary history of these insular *Podarcis* populations might be supported by morphological and morphometric differences found among insular populations (Galán, 2003; Băncilă et al., 2010; Băncilă and Arntzen, 2016; data unpublished). Insular populations of *P. g. lusitanicus* show larger body size than mainland populations, being also significantly different among islands, with the largest individuals occurring in small islets of *Ría de Arousa* (Galán, 2003, data unpublished). This survey will serve as a baseline for future studies focused on the evolutionary history of wall lizards in this insular mainland system, as well as to investigate the evolutionary and conservation implications of extremely small and isolated populations, where the exacerbated effects of genetic drift and potential adaptive pressures impact the genome-wide diversity and boost phenotypic and genetic differentiation (Velo-Antón et al., 2012).

Figure 3. *Podarcis guadarramae lusitanicus* in Noro (A), Vionta (B), San Martiño (C), Faro (D), Herbosa (E-F). *Podarcis bocagei* in Cortegada (G), and Areoso (H).

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