Morphometric differences in two calanoid sibling species, *Boeckella gracilipes* and *B. titicacae* (Crustacea, Copepoda)

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ABSTRACT. Calanoid copepods are abundant in South American inland waters and include widespread species, such as *Boeckella gracilipes* (Daday, 1902), which occurs from the Ecuador to Tierra del Fuego Island. This species occurs under various environmental conditions, and is found in oligotrophic lakes in Patagonia (39-54°S) and in shallow mountain lakes north of 39°S. The aim of the present study is to conduct a morphometric comparison of male specimens of *B. titicacae* collected in Titicaca and *B. gracilipes* collected in Riñihue lakes, with a third population of *B. gracilipes* collected in shallow ponds in Salar de Surire. Titicaca and Riñihue lakes are stable environments, whereas Salar de Surire is an extreme environment. These ponds present an extreme environment due to high exposure to solar radiation and high salinity levels. The results of the study revealed differences among the three populations. These results agree well with systematic descriptions in the literature on differences between the populations of Titicaca and Riñihue lakes, and population of Salar de Surire differs slightly from the other two populations. It is probable that the differences between the population of Salar de Surire and the other two populations result from the extreme environment in Salar de Surire. High exposure to solar radiation, high salinity and extreme variations in temperature enhance genetic variations that are consequently expressed in morphology.

KEYWORDS. *Boeckella*; fifth thoracopods; morphology; populations.

RESUMEN. Diferencias morfométricas en dos especies hermanas *Boeckella gracilipes* y *Boeckella titicacae* (Crustacea, Copepoda). Los copépodos calanoideos son abundantes en aguas continentales sudamericanas e incluyen especies de amplia distribución geográfica como *Boeckella gracilipes* (Daday, 1902) que se encuentra desde Ecuador hasta la isla de Tierra del Fuego. Esta especie vive bajo varias condiciones ambientales, y se encuentra en lagos oligotróficos en la Patagonia (39-54°S) y en lagunas superficiales de montaña al norte de los 39°S. El objetivo del presente trabajo es realizar un estudio comparativo morfométrico de machos de *B. titicacae* colectado en el lago Titicaca y *B. gracilipes* colectado en el lago Riñihue, ambos son ambientes estables, con una tercera población colectada en lagunas superficiales en el Salar de Surire. Estas lagunas tienen condiciones ambientales extremas debido a alta exposición a la radiación solar y altos niveles de salinidad. Los resultados del presente estudio encontraron diferencias entre las tres poblaciones. Estos resultados concordarían con las descripciones sistemáticas en la literatura sobre las diferencias de las poblaciones de los lagos Titicaca y Riñihue, y la población del salar de Surire tuvo leves diferencias respecto a las dos poblaciones anteriores. Es probable que las diferencias entre la población del Salar de Surire y las otras dos se deban a alta exposición a la radiación solar, salinidad y condiciones extremas de temperatura que acelera las diferencias genéticas las que se expresan en diferencias morfológicas.

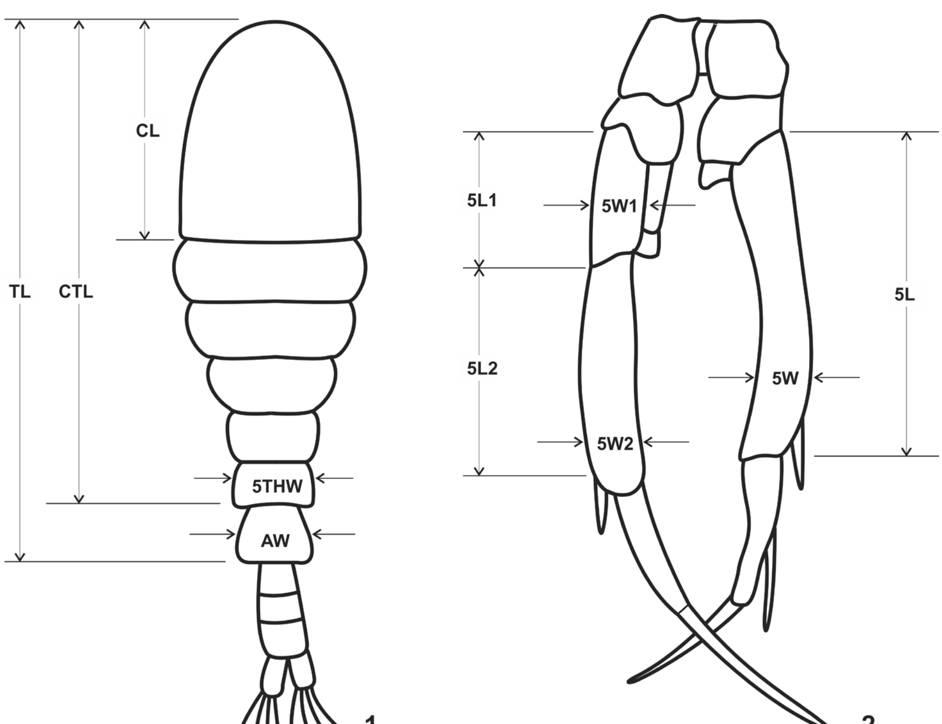
PALABRAS-CLAVE. *Boeckella*; quinto toracópodo; morfología; poblaciones.

Calanoid copepods are widespread in South American inland waters and are represented by two families, Centropagidae and Diaptomidae (Soto & Zúñiga, 1991; Menu-Marque *et al.*, 2000). Calanoids are abundant in South American inland waters because this group is tolerant to the oligotrophy of these ecosystems (De los Ríos & Soto, 2006), whereas in Andean lakes this group tolerates high-to-moderate salinity (< 90 g/l; De los Ríos & Crespo, 2004; De los Ríos & Contreras, 2005). This group includes widespread species that are found from tropical to temperate and subpolar latitudes, such as *B. gracilipes* (Daday, 1902), *B. gracilis* (Daday, 1902) and *B. poopoensis* (Marsh, 1906) (Menu-Marque *et al.*, 2000). Certain species inhabit different environmental gradients. For example, *B. poopensis* can tolerate salinities between 5-90 g/l (De los Ríos & Contreras, 2005), and *B. gracilipes* and *B. gracilis* inhabit shallow ponds and large lakes (Menu-Marque *et al.*, 2000). If we consider the environmental variation of these habitats and the exposure to extreme conditions that may include temperature variation, high salinity or natural ultraviolet radiation exposure, it is probable that substantial interpopulational variation occurs for each species as a consequence of the distinct geographical characteristics of different populations (Scheihing *et al.*, 2010). The species cited above include *B. gracilipes*, which is found from Ecuador to Tierra del Fuego Island (Bayly, 1992a; Menu-Marque *et al.*, 2000). It inhabits large, deep Patagonian lakes as well as shallow Andean and Patagonian lakes and ponds. These lakes and ponds are located primarily in the northern Andes mountains or Patagonian plains. Many of these habitats are oligotrophic, with low conductivity (3.1 mS/cm) and with high exposure to natural ultraviolet radiation (De los Ríos-Escalante, 2010). *Boeckella titicacae* Harding, 1955 was described as a species that inhabits Titicaca Lake and surrounding bodies of water (Bayly, 1992a; Scheihing *et al.*, 2010). Bayly (1992a,b) suggested that this species differs from others in the dimensions of the fifth thoracopod. Nevertheless, Bayly (1992a,b) does not characterise *B. gracilipes* and *B. titicacae* as different species or as morphotypes. This structure has a role in reproductive isolation because it allows the transfer of the spermatophore to the female during mating (Othsuka & Huys, 1991; Ferrari & Ueda, 2005). In contrast, Menu-Marque *et al.* (2000) stated that *B. titicacae* is a synonym of *B. gracilipes*. Scheihing *et al.* (2010) rejected this argument and proposed that the populations of Titicaca Lake represent a distinct to the species *B*. *titicacae*. This proposal is based on molecular evidence and on features of body morphology described by Villalobos & Zúñiga (1991).

Previous descriptions proposed that the morphology of the fifth thoracopod is sensitive to extreme environments (Pandourski & Evtimova, 2006, 2009). It is possible to find marked differences in the morphology of the fifth thoracopod in populations of the same species, as observed for *B*. *poppei* (Adamowicz *et al.*, 2007). The aim of the present study is to perform a morphometric comparison of males of *B*. *gracilipes* collected in a Patagonian Lake (Riñihe Lake) with males of *B*. *titicacae* from Titicaca Lake and with males of a third population of *B. gracilipes* collected in shallow ponds of Salar de Surire. This comparison will allow evaluation of the two different viewpoints existing in the literature (Villalobos & Zúñiga, 1991; Bayly, 1992a,b). Special consideration will be given to the morphometry of the fifth thoracopod, a structure that may be important for speciation because it can serve as an isolating mechanism in copepods. This structure can be used as a single trait to discriminate *B*. *gracilipes* and *B*. *titicacae* populations.

MATERIALS AND METHODS

Adult males were collected at two different sites. The first site was Copacabana Bay, Titicaca Lake, Bolivia (16°09'S; 69°04'W). The specimens from this site would correspond to *B*. *titicacae* (Bayly, 1992a,b). The annual temperature variation at the site is 3-25°C (Rieckerman *et al.*, 2006; Canales-Gutiérrez, 2010). The second population of *Boeckella gracilipes* was sampled at the Salar de Surire (18°51'S; 69°07'W), Chile, a saline deposit with pools at 3800 m a.s.l (Zúñiga *et al.*, 1999). The pools show a wide salinity gradient and are exposed to a daily temperature variation of 15°C. The minimum temperatures varied between 0-13°C from June through September, and the maximum temperatures vary between 18-20°C in December and January (Garcés, 2011). The third population of *Boeckella gracilipes* was sampled at the oligo-mesotrophic Riñihue Lake (Daday, 1902; Villalobos & Zúñiga, 1991; Soto & Zúñiga, 1991; De los Ríos & Soto, 2007), Chile (39°49'S; 72°19'W, 107 m a.s.l) a North Patagonian Lake with a surface area of 77.5 km^2 and an annual temperature variation of 9-20°C (Woelfl *et al.*, 2003). The specimens were fixed in absolute ethanol and identified according to the descriptions in Bayly (1992a,b). Thirty male specimens were selected for each population. A morphometric analysis of the body and fifth thoracopod was conducted (Villalobos & Zúñiga, 1991; Figs 1, 2). The characteristics measured were the total length (TL), cephalotorax length (CTL), cephalic length (CL), 5th thoracic segment width (5THW), abdominal segment width (AW), fifth thoracopod right segment length (5L), fifth thoracopod first right segment length



Figs. 1, 2. Morphological parameters considered in this study: 1, parameters considered in body (according Villalobos & Zúñiga, 1991); 2, parameters considered in fifth thoracopod (according Bayly, 1992a,b) (TL, total length; CTL, cephalotorax length; CL, cephalic length; 5THW, 5th thoracic segment width; AW, abdominal segment width; 5L, fifth thoracopod right segment length; 5L1, fifth thoracopod first right segment length; 5L2, fifth thoracopod second right segment length; 5W, fifth thoracopod right segment width; 5W1, fifth thoracopod first right segment width; 5W2, fifth thoracopod second right segment width).

(5L1), fifth thoracopod second right segment length (5L2), fifth thoracopod right segment width (5W), fifth thoracopod first right segment width (5W1), and fifth thoracopod second right segment width (5W2). The second viewpoint for morphometric comparison was included by measuring the following characteristics (Bayly, 1992a,b): the right segment length-to-width ratio (5L/5W); the second right segment length-to-width ratio (5L2/5W2); the first right segment length-to-width ratio (5L1/5W1); and the ratio between the sum of the total lengths of the first and second segments to the total length (5L1+5L2)/5L)). The ratios between the different values of length and width and the total length were also considered. A discriminant analysis was applied to the data. SPSS v.12.0 software was used for the analysis.

RESULTS AND DISCUSSION

We hypothesised that the three populations can be distinguished morphologically. We therefore defined *a priori* three groups of specimens: Titicaca Lake, Salar de Surire and Riñihue Lake. We were particularly interested to determine the morphological distances between our populations and to compare these distances with the geographical distances. The results revealed the large morphological differences between Titicaca and Salar de Surire and between Titicaca and Riñihue Lakes. However, only a slight morphological distance was detected between the Salar de Surire and Riñihue Lake populations (Fig. 3). Almost all of the parameters studied differed significantly (Tab. I). In general, the population of Titicaca Lake is large-bodied relative to the other two populations. The measurements of the fifth thoracopod (length and width, Tab. I) showed a similar trend. In contrast, the ratios involving different measurements of the fifth thoracopod were significantly higher for the population of Riñihue Lake in comparison to the other two populations. The results indicates that the populations were distinct based on the morphometric parameters (Fig. 3). Our findings for the Titicaca Lake population agree with the description in Bayly (1992a,b) of the differences between *B. gracilipes* and *B. titicacae*, and our findings for the population of Salar de Surire agree with the description of *B. titicacae* in Bayly (1992a,b) (Tab. II). Our findings for the population collected in Riñihue Lake do not agree with this description of *B. titicacae*, but they agree partially with the description of *B. gracilipes* in Bayly (1992a,b) (Tab. II).

According to the results of the discriminant analysis, the males of the three populations show marked morphological differences (Fig. 3). This finding may reflect the marked environmental characteristics of the different habitats. Riñihue and Titicaca Lakes are large and deep. Their environments are relatively stable. In contrast, the Salar de Surire is a habitat with extreme environmental conditions. Specifically, this habitat shows marked temperature variations and is exposed to high levels of natural ultraviolet radiation (Scheihing *et al.*, 2010). The morphological variation described in the current study agrees with the descriptions in Villalobos & Zúñiga (1991). Those authors found variation in populations that were described in the literature as *B. gracilipes*, not as *B. titicacae*. These populations were represented by specimens from Chungará and Villarrica Lakes (Chile) and from Parinacota and Negra lagoons

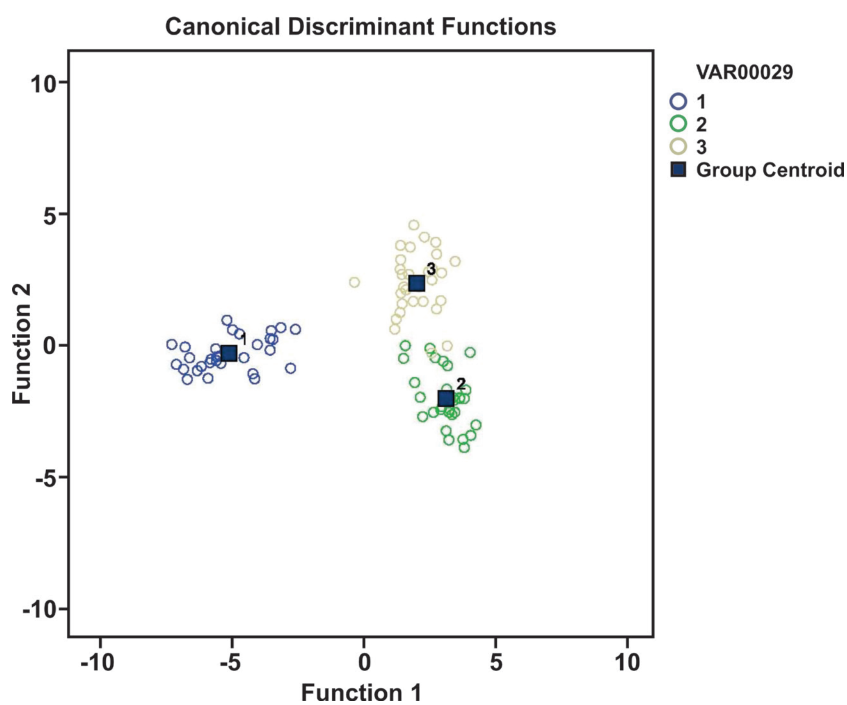


Fig. 3. Results of discriminant analysis for three populations of *Boeckella gracilipes* (Daday, 1902) studied: (1) Titicaca Lake; (2) Salar de Surire; (3) Riñihue Lake.

Tab. I. Average ± standard deviation and results of first step of discriminant analysis for parameters considered for three *Boeckella gracilipes* (Daday, 1902) populations considered in the present study (*P* values lower than 0.05 denotes significant differences)(TL, total length; CTL, cephalotorax length; CL, cephalic length; 5THW, 5th thoracic segment width; AW, abdominal segment width; 5L, fifth thoracopod right segment length; 5L1, fifth thoracopod first right segment length; 5L2, fifth thoracopod second right segment length; 5W, fifth thoracopod right segment width; 5W1, fifth thoracopod first right segment width; 5W2, fifth thoracopod second right segment width).

	Titicaca Lake (mm)	Salar de Surire (mm)	Riñihue Lake (mm)	F	P
TL	850.6±41.9	748.0±66.8	644.6±41.6	119.993	<0.001
CTL	664.6±40.2	535.2±111.2	500.6±30.8	45.035	<0.001
CL	281.3±28.2	299.1±111.7	229.3±14.6	8.782	<0.001
5THW	124.7±13.5	115.2±13.6	130.1±37.1	7.486	<0.001
AW	104.7±13.6	97.07±13.2	96.0±24.7	2.916	0.059
5L	287.6±18.2	249.3±22.1	312.0±23.6	2.067	0.133
5L1	59.7±5.4	55.0±14.3	87.9±15.4	65.280	<0.001
5L2	175.5±7.6	158.7±20.1	162.7±10.5	60.533	<0.001
5W	42.4±3.8	43.7±8.1	38.4±6.9	12.076	<0.001
5W1	61.1±4.9	49.0±6.1	50.7±2.6	5.338	0.007
5W2	54.0±5.8	43.3±6.6	45.2±3.5	56.518	<0.001
Ratios ± standard deviation of different ratios of fifth thoracopod regions, and other body zones					
5L2/5W2	3.3±0.4	3.74±0.7	3.6±0.4	56.518	<0.001
5L1/5W1	6.8±0.8	5.9±1.3	8.4±1.6	32.482	<0.001
(5L1±5L2)/5L	0.8±0.1	0.8±0.1	0.8±0.1	7.079	0.001
CTL/TL	0.782±0.031	0.717±0.148	0.778±0.043	62.738	<0.001
CL/TL	0.331±0.032	0.402±0.155	0.357±0.032	28.495	<0.001
LW/TL	0.218±0.031	0.283±0.148	0.222±0.043	4.079	0.020
5THW/TL	0.147±0.015	0.155±0.019	0.203±0.058	4.740	0.011
THAW/TL	0.123±0.015	0.130±0.019	0.150±0.040	4.497	0.014
5L/TL	0.339±0.025	0.335±0.037	0.486±0.050	4.739	0.011
5L1/TL	0.070±0.007	0.074±0.021	0.137±0.026	20.310	<0.001
5L2/TL	0.207±0.010	0.213±0.030	0.253±0.020	7.804	0.001
5W/TL	0.050±0.006	0.059±0.013	0.060±0.011	148.516	<0.001
5W1/TL	0.072±0.005	0.066±0.010	0.079±0.006	108.103	<0.001
5W2/TL	0.064±0.007	0.059±0.012	0.070±0.006	40.205	<0.001

(Chile). The first studies of the problem do not indicate whether *B. titicacae* is a morphotype or subspecies of *B. gracilipes* or state whether the two taxa are actually different species (Bayly, 1992a,b; Menu-Marque *et al.*, 2000). Nevertheless, Scheihing *et al*. (2010) proposed that the population of Titicaca Lake belongs to the species *B. titicacae*. This proposal was based on morphological and molecular analysis.

A perspective from the viewpoint of reproduction would consider the important role of the fifth thoracopod pair as a mechanical isolating mechanism (Maly & Maly, 1991; Ohtsuka & Huys, 1991; Bayly, 1992a,b). This perspective would recognise the differences between *B. titicacae* and *B. gracilipes*, the morphometric discriminant parameters for *B. gracilipes* and *B. titicacae* described by Bayly (1992a,b) agree with the results for the populations of Titicaca Lake and Salar de Surire (Tab. II), but these descriptions do not agree with the results for the population of Riñihue Lake (Tab. II). A possible explanation of this apparent discrepancy would be that the descriptions of *B. gracilipes* in Bayly (1992b) are based on specimens collected in shallow Patagonian ponds. In that study, no descriptions are included for the populations of large, deep Patagonian lakes, such as Riñihue Lake or similar lakes, that are habitats of this species (Bayly 1992b; Menu-Marque *et al.*, 2000).

Suppose that one species, *B. gracilipes* (Menu-Marque *et al.*, 2000; Scheihing *et al.*, 2010), inhabits a wide geographical gradient and variety of habitats that includes lakes, ponds and pools between Ecuador and Tierra del Fuego island (Menu-Marque *et al.*, 2000), including subsaline lakes of the South American Altiplano (Bayly, 1993, 1995; De los Ríos & Contreras, 2005). It is possible to find differences in the fifth thoracopod pair within the same species. Similarly, these descriptions are consistent with the results of comparative studies of the frontal knobs in males of the brine shrimp *Artemia* (Crustacea, Branchiopoda) exposed to extreme environments, primarily to variation in salinity and temperature (De los Ríos & Zúñiga, 2000; De los Ríos & Asem, 2008). The salinity tolerance of *B. gracilipes* is low, varying between 0.1-3.7 g/L (De los Ríos & Contreras, 2005; Bayly & Boxshall, 2008). This species is exposed to high levels of ultraviolet radiation in tropical and subtropical latitudes (Cabrera *et al.*, 1997; Helbling *et al.*, 2002; Scheihing *et al.*, 2010) and in Patagonian inland waters (Marinone *et al.*, 2006). Salinity variations and ultraviolet radiation exposure are accelerators of molecular changes in aquatic crustaceans (Hebert *et al.*, 2002). These stressors

Tab. II. Results of morphometric criteria observed for discriminate *Boeckella gracilipes* (Daday, 1902) and *Boeckella titicacae* Harding, 1955, according to descriptions of Bayly (1992a,b) (5L, fifth thoracopod right segment length; 5L1, fifth thoracopod first right segment length; 5L2, fifth thoracopod second right segment length; 5L2, fifth thoracopod second right segment length; 5W, fifth thoracopod right segment width; 5W1, fifth thoracopod first right segment width; 5W2, fifth thoracopod second right segment width).

	B. gracilipes	*B. titicacae*
5W2/5L2	4.5×	3× Titicaca Lake Salar de Surire
(5L1±5L2)/5L	1×	0.7-0.8× Titicaca Lake Salar de Surire
(5L/5W)	5.5-6.0× Titicaca Lake	6.0-7.5× Titicaca Lake Salar de Surire

Tab. III. Results of discriminant analysis for studied parameters for three populations of *Boeckella gracilipes* (Daday, 1902).

Function	Eighenvalue	% Variance	% accumulated	Canonical correlation
1	13.823	80.4	80.4	0.996
2	3.366	19.6	100.0	0.878

could have potential teratological effects. These effects would be expressed in morphology such morphological differences have been described for *B. poppei* (Pandourski & Chipiev, 1999), a species that occurs at polar and subpolar latitudes in extreme environments with variations in temperature and levels of ultraviolet radiation similar to those cited for *B. gracilipes*. Similar results were described for *Eurytemora velox* Lilljeborg, 1853, *Eucyclops serrulatus* (Fisher, 1851), *Paracyclops fimbriatus fimbriatus* (Fisher, 1853) and *Acanthocyclops vernalis* (Fisher, 1853)(Pandourski & Evtimova, 2005).

In this scenario, the natural ultraviolet radiation exposure (Zagarese *et al.*, 1998; Helbling *et al.*, 2002; Tartarotti *et al.*, 2004) and salinity variations (De los Ríos & Contreras, 2005; Bayly & Boxshall, 2008) reported for the South American Altiplano and their potential effects as accelerators of molecular changes in aquatic crustacean species (Hebert *et al.*, 2002) would allow the occurrence of a speciation that would produce two different species, *B. gracilipes* and *B. titicacae* (Scheihing *et al.*, 2010). The results of the present study reveal the differences between the populations from Riñihue Lake that was described as *B. gracilipes* (Villalobos & Zúñiga, 1991; Soto & Zúñiga, 1991; De los Ríos & Soto, 2007) and the populations of Salar de Surire and Titicaca Lake (Fig. 3). The presence of two separate species would also be consistent with the descriptions in Scheihing *et al*. (2010). Although the morphological approach used in the present study differs from the approach used by Scheihing *et al.* (2010), the similar results of the two studies reveal the differences between *B. gracilipes* and *B. titicacae*. On this basis, it would be necessary to conduct further comparative studies of populations of both species and to include considerations of the marked environmental variation of the habitats of both species in these studies. The aim of this research would be to understand the potential genetic isolation of the populations (Gajardo & Beardmore, 2002).

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