

Is *Munida gregaria* (Crustacea: Decapoda: Munididae) a truly transpacific species?

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Abstract The “East Pacific Barrier” has been recognized as the World’s largest marine biogeographic barrier. *Munida gregaria* is the only species of its family with transpacific populations; however, it still remains to be elucidated whether these two distantly located populations belong to the same species. In this study, we investigated the genetic cohesion of *M. gregaria* across the East Pacific Barrier by analyzing mitochondrial markers. Cytochrome oxidase subunit I and NADH dehydrogenase subunit 1 genes were sequenced for individuals from different areas, i.e., the southeast Pacific, the southern tip of South America, the southwest Atlantic, and the southwest Pacific. A median-joining network, pairwise F_{ST} s, genetic diversity statistics, and neutrality tests were computed. Our results, i.e., the absence of different haplogroups on both sides of the East

Pacific Barrier and existence of shared haplotypes, showed that populations on both sides of this barrier belong to the same species. At a population genetic level, our results suggest that individuals from both regions have been connected, since although some differentiation was found between the southern tip of South America and the southwest Pacific, the southeast Pacific and southwest Atlantic showed no signs of differentiation from the southwest Pacific. In addition, our results provided evidence of a population expansion in southern South America during the Pleistocene. The role of Pleistocene glaciations and the Antarctic Circumpolar Current in shaping the distribution of sub-Antarctic marine invertebrates is discussed.

Keywords Marine biogeography · Squat lobsters · East Pacific Barrier · Antarctic Circumpolar Current · COI · ND1

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Introduction

The vast extension of deep water that separates the east Pacific (EP) from the central Pacific (4,000–7,000 km), a.k.a. East Pacific Barrier, has been recognized as the world’s largest marine biogeographic barrier (Lessios and Robertson 2006 and references therein). Several groups of fishes and invertebrates include “transpacific” species (Lessios et al. 1998; Lessios and Robertson 2006; Duda and Lessios 2009; Schnabel et al. 2011a). However, many of these are diagnosed on the basis of morphological characters, which may be misleading when the populations on either side of the barrier have undergone cryptic speciation (Lessios and Robertson 2006). Most studies investigating the effectiveness of this barrier to gene flow have involved tropical marine organisms (Lessios et al. 1998; Lessios and

Robertson 2006; Baums et al. 2012). However, the barrier is more pronounced at southern temperate latitudes. South America (EP) and New Zealand (NZ)—west Pacific (WP)—are separated by 7,500 km without islands, which would favor the dispersal of shallow-marine organisms through a stepping-stone migration process (Wood et al. 2014).

Squat lobsters are highly diversified and widespread anomuran decapods belonging to six families: Chirostyliidae, Eumunididae, Kiwaidae, Galatheidae, Munidopsidae, and Munididae (Baba et al. 2008; Ah Yong et al. 2010; Schnabel and Ah Yong 2010; Schnabel et al. 2011b). Species richness is highest in the WP Ocean, i.e., 80 % of the world's species of squat lobsters inhabit the Pacific Ocean, whereas only 11 % live in the EP region (including Hawaii), 23 % in the Indian Ocean, and 15 % in the Atlantic Ocean (Schnabel et al. 2011a). Macpherson et al. (2010) proposed the existence of a fundamental biogeographic division for squat lobsters between the Western–Central and EP, which is coincident with the East Pacific Barrier. Furthermore, the occurrence of endemic genera on both margins of the Pacific Ocean supports the hypothesis of long-term isolation between squat lobsters from both these regions (Macpherson et al. 2010; Schnabel et al. 2011b). On the other hand, the East Pacific Barrier was postulated to be permeable due to the existence of twelve transpacific species (Schnabel et al. 2011a).

Munida is the most diverse genus of the family Munididae comprising 242 species (Baba et al. 2008). Its members are generally found at continental shelf or slope depths in all major ocean basins (Baba et al. 2008), but diversity is highest in the south WP Ocean (SWP, Schnabel et al. 2011a). Of the 242 species described for this genus, only 43 are known to inhabit the Atlantic (Baba et al. 2008) and 17 the EP Ocean (Hendrickx 2003), in agreement with the general pattern of biodiversity described for squat lobsters. Recent molecular phylogenetic studies involving species of *Munida* from the SWP and related genera suggested a rapid radiation of the former in this area since the Middle or Late Miocene (7–14 mya, Machordom and Macpherson 2004).

Only five species of *Munida* are distributed around southern South America, i.e., *M. gregaria*, *M. montemaris* and *M. curvipes* in the Pacific Ocean (Hendrickx 2003), and *M. gregaria*, *M. spinosa*, and *M. iris* in the Atlantic Ocean (Spivak 1997). In particular, *M. gregaria* is found around NZ and southern Australia, from 36°S to 51°S, and around southern South America, from 41°S to 55°S in the Pacific Ocean and from 35°S to 55°S, including the Islas Malvinas/Falkland Islands, in the Atlantic Ocean (Tapella et al. 2002; Ah Yong and Poore 2004; Baba et al. 2008).

The Antarctic Circumpolar Current encircles Antarctica and connects the major ocean basins, i.e., Pacific, Atlantic, and Indian Oceans. It flows eastwards between about 40° and 60°S (Orsi et al. 1995; Reddy 2001), and currently represents

the largest ocean current in the world (Barker et al. 2007). New Zealand (NZ) and southern South America have been potentially connected since the establishment of this current during the Late Miocene (Dalziel et al. 2013). Despite this fact, *M. gregaria* is the only species of Munididae distributed on both sides of the East Pacific Barrier. It still remains to be elucidated whether the two distantly located populations belong to the same species.

Truly transpacific species share certain life history traits that could favor long-distance dispersal, i.e., planktonic larvae, long larval durations, and adult pelagic dispersal ability (Lessios et al. 1998; Robertson et al. 2004; Lessios and Robertson 2006). The larval development of *M. gregaria* consists of five or six zoeal stages and a megalopa, with a pelagic larval duration of about 4 months at 8 °C (Roberts 1973; Pérez-Barros et al. 2007). The larvae of this species are present in the plankton from August to March, i.e., from the end of winter throughout summer (Zeldis 1985; Lovrich 1999; Meerhoff et al. 2013; Dellatorre et al. 2014). In addition, its juveniles and adults may have a pelagic habit and swarming behavior that may facilitate their dispersal (Zeldis 1985; Diez et al. 2012).

The above-mentioned characteristics of *M. gregaria*, together with the potential capability of the Antarctic Circumpolar Current to carry propagules across the East Pacific Barrier, led us to hypothesize that gene exchange across the barrier has been sufficient to maintain species cohesion. In this study, we analyzed molecular data to investigate whether populations of *M. gregaria* on the two sides of the East Pacific Barrier belong to the same species.

Materials and methods

Sampling

Individuals of *M. gregaria* (morphs *gregaria* and *subrugosa*, see Pérez-Barros et al. 2008) were collected for molecular analysis between 2003 and 2009 from different localities, three in the southeast Pacific (SEP), i.e., southern Chile from Puerto Montt to Darwin Channel (Chonos Archipelago); four in the southwest Atlantic (SWA), i.e., Banco Burdwood, Islas Malvinas/Falkland Islands, Golfo San Jorge, and Golfo Nuevo; two in the southern tip of South America (STSA), i.e., Beagle Channel and Magellan Straits; and one in the SWP, at Otago, New Zealand (NZ) (Table 1; Fig. 1). Because of the dispersal capacity of this species, samples from each area, i.e., SEP, SWA, STSA, and SWP, were pooled as a single locality for all analyses (Fig. 1). All animals were fixed in EtOH 96 %.

Sequences from the Beagle Channel, Magellan Straits, and Banco Burdwood were obtained in a previous study (Pérez-Barros et al. 2008, Online Resource 1).

Table 1 Number of individuals of *Munida gregaria* per sampling area and their respective diversity indices based on the combined COI + ND1 mtDNA sequences

Sampling area	<i>N</i>	<i>k</i>	<i>H</i>	<i>S</i>	<i>Π</i>	<i>π</i>
Southeast Pacific	11	6	0.73	10	2.91	0.0032
Southern tip of South America	19	15	0.94	27	2.84	0.0031
Southwest Atlantic	21	13	0.86	20	2.97	0.0033
Southwest Pacific	13	9	0.94	14	3.9	0.0044
Total	64	37	0.90	50	3.18	0.0035

N specimens analyzed, *k* haplotype number, *H* haplotypic diversity, *S* polymorphic sites, *Π* mean number of pairwise differences, *π* nucleotide diversity

DNA extraction, amplification, and sequencing

Deoxyribonucleic acid (DNA) was extracted from gills/muscle using a salting-out protocol (Reiss et al. 1995). Fragments of two mitochondrial genes, cytochrome oxidase subunit I (COI) and NADH dehydrogenase subunit 1 (ND1), were amplified using primers LCO1490 and HCO2198 (Folmer

et al. 1994), and ND1af-P (5'-CGG TTG ATC TTC AAA TTG TAA-3') and ND1ar-P (5'-AAG CTT ATC ATA TCG TAA ACG A-3') (Pérez-Barros et al. 2008), respectively. Polymerase chain reactions (PCRs) were performed using Applied Biosystems, Primus and BioNer thermal cyclers in 10, 20, and 50 μ l reactions consisting of 20 ng of DNA, 0.2 mM of each dNTP, 2 mM/3 mM MgCl₂, 0.15 μ M of each primer, 0.025 U μ l⁻¹ of Taq, the corresponding buffer, and ddH₂O. Thermal cycling conditions consisted of an initial denaturation step of 94 °C for 3 min followed by 35–38 cycles at 94 °C for 30 s, 40 °C to 50 °C for 50 s, 72 °C for 1 min, and a final extension at 72 °C for 7 min.

Amplification products were cycle-sequenced in the sequencing facility of the Department of Ecology, Genetics and Evolution of the University of Buenos Aires.

Phylogeographic data analyses

Cytochrome oxidase subunit I and ND1 sequences were edited and aligned independently using BioEdit version

Fig. 1 Study locations included in the phylogeographic analysis of *Munida gregaria*. SEP southeast Pacific, STSA southern tip of South America, SWA southwest Atlantic, SWP southwest Pacific. Arrows indicate the approximate position of the Antarctic Circumpolar Current (ACC). EPB East Pacific Barrier



7.1.3 (Hall 1999). Sequences were translated into amino acids in MEGA version 5.1 (Kumar et al. 2001) to check for sequencing errors and for the presence of pseudogenes. All haplotype sequences were deposited in GenBank (Online Resource 1). COI and ND1 sequences belonging to the same individual were concatenated for further analysis.

Genealogical relationships between haplotypes were reconstructed as a median-joining network using Network version 4.6 (Bandelt et al. 1999). The level of genetic differentiation between individuals of different sampling areas was investigated by calculating pairwise F_{ST} s and their significance tested by 10,000 permutations. The level of polymorphism in *M. gregaria* from different sampling areas was determined by means of standard genetic diversity indices: haplotype number (k), number of segregating sites (S), haplotype diversity (H), and nucleotide diversity (π). Departures from neutral expectations/constant population size were investigated combining the sequences of all areas and for each area individually, by calculating Tajima's D (1989a, b) and Fu's F_s (1997) statistics, and their significance was estimated by performing 1,000 coalescent simulations. A mismatch analysis was conducted by combining the sequences of all areas, and for each area individually, in order to investigate the fit of the observed mismatch distribution to the one expected under an exponential population growth model (Librado and Rozas 2009). Possible expansions were dated following the expression $T = \tau/2\mu k$, where τ is the estimated number of generations since the expansion, μ is the mutation rate per site per generation, and k is the sequence length. Since the only calibrated mutation rate available corresponds to the COI gene, only COI sequences were used to calculate the τ used to time the expansion. Ho et al. (2005) recently described a dependency of molecular evolutionary rates on time, i.e., molecular population-level studies (1–2 myr) have much higher mutation rates, tenfold higher, than the long-term substitution rates inferred from phylogenetic studies (Ho et al. 2005, 2007). In this study, we used a COI substitution rate of 1.015 % per lineage per million years [average between rates reported for other decapods by Knowlton et al. (1993) and Schubart et al. (1998)]. However, since our estimates may be biased due to the time dependency of molecular evolutionary rates, a tenfold correction was also applied. A mean generation time of 2 year (see Tapella 2002) was used.

Pairwise F_{ST} s, genetic diversity indexes, Tajima's D , and Fu's F_s were calculated using Arlequin version 3.5 (Excoffier and Lischer 2010). The mismatch analyses were conducted in DnaSP 5.10 (Librado and Rozas 2009).

Results

Alignment lengths of the COI and ND1 sequences of the 64 *M. gregaria* analyzed were 516 and 397 bp, respectively

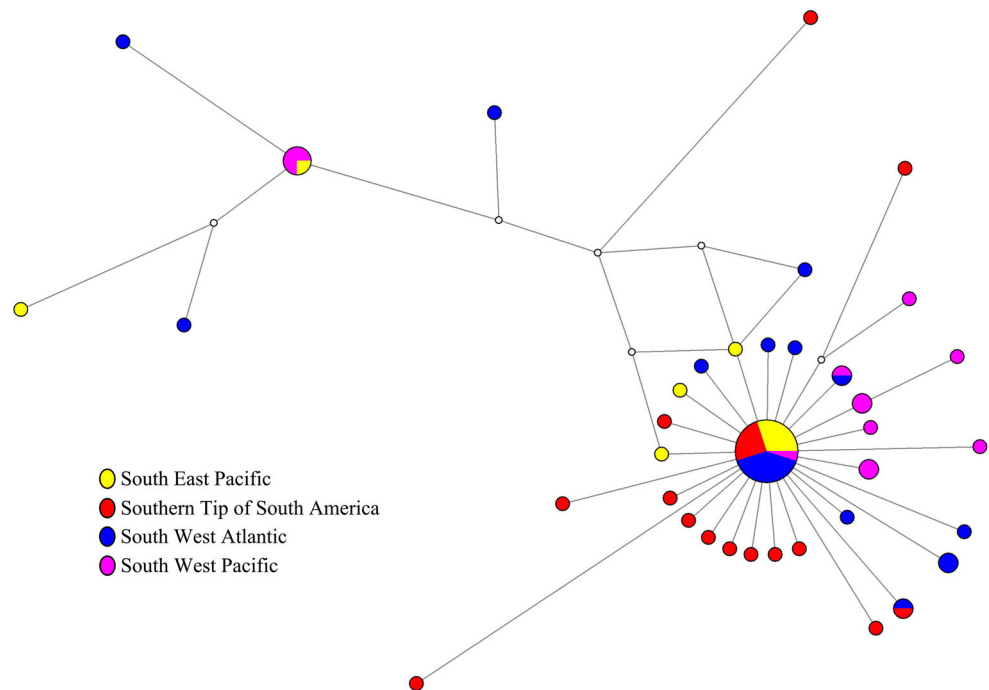
(Table 1, Online Resource 1). The concatenated dataset totaled 913 bp, with 37 haplotypes determined by 50 variable sites (23 in COI and 27 in ND1), 15 of which were parsimony informative (four in COI and 11 in ND1).

The genealogical relations between the samples of *M. gregaria* from both sides of the East Pacific Barrier showed no subdivision into eastern and western haplogroups (Fig. 2). Furthermore, three out of 37 mtDNA haplotypes were found both around southern South America and in the SWP. The most common haplotype (found in 20 individuals) was present in all areas, and most of the remaining haplotypes differed from the most common one in one or a few mutational steps (Fig. 2). The second most common haplotype (found in four individuals, three of which were from the SWP and one from the SEP) was separated from the most common one by six mutational steps and gave rise to three other haplotypes that were found around South America. This star-shaped pattern and the occurrence of a large proportion of very low frequency mutations could be explained by a sudden population expansion (Schneider and Excoffier 1999) or a selective sweep (Nordborg 2007). Pairwise F_{ST} s calculated among the four areas were not significant except for one, which evidenced that differentiation between the STSA and the SWP was low but significant ($F_{ST} = 0.054$, $P < 0.05$).

Genetic diversity indices such as the haplotype and nucleotide diversities were similar between areas (Table 1). Haplotype diversity was always higher than 0.70, while nucleotide diversity was always lower than 0.005 (Table 1). High haplotype diversity and low nucleotide diversity can be attributed to an expansion after a period of low effective population size (Grant and Bowen 1998).

Neutrality tests performed on the entire dataset indicated a departure from neutral expectations. Tajima's D and Fu's F_s were negative and highly significant ($D = -2.34$, $P < 0.05$; $F_s = -26.51$, $P < 0.02$), suggesting either a population expansion or purifying selection in the first case, and an excess in the number of haplotypes as would be expected from a recent population expansion or from genetic hitchhiking in the second case (Holsinger 2012). The mismatch analysis on the entire dataset could not reject the hypothesis of a sudden population expansion (Online Resource 2). When neutrality tests were performed for each area separately, only samples from the STSA ($D = -2.49$, $P \ll 0.05$; $F_s = -11.67$, $P \ll 0.02$) and from the SWA ($D = -1.75$, $P < 0.05$; $F_s = -6.43$, $P < 0.02$) showed departures from neutral expectations, suggesting the population expansion (or selection) occurred in these localities. Regarding the mismatch analyses, the population growth hypothesis was not rejected for any area (Online Resource 2). The onset of the possible expansion in southern South America was estimated in ca. 220,000 and 160,000 years ago ($\tau = 1.158$ and $\tau = 0.848$) for the STSA and the SWA,

Fig. 2 Median-joining network of mitochondrial COI + ND1 haplotypes of *Munida gregaria*. Each circle represents a distinct haplotype; circle area and line length are proportional to haplotype frequency and number of mutational steps, respectively. Small empty circles represent median vectors. The area of the smallest color circle corresponds to a frequency of one. Colors indicate sampling location. (Color figure online)



respectively. However, if we apply the tenfold correction suggested by Ho et al. (2005, 2007), these estimates become 22,000 and 16,000 for each area, respectively.

Discussion

In the present study, we analyzed the phylogeography of *M. gregaria*. The analyses conducted provided evidence that *M. gregaria* is a truly transpacific species. Furthermore, some indication of population-level genetic differentiation between transpacific populations of *M. gregaria* (STSA vs. SWP) was found. Finally, our results also suggested the occurrence of a population expansion during the Pleistocene.

Munida gregaria is distributed on the continental shelf and upper slope off southern South America, New Zealand, and southern Australia (Baba et al. 2008; Schnabel et al. 2011a). This apparent disjoint distribution hinted at the possibility of a cryptic speciation process between populations on both sides of the East Pacific Barrier. Our results, i.e., the absence of different haplogroups for each area and existence of shared haplotypes, showed that populations on both sides of the East Pacific Barrier belong to the same species.

At a population genetic level, some degree of genetic differentiation was found between the STSA and the SWP. Notwithstanding, our results suggest that individuals from both regions have been connected, since although some differentiation was found between STSA and SWP, the

SEP and SWA showed no signs of differentiation from the SWP. It should be pointed out, however, that genetic homogeneity inferred from indirect measures of gene flow can have many possible explanations that are not readily distinguishable from each other, i.e., current gene flow, balancing selection on markers, and lack of resolution of markers (retention of shared ancestral polymorphisms) (Bossart and Pashley Prowell 1998). Future studies employing direct measures of gene flow, i.e., population assignment methods, are needed to test whether connectivity still exists.

Most studies addressing the circumpolar phylogeography of marine invertebrates at high southern latitudes have been conducted on Antarctic organisms (Raupach et al. 2010; Bortolotto et al. 2011; Janosik et al. 2011). Raupach et al. (2010) found no genetic differentiation among circumantarctic populations of the Antarctic shrimps *Chorismus antarcticus* and *Nematocarcinus lanceopes*. Bortolotto et al. (2011), who studied the circumpolar Antarctic krill *Euphausia superba*, reported genetic homogeneity over a large geographic scale and attributed this result to the tight link between krill and circumantarctic ocean currents. Furthermore, Janosik et al. (2011) suggested that the genetic structure of *Odontaster validus* from Antarctic waters was being homogenized by the Antarctic Circumpolar Current. To date, the only study focused on the circumpolar phylogeography of sub-Antarctic marine crustaceans is that of Nikula et al. (2010). Although the two species studied exhibited wide-scale circumpolar distributions of single haplotypes, these results

correspond to a particular scenario. Indeed, both species are associated with kelp holdfasts and would have achieved circumpolar dispersal by rafting on buoyant macroalgae via the Antarctic Circumpolar Current.

Connectivity between distant populations is possible if the ecological requirements of both larvae and adults are met during transport (Lessios and Robertson 2006; Luiz et al. 2012). *Munida gregaria* is a cold-temperate species inhabiting the Southern Hemisphere between 40° and 56°S. It is the only transpacific species in its family, meaning that, in contrast to the other species of Munididae studied so far, it was able to disperse and settle on both sides of the East Pacific Barrier. The southernmost distribution limit of *M. gregaria* is the Beagle Channel, where it reaches high densities throughout the year (Gutt et al. 1999; Tapella et al. 2002; Pérez-Barros et al. 2004). Here, minimum water temperature in winter is 4.4 °C (Balestrini et al. 1998), which is below that registered during summer (6 °C) in the sub-Antarctic Front of the Antarctic Circumpolar Current (Whitworth 1988). This fact suggests that dispersal may have taken place via the Antarctic Circumpolar Current. Taking into account a surface speed of 77 cm s⁻¹ (2.8 km h⁻¹) inside the jets of the current (Whitworth 1988), the distance of 7,500 km between NZ and southern South America may be covered in about 113 days. On the other hand, the eastward distance between southern South America and NZ is 13,000 km, and may be travelled by passively drifting in the current during 196 days. At this point, it should be noted that, first, there are no records of *M. gregaria* off the sub-Antarctic islands between South America and Australia/NZ (i.e., Bouvet, Arntz et al. 2006; Crozet, Kerguelen, Cherel et al. 2000; Macpherson and Saint Laurent 2002; Pruvost et al. 2005; GBIF 2013); and second, 196 days exceed the pelagic larval duration of *M. gregaria* (ca. 111 days, Pérez-Barros et al. 2007). Thus, dispersal from NZ to southern South America would emerge as the most probable route. However, the alternative dispersal direction must not be ruled out since *M. gregaria* can remain pelagic after metamorphosis (Diez et al. 2012 and references therein) for up to six months (Zeldis 1985).

Species experienced changes in distribution as a result of the severe climatic fluctuations produced by glaciation events (Hewitt 2000). Patagonia has experienced multiple glaciations of varied duration and intensity since the latest Miocene, with the consequent changes in sea level and coastline (6 mya, Rabassa et al. 2011). Several glaciations took place during the Pleistocene, since the Great Patagonian Glaciation (GPG) 1 mya, i.e., post-GPG 1 (<1, >0.760 mya), post-GPG 2 (<0.760, >0.315 mya), post-GPG 3 (<0.260, >0.150 mya), and the “Last Glaciation” (LG, 0.025–0.015 mya) (after Rabassa et al. 2011). During GPG and other Middle Pleistocene Glaciations, the ice extended from the Andes to the present Atlantic submarine shelf south of Río Gallegos ca. 54°S (Rabassa et al. 2011).

Sea-level changes during full glacial episodes (i.e., decreases of up to 100–140 m) caused large extensions of the present Argentine continental shelf to be exposed. This almost doubled the size of continental areas, leading to a pronounced climate continentalization, which decreased sea surface temperatures (Cavallotto et al. 2011; Rabassa et al. 2011). Pérez-Barros et al. (2008) reported evidence of a recent population expansion for *M. gregaria* and hypothesized that, during some glacial period, its distribution would have been restricted to lower latitudes. This was probably followed by a southward population expansion when seawater temperature increased. Our estimated time of expansion ranged between 220,000 and 160,000 years ago, coinciding with the Middle Pleistocene, during Post-GPG 3. However, if the tenfold correction of the mutation rate due to the time dependency of molecular evolutionary rates (population-level vs. phylogenetic) is considered, our estimations (22,000–16,000 years ago) would fit to the LG. The pattern of genetic variation observed in *M. gregaria*, i.e., negative values of neutrality tests and star-shaped genealogy, can also be explained by a selective sweep (Nordborg 2007). The fact that other sub-Antarctic and Antarctic organisms would have experienced population expansions during a similar period of time (Raupach et al. 2010; Ceballos et al. 2012) makes the expansion hypothesis more plausible than the selective one. Notwithstanding, the analysis of nuclear markers is necessary to further support or refute this hypothesis.

In conclusion, *M. gregaria* constitutes a truly transpacific species. There has been enough gene flow between populations on both sides of the East Pacific Barrier to maintain species cohesion.

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