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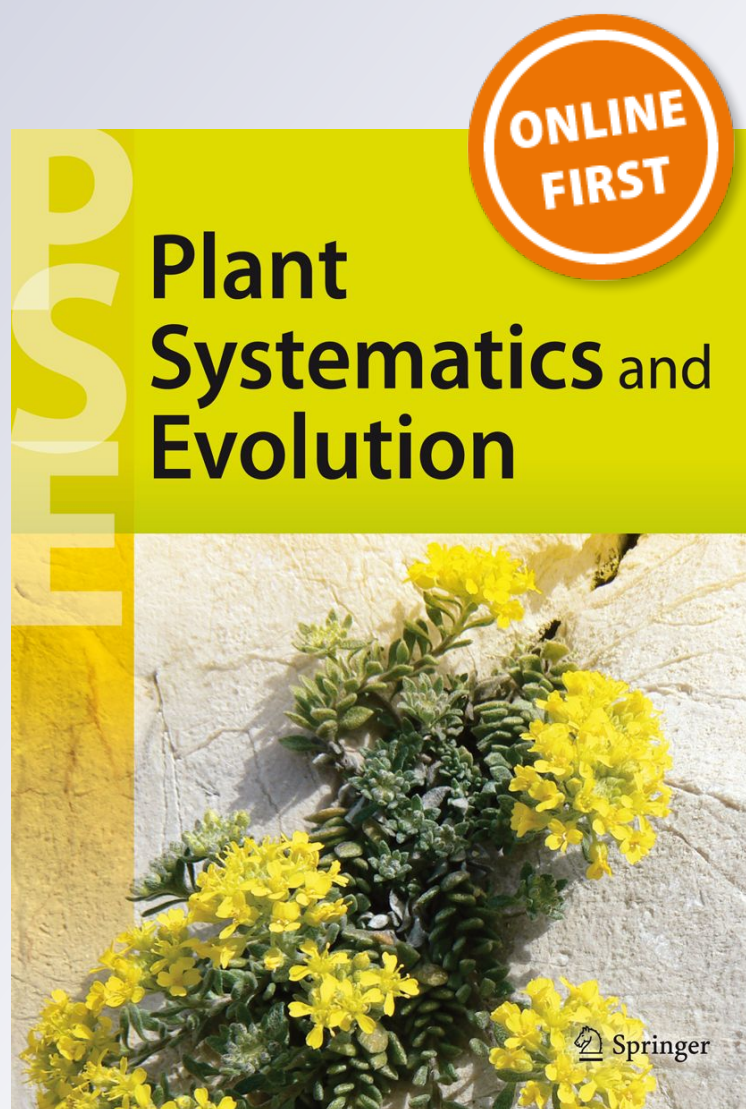
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# Unraveling the phylogenetic relationships of *Nectouxia* (Solanaceae): its position relative to *Salpichroa*

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**Abstract** *Nectouxia* (Solanaceae) is a monospecific genus endemic to Mexico and southern United States of America. Morphological and phylogenetic evidence supports a close relationship between *Nectouxia* and the Andean genus *Salpichroa*, but the phylogenetic analyses completed to date have included very few *Salpichroa* species. A comprehensive phylogenetic analysis including *Nectouxia* and all *Salpichroa* species was carried out to shed light on the relationship between the two genera. Maximum parsimony and Bayesian inference analyses were done using sequences from three markers (ITS, *psbA-trnH*, and *ndhF-rpl32*). The results of both analyses are congruent regarding the strongly supported clades while incongruences are observed in weakly supported clades that can be explained by rapid species radiation. *Salpichroa* species are divided in two main clades with

strong support, while *Nectouxia* is resolved within one of them. Our results indicate that the two genera should be combined into a single genus or *Salpichroa* will be paraphyletic as currently circumscribed. The name *Nectouxia* has priority but the conservation of *Salpichroa* has been proposed. At the suprageneric level, the *Nectouxia* + *Salpichroa* clade is not closely related to *Jaborosa*, which is further evidence that the previously recognized tribe Jaboroseae is not monophyletic.

**Keywords** Jaboroseae · *Nectouxia* · Neotropics · Phylogeny · *Salpichroa* · Taxonomy

## Introduction

*Nectouxia* (Solanaceae) is a monospecific genus endemic to Mexico and the southern United States of America (Hunziker 2001). *Nectouxia* is considered to be closely related to *Salpichroa* (Olmstead et al. 2008), a relatively small genus from the Andes of South America (21 species; Gonzáles et al. in prep.). The suprageneric position of *Nectouxia* and *Salpichroa* within subfamily Solanoideae is still unresolved. D'Arcy (1991) and Hunziker (2001) placed both genera along with *Jaborosa* in tribe Jaboroseae, based mostly on morphological characters. However, in phylogenetic reconstructions of the family (Olmstead et al. 2008; Särkinen et al. 2013) as well as in phylogenetic analyses of the genus *Jaborosa* (Moré et al. 2015), *Nectouxia* and *Salpichroa* were not resolved as closely related to *Jaborosa*. In fact, *Nectouxia* and *Salpichroa* are sister genera grouped in the “Salpichroina” clade (Olmstead et al. 2008). In addition, Moré et al. (2015) found the single *Nectouxia* species nested within *Salpichroa*. However, the relationship between the two genera is not thoroughly understood due to the small

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number of *Salpichroa* species included in the phylogenetic analyses completed to date (1–3 out of 21 *Salpichroa* species). Therefore, a comprehensive phylogenetic analysis including *Nectouxia* and all *Salpichroa* species was carried out to shed light on the relationship between the two genera and to ultimately decide about the taxonomic status of *Nectouxia*.

## Materials and methods

The single *Nectouxia* species, *N. formosa*, together with the 21 *Salpichroa* species (González et al. in prep.) were included in the phylogenetic analyses; a single accession was used in each case except for *N. formosa*, *S. organifolia*, *S. scandens*, and *S. tristis* (Online Resource 1). Seventeen species from nine genera representing different Solanaceae tribes/clades (after Olmstead et al. 2008) were selected as outgroup (Online Resource 1), but only *Nicotiana* species were defined as the outgroup in the analyses.

DNA was extracted from silica gel-dried leaves using the DNeasy Plant Mini kit (Qiagen, Valencia, CA, USA) following the manufacturer's instructions. Three molecular markers were sequenced: the intergenic spacers *psbA-trnH* and *ndhF-rpl32* from the chloroplast genome, both of them used in the *Jaborosa* phylogeny, providing ca. 12% of parsimony-informative data (Moré et al. 2015), and ITS from the nuclear ribosomal genome, a marker largely used in plant phylogenetic studies, considered particularly useful at the species level [see Nieto Feliner and Rosselló (2007) for a review]. The three markers were amplified by PCR following published protocols using the primers specified by the authors: Sang et al. (1997) for *psbA-trnH*, Miller et al. (2009) for *ndhF-rpl32*, and White et al. (1990) for ITS (forward ITS5/leu1, reverse ITS4); eventually, an internal primer, designed for this study (ITS-X 5'-CCGYTGC-CRARAGTCGTT-3'), was used for partial ITS sequencing toward ITS5/leu1. PCR products were cleaned using a combination of the enzymes exonuclease I (Exo I, Thermo Scientific) and thermosensitive alkaline phosphatase (FastAp, Thermo Scientific), according to Werle et al. (1994), and sequenced on an automated capillary sequencer (CERELA-CONICET, Tucumán, Argentina). New sequences for the three markers were obtained from most *Salpichroa* samples [except for those used by Moré et al. (2015); Online Resource 1]. Sequences retrieved from GenBank were used for most outgroup species or were obtained in this study (Online Resource 1). ITS sequences were not available for several *Jaborosa* species (Online Resource 1).

DNA sequences from the three markers were aligned in a single concatenated dataset (Online Resource 2) using MEGA 5.1 (Tamura et al. 2011) and analyzed in PAUP\* 4.0b10 (Swofford 2003) for maximum parsimony (MP)

analysis. A heuristic search was done with tree-bisection–reconnection (TBR) branch swapping; 1000 random addition replicates were performed, saving ten trees each. All characters were unordered and equally weighted. A bootstrap analysis was done to test support for the clades (1000 pseudo-replicates using TBR branch swapping, holding ten trees at each step, with random addition and 100 replicates). Clades with bootstrap percentages (BP) above 80% are considered strongly supported. Partitioned datasets including plastid (*psbA-trnH* and *ndhF-rpl32*) and nuclear (ITS) sequences separately were also used for MP analyses, but conclusions were drawn only from the concatenated dataset. The concatenated dataset was also analyzed through Bayesian inference (BI) in MrBayes 3.2.2 (Ronquist et al. 2012), using a Markov chain Monte Carlo (MCMC) search with five million generations. The first 25% of the trees was discarded as burn-in; the remaining trees were used to build a majority-rule consensus tree along with posterior probability values. Posterior probabilities (PPs) above 0.94 are considered as high support, between 0.94 and 0.70 as moderate support, and below 0.69 as weak support. The nucleotide substitution model was selected a priori following the Akaike Information Criteria in JModelTest version 2.1.3 (Darriba et al. 2012); the model that best fitted the data was the GTR + I + G.

## Results

The concatenated matrix had 2134 total characters and had 2.5% missing data. One single most parsimonious tree (1018 steps, CI 0.632, RI 0.807) was obtained from the MP analysis (Fig. 1a); 23.2% characters were variable and 16.03% were potentially parsimony informative. Statistics for the plastid, nuclear, and combined datasets are summarized in Table 1. The most parsimonious tree and the majority-rule consensus of the BI analysis were highly congruent regarding well-supported branches, with several weakly supported incongruences (Fig. 1). *Salpichroa* is resolved as a strongly supported monophyletic group (PP 1, BS 100%) if *N. formosa* is included within the genus (Fig. 1). The same result was obtained after MP analyses of plastid and nuclear datasets separately (BS 100 and 86%, respectively; not shown).

*Salpichroa* is divided in two main clades (Fig. 1), one formed by *S. lehmannii*, *S. organifolia*, *S. scandens* and also *N. formosa* (PP 0.83, BS 63%), and the other including the remaining species of the genus (PP 1, BS 100%). These two clades are identified as clades *organifolia* and *tristis*, respectively (after the most widespread species within each one). Clade *organifolia* was also resolved as a monophyletic group after MP analyses of plastid and nuclear datasets, with moderate support (BS 59 and 63%, respectively), while clade



**Fig. 1** Phylogenetic relationships of *Nectouxia* and *Salpichroa*. **a** Single most parsimonious tree (1018 steps, CI 0.632, RI 0.807). Bootstrap support values (> 50%) are indicated by each branch. **b** Bayesian majority-rule consensus tree. Posterior probabilities values are indicated by each branch. **a** and **b** were obtained from a combined data set (nuclear ITS, chloroplast intergenic spacers *psbA-trnH* and *ndhF-rpl32*). The arrows indicate the origin of the clade *Nectouxia* + *Salpichroa*; *N. formosa* samples are highlighted in red

**Table 1** Statistics from maximum parsimony analyses of plastid, nuclear, and combined datasets

	cpDNA ( <i>psbA-trnH</i> , <i>ndhF-rpl32</i> )	ITS	Combined
Aligned length	1442	692	2134
Number of variable characters	272 (18.86%)	223 (32.23%)	495 (23.2%)
Parsimony-informative characters	187 (12.97%)	155 (22.4%)	342 (16.03%)
Number of maximum parsimony trees	36	1165	1
Tree length	427	568	1018
Consistency index	0.747	0.570	0.632
Retention index	0.893	0.738	0.807

tristis was strongly resolved analyzing plastid sequences (BS 100%) but paraphyletic analyzing nuclear data (not shown).

Most relationships within clade *origanifolia* are strongly resolved, with *N. formosa* recovered as sister to the other species included in this clade (Fig. 1). The interspecific relationships are fully resolved within clade *tristis* in the most parsimonious tree (Fig. 1a) while several polytomies are observed in the BI phylogram (Fig. 1b); in both analyses, the support for the clades is overall moderate to low or null, except for a few pairs of sister species (e.g., *S. ramosissima* and *S. micrantha*). Several incongruences, with low or no support, are observed within clade *tristis* between the MP tree and the BI phylogram (Fig. 1).

The species of the other genera included in the analyses are segregated into four strongly supported clades (Fig. 1) identified as tribes Solanaceae (*Solanum* spp.) and Physalideae (*Physalis peruviana*, *Saracha punctata*, *Vassobia dichotoma*, and *Dunalia brachyacantha*), and the paraphyletic group “Atropina” (after Olmstead et al. 2008; *Lycium* spp., *Nolana* spp., and *Jaborosa* spp.). *Solanum* was recovered as sister group to the clade *Nectouxia* + *Salpichroa*, with contrasting support (PP 1, BS 64%).

## Discussion

*Nectouxia* and *Salpichroa* were resolved as highly supported sister groups in the phylogenetic reconstructions of Solanaceae done by Olmstead et al. (2008) and Särkinen et al. (2013), and they are recognized as the only members of the small and informal “Salpichroina” clade. These molecular studies encompassed the majority of the Solanaceae genera but only one species of *Salpichroa* (*S. origanifolia*) and the single species of *Nectouxia*. Recently, Moré et al. (2015) proposed a phylogenetic reconstruction for *Jaborosa*, a genus traditionally considered close to *Salpichroa* and *Nectouxia* (D’Arcy 1991; Hunziker 2001). Moré et al. (2015) sampled 18 *Jaborosa* species, as well as three *Salpichroa* species (*S. origanifolia*, *S. lehmannii*, and *S. tristis*) and *N. formosa*. Again, *Nectouxia* and *Salpichroa* were resolved in a strongly supported clade, with *N. formosa* nested among

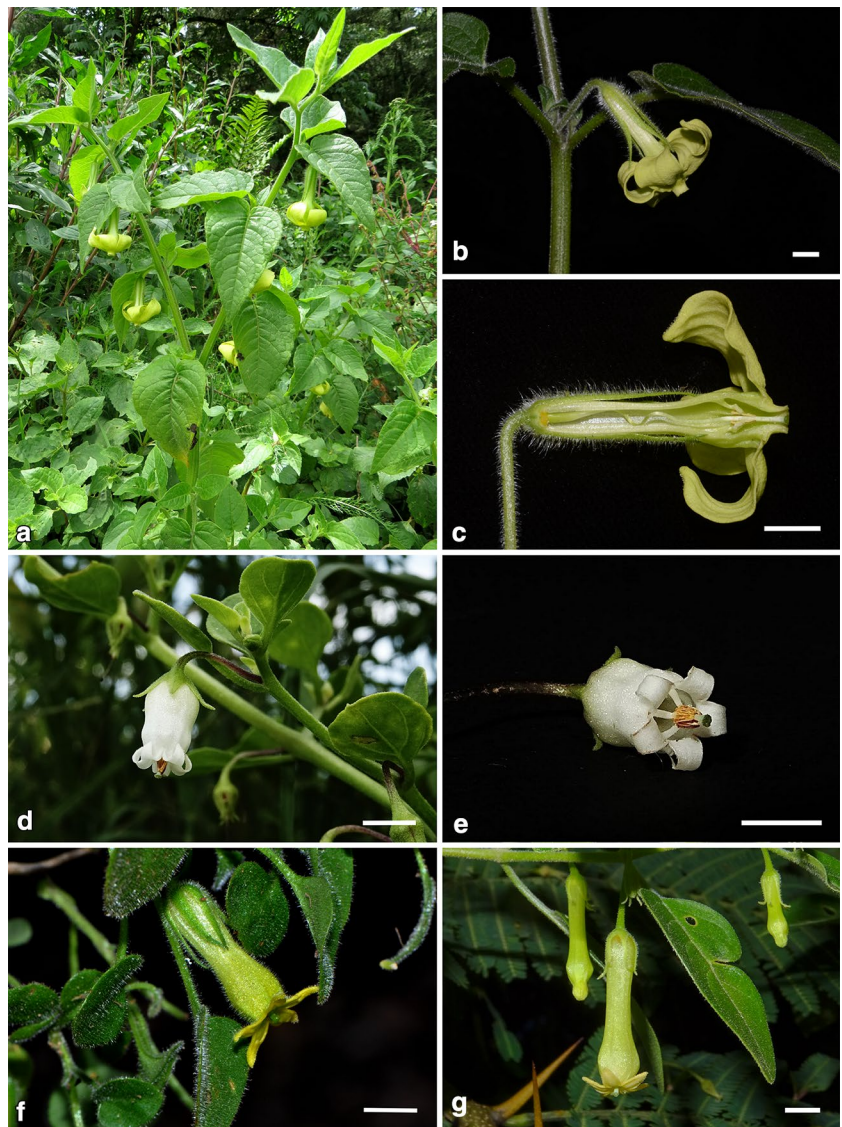
*Salpichroa* species (to be precise, as sister to the species now resolved in clade *origanifolia*); the *Nectouxia* + *Salpichroa* clade was not closely related to the *Jaborosa* clade. The phylogenetic reconstructions obtained in this analysis, which includes all *Salpichroa* species and *N. formosa*, indicate that the two genera should be merged since *Salpichroa* would be paraphyletic as currently circumscribed.

The name *Nectouxia* was validly published by Kunth (1818) and therefore it antedates *Salpichroa* (Miers 1845). To recognize the monophyletic clade *Nectouxia* + *Salpichroa* as a single genus, nomenclatural changes are required. Options include renaming the 21 *Salpichroa* species as *Nectouxia* by strictly applying the principle of priority of ICN Art. 11.3 (McNeill et al. 2012) or, alternatively, proposing the conservation of *Salpichroa* against *Nectouxia*. This latter option has been recently proposed (Barboza et al. 2016) in order to avoid disadvantageous nomenclatural changes and preserve the stability of current nomenclature (Art. 14.1 & 14.2, ICN McNeill et al. 2012).

Morphologically, *Nectouxia* is characterized by its herbaceous habit (Fig. 2a), a prominent ring-like crown in the mouth of the corolla (Fig. 2b, c; Hunziker 2001) and, like *Salpichroa*, having aerial parts that darken upon drying, ovate leaf blades that are cordate at the base, solitary axillary flowers (Fig. 2a), deeply divided calyces (Fig. 2a, b), dorsifixed anthers, filaments inserted in the upper part of the corolla tube (Fig. 2c), thickened connectives, a conspicuous colored nectary around the ovary (Fig. 2c), and ovoid juicy berries with persistent accrescent calices (Whalen 1984; Hunziker 2001). Many authors previously suggested the resemblance of *Nectouxia* to *Salpichroa* (Miers 1849; Bentham and Hooker 1876; Wettstein 1895; Whalen 1984; Nee 1986; Hunziker 2001), but due to the lack of more information about many characters (palynological, phytochemical, karyological, cf. Hunziker 2001), they maintained the two genera as separate.

*Nectouxia formosa* was resolved within *Salpichroa* clade *origanifolia* as sister to a clade comprising *S. scandens*, *S. lehmannii*, and *S. origanifolia*, but it is not closer to any particular species. In this regard, considering the moderate support for *N. formosa*’s position (BS 63%, PP 0.83), it may

**Fig. 2** a–c *Nectouxia formosa*, a flowering branch, b flower, c flower in longitudinal section. d, e *Salpichroa organifolia*, d flower, e flower in upper view. f *Salpichroa lehmannii*, flower. g *Salpichroa scandens*, flower. Observe the style exceeding the corolla tube in c–g, and the structure-like staminal cone formed by the anthers in c and e. Scale bars: 0.5 cm. Photographs by F. Chiarini (a), G. Salazar Chávez (b, c), P. Gonzáles (f), and C. Carrizo García (d, e, g)



eventually be considered a separate lineage, in its own clade sister to the clade organifolia. Actually, of all the species of clade organifolia, *N. formosa* is the only one with a different habit and range; it is a perennial herb endemic to the southern USA and Mexico (Whalen 1984; Nee 1986; Rzedowski & Rzedowski 2001) while the three *Salpichroa* species are South American scandent shrubs, found from southern Peru up to northern Chile, northwestern-central Argentina, Paraguay, Uruguay, and southern Brazil (Keel 1984; Chiarini et al. 2007; Basso and Barboza 2013). *Salpichroa organifolia* has a cosmopolitan distribution (Barboza et al. 2016); the presence of underground rhizomatous stems in this species may favor invasive plant behavior. Morphologically, each of the four species is very distinctive (Fig. 2b–g) and all share only two features, glandular pubescence (glandular trichomes not always present in *S. organifolia*) and the style exceeding the corolla tube (Fig. 2c–g); it is worth

mentioning that these features are not exclusive of clade organifolia, e.g., glandular trichomes present in *S. glandulosa*, exerted style observed in *S. amoena*. In addition, three species, *N. formosa* (Fig. 2c), *S. organifolia* (Fig. 2e), and *S. scandens*, have stamens that are bent toward the center of the flower, placing the five anthers over the style in a structure-like staminal cone. Finally, an interesting character shared by all three *Salpichroa* species of clade organifolia is the production of withanolides known as salpichrolids (Nicotra et al. 2013; Basso et al. 2017), while *Nectouxia* is phytochemically under study (V. Nicotra personal comm.). In this regard, 12 out of 18 species from *Salpichroa* clade tristis were tested for the presence of withanolides and they were all negative (Basso et al. 2017); therefore, if salpichrolids are found to be present in *N. formosa*, the production of these metabolites would be a synapomorphy of the entire clade organifolia.

As regards, the relationships within clade *tristis*, the short length of the internal branches, and the general low support (except for a few well-supported sister species) may be evidence of rapid radiation evolution after the divergence of the clade. In fact, there has been much confusion regarding species circumscription within the clade, an issue that is currently being addressed by our team (González et al. in prep.). The phylogenetic analysis presented here provides evidence for reinstating some names currently considered synonyms (*S. amoena*, *S. tenuiflora*, and *S. diffusa* var. *longiflora*) and elevating two infraspecific taxa to the species level (*S. lehmannii* and *S. weddellii*) (Fig. 1). However, further analyses need to be done to better understand the interspecific affinities within clade *tristis*.

Divergence times were calculated using the estimations done by Särkinen et al. (2013); however, the results were left out in view of the recent findings by Wilf et al. (2017). Indeed, a new fossil record from Patagonia (Argentina) identified as member of *Physalis* (*P. infinemundi* Wilf) has been dated at 52.2 Myr (Wilf et al. 2017). Considering that the divergence time for the entire family Solanaceae was previously dated at ca. 30 Myr (Särkinen et al. 2013), this new evidence would completely change previous estimates of divergence times. Therefore, until these discrepancies are resolved, we are holding off on undertaking further analyses.

In reference to *Nectouxia* + *Salpichroa* suprageneric affinities, just a single reliable conclusion can be drawn from the present results due to the limited diversity of the outgroups used. As found by previous authors (Olmstead et al. 2008; Särkinen et al. 2013; Moré et al. 2015) and also in this analysis, *Nectouxia* + *Salpichroa* are not closely related to *Jaborosa*. *Jaborosa* belongs to a different informal group, namely “Atropina,” which in our analysis is paraphyletic (Fig. 1). According to different analyses, *Jaborosa* groups with members of tribe Hyoscyameae and the genera *Lycium*, *Nolana*, *Sclerophylax*, and *Latua* (Olmstead et al. 2008; Tu et al. 2008, 2010; Levin et al. 2011; Särkinen et al. 2013; Moré et al. 2015; Chiarini et al. 2017), all of them also placed in the Atropina clade by Olmstead et al. (2008). The traditional tribe Jaboroseae (i.e., *Jaborosa*, *Salpichroa*, and *Nectouxia*) does not represent a monophyletic group and is here formally dismembered. In contrast, *Nectouxia* and *Salpichroa* are merged into a single genus, whose name will depend on the acceptance or rejection of the proposal to conserve *Salpichroa* (Barboza et al. 2016); thus, *Nectouxia* or *Salpichroa* is recognized as the single genus of the *Salpichroina* clade, whose suprageneric affinities still need to be clarified.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Human and animal rights** This article does not contain any studies with human participants or animals performed by any of the authors.

#### Information on Electronic Supplementary Material

**Online Resource 1.** Table of materials studied and GenBank accession numbers.

**Online Resource 2.** Alignment of concatenated *psbA-trnH*, *ndhF-rpl32*, and ITS sequences in nexus format.

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