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Allium littoricola, a new species from Zhejiang, East China

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ABSTRACT: A new species of *Allium* L. (Amaryllidaceae) from Zhejiang, eastern China, namely *A. littoricola*, was described and illustrated. Morphological analysis indicates this new species is similar to *A. longistylum* Baker, but differs in having ovoid bulb, tunic white, light-purple, membranous, leaf blades ascending, scape lateral, hollow in cross section or solid at base, perianth segments 5–6 × 2–3 mm, inner filaments base 1-toothed at each side; low altitude and coastal hillside habitat. Molecular phylogenetic analyses also support it as a new species and suggest that it is closely related to *A. longistylum* Baker.

KEY WORDS: *Allium chinense*, *Allium longistylum*, *Allium sacculiferum, Allium thunbergii,* phylogeny.

INTRODUCTION

Allium L. is one of the largest genera in Amaryllidaceae (Friesen *et al.,* 2006; Fritsch *et al.*, 2010; Li *et al.,* 2010; Herden *et al.,* 2016). The majority of *Allium* species are located in the Northern Hemisphere, particularly in regions with seasonal dryness. The diversity center of *Allium* is Southwest and Central Asia, with a secondary species diversity centre in North America (Friesen *et al.,* 2006; Nguyen *et al.,* 2008; The angiosperm phylogeny group, 2009; Li *et al.,* 2010; Khassanov, 2018).

Over the last few years, numerous morphological and anatomical studies on *Allium* plants have been undertaken, culminating in the publication of a wealth of data on newly described taxa (e.g. Brullo *et al.,* 1991; Fritsch and Friesen, 2009; Balos, 2022; Bartolucci *et al.,* 2022; Ioannidis and Tzanoudakis, 2022; Memariani *et al.,* 2022; Özdöl *et al.,* 2022; Balos and Geçit, 2023; Balos *et al.,* 2023; Balos and Sonay, 2024; Çeçen *et al.,* 2024; Eker, 2024; Koçyiğit *et al.,* 2024; Sonay *et al.,* 2024; Vojtěchová *et al.,* 2024; Yıldırım *et al.,* 2024; Özüdoğru and Eker, 2025) and regional revisions (e.g. Cheremushkina, 1992; Hanelt and Fritsch, 1994; Friesen, 1995; Mathew, 1996; Khassanov *et al.,* 1997; Xu and Kamelin, 2000; Dale *et al.,* 2002; Kovtonyuk *et al.,* 2009; Li, *et al.,* 2010). The International Plant Names Index (IPNI) reports that around ten new *Allium* species are identified annually (Seregin *et al.,* 2015). According to the original count by POWO (2025), *Allium* now consists of 1,089 species.

Recent taxonomic revisions and studies indicate that about 145 *Allium* species in China, including 51 that are endemic (Choi and Oh, 2011; Seregin *et al.,* 2015; Herden *et al.,* 2016; Shukherdorj *et al.,* 2018; Li *et al.,* 2019; Jie *et al.,* 2019; Xie *et al.,* 2020, 2024; Huang *et al.,* 2021; She *et al.,* 2023). These Chinese species represent approximately one-sixth of the global *Allium* species, covering 13 out of 15 subgenera and nearly half of the sections within the genus. They are predominantly found in the southwestern, northwestern, northern, and northeastern parts of China.

In March 2014, during the investigation of plant resources in Ningbo City, co-author Zheng-Hai Chen made an initial discovery of an unusual *Allium* plant on Nantian Island in Xiangshan County of eastern Zhejiang, China. The plant grows in the grass on sunny slopes along the coast at an altitude of 20–75 meters. While preparing the new edition of *Flora of Zhejiang* (2014–2021), our attention was captured by this plant, prompting us to investigate its native habitat and neighboring areas during the flowering and fruiting periods. We also introduced it to several sites in Hangzhou City (Zhejiang Forest Resources Monitoring Centre, Zhejiang Museum of Natural History, Zhejiang Qingliangfeng National Nature Reserve, Zijingang Campus of Zhejiang University) and Jinhua City (Wuyi County and Yongkang County) for cultivation and observation. After careful morphological and molecular phylogenetic analyses, the species was identified as a new species of *Allium* and named *A. littoricola* Z.H. Chen, Y.L. Xu & P. Li.

MATERIALS AND METHODS

Sampling and morphology: A comprehensive morphological study of the unidentified live plants was conducted using a Leica DFC320 stereomicroscope (Japan)

Table 1. Diagnostic morphological characters of ***A. littoricola*, *A. longistylum*, *A. sacculiferum*, *A. thunbergii*** and ***A. chinense***.

Characters	*A. littoricola* $	*A. longistylum**,#	*A. sacculiferum**,#	*A. thunbergii**,#	*A. chinense*#
Bulb	solitary or clustered, ovoid	solitary or clustered, cylindrically ovoid	solitary or clustered, cylindrically ovoid to ovoid	solitary or clustered, ovoid	densely clustered, narrowly ovoid
Tunic	white, light purplish, membranous	papery, brown	brown, papery	brown, papery	white, sometimes tinged with red, membranous
Leaf sheath	exposed above ground, 1.0–4.0 cm high, striped green or light purplish	exposed above ground, 5.1–16.0 cm high, striped green	clearly exposed above ground, 7.5–42.0 cm high, striped green	not exposed above ground, 3.1–13.5 cm high, striped green	/
Leaf blade	ascending, linear, subterete, subequaling scape	curved, linear, terete, subequaling scape	ascending, linear, 3-angled, shorter than scape	curved, near flat, subequaling scape	curved, linear, 3–5-angled, subequaling scape
Scape	lateral, hollow in cross section, or solid at base	terminal, solid in cross section	terminal, solid in cross section	terminal, solid in cross section	Lateral, /
Umbel	hemispheric, usually densely 8–57-flowered	subglobose, 11–82-flowered	subglobose, usually densely 10–163-flowered	subglobose, 7–78-flowered	hemispheric, laxly flowered
Pedicel	7.0–16.0 mm long	7.0–15.6 mm long	8.1–26.0 mm long	7.0–19.3 mm long	8.0–24.0 mm long
Perianth & segment	reddish purple to purple, segments elliptic, 5–6 × 2–3 mm	reddish purple to purple, segments oblong, 3.5–4.5 × 1.8–2.3 mm	reddish lilac to purple, segments elliptical, 4.3–5.1 × 2.0–2.6 mm	purple to dark purple, segments elliptical, ovate-elliptical to oval, 4.5–6.1 × 2.1–3.6 mm	pale purple to dull purple, segments broadly elliptic to suborbicular, 4–6 × 3–4 mm
Filament	ca. 1.3 × as long as perianth segments, outer ones entire, inner ones 1-toothed on each side	ca. 2 × as long as perianth segments, entire, or inner ones small 1-toothed on each side	1.2–1.7 × as long as perianth segments, entire, or inner ones occasionally 1-toothed on each side	1.1–1.6 × as long as perianth segments, entire, or inner ones small 1-toothed on each side	ca. 1.5 × as long as perianth segments, outer ones subulate, inner ones broadened at base, 1-toothed on each side

Based on *: Choi & Oh, 2011, #: Xu & Kamelin, 2000 and $: our own measurements at ZM; /, No data available

and microcolour photographs of seeds were taken by a 10× microscope objective (Mitutoyo, Japan). Additionally, we reviewed all available type specimens and protologues, as well as specimens (digital images) preserved in various herbaria including AU, BJFC, BJM, BNU, CSH, E, G, GH, HBNU, HBU, HHBG, HIB, HNWP, HSIB, HTC, HZU, IATM, IBK, IBSC, IFP, IGA, JLSLKY, JSPC, K, KUN, NAS, NEFI, NKU, P, PE, PEY, SXU, SYAU, TI, TIE, WUK, ZJFC, and ZM (herbarium abbreviations follow Thiers 2020). A total of 12 characters were selected for comparison. Detailed differences among *A. littoricola* and *A. longistylum* Baker (1874), *A. sacculiferum* Maxim. (1859), *A. thunbergii* G. Don (1827) and *A. chinense* G. Don (1827) are listed in Table 1, based on Choi and Oh (2011), Xu and Kamelin (2000), and our own measurements of over 30 individuals from six collection numbers of *A. littoricola*.

DNA sequencing, assembly, and phylogenetic analyses: The fresh leaves were taken from living plants and dried in silica gel. DNA was extracted by Plant DNAzol (Shanghai, China) using the manufacturer's protocol. Sequencing libraries were prepared at China National GenBank (CNGB, Shenzhen, China) and paired-end reads of 150 bp were generated on the Illumina HiSeq X10 platform. The complete plastome and ITS (ITS-1, 5.8S, and ITS-2) sequences were assembled by GetOrganelle (Jin *et al.,* 2020) with default settings. MAFFT v7.487 (Katoh and Standley, 2013) was used to align the complete plastome sequences, and the low-quality sequences were trimmed manually in Geneious v.24.0.5 (Kearse *et al*., 2012). The aligned sequences were concatenated into a supermatrix. Maximum likelihood (ML) analyses were performed in IQ-TREE 2 (Minh *et al.,* 2020) with 1000 bootstrap replicates and Modelfinder (Kalyaanamoorthy *et al.,* 2017) for gene partitions and best models. The final tree graph was displayed and exported in FigTree v.1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/).

RESULTS AND DISCUSSION

Morphology: Through field observation and dissection of living plants, the morphological characteristics of the new species, such as bulbs, leaves, scapes, inflorescences, and flowers, were comprehensively studied and compared with related species. The results showed that the new species is clearly different from other related species.

It is mainly distinguished from them by the bulb ovoid, tunic white, light purplish; scape lateral and hollow in cross section, or solid at base; rocky coastal habitat. The distinguishing characteristics of the new species and the four relatives are listed in detail in Table 1. The morphological analysis reveals that although the new species, *A. longistylum*, *A. sacculiferum*, *A. thunbergii* and *A. chinense* share similarities in certain traits, they exhibit distinct characteristics. *Allium longistylum* differs from *A. littoricola* by having papery and brown tunic,

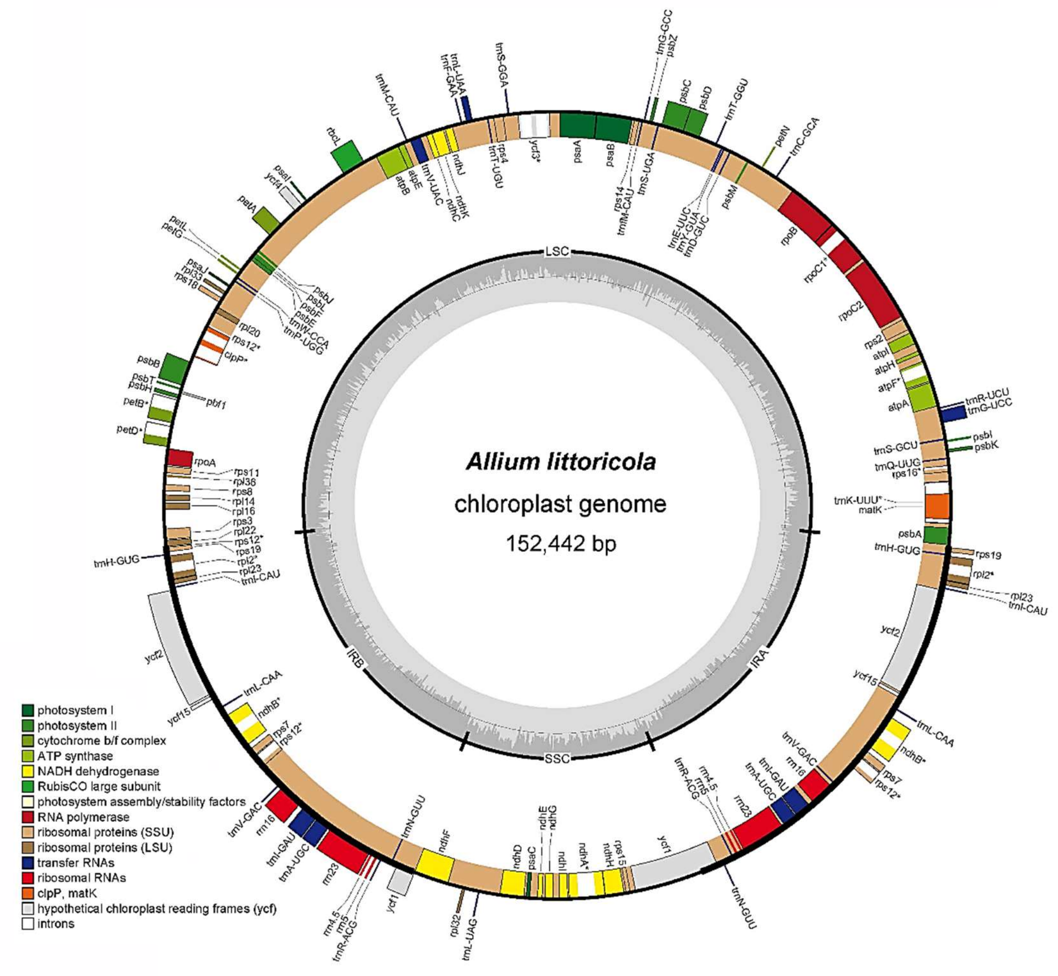

Fig. 1. Gene map of assembled ***Allium littoricola*** plastome. The genes located inside the circles are transcribed in a clockwise direction, while those outside the circle are transcribed counterclockwise.

curved leaf blades, central and solid scape, 1 500 – 3 000 m altitude, slopes, plains and sunny meadows of riversides habitat. Compared to *A. littoricola*, *A. sacculiferum* bears brown papery tunic; leaf sheath clearly exposed above ground, 7.5–42.0 cm tall; leaf blades linear, 3-angular, shorter than scape; scape central, solid; filaments entire, or inner ones occasionally with 1 tooth on each side. By contrast, *A. thunbergii* has leaf blades curved, nearly flat; leaf sheaths not exposed above ground; scape terminal and solid in cross section. The main difference between *A. chinense* and *A. littoricola* is the densely clustered, narrowly ovoid bulbs, 3–5 angled linear leaf blades, laxly 4–28 flowered umbels, seeds with a convex cross-section and a short-obtuse micropyle apex, summer-wilting habit, and habitats in vegetable fields, forest margins, and roadsides on hillsides.

Observations over the past decade have indicated that under cultivation conditions, *A. littoricola* has exhibited changes only in quantitative traits (such as flower stalk height reaching up to 60.5 cm, bulb diameter up to 3.0 cm, leaf length up to 100 cm, and diameter up to 4.3 cm), while all other identification traits have remained stable. The changes in the aforementioned quantitative traits do not affect their key distinguishing characteristics, which further supports the stability of the species.

Plastome Features: The complete plastome sequence length of *Allium littoricola* is 152,422 bp (Fig. 1). The plastome shows a typical quadripartite structure with two IR regions (26,507 bp), the large single-copy (LSC) region (81,251 bp), and the small single-copy (SSC) region (18,177 bp). The total GC content of plastome is 36.8%, with the IR regions showing the highest GC content (42.6%), followed by the LSC region (34.6%) and the SSC region (29.3%).

Molecular phylogenetics: Phylogenetic analyses of plastome included 116 *Allium* species: four newly sequenced (*A. paepalanthoides*_PQ248063, *A. thunbergii*_PQ248065, *A. tianmuense*_PQ248066 and *A. littoricola*_PV026310, followed by the Genebank number, the same as ITS sequence) and 112 downloaded from the National Centre for Biotechnology Information, with *Clivia miniata* as the outgroup (Fig. 2). The complete

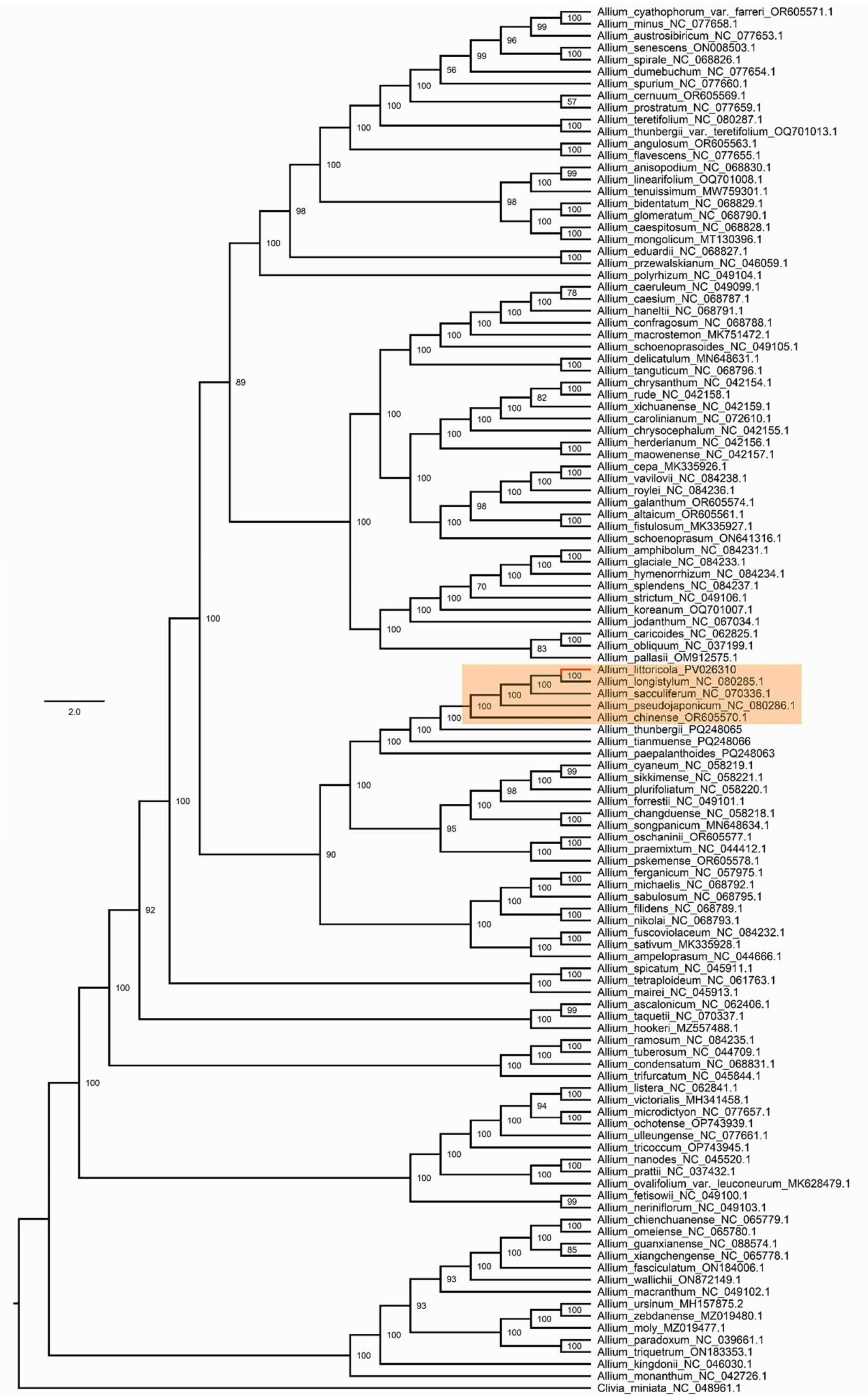

Fig. 2. Plastid phylogenetic tree of ***Allium*** based on the full-length plastome sequences.

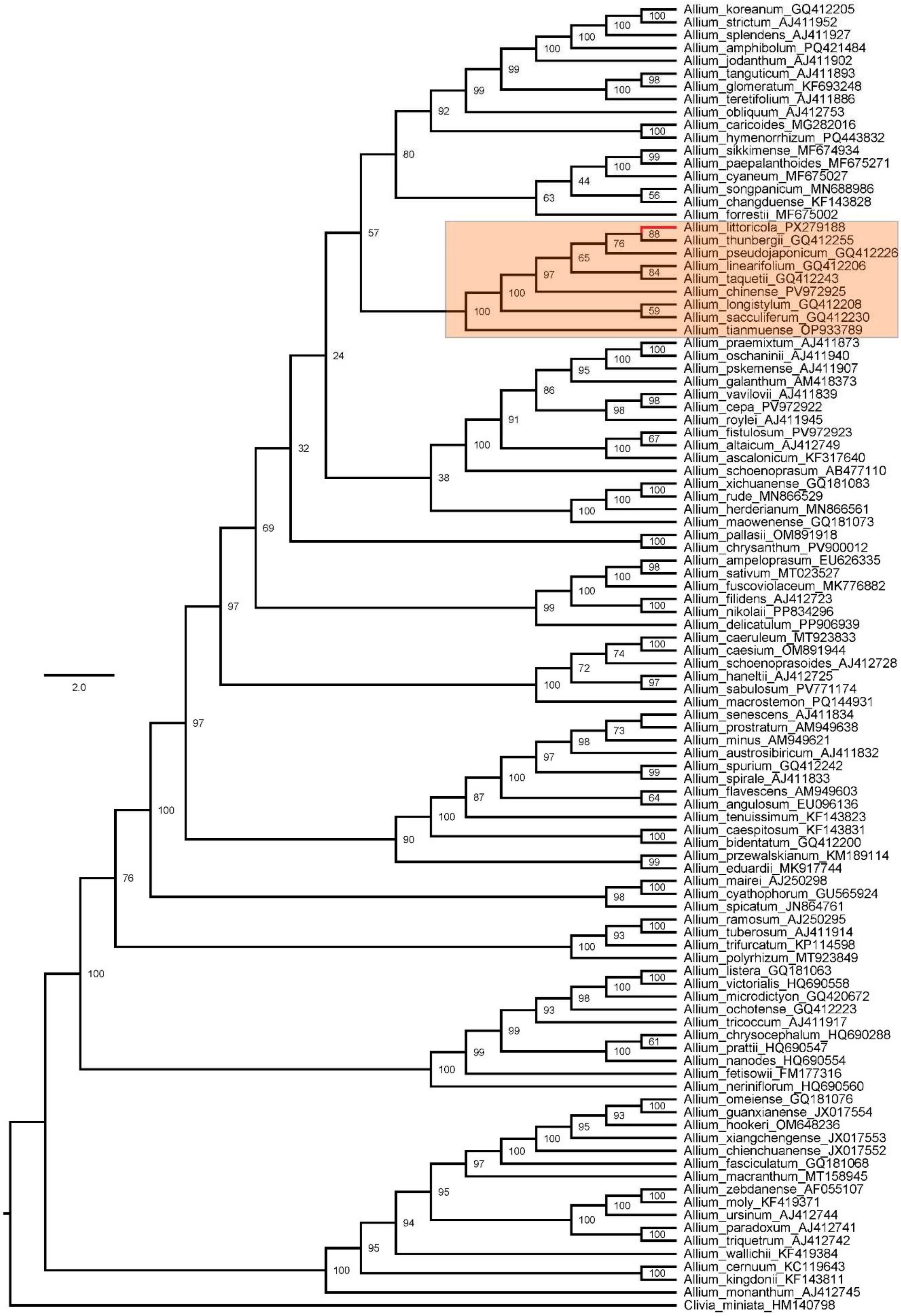

Fig. 3. Phylogenetic tree of ***Allium*** based on ITS sequences.

Fig. 4. Habitat and habit of ***Allium littoricola***. **A.** Habitat; **B.** Population (a. early spring; b. flowering period; c. fruiting period); **C.** Plants.

plastome sequences length of *Allium littoricola* was 152,422 bp (Fig. 1). The supermatrix of 116 complete plastome genomes with 193,176 bp was combined in Geneious v.24.0.5 (Kearse *et al*., 2012) and used for phylogenetic tree reconstruction. The plastome phylogeny supported that *A. littoricola* belongs to Sect. *Sacculiferum* and is sister to *A. longistylum* with full support, highlighting the close relationship at the plastome level (Fig. 2).

To further evaluate species delimitation, nuclear ribosomal ITS sequences of 101 *Allium* species were used to construct a phylogenetic tree with a supermatrix length of 931 bp. The results also confirmed that *A. littoricola* belonged to Sect. *Sacculiferum*, and importantly, it was recovered as sister to *A. thunbergii* with moderate bootstrap support (Fig. 3). This suggests that *A. littoricola* is distinguishable from *A. longistylum* at the nuclear ITS level. The differing sister relationships between plastid and nuclear markers may reflect incomplete lineage sorting or historical hybridization events within the Sect. *Sacculiferum*, and this warrants further investigation. Although the phylogenetic results based on the two markers were different, they both indicated that *A. littoricola* was genetically differentiated from its closely related species, supporting its status as an independent species.

TAXONOMIC TREATMENTS

Allium littoricola Z.H. Chen, Y.L. Xu & P. Li, ***sp. nov.***
滨海葱 Figs. 4–6

Type: CHINA. Zhejiang, Ningbo City, Xiangshan County, Hepu Town, Nantian Island, Yangliukeng Village, Bainiuwai, in the grassof the coastal hillside, 121°55'58.44"E, 29°3'26.16"N, alt. 20 m, 19 Nov. 2021, *Zheng-Hai Chen , Gen-you Li & Yue-Liang Xu, et al., Xu2734* (holotype: ZM, barcode: ZMNH0067407!; isotypes: ZM!, HZU!). (Fig. S1)

Fig. 5. Morphology of ***Allium littoricola***. **A.** Plant; **B.** Bulb (showing different colors of the tunic); **C.** Cross section of leaf blade; **D.** Cross section of scape; **E.** bracteole; **F.** Inflorescence; **G.** Flower; **H.** Anatomy of a flower; **I.** Infructescence; **J.** Seed.

Diagnosis: This new species is similar to *A. longistylum* Baker, but differs in having bulb ovoid (*vs.* cylindrically ovoid), tunic white, light purplish, membranous (*vs.* brown, papery), leaf blades ascending (*vs.* curved), scape lateral, hollow in cross section, or solid at base (*vs.* central, solid in cross section), perianth segments 5–6 × 2–3 mm (*vs.* 3.5–4.5 × 1.8–2.3 mm), filament 6.4–8.2 mm long, outer ones entire, inner ones with 1-toothed on each side (*vs.* 8.0–9.5 mm long, margin entire or inner ones with 1-toothed on each side), below 75 m altitude, sunny coastal hillside habitat (*vs.* 1,500–3,000 m altitude, slopes, plains and sunny meadows of riversides). Then, it is morphologically similar to *A. chinense* G. Don, but differs in having bulb solitary or clustered, ovoid (*vs.* densely clustered, narrowly ovoid), leave blades rounded, or with obtuse angles at lower part (*vs.* 3–5 sharply-angled), umbel with 8–57-flowered (*vs.* 4-28-flowered), seeds flat in cross section, micropyle apex acuminate (*vs.* convex in cross section, micropyle apex short-obtuse).

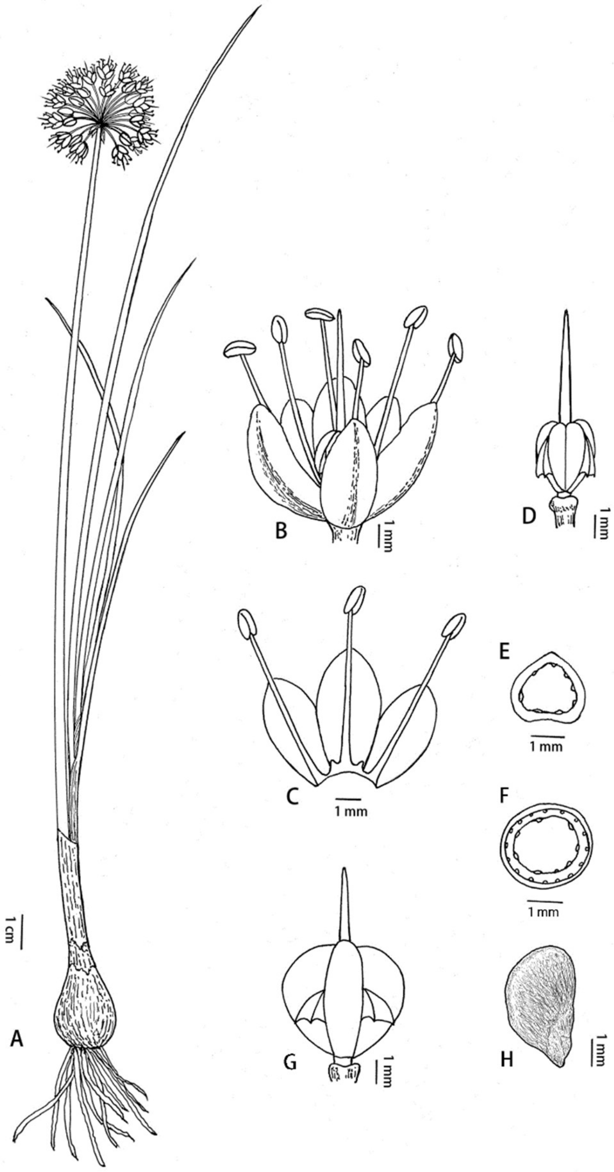

Fig. 6. Ink line diagram of ***Allium littoricola***. **A.** Whole plant; **B.** Flower; **C.** Tepals and filament; **D.** Pistil; **E.** Crosssection of leaf blade; **F.** Crosssection of scape; **G.** Capsule; **H.** Seed.

Description: Herbs perennial, with onion-garlic odor. Rhizome condensed, erect, 1.5–4.5 mm. Bulb solitary or clustered, ovoid, without bulbils, 8.5–23.0 mm in diam.; tunic white, light purplish, membranous, entire; fibrous roots growing from base of bulb, slender. Leaves 3–5; leaf sheaths exposed above ground, 1–4 cm high, striped green or light purplish; leaf blades ascending, 10–45 cm × 1–2 mm, linear, subterete, hollow in cross section, wall 0.4–0.5 mm thick. Scape lateral, terete, 14–45 cm × 2–3 mm, hollow in cross section, or solid at base, covered with leaf sheaths only at base. Spathe 1–3-valved, 10–12 mm long, persistent. Umbel nearly hemispheric, 35–55 × 45–60 mm, usually densely 8–57 flowered, without bead buds. Pedicels subequal, 7–16 mm long, only a few bracteolate at base, 1.2–3.0 × 1.5–3.0 mm. Flowers bisexual; perianth campanulate, reddish purple to purple; segments 6, in 2 whorls, elliptic, 5–6 × 2–3 mm, apex obtuse, inner ones slightly longer. Filaments subequal, 6.4–8.2 mm long, connate and adnate to perianth segments only at base; outer ones slightly broadened at base, entire; inner ones broadened at base, 1-tooth on each side. Ovary obovoid, 3-loculed, ovules 2 per locule, with concave nectaries covered by hoodlike projections at base. Styles 4.2–4.9 mm long, exserted, stigma simple, entire. Capsules cordiform, trigonous, 4.8–5.3 × 5.3–5.6 mm. Seeds oval, flat in cross section, 4.3–4.4 × 2.6–2.7 mm.

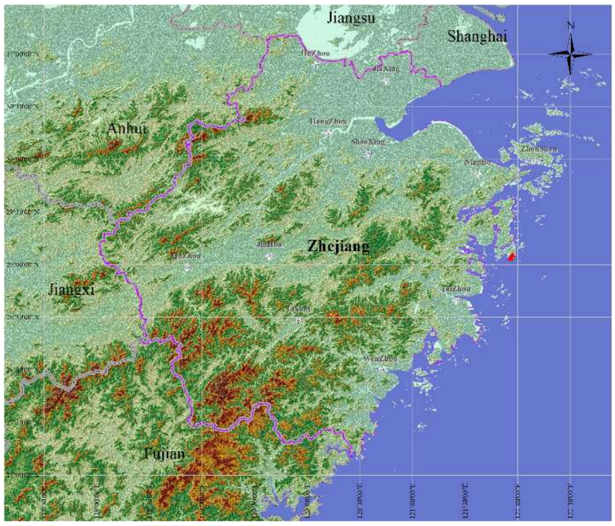

Fig. 7. Geographic distribution of ***Allium littoricola***. The red triangles represent the distribution sites.

Distribution: The new species is only found at Nantian Island in Xiangshan County, eastern Zhejiang (Fig. 7).

Habitat: It grows in the grass of the sunny coastal hillside at an elevation of 20–75 m.

Phenology: Flowering from November to December, fruiting from December to January of the following year.

Conservation status: Conservation assessment. We calculated conservation metrics for *Allium littoricola* using GeoCAT (Bachman *et al.,* 2011) based on its known localities to date, yielding an Area of Occupancy (AOO) of 4.000 km² and Extent of Occurrence (EOO) of 0.011 km². As stated by IUCN criteria (2024), “if EOO is less than AOO, EOO should be changed to make it equal to AOO to ensure consistency with the definition of AOO as an area within EOO”, therefore, the EOO should be calculated as 4.000 km² as AOO. Field investigations have documented clear reductions in habitat area and population size in recent years due to public infrastructure construction and local citrus industry development. Based on IUCN criteria (2024), *A. littoricola* is assessed as Critically Endangered [CR B1ab(iii)+B2ab(iii)].

Etymology: The specific epithet ‘littoricola’ refers to the habitat of the new species.

Growth trial: After 12 years (2014–2025) growth trials, this species exhibits robust vegetative growth while maintaining stable floral morphology without significant changes in inflorescence structure or size. Bulbs up to 23 mm in diam, leaf blades up to 100 cm × 4.3 mm, scape up to 60.5 cm length, Pedicels up to 24.7 mm length.

Additional specimen examined: CHINA. Zhejiang Province, Ningbo City, Xiangshan County, Hepu Town, Nantian Island, Yangliukeng Village, Bainiuwai, in the rock crevices of the coastal hillside, 121°56'0.36"E, 29°3'27.48"N, alt. 52 m, 9 Jan. 2025, *Zheng-Hai Chen, Yue-Liang Xu et al., Xu 3017* (ZM); the same locality, Yangliukeng Village, 121°55'58.8"E, 29°3'29.8"N, alt. 75 m, 9 Jan. 2025, *Zheng-Hai Chen, Yue-Liang Xu et al., Xu 3018* (ZM); the same locality, Xiaonantian Village, 121°55'52.9"E, 29°3'32.4"N, alt. 55 m, 9 Jan. 2025, *Zheng-Hai Chen, Yue-Liang Xu et al., Xu 3019* (ZM); Hangzhou City, Shangcheng District, Huajiachi, cultivated in Zhejiang Forest Resources Monitoring Centre (plants originally introduced from Yangliukeng, Nantian Island, Xiangshan County by Zheng-Hai Chen in November 2014), 6 Dec. 2021, *Zheng-Hai Chen*, *XS21120603* (ZM); the same locality, 23 Dec. 2024, *Zheng-Hai Chen*, *XS24122301* (HZU).

Key to *Allium littoricola* and its similar species

1a. Leaf blades without ridges ………….…………………………… 2
1b. Leaf blades with ridges …………………………..……………… 4
2a. Leaf blades terete or subterete; leaf sheaths exposed above the ground ………………………………….……………………… 3
2b. Leaf blades nearly flat; leaf sheaths not exposed above the ground; scapes terminal ……………………………………… ***A. thunbergii***
3a. Leaf blades subterete, ascending; scapes lateral, cross-section hollow or solid at the base; leaf sheaths 1.0–4.0 cm high ………. ***A. littoricola***
3b. Leaf blades terete, curved; scapes terminal, cross-section solid; leaf sheaths 5.1–16.0 cm high ………..………………… ***A. longistylum***
4a. Leaf blades 3-anguled, erect, withering in summer; scapes terminal ………………………………………..… ***A. sacculiferum***
4b. Leaf blades 3–5-angled, curved, evergreen in summer; scapes lateral ………………………………….……………… ***A. chinense***

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