

Distribution over the Equator;
the first record of *Yonagunia taiwani-borealis*
S.-M.Lin, Y.-C.Chuang & De Clerck
(Halymeniales, Rhodophyta) in Southern Indonesia

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ABSTRACT

Disjunct distributions provide an intriguing issue for our understanding of the biogeography of marine algae because of their lack of the active dispersal potential. The present morphological and molecular study reports the unexpected occurrence of a grateloupiacean red alga *Yonagunia taiwani-borealis* S.-M.Lin, Y.-C.Chuang & De Clerck from Lembongan Island, Southern Indonesia, a species which was considered endemic to northern Taiwan. Indonesian specimens were examined and are in good morpho-anatomical agreement with the Taiwanese type material. Plastid *rbcl* sequence divergence of both Indonesian and Taiwanese specimens was 0.08%. The disjunct distribution of *Y. taiwani-borealis* across the Equator likely represents a refugia population in an upwelling area that was isolated from formerly widespread populations. *Yonagunia taiwani-borealis* was large in height and abundant, likely functioning as foundation species of rocky shore community. This is the first record of *Y. taiwani-borealis* outside of northern Taiwan. This result raises the likelihood of other disjunct distributions of red algae between these two opposite areas of coastal upwelling in Southeast Asia.

KEY WORDS

Disjunct distribution,
Miocene,
rbcl,
red algae,
upwelling area.

RÉSUMÉ

Répartition au-delà de l'équateur; première observation de Yonagunia taiwani-borealis S.-M.Lin, Y.-C. Chuang & De Clerck (Halymeniales, Rhodophyta) dans le sud de l'Indonésie.

Les distributions disjointes constituent un sujet intrigant pour notre compréhension de la biogéographie des algues marines en raison de leur faible potentiel de dispersion active. La présente étude morphologique et moléculaire fait état de la présence inattendue d'une algue rouge de la famille des grateloupiacées, *Yonagunia taiwani-borealis* S.-M.Lin, Y.-C.Chuang & De Clerck, sur l'île de Lembongan, au sud de l'Indonésie, une espèce considérée comme endémique au nord de Taïwan. Les spécimens indonésiens ont été examinés et présentent une bonne concordance morpho-anatomique avec le matériel type taïwanais. La divergence de la séquence du gène chloroplastique *rbcl* des spécimens indonésiens et taïwanais était de 0,08 %. La distribution disjointe de *Y. taiwani-borealis* de part et d'autre de l'équateur représente probablement une population refuge dans une zone d'upwelling qui a été isolée des populations autrefois répandues. *Yonagunia taiwani-borealis* était grande et abondante, et jouait probablement le rôle d'espèce fondatrice de la communauté des côtes rocheuses. Il s'agit de la première observation de *Y. taiwani-borealis* en dehors du nord de Taïwan. Ce résultat augmente la probabilité d'autres distributions disjointes d'algues rouges entre ces deux zones opposées d'upwelling côtier en Asie du Sud-Est.

MOTS CLÉS

Distribution disjointe,
Miocène,
rbcl,
algues rouges,
zone d'upwelling.

INTRODUCTION

Yonagunia Kawaguchi & Masuda is a red algal genus in the Grateloupiaceae Schmitz that includes 10 species (Kim *et al.* 2021; Rodríguez-Prieto *et al.* 2022; Guiry & Guiry 2024). The genus was established to accommodate two species, the generitype *Y. tenuifolia* Kawaguchi & Masuda and the other previously known as *Prionitis formosana* (Okamura) Kawaguchi & Nguyen based on female auxiliary cell ampullar filaments and an *rbcL* phylogenetic analysis (Kawaguchi *et al.* 2004). *Yonagunia* was distinguished from other genera in the family by developing primary and secondary ampullar filaments simultaneously that form grape-like clusters of small globular cells that subsequently elongate and produce involucre filaments to laxly surround the maturing carposporophyte. About ten years later, three species have been added to *Yonagunia* based on *rbcL* phylogenetic and morphological evidence, one from southern Indonesia (Boo *et al.* 2013) and two from southern Madagascar (Manghisi *et al.* 2015). Recently, Lin *et al.* (2020) described three *Yonagunia*, two from Taiwan and one widespread species in the Indo-Pacific. Rodríguez-Prieto *et al.* (2022) described two more species from Taiwan, and thus Taiwan is considered the diversity center of *Yonagunia* (seven out of 10 species in the world). The estimation of the divergence time revealed that *Yonagunia* likely originated in the Eocene-Oligocene and diversified its species mainly in the Miocene (Lin *et al.* 2020).

In Indonesia, Boo *et al.* (2013) reported *Yonagunia zollingeri* G.H.Boo, J.K.Park & S.M.Boo in Malang, Java, which was for a long time known as *Gelidium zollingeri* Sonder Sonder (1854). During collection trips in southern Indonesia, we collected several specimens of *Yonagunia* from the Lembongan Islands, Bali. Here, it was found as a fairly large species up to 12 cm in height and growing in abundance on the lower intertidal rocky beds where it looked to be a foundational species. Morphological and *rbcL* sequence analyses of the *Yonagunia* sp. demonstrated its identification as *Y. taiwani-borealis* S.-M.Lin, Y.-C.Chuang & De Clerck there, which has been considered endemic to northern Taiwan.

MATERIAL AND METHODS

Specimens were collected in June 2017 in the intertidal zone at Dream Beach (8°41'28.80"S, 115°26'0.77"E), Lembongan Island, Bali on the southern coast (Table 1). The specimens were mounted on herbarium sheets and subsamples were dehydrated in silica gel for DNA sequencing. For anatomical observations, plants were sectioned using razor blades and were stained with 1% aqueous aniline blue. Photographs were taken with a DP-71 camera (Olympus, Tokyo, Japan) mounted on a BX-51 microscope (Olympus). Voucher specimens are housed at the Herbarium of the Department of Marine Biology, Pukyong National University, Busan, Korea (PKNU). DNA extraction, polymerase chain reaction amplification, and sequencing procedures followed Boo *et al.* (2016, 2022). The primer set used for amplifying and sequencing was

F145, F762, R898 and R1442 for *rbcL* (Kim *et al.* 2010). All sequences were aligned together with publicly available sequences of *Yonagunia* from previous studies (Lin *et al.* 2020; Rodríguez-Prieto *et al.* 2022), using the MUSCLE algorithm in MEGA7 (Kumar *et al.* 2016) with default parameters and the alignment was manually adjusted. Sequences generated in the present study were deposited in GenBank (Table 1).

Phylogenies of *rbcL* sequences were reconstructed using maximum likelihood (ML) and Bayesian inference (BI). The ML analysis was performed using the W-IQ-tree webserver (Trifinopoulos *et al.* 2016) with 1,000 ultrafast bootstrap (BS) replications (-bb 1000) and model test option (-m TEST). The BI analysis was performed with MrBayes v.3.2.1 (Ronquist *et al.* 2012) using the Metropolis-coupled Markov Chain Monte Carlo (MC3) with the best-fitting substitution model selected by iqtree. Four million generations of two independent runs were performed with four chains and sampling trees every 100 generations. The burn-in period was identified graphically by tracking the likelihoods at each generation to determine whether they reached a plateau. Twenty-five percent of saved trees were removed, and the remaining trees were used to obtain Bayesian posterior probabilities (BPP).

RESULTS

Family GRATELOUPIACEAE Schmitz
Genus *Yonagunia* S.Kawaguchi & M.Masuda

Yonagunia taiwani-borealis
S.-M.Lin, Y.-C.Chuang & De Clerck
(Fig. 1)

Journal of Phycology 56: 1550, figs 6, 7 (Lin *et al.* 2020).

SPECIMENS EXAMINED. — **Indonesia** • Bali, Nusa Lembongan Island, on the left side of Dream Beach; 23.VI.2017; S.M. Boo leg.; PKNU00668 (G76376); GenBank: PV030967; PKNU00669 (G76377), GenBank: PV030968; PKNU00670 (G76378), GenBank: PV030969; PKNU00671 (G81651), GenBank: PV030970.

DESCRIPTION

Thalli (Fig. 1A) were found epilithic on rocky intertidal beds and also to the shallow sublittoral zone, up to 12 cm in height, bushy, erect, bright to dark red. Single to several blades arise from discoidal to crustose holdfast. Main axes were terete basally and then gradually becoming compressed to flattened. Branches were feather-like to subdichotomously branched four to six orders. Blade structure was multiaxial, consisting of a cellular cortex and a compact medulla. Cortices were unilaterally thickened, while the medulla was filled with secondarily produced, densely entwined filaments.

Tetrasporangial sori were formed on the margins of blades and roundish, heart-shaped, or elongate (Figs 1B, C). Tetrasporangial initials were cut off from inner cortical cells and elongated. Tetrasporangia were ellipsoidal, cruciate or decussate, and 10–13 µm in width and 27–44 µm in length

TABLE 1. — Sample information of *Yonagunia taiwani-borealis* S.-M.Lin, Y.-C.Chuang & De Clerck collected in this study.

Species	Voucher-code	Collection information	<i>rbcL</i>
<i>Yonagunia taiwani-borealis</i> S.-M.Lin, Y.-C.Chuang & De Clerck	PKNU00668	Dream beach, Lembongan Island, Bali, Indonesia (8°41'28.80"S, 115°26'0.77"E); 23.VI.2017; <i>SMB G76376</i>	PV030967
<i>Yonagunia taiwani-borealis</i>	PKNU00669	Dream beach, Lembongan Island, Bali, Indonesia (8°41'28.80"S, 115°26'0.77"E); 23.VI.2017; <i>SMB G76377</i>	PV030968
<i>Yonagunia taiwani-borealis</i>	PKNU00670	Dream beach, Lembongan Island, Bali, Indonesia (8°41'28.80"S, 115°26'0.77"E); 23.VI.2017; <i>SMB G76378</i>	PV030969
<i>Yonagunia taiwani-borealis</i>	PKNU00671	Dream beach, Lembongan Island, Bali, Indonesia (8°41'28.80"S, 115°26'0.77"E); 23.VI.2017; <i>SMB G81651</i>	PV030970

(Fig. 1D). Female and male thalli were not found in the present collections.

PLASTID *rbcL* ANALYSIS

Four *rbcL* sequences (1 205 bp) of *Yonagunia taiwani-borealis* generated in the present study were identical in sequence. The pairwise sequence difference between the southern Indonesia and the Taiwanese type material (MT501503) was 0.08%. Phylogenetic analysis of the *rbcL* gene sequences revealed that *Y. taiwani-borealis* both Indonesian and Taiwanese specimens are positioned in a poorly resolved clade (70% MLBS, less than 0.9 BPP) with *Y. zollingeri* from Indonesia (Fig. 2). The ancestor of these two species again formed a well resolved clade with *Y. maillardii* (92% MLBS, 1.0 BPP).

DISCUSSION

The present study demonstrates the occurrence of *Yonagunia taiwani-borealis* in Lembongan Islands, Bali, Southern Indonesia. Indonesian specimens are mostly large (up to 12 cm), bushy, erect, and have discoidal holdfasts. Their axes are naked (lacking branches in the lower thallus) and have conspicuous to inconspicuous midribs in the upper thallus. The branching is subdichotomous to pinnate, elongate, roundish, and display heart-shaped tetrasporangial sori. Young plants of *Y. taiwani-borealis* are very similar to *Y. maillardii* in their lacking discoidal holdfast and a conspicuous midrib on the main axes based on our observation as well as findings by Lin *et al.* (2020), while *Y. maillardii* has less densely arranged branchlets (Rodríguez-Prieto *et al.* 2022). *Yonagunia taiwani-borealis* is also similar to *Y. stipitata* in its having stipitate main axes and bushy habit based on our observation, while, in *Y. stipitata*, main axes are not pinnately branched (Rodríguez-Prieto *et al.* 2022). Female reproductive structures and tetrasporangial anatomy have been well described and illustrated by Lin and her colleagues (Lin *et al.* 2020; Rodríguez-Prieto *et al.* 2022). A key including all 10 species of *Yonagunia* made by Rodríguez-Prieto *et al.* (2022) is very useful for identifying species,

however, DNA data are needed to conclusively confirm the identify of species of *Yonagunia* because of their thallus variability which depends on collection locality and growth stage.

The disjunct distribution of *Yonagunia taiwani-borealis* between southern Indonesia and northern Taiwan (c. 3 900 km apart) found in the present study casts an intriguing issue on when and how the distribution was shaped. The molecular estimation of *Yonagunia* revealed that *Y. taiwani-borealis* and *Y. zollingeri* diverged from the most recent common ancestor in the late Miocene (Lin *et al.* 2020). Since its divergence, *Y. taiwani-borealis* was likely widespread from southern Indonesia to northern Taiwan. *Yonagunia taiwani-borealis* might have persisted to favorable habitats in northern Taiwan and southern Indonesia where coastal upwelling has replaced nutrient-poor, warm surface waters with cold, nutrient-rich, deep waters (Wu *et al.* 2008; Fontana *et al.* 2024; Gallagher *et al.* 2024). Both northern Taiwan and southern Indonesia are hypothesized to be refugia for relict populations, being similar to vicariance events reported in coral reef fishes and red algae in Southeast Asia (Cowman & Bellwood 2013; Leliaert *et al.* 2018; Boo *et al.* 2022). The alternate hypothesis is that a long-distance dispersal event took place between these two disjunct areas. In this scenario, *Y. taiwani-borealis* is subject to assuming an origin center around the middle Philippines between the northern and southern hemispheres. The Kuroshio current is assumed to have driven its dispersal to northern Taiwan, while the Mindanao Current and Indonesian Throughflow (Gallagher *et al.* 2024) likely drove its dispersal to Southern Indonesia. However, the dispersal hypothesis is not currently supportable because of the lack of records of *Y. taiwani-borealis* between northern Taiwan and southern Indonesia. This hypothesis requires further verification through additional sampling in the intermediate region. The estimation of divergence time between these two isolated populations could further challenge the hypotheses of disjunct distribution over the equator using the mitochondrial COI-5P sequences data which is more sensitive than *rbcL* gene sequences at population levels (Boo *et al.* 2020).

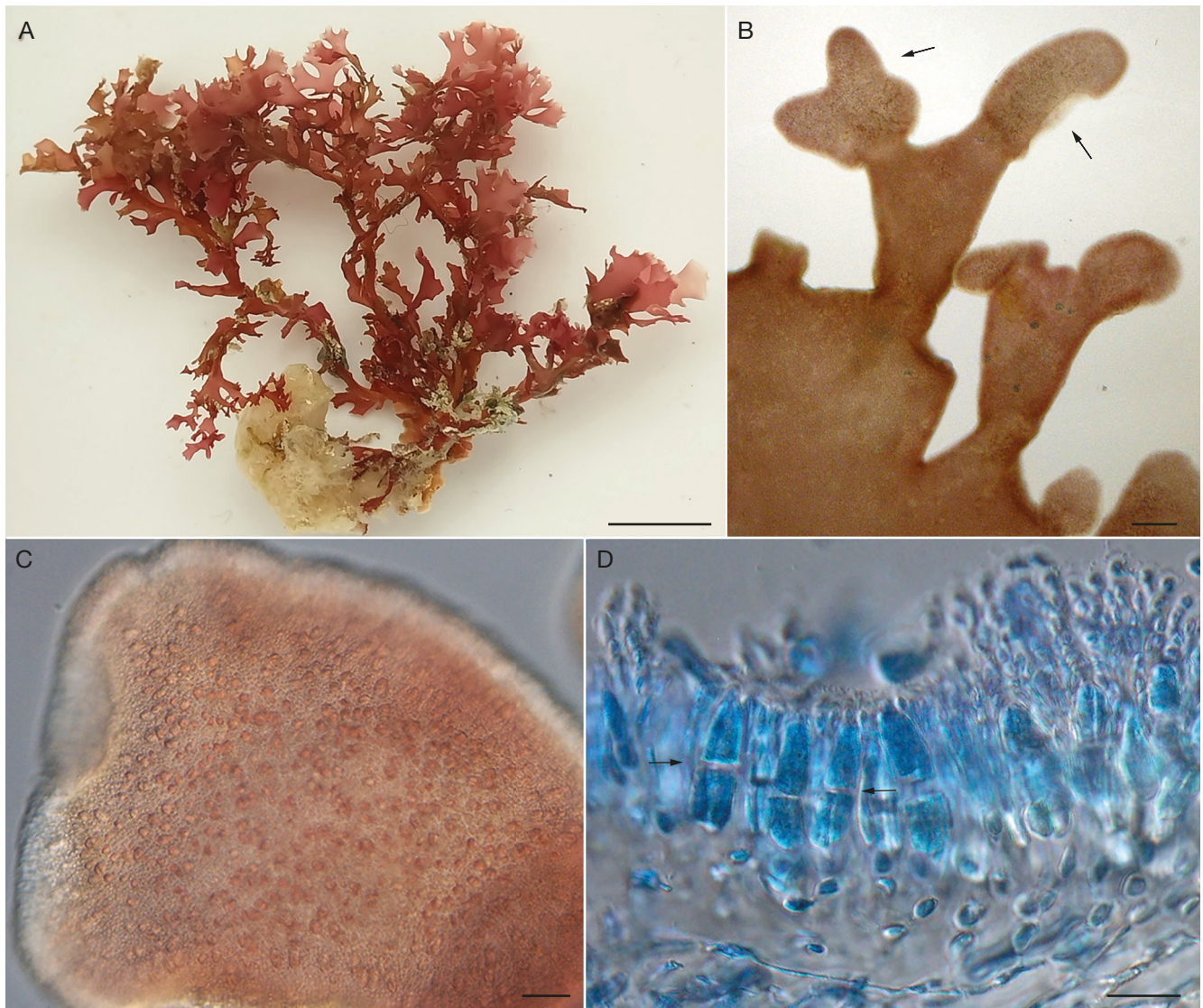


FIG. 1. — Morphology of *Yonagunia taiwani-borealis* S.-M.Lin, Y.-C.Chuang & De Clerck from Lembongan Island, Bali, Indonesia: **A**, habit of thallus; **B**, tetrasporangial stichidia (arrows) on the margins of branches; **C**, enlargement of tetrasporangial stichidium; **D**, transverse section of tetrasporangial stichidium showing tetrasporangia (arrows). Scale bars: A, 1 cm; B, 200 µm; C, 50 µm; D, 20 µm.

Plastid *rbcL* sequences of type and/or topotype material for all species of *Yonagunia* have been analyzed since its establishment by Kawaguchi *et al.* (2004) and greatly contributed to its taxonomy and biogeography (Boo *et al.* 2013; Manghisi *et al.* 2015; Lin *et al.* 2020; Rodríguez-Prieto *et al.* 2022). Pairwise divergence of the *rbcL* gene sequences between Indonesian and Taiwanese specimens of *Y. taiwani-borealis* (0.08%) is within the reported range of intraspecific divergence (up to 0.4%) in other species of *Yonagunia* (Lin *et al.* 2020). Compared to the plastid *rbcL* gene, mitochondrial COI-5P is more informative and as a result better at explaining distribution patterns of red algal species (Boo *et al.* 2020; Fumo & Sherwood 2023). However, it is regrettable that COI-5P sequences are currently unavailable in *Yonagunia* except *Y. atimo-vatae*, *Y. lingulata*, and *Y. zollingeri* (Boo *et al.* 2013; Manghisi *et al.* 2015).

The present study reveals the disjunct distribution of *Yonagunia taiwani-borealis* between two opposite areas of coastal

upwelling, which has been divided by the boundary of the Equator. *Yonagunia taiwani-borealis* is also an example showing the risks of defining endemism of marine algae without more extensive sampling data on less studied areas. To the best of our knowledge, this is the first study to report a red algal species in the Grateloupiaceae that has jumped the equatorial boundary. This result opens up further insights into distinct distributions and phylogeographic questions of red algae in Southeast Asia.

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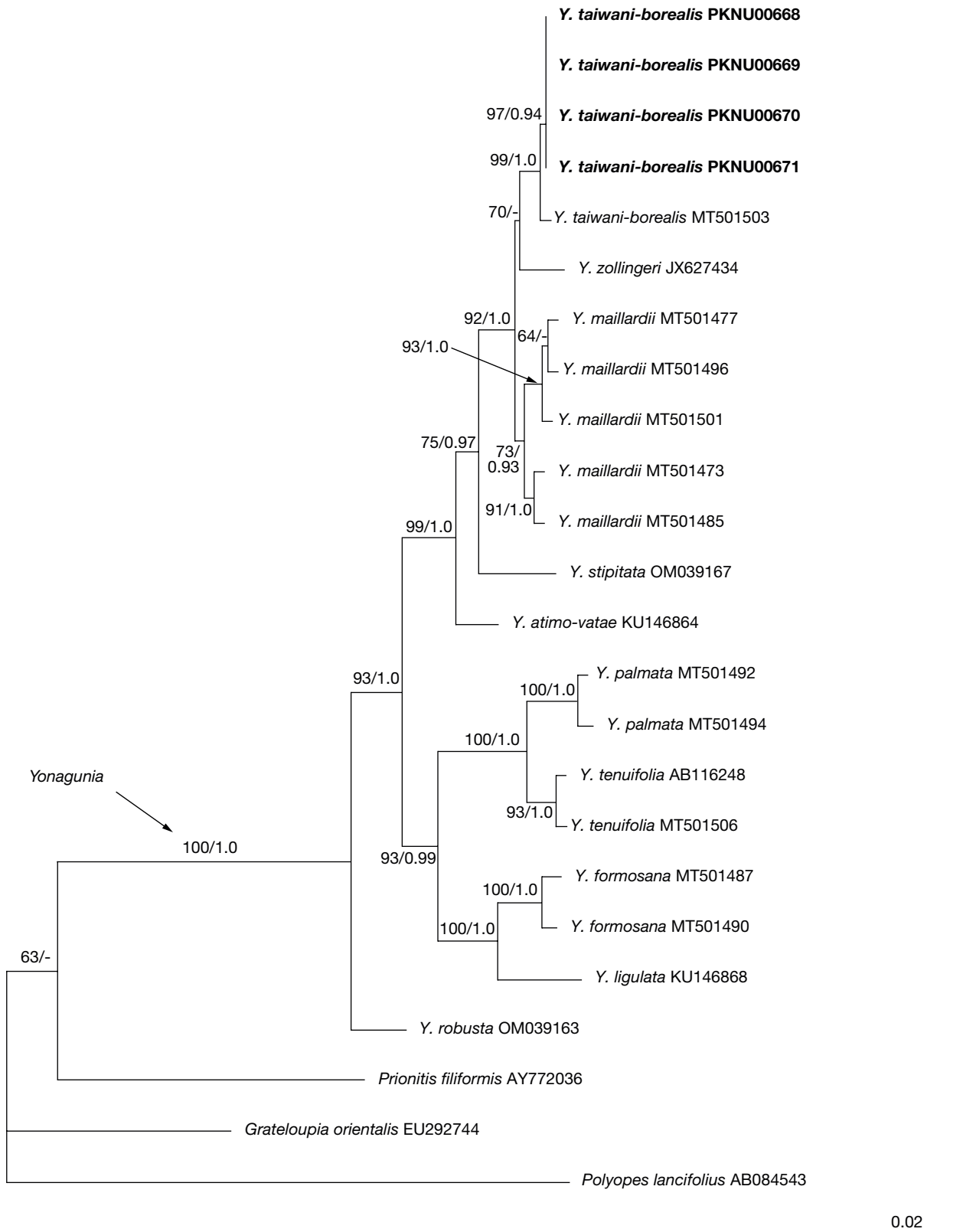


FIG. 2. — Maximum likelihood tree of *rbcL* sequences of *Yonagunia* spp. and *Yonagunia taiwani-borealis* S.-M.Lin, Y.-C.Chuang & De Clerck from Lembongan Island, Bali, Indonesia. The numbers above or below the nodes are ML bootstrap values and Bayesian posterior probabilities. Only bootstrap values $\geq 50\%$ and Bayesian posterior probabilities ≥ 0.90 are shown in the tree. **Bold** indicates newly analyzed sequences in the present study.

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