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Systematic revision of *Elaphoglossum* (Dryopteridaceae) in French Polynesia, with the description of three new species

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Species descriptions and a key for the nine species of *Elaphoglossum* (Dryopteridaceae) in French Polynesia are provided. Three new species are described: *E. austromarquesense* from the southern Marquesas Islands, *E. florencei* from Raiatea and Moorea, and *E. meyeri* from Rapa. Each species is illustrated by a line drawing of the habit, and spore images using a scanning electron microscope. Images of scales, one of the most important diagnostic characters in the genus, are also included. © 2008 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2008, **158**, 309–331.

ADDITIONAL KEYWORDS: ferns – insular flora – Marquesas Islands – Monilophytes – Pacific islands – Pteridophytes – Rapa – Society Islands – spores – taxonomy.

INTRODUCTION

Elaphoglossum contains about 600 species and ranks as one of the world's largest fern genera. Nearly 75% of the species are epiphytes. It occurs in both the New and Old World tropics, but is by far most species-rich in the Neotropics, where about 80% of the species occur, including all of the sections and subsections. The genus is related to *Bolbitis, Teratophyllum* and *Lomagramma* as evidenced by plastid DNA sequence data (Liu *et al.*, 2007; Schuettpelz & Pryer, 2007) and morphological characters, such as acrostichoid sori, sterile-fertile leaf dimorphy, an elongated (in crosssection) ventral vascular bundle in the rhizomes, and this ventral vascular bundle bearing all the roots (thus the roots appear to be borne only on the ventral surface of the rhizomes: Holttum, 1978; Kramer & Green, 1990). These genera are currently placed in Dryopteridaceae, a placement well supported by molecular phylogenetic studies (Smith *et al.*, 2006; Liu *et al.*, 2007; Schuettpelz & Pryer, 2007).

The infrageneric classification of *Elaphoglossum* is now firmly established thanks to morphological and molecular studies. Mickel & Atehortúa (1980) proposed a classification based on morphology, and this has been largely supported by the molecular phylogenetic studies of Rouhan *et al.* (2004) and Skog *et al.* (2004). A study of spores in relation to phylogeny further supported many of the infrageneric groups (sections and subsections) (Moran, Garrison-Hanks & Rouhan, 2007a).

The main clades in *Elaphoglossum* can now be characterized as follows. Section *Amygdalifolia* is

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Figure 1. Map of the islands of French Polynesia with the relative geological ages of the archipelagos.

sister to the rest of the genus (Rouhan et al., 2004). It consists of a single species [E. amygdalifolium (Mett. ex Kuhn) Christ] that has long-creeping rhizomes, phyllopodia and hydathodes – a unique character combination in the genus. Its reddish young leaves are also unique within the genus. Section Elaphoglossum is characterized by phyllopodia and usually thick, glabrous to very sparsely scaly blades. Based on molecular evidence (Rouhan et al., 2004), it consists of two main clades: subsections Pachyglossa and Platyglossa. No known macromorphological characters separate these two groups; however, their perispores differ: subsection Pachyglossa has nonperforate perispores, whereas they are perforate in subsection Platyglossa (Moran et al., 2007a). Section Squamipedia is characterized by long-creeping rhizomes, paired peg-like aerophores on the rhizomes near the petiole bases, pale brownish flaccid rhizome scales and a lack of phyllopodia. The subulate-scaled clade ('Subulata' in Rouhan et al., 2004) is characterized by leaves with subulate scales - erect hair-like

scales enrolled at the bases and often all the way to the tip. This clade comprises two subsections: subsection *Polytrichia*, which lacks hydathodes, and subsection *Setosa*, which possesses hydathodes. The last section, *Lepidoglossa*, is characterized by laminar scales with marginal teeth consisting of acicular cells (all other *Elaphoglossum* species have laminar scales with marginal teeth consisting of glandular or bulbous marginal cells, or gland-tipped marginal processes).

French Polynesia is a political entity that comprises 118 islands spread across five million square kilometres of the southern Pacific Ocean (Fig. 1). The islands form five archipelagos: the Society Islands, the Marquesas Islands, the Austral Islands (or Tubuai Islands), the Tuamotu Islands and the Mangareva Group (or Gambier Islands). The Societies, Marquesas, Australs and Mangareva Group (the latter group comprises the remaining peaks of a once single large island) are, with a few exceptions, made up of high islands that are volcanic in origin. The 78 islands of

| Archipelago | Number of islands | Range of age (Myr) | Latitude | Longitude | Land area (km ²) |
|---------------------------|----------------------|--------------------|---|----------------------|------------------------------|
| Society Islands | 14 | < 0.5-4.5 | 15°48′ and 17°53′S | 148°05′ and 154°43′W | 1536 |
| Marquesas Islands | 15 | 1.3 - 8.8 | 7°50' and 10°35'S | 138°25′ and 140°50′W | 1189 |
| Tuamotu Islands | 78 | 47.4* | 14°00' and 23°00'S | 135°00′ and 149°00′W | 826 |
| Mangareva Group (Gambier) | 4 | 5.2 - 7.2 | 23°00' and 23°15'S | 134°50′ and 135°00′W | 28 |
| Austral Islands | 7 | 3.5 - 27 | 21°45' and 28°00'S | 143°30′ and 155°00′W | 174 |
| Total (French Polynesia) | 118 | < 0.5 - 47.4 | $7^\circ 50'$ and $28^\circ 00' \mathrm{S}$ | 134°50′ and 155°00′W | 3753 |

Table 1. Overview of the geography and geology of French Polynesia

*From a single volcanic sample (Schlanger et al., 1984).

the Tuamotu chain, with the exception of the uplifted limestone island of Makatea, are low-lying atolls.

The indigenous vascular plant flora of French Polynesia has been estimated to be approximately 960 species (Florence, 1987) with an endemism of 58%. For monilophytes and lycophytes, endemism is estimated to be approximately 35% (J. Florence, IRD, Paris, pers. comm.). In his phytogeographical analyses of the Pacific, Van Balgooy (1971) placed French Polynesia in the South-eastern Polynesia Province. The floristic affinities of these isolated archipelagos, located 6000 km from North America and 9000 km from Japan, have a strong Indo-Malaysian influence (Mueller-Dombois & Fosberg, 1998). However, *Elaphoglossum* appears to have its origins in the New World tropics (Rouhan *et al.*, 2004).

Elaphoglossum species presently occur only on the wet, high islands in the Marquesas and the Societies and on the island of Rapa in the Australs. Each archipelago is a geological timeline of islands that emerged when the Pacific Tectonic Plate moved slowly to the north-west over volcanic hotspots (Duncan & Clague, 1985). Each archipelago was therefore laid down in linear progression, with the islands in the north-west being the oldest and those in the southeast being the youngest (Table 1, Fig. 1). The Austral chain is the most ancient of the remaining high islands. Rapa in the south-eastern end (younger end) of the Austral archipelago is estimated to be 5.9 Myr in age (Duncan & Clague, 1985). The Marquesas Islands range from 8.8 to 1.3 Myr in age (Brousse et al., 1990) and the Society Islands are 4.5 to < 0.5 Myr in age (Mehetia Island is still active; Duncan & Clague, 1985).

Morphological and phylogenetic data (Rouhan *et al.*, 2004; Moran, Motley & Rouhan, 2007b) suggest that French Polynesia has been colonized by species of *Elaphoglossum* at least three times. The most likely ancestral source areas are the New World tropics. The hypothesis for three distinct colonization events was derived from data indicating that the

French Polynesian species of *Elaphoglossum* belong to different taxonomic sections which are located on three separate well-supported branches of the phylogenetic tree for the genus (Rouhan et al., 2004). Two species (E. austromarquesense and E. tovii) belong to section Lepidoglossa, four species (E. florencei, E. meyeri, E. rapense and E. samoense) are in subsection Setosa of section Subulata, and the remaining three species (E. feejeense, E. marquisearum and E. savaiense) are members of section Elaphoglossum subsection Pachyglossa. Most of the French Polynesian species are endemic to a single archipelago, with the exception of *E. savaiense*, which occurs in both the Australs and the Societies, and E. feejeense, which is indigenous to the Societies and to other regions in the western Pacific. At least two colonization events must be invoked to explain the derivation of *Elaphoglos*sum on each archipelago. The Marquesas, with three endemic species, harbours two members of section Lepidoglossa and one species in section Elaphoglossum. The Societies contain two endemic species in section Subulata and the two widespread species in section Elaphoglossum. Rapa, in the Australs, is inhabited by two endemic species in section Subulata and E. savaiense (section Elaphoglossum), which also occurs in the Societies. Geiger et al. (2007) hypothesized that trade winds and storms were responsible for the colonization of several fern genera to the Hawaiian Islands that had Neotropical sister relationships. This same scenario is also the most likely explanation for the long-distance dispersal of Elaphoglossum to French Polynesia.

Despite progress in understanding the phylogeny and circumscription of the main infrageneric groups, taxonomic treatments of the species of *Elaphoglossum* are still lacking for many regions of the world, making it a challenge to identify specimens and compare the floras of different regions. Identification has been a particular problem because the genus is morphologically uniform (nearly all the species have simple, entire leaves and free veins), and herbarium

specimens are often misidentified. Within the past 20 years, several useful taxonomic treatments have appeared for certain regions, such as Mesoamerica (Mickel, 1995a), Mexico (Mickel & Smith, 2004), Venezuela (Mickel, 1995b), Peru (Mickel, 1991), tropical East Africa (Mickel, 2002), Hawaii (Palmer, 2003) and islands of the Indian Ocean (Lorence & Rouhan, 2004). However, no treatment exists for French Polynesia. The purpose of this paper is to provide such a treatment for the French Polynesian species of *Elaphoglossum*.

MATERIAL AND METHODS

PLANT MATERIAL

This revision is based on the examination of over 300 herbarium specimens and on field observations of all nine *Elaphoglossum* species. Specimens from the following herbaria (abbreviated according to Holmgren, Holmgren & Barnett, 1990) were examined and annotated during this study: BISH, G, K, MICH, MPU, NY, P, PAP, PTBG, US. All measurements, colours and other details included in the descriptions were based on herbarium specimens and data derived from field notes. In evaluating the variability of each

species, habitat and ecology were noted in the field, but information on these features was also taken from herbarium labels.

SPORE MICROMORPHOLOGY

Spores were obtained from herbarium specimens of *Elaphoglossum* at NY and P. Generally, one specimen per species and 20–100 spores per stub were examined. The spores were transferred with dissecting needles from herbarium specimens to aluminium scanning electron microscope (SEM) stubs coated with an asphalt adhesive. The stubs were then coated with gold–palladium in a sputter coater for 2.5 min, and the spores were imaged digitally using a JEOL JSM-5410LV SEM equipped with a JEOL Orion 5410 software interface. The accelerating voltage was 15 kV.

TAXONOMIC TREATMENT

Elaphoglossum Schott ex J.Sm., J. Bot. (Hook.) 4(27): 148. Aug. 1841, nom. et typ. cons. TYPE: *E. conforme* (Sw.) J.Sm., J. Bot. (Hook.) 4(27): 148. 1841. *Acrostichum conforme* Sw., Syn. Fil. (Sw.) 10, 192. 1806.

DIAGNOSTIC KEY TO SPECIES OF THE GENUS ELAPHOGLOSSUM IN FRENCH POLYNESIA

| 1. | Sterile blades glabrous or bearing scattered, inconspicuous, minute, appressed, scales less than 1 mm long, scales |
|----|--|
| | substellate with margins bearing gland-tipped cilia |
| 2. | Veins free apically; rhizomes short-creeping (Society Islands)2. E. feejeense |
| 2. | Veins uniting apically into a continuous intramarginal vein; rhizomes moderately creeping to long-creeping |
| 3. | Scales of blades like numerous blackish dots; petioles scaly in the proximal half; usually epiphytic (Marquesas |
| | Islands) |
| 3. | Scales of blades brown; petioles subglabrous even in the proximal half; usually terrestrial on organic soils, able to |
| | form large populations (Austral and Society Islands)8. E. savaiense |
| 1. | Sterile blades bearing scattered to imbricate, conspicuous, ovate to narrowly ovate or subulate and acicular scales |
| | on both surfaces |
| 4. | Scales of blades flat, with margins bearing hair-like teeth; veins not forming hydathodes apically |
| 5. | Blades bearing scattered scales up to 1.5 mm long, not forming a marginal fringe (Marquesas Islands: Fatu Hiva, |
| | Hiva Oa, Tahuata)1. E. austromarquesense |
| 5. | Blades densely scaly, scales 2-6 mm long, forming a distinct fringe along the margins of the blades (Marquesas |
| | Islands: Nuku Hiva, Ua Huka, Ua Pou)9. E. tovii |
| 4. | Scales of blades subulate and acicular (at least bases being cochleariform), with subentire or serrulate margins; |
| | veins forming hydathodes apically |
| 6. | Rhizomes erect; blades 5.0-9.8 cm wide, bases rounded to obtuse; plants terrestrial (Austral Islands) |
| | |
| 6. | Rhizomes short-creeping; blades 1.0-3.5(7.0) cm wide, bases acute to cuneate; plants epiphytic, saxicolous or |
| | occasionally terrestrial (Austral and Society Islands) |
| 7. | Scales of petioles flat, spreading, with margins serrulate throughout (Society Islands) |
| 7. | Scales of petioles obviously subulate, erect, with margins entire or subentire |
| 8. | Scales of petioles and blades $1.5-2.5 \times 0.1-0.25$ mm; blades apically obtuse (rarely acute); terrestrial or saxicolous |
| | (Austral Islands) |
| 8. | Scales of petioles 5–8 mm long, scales of blades 3–5 mm long; blades apically acute to attenuate (rarely rounded); |
| | epiphyte (Society Islands) |



Figure 2. A–D, *Elaphoglossum austromarquesense* (*Lorence 9011*, NY): A, habit; B, rhizome scales; C, petiole scale; D, abaxial surface of blade. E–H, J, *Elaphoglossum meyeri* (*Motley 2875*, NY): E, habit; F, rhizome scale; G, petiole scale; H, abaxial surface of blade; J, abaxial surface of costa. All scale bars 1 mm unless otherwise indicated. Drawing by H. Fukuda.

1. **ELAPHOGLOSSUM AUSTROMARQUESENSE** ROUHAN & LORENCE SP. NOV.

Type: Marquesas, Fatu Hiva, trail from Omoa-Hanavave road leading to Teavapuhiau peak, just S of Teavapuhiau peak, 10°28'S, 138°38'W, 610–630 m, 6.ii.2003, D. H. Lorence 9011, with L. Dunn, S. Perlman, K. Wood, J.-Y. Meyer (holotype P!; isotypes) BISH!, NY!, PAP!, PTBG!, US!). Figures 2A–D, 10, 11.

Etymology: From the Latin '*austro*' (south) and '*marquesense*' (the Marquesas Islands), referring to the part of the archipelago in which the species occurs.



Figures 3-10. Close-up of abaxial surface of blades of species of *Elaphoglossum* from French Polynesia. Fig. 3. *E. feejeense* (*Birnbaum 113*, P). Fig. 4. *E. marquisearum* (Lorence 9020, P). Fig. 5. *E. rapense* (St John et al. 15644, P). Fig. 6. *E. meyeri* (Florence 6507, P). Fig. 7. *E. samoense* (Jacq 424, P). Fig. 8. *E. florencei* (Florence 8348, P). Fig. 9. *E. tovii* (Florence 4203, P). Fig. 10. *E. austromarquesense* (Lorence 9011, P). Scale bar, 1 cm.

Diagnosis: Rhizomata repentes *c.* (4)6–8 mm diam, paleis castaneis anguste ovatis. Laminae steriles anguste ellipticae, ad apicem acutae, ad basim cuneatae, paleis orbicularibus vel suborbicularibus ad 1.5 mm longis, setiferis marginibus.

Description: RHIZOMES short-creeping, (4-)6-8 mm in diameter (excluding the dense covering of scales), unbranched, bearing erect fronds borne in 2(3) ranks, spaced 2–5 mm; rhizome scales $4-11 \times 0.5-1.0$ mm, narrowly ovate to linear, bases cordate, apices attenuate and sinuate, dark reddish brown, lustrous, chartaceous, margins entire to subentire with few short teeth occasionally glandular, cells short to elongate. PHYLLOPODIA 4–7 mm long, dull brown, bearing scales as on rhizomes. STERILE FRONDS simple, (10)17–38 × (1.0)1.5–3.7 cm; petioles (3/10)2/5–9/10 the sterile blade length, 1.0–1.5 mm wide, with dense to scattered (glabrescent), reddish brown to pale reddish brown scales of two types in various proportions, the small scales orbicular to ovate, 0.5–2.0 mm, basifixed, bases cordate to auriculate, margins with 4–8 hair-teeth on each side, the larger scales narrowly ovate, up to 9 mm long, bases cordate, margins with few hair-teeth in the basal half part. BLADES narrowly elliptic, bases cuneiform, apices acute, coriaceous, both surfaces of blades bearing closely appressed, glabrescent, suborbicular scales as the smaller ones on the petioles but not larger than 1.5 mm, costae rounded abaxially, canaliculate adaxi-



Figures 11–19. Scales of the nine species of *Elaphoglossum* from French Polynesia (*a*, laminar scales; *b*, petiole scales; *c*, rhizome scales). Fig. 11. *E. austromarquesense*. Fig. 12. *E. tovii*. Fig. 13. *E. florencei*. Fig. 14. *E. rapense*. Fig. 15. *E. samoense*. Fig. 16. *E. meyeri*. Fig. 17. *E. feejeense*. Fig. 18. *E. marquisearum*. Fig. 19. *E. savaiense*. Scale bar, 1 mm (except Figs 11*a*, *b*, 16*a*, 18*a*: scale bar, 0.5 mm; Fig. 19*a*: scale bar, 0.3 mm).

ally. VEINS free, simple or once bifurcate. HYDATH-ODES absent. FERTILE FRONDS shorter or longer than the sterile, blades similar in shape but narrower, (5)7–14 mm wide; intersporangial scales absent. SPORES $34-50 \times 31-35 \mu m$, perispores with broad continuous folds, tubercles on surfaces between folds, lacking perforations and spines, margins of folds smooth (entire) (Fig. 20). Discussion: Based on its morphological characters, especially its scaly fronds, *E. austromarquesense* belongs to section *Lepidoglossa*. Specimens of this species were previously identified as *E.* sp., *E.* cf. *marquisearum*, *E. marquisearum* or *E. tovii. Elaphoglossum austromarquesense* is distinguished from *E. marquisearum* Bonap., which has glabrate blades typical of section *Elaphoglossum*. The most similar



Figures 20–28. Spores of the nine species of *Elaphoglossum* from French Polynesia. Fig. 20. *E. austromarquesense* (Lorence 9011, P). Fig. 21. *E. tovii* (Florence 7282, P). Fig. 22. *E. feejeense* (Florence 9807, P). Fig. 23. *E. samoense* (Florence & Birnbaum 9938, P). Fig. 24. *E. florencei* (Jacq 463, P). Fig. 25. *E. meyeri* (Motley 2875, NY). Fig. 26. *E. rapense* (St John & Maireau 15529, P). Fig. 27. *E. savaiense* (Florence 12133, P). Fig. 28. *E. marquisearum* (Wood 6390, NY). Scale bar, 10 μm.

species is *E. tovii* E.D.Br., which also belongs to section *Lepidoglossa*. However, *E. austromarquesense* differs by the smaller, narrower fronds and less scaly blades with suborbicular and smaller scales. In *E. tovii*, the abundant laminar scales form a red-brown fringe along the margins of the blades, whereas this is absent in *E. austromarquesense*.

Both *E. tovii* and *E. austromarquesense* are endemic to the Marquesas. Morphologically, the specimens were separated and attributed to one or other species. Specimens also segregated geographically into the North and South Marquesas: *E. tovii* is restricted to the northern islands, whereas *E. austromarquesense* occurs only in the southern islands of Fatu Hiva, Hiva Oa and Tahuata.

Distribution and habitat: Marquesas Islands, in the southern islands only: Fatu Hiva, Hiva Oa, Tahuata.

Epiphyte, on mossy trunks, in wet crest forests of *Metrosideros*, *Weinmannia*, *Cyathea*, *Pandanus* and *Hibiscus*, from 550 to 1160 m.

Other specimens examined: FATU HIVA: Haute vallée de la Vaitopii, piste de Ouia, 148°38'W, 10°29'S, 640 m, 27.ii.1986, Florence 7359 (P, PAP); Epaulement SW du Mt. Touaouoho, 138°38'W, 10°29'S, 770 m, 23.vii.1988, Florence et al. 9538 (BISH, P, PAP 2 sheets, US); trail from Omoa along Punaitai ridge crest to base of Tekou peak, 550–840 m, 23.vii.1988, Lorence et al. 6172 (BISH, PAP, PTBG); trail from Omoa-Hanavave road leading to Teavapuhiau peak, just S of Teavapuhiau peak, 10°28'S, 138°38'W, 610–630 m, 6.ii.2003, Lorence 9004 (PTBG, US), Lorence et al. 9011 (BISH, NY, P, PAP, PTBG, US); Sentier d'Ouia, W du col, lieu-dit Tahuna, 620 m, 21.ix.1975, Schäfer 5802 (MPU);

Tevaiua, 871 m, 15.ii.2003, *Wood 10141* (PTBG, US); Teavapuhiau, 640 m, 6.ii.2003, *Wood 10088* (BISH, P, PAP, PTBG, US).

HIVA OA: Region Atuona, > 800 m, 15.i.1922, Brown & Brown 1021a (BISH); Atuona, piste de Hanamenu, NW du Mt. Temetiu, 139°5'W, 9°48'S, 1080-1160 m, 30.vii.1988, Florence et al. 9631 (BISH, P, PAP), Florence et al. 9647 (PAP); along old Atuona-Hanamenu trail, on high ridge leading to Mt. Feani, 1050-1150 m, 30.vii.1988, Lorence et al. 6244 (PAP, PTBG); ridge crest leading to Mt. Temetiu, S of Teakatau, along ridge heading W towards Hanamenu. 139°4'30"W, 9°48'S, 1000 m, 30.i.2003, Lorence 8937 (P, PTBG), Lorence 8938 (PTBG, US); Tenatinaei, crest N of summit of Mt. Temetiu, 3620 ft, 24.vii.1929, Mumford & Adamson 474 (BISH); Mt. Feani, trail from Atuona to Hanamenu, 1080 m, 11.ii.1975, Oliver & Schäfer 3112 (BISH, MPU, PTBG, US); Atuona-Feani trail, upper part of trail just below crest of ridge, 1200 m, 24-26.ix.1963, Sachet & Decker 1136 (PTBG, US); Mt. Ootua, 2400-2500 ft, Wood & Perlman 4351 (BISH, PAP, PTBG, US); Temetiu region, drainage to south-east of Vaimete et Vaiumioi, headwaters of Hanamenu, 1067 m, 29.i.2003, Wood 10040 (BISH, NY, P, PAP, PTBG, US).

TAHUATA: Haaoiputeomo near satellite dish, NE from Vaitahu to summit ridge, 2000–2500 ft, 1–2.ix.1995, *Wood 4434* (BISH, MO, P, PAP, PTBG, US).

2. ELAPHOGLOSSUM FEEJEENSE BRACK.

U.S. Expl. Exped., Filic. 16: 72 (1854). Acrostichum feejeense (Brack.) Hook., Sp. Fil. 5: 199 (1864). TYPE: Fiji Islands, on trees, vicinity of Sandal-wood Bay, 1838–1842, Wilkes s.n. (holotype US!). Figures 3, 17, 29G–J.

Synonyms: Elaphoglossum tahitense Brack., U.S. Expl. Exped., Filic. 16: 73 (1854) **Syn. Nov.** Acrostichum tahitense (Brack.) Carruth. in Seemann, Fl. Vit.: 373 (1873). TYPE: Society Islands, Tahiti, terrestrial, in mountain forests, 1838–1842, Wilkes s.n. (holotype US!).

Acrostichum conforme sensu Drake, Fl. Polynésie Franç. 319 (1892), non A. conforme Sw., Syn. Fil. 10: 192, fig. 1(1) (1806).

Elaphoglossum vanuaënse Krajina. TYPE: Fiji, Vanua Levu: Thakaundrove, south-western slope of Mt. Mbatini, 300–700 m, dense forest, 28–29.xi.1933, epiphyte, *A.C. Smith 675* (holotype K, photo P!; isotypes BISH!, NY!, UC, US!).

Etymology: The specific epithet '*feejeense*' refers to the Fiji Islands, where the type specimen was collected.

Description: RHIZOMES short-creeping, 5-8 mm in diameter (excluding the dense covering of scales), unbranched, bearing erect fronds, borne in 2(3) ranks, spaced 2–5 mm; rhizome scales $6-10 \times 1.0-1.5$ mm, narrowly ovate, bases cordate to auriculate with lobes overlapping, apices attenuate, yellowish to light reddish brown, dull, papyraceous, margins subentire with some glandular-tipped cilia, cells short to elongated. PHYLLOPODIA distinct, to 1.5 cm long, darker, bearing basally few scales similar to those of the rhizomes. STERILE FRONDS simple, $20-58 \times 1.8-$ 6.0 cm; petioles 1/6-1/2 the sterile blade length, 1.5-2.5 mm wide, subglabrous but bearing numerous reddish resinous dots. BLADES narrowly elliptic to oblong, bases attenuate and decurrent, apices obtuse to rounded, coriaceous, lustrous adaxially, margins revolute, both surfaces of blades subglabrous but bearing (at least when young) usually numerous shiny, reddish, resinous dots; costae prominent on both faces, rounded abaxially, canaliculate adaxially, bearing resinous dots. VEINS indistinct, free, simple or bifurcate. HYDATHODES absent. FERTILE FRONDS shorter to equalling the sterile; petioles 2/5-3/5 the fertile blade length, fertile blades linear, 1.2-2.2 cm intersporangial scales absent. wide: SPORES $34-50 \times 19-29 \,\mu\text{m}$, perispores with broad continuous folds or cristae, perispore surfaces smooth between ridges, no perforations or spines, margins of folds smooth (Fig. 22).

Discussion: Elaphoglossum feejeense belongs to section Elaphoglossum, characterized by nearly glabrous blades. It is most similar to *E. savaiense*, which also has reddish resinous dots on the blades. *Elapho*glossum feejeense is primarily distinguished by the free veins and obtuse fronds.

The name *E. tahitense* was published in the same book as the name E. feejeense, the latter appearing first. With a fertile frond well developed and apices of sterile blades preserved, the holotype specimen of E. feejeense is a better specimen than that of E. tahitense. For this reason, we decided to place E. tahitense in synonymy under E. feejeense. Information about the type locality in the protologue (Tahiti, Society Islands) disagrees with information typed on the sheet label (Philippine Islands) housed at US. Nevertheless, the sheet bears another label, handwritten, bearing the annotation '12/ Elaphoglossum tahitense sp. nov.?'. The number '12' matches the taxon number figured in the protologue. For this reason, we believe that the specimen housed in US is the holotype, and we conclude that the type locality 'Philippine Islands' on the sheet is probably a mistake.

Distribution and habitat: Society Islands: Raiatea and Tahiti. Also present in Fiji, Samoa, Tonga and Vanuatu. Epiphyte in wet forests, from 80 to 400 m.



Figure 29. A-F, *Elaphoglossum marquisearum* (*Lorence 9020*, P): A, habit; B, rhizome scale; C, petiole scale; D, abaxial surface of blade; E, scales on abaxial surface of blade; F, adaxial surface of blade. G, H, J, *Elaphoglossum feejeense* (*Florence & Birnbaum 9936*, P): G, habit; H, rhizome scales; J, adaxial surface of blade. All scale bars 1 mm unless otherwise indicated. Drawing by H. Fukuda.

Other specimens examined: RAIATEA: Faaroa, partie Ouest, Inventaire Forestier, 25.viii.2003, *Jacq 222* (PAP); Faaroa, partie Est, *Jacq 337* (PAP).

TAHITI: Vallée de la Faonee, rivière de la Mapuauta, 17°41'S, 149°20'W, 150 m, *Birnbaum 113* (P, PAP); Vallée de la Mahaena, 17°35'S, 149°20'W,

80 m, 20.x.1988, *Birnbaum 147* (PAP, 2 sheets); Vallée de Mahaena, lit majeur, rive droite, 17°36'S, 149°21'W, 27.x.1988, *Chaine 16* (PAP); Papenoo, moyenne Vaitopaa, flanc gauche, 17°39'S, 149°26'W, 390 m, 19.ix.1986, *Florence 7829* (P); Papeari, rive gauche de la moyenne Vaite, 17°43'S, 149°24'W,

160 m, 30.x.1986, Florence 8010 (PAP); Presqu'île, côte Est, branche droite de la haute Aiurua, 17°50'S. 149°10′W, 195 m, 6.iii.1987, Florence 8121 (P); Tautira, haute Vaitepiha, rive gauche, 17°49'S, 149°11′W, 270 m, 21.xi.1987, Florence 8811 (PAP); Tevaitoa, branche centrale de la moyenne Tooroa, 16°49'S, 151°27'W, 400 m, 25.xi.1987, Florence 8845 (P); Basse vallée de la Mapuaura, 17°41'S, 149°20'W, 75 m, 15.x.1988, Florence & Birnbaum 9782 (PAP); Branche droite de la moyenne Tahaute, 17°37'S, 149°22'W, 120 m, 27.x.1988, Florence et al. 9807 (BISH, P, PAP); Tiarei, moyenne Orohena, branche centrale, 17°34'S, 149°24'W, 360 m, 15.xi.1988, Florence et al. 9871 (BISH, P); Tiarei, movenne Orohena, branche centrale, 17°35'S, 149°24'W, 390 m, 10.xi.1989, Florence & Birnbaum 9936 (BISH, P, PAP); Hitiaa, Puunui, 1025 ft, 15.xi.1930, Grant 4498 (BISH, 2 sheets); Tehupoo, Ronui, 980 ft, 1.vii.1930, Grant 3888 (BISH, UC); Orohena, 3.ix.2005, Jacq 521 (PAP); Vallée de la Papenoo, 13.v.1896, Nadeaud s.n. (P. 3 sheets).

3. ELAPHOGLOSSUM FLORENCEI ROUHAN, SP. NOV.

Type: Moorea, Haumi, Mt. Tohiea, vallon entre les deux sommets, 17°33'S, 149°49'W, 1140 m, épiphyte sur *Ilex* en station sciaphile, 9.vii.1987, *Florence* 8348 (holotype P!; isotypes BISH!, PAP!, 3 sheets). Figures 8, 13, 30A–E.

Etymology: The author is pleased to name this species in honour of Dr Jacques Florence, colleague and botanist at the Institut de Recherche pour le Développement, for his many important contributions towards our knowledge of the vascular plant flora of French Polynesia, including the type of this species.

Diagnosis: Rhizomata repentes c. 1.5–4 mm diam. Laminae steriles ellipticae, ad apicem acutae vel acuminatae, ad basim cuneatae, paleis serrulatis, hydathodi praesentes.

Description: RHIZOMES short-creeping somewhat ascending, 1.5–4.0 mm in diameter (excluding the dense covering of scales), possibly branched, bearing erect, caespitose fronds; rhizome scales $5-9 \times 0.5$ mm, narrowly ovate to linear, bases cordate, apices attenuate, dark reddish brown, lustrous, papyraceous, margins subentire with some short teeth, cells fusiform. PHYLLOPODIA indistinct, covered by scales similar to those of the rhizomes. STERILE FRONDS simple, $9-25 \times (0.9)1.5-3.3$ cm; petioles 1/2 to equalling the sterile blade length, 0.5–1.5 mm wide, with dense to scattered, reddish brown scales, sometimes darker in the centre, $2-3 \times 0.2-0.4$ mm, bases flat or somewhat inrolled or cochleariform, margins distinctly serrulate over the entire length with teeth directed acroscopically, scales spreading but not erect perpendicular to the petioles. BLADES elliptic to slightly ovate, bases acute, apices acute to acuminate, subcoriaceous, both surfaces of blades bearing scattered, yellowish to reddish brown scales, $2-3 \times 0.25$ mm, papyraceous, more or less subulate and acicular (bases inrolled but not always closed and most often distally flat), margins serrulate; broader scales, 0.5-0.75 mm, form an obvious and persistent fringe along the margins of the blades, even after other scales of the blades fall; costae rounded to flattened abaxially, slightly canaliculate adaxially. VEINS distinct, free, simple to twice bifurcate. HYDATHODES present. FERTILE FRONDS shorter than the sterile; petioles approximately 4-5 times longer than the fertile blade length, fertile blades similar in shape to the sterile, 0.7-1.0 cm wide; intersporangial scales absent. SPORES $30-36 \times 17-26 \,\mu\text{m}$, perispores with discontinuous low folds, sparsely perforate, tubercles on surfaces between folds, margins of folds with few spines (Fig. 24).

Discussion: Based on the subulate and acicular scales of the blades, *E. florencei* belongs to the group *Subulata sensu* Rouhan *et al.* (2004). Within the group, it belongs to subsection *Setosa* because of the presence of hydathodes.

In French Polynesia, *E. florencei* is morphologically similar to other species having hydathodes and subulate scales on blades. Nevertheless, *E. florencei* differs from *E. rapense* and *E. samoense* by its thinner rhizomes covered with smaller scales. It differs from *E. samoense* and *E. meyeri* by serrulate petiolar scales that are rather flat and not erect (vs. distinctly subulate and erect in *E. samoense* and *E. meyeri*). Furthermore, *E. florencei* can be distinguished from *E. rapense* and *E. meyeri* by its epiphytic habit.

Distribution and habitat: Society Islands, endemic to Moorea and Raiatea. Epiphyte in sciaphilous stations of wet forests, from 1000 to 1140 m.

Other specimens examined: MOOREA: Tohiea, 19.vii.2004, Jacq et al. 314 (PAP).

RAIATEA: To'omaru, en sous-bois sur la crête Tefauta, entre les deux sommets, 9.ix.2005, *Jacq et al. 463* (PAP).

4. ELAPHOGLOSSUM MARQUISEARUM BONAP.

Notes Pteridol. 7: 413 (1918). TYPE: Iles Marquises, Hiva-Oa, saxatile et épiphyte, *Henry s.n.* (holotype P!). Figures 4, 18, 29A–F.



Figure 30. A–E, *Elaphoglossum florencei* (*Florence 8348*, P): A, habit; B, rhizome scale; C, petiole scale; D, adaxial surface of blade; E, scale from blade margin. F–H, J, K, *Elaphoglossum tovii* (*Florence 4203*, P) : F, habit; G. rhizome scale; H, petiole scales; J, abaxial surface of blade; K, adaxial surface of blade. All scale bars 1 mm unless otherwise indicated. Drawing by H. Fukuda.

Synonym: Elaphoglossum marquisearum var. tahuatense E.D.Br., Flora of Southeastern Polynesia. II. Pteridophytes, Bernice P. Bishop Mus. Bull. 89(21): 95 (1931). TYPE: Marquesas, Tahuata, Mt. Amatea, 100 m, 27.xi.1922, Jones 1792 (holotype BISH!). *Etymology:* The specific epithet '*marquisearum*' refers to the Marquesas Islands, where the species is endemic.

Description: RHIZOMES moderately long-creeping, 2.5–8.0 mm in diameter (excluding the dense covering of

scales), unbranched, bearing erect fronds, borne in two ranks, spaced 5-20 mm; rhizome scales (5)10- $18 \times (0.5)$ 1.0–2.0 mm, narrowly ovate, bases cordate to auriculate with lobes overlapping, apices attenuate, yellowish to light reddish brown, dull, papyraceous, margins subentire with rare glandular-tipped cilia, cells short to elongated. PHYLLOPODIA distinct, to 3 cm long, bearing scales similar to those of the rhizomes, but sparser. STERILE FRONDS simple, $24-91 \times 2.9-5.5(6.5)$ cm; petioles 2/5 to equal the sterile blade length, 1.5-4.0 mm wide, sparsely paleaceous at least in the lower half to subglabrous in the upper half, scales similar to those of the rhizomes but shorter, darker, and margins with more glandulartipped cilia. BLADES elliptic, bases attenuate and decurrent, apices acute, coriaceous, margins cartilaginous and translucent, both surfaces of blades bearing scattered scales but adaxial surfaces usually glabrescent; laminar scales dark brown with black centre, appressed, substellate, 0.25-0.5 mm in diameter, margins with bulbous-tipped cilia; costae rounded abaxially, canaliculate adaxially, bearing scales similar to those of the blades or elongated, up to 2 mm long, on and along the abaxial surfaces. VEINS usually indistinct, free, simple or bifurcate, uniting apically into a continuous intramarginal vein. HYDATHODES absent. FERTILE FRONDS somewhat shorter than the sterile; petioles 3/5-4/5 the fertile blade length, fertile blades narrowly elliptic to linear, 1.6-2.8 cm wide; intersporangial scales absent. SPORES $33-47 \times 26-37 \,\mu\text{m}$, perispores with many cristae, perforate, surfaces between cristae perforate, few tubercles, margins of cristae sparsely spiny (Fig. 28).

Discussion: Elaphoglossum marquisearum belongs to section Elaphoglossum, characterized by nearly glabrous blades. According to the molecular phylogenetic results (Rouhan *et al.*, 2004), the species belongs to subsection *Pachyglossa*.

In the Marquesas, *E. marquisearum* is distinguished by its minute, black blade scales, and veins uniting apically into a continuous intramarginal vein (this is often difficult to observe because of the coriaceous blades). Although greatly resembling *E. savaiense* of the Society Islands and Rapa, *E. marquisearum* differs by the presence of minute, black blade scales primarily on the abaxial surfaces, the presence of scales on the lower half of the petioles and a usually epiphytic habit.

Distribution and habitat: Endemic to the Marquesas Islands: Fatu Hiva, Hiva Oa, Nuku Hiva, Tahuata, Ua Huka, Ua Pou. Epiphyte or rarely terrestrial in mats of bryophytes, in wet ravine forests or in summit forests, from 610 to 1200 m. Other specimens examined: FATU HIVA: Haute vallée de la Vaitopii, piste de Ouia, 10°29'S, 148°38'W, 660 m, 26.ii.1986, Florence 7339 (P); Epaulement SW du Mt. Touaouoho, 10°29'S, 138°38'W, 770 m, Florence et al. 9539 (P); Omo'a-Ouia-Mounanui Trail, 690 m, 17.ix.1988, Gagné & Montgomery 2330 (BISH); Omo'a, 500–900 m, 6.xii.1922, W.B. Jones 1842 (BISH); trail leading from Vaieenui Cascade along ridges to Omoa–Hanavave road, 600–640 m, 21.vii.1988, Lorence et al. 6151 (BISH, PTBG); trail from Omoa–Hanavave road leading to Teavapuhiau peak, just S of Teavapuhiau peak, 10°28'S, 138°38'W, 610–630 m, 7.ii.2003, Lorence et al. 9020 (P, PAP, PTBG, US).

HIVA OA: Atuona, 800 m, 20.i.1922, F.B.H. Brown & E.D.W. Brown 14 (BISH); Atuona region, 800 m, 15.i.1922, F.B.H. Brown & E.D.W. Brown 1021(A) (BISH); Ootua, 800-900 m, 15.i.1922, F.B.H. Brown & E.D.W. Brown 1100 (BISH); Maguis sommital Mt. Feani, 1100 m, 11.xi.1989, Cherrier in McKee 44691 (P, PAP); Atuona, piste de Hanamenu, crête centrale, 9°48'S, 139°5'W, 950 m, 29.vii.1988, Florence et al. 9616 (P); Hana Iafa, 700 m, 29.x.1922, W.B. Jones 1607 (BISH, BKL); base camp, near Vaitumete to ridge crest south of Teakatau, 1200 m, 29.i.2003. Lorence & Price 8934 (PAP, PTBG, US); NE slopes of Mt. Temetiu, 700 m, 23.ii.1929, Mumford & Adamson 39 (BISH); above Atuona, 6.x.1930, Pacific Entomol. Surv. Ex 39 (BISH); road from Atuona to Puamau, just below Mt. Cotua, 660-690 m, 22.i.1975, Sachet et al. 2122 (BISH, MPU, PTBG, US); Temetiu region, drainage to south-east of Vaimete et Vaiumioi, headwaters of Hanamenu, 1067 m, 23.i.2003, Wood 10042 (PTBG).

NUKU HIVA: Tovii, épaulement S du Mt. Ooumu, 8°51'S, 140°08'W, 850 m, 1.xii.1982, Florence 4217 (P, PAP); Tovii, épaulement SE du Mt. Tekao, 8°51'S, 140°10'W, 985 m, 28.v.1984, Florence 6801 (BISH, P); Tovii, flanc sud du Mt. Ooumu, 8°51'S, 140°09'W, 1000 m, 28.vii.1987, Florence 8396 (BISH, P); Toovii region, NW of l'Economie Rurale complex along new road to airport over flanking mountains, 1060 m, 16.vii.1988, Lorence et al. 6090 (PAP, PTBG, US); Tovii, ridge above l'Economie Rurale to Ooumu, 940 m, 17.vii.1988, Wagner et al. 6113 (BISH, P, PTBG, US); Tovii, Ooumu area, top of Tapueahu valley off new Hwy., 1060–1130 m, 20–22.ix.1995, Wood & Perlman 4593 (BISH, MO, P, PAP, PTBG).

TAHUATA: Région du sommet de Tahuata, 17.iii.1973, Hallé 2174 (P).

UA HUKA: summit of Hitikau area, 8°54'201"S, 139°31'622"W, 838 m, 15.vi.2004, *Perlmann & Wood 19021* (P, PAP, PTBG, US); Hitikau region, ascended via the Matukuoha ridge over-looking Hane, constitutes the summit of the single crater of Ua Huka, 730 m, 5.xii.2003, *Wood 10503* (PAP, PTBG, US);

Hitikau summit area, 8°54′22″S, 139°31′66″W, 2700–2900 ft, 28.vi.1997, *Wood et al. 6390* (P, PAP, PTBG, US).

UA POU: forested ridge and slopes up to Teavahaakiti, north-west side, 914 m, 24.xi.2003, *Wood 10445* (PAP, PTBG, US); ridge above Anakooma river and below Oave, 9°40'S, 140°8'W, 732 m, 17.vii.2003, *Wood & Meyer 10304* (PAP, PTBG, US).

5. ELAPHOGLOSSUM MEYERI ROUHAN, SP. NOV.

Type: Rapa, Crête sud du Mt. Mamuere, 27°36'S, 144°22'W, 450 m, 6.ii.1984, terrestre et saxicole, *Florence 6507* (holotype P!; isotype PAP!). Figures 2E–J, 6, 16.

Etymology: The species is named in honour of Dr Jean-Yves Meyer, at the Délégation à la Recherche in French Polynesia, for his years of research in French Polynesia on invasive species, plant conservation and floristics. He was instrumental in coordinating and participated in many of the expeditions that led to the discovery of this new species and many others.

Diagnosis: Rhizoma repentes c. 3-5 mm diam. Laminae sterilis ellipticae, ad apicem acutae vel obtusae, ad basim cuneatae vel acutae, paleis subulatis, hydathodi praesentes.

Description: RHIZOMES short-creeping, 3-5 mm in diameter (excluding the dense covering of scales), occasionally branched, bearing erect, caespitose fronds; rhizome scales $5-12 \times 0.5-1.0$ mm, linear, bases cordate, apices long-attenuate, dark reddish brown to dark brown, lustrous, papyraceous, margins entire, cells fusiform. PHYLLOPODIA indistinct, covered by a dense layer of scales similar to those of the rhizomes. STERILE FRONDS simple, $7-34 \times 1.0-$ 4.4 cm; petioles 2/5 to equalling the sterile blade length, 0.5-1.5 mm wide, with dense to scattered, spreading, pale reddish brown, dull scales, 1.5- 2.5×0.1 –0.25 mm, papyraceous, subular and acicular. BLADES narrowly elliptic to oblong, bases acute to cuneate, apices obtuse (rarely acute), subcoriaceous, both surfaces of blades and margins covered by numerous, pale vellowish to reddish brown scales, $1.5-2.5 \times 0.1-0.25$ mm, linear except at the bases that are enlarged and more or less closed (i.e. not distinctly subulate), darker and resinous leaving a distinct dark reddish brown to black punctuation after scale falls; costae rounded abaxially, shallowly canaliculate adaxially. VEINS distinct, free, simple to twice bifurcate. HYDATHODES present but not always distinct. FERTILE FRONDS shorter than the sterile; petioles 3/5 to equalling the fertile blade length, fertile blades oblong to oblong-ovate, $2.5-3.8 \times 0.8-1.0$ cm.

SPORES $29-38 \times 21-29 \mu m$, perispores with continuous cristae, highly perforate, perforations on surfaces between cristae, few tubercles; margins of cristae with spines (Fig. 25).

Discussion: Based on the subulate and acicular scales of the blades, *E. meyeri* belongs to the group *Subulata* sensu Rouhan et al. (2004). Within the group, it belongs to subsection *Setosa*, because of the presence of hydathodes.

Elaphoglossum meyeri resembles E. samoense. Both species have similar scales on all parts, but, in E. meyeri, the petiolar and laminar scales are shorter, narrower and less dense, and the blades are obtuse. Also, E. meyeri differs by its ecology, being terrestrial or saxicolous and forming large populations at lower elevations (vs. rather isolated and epiphytic in cloud forests).

In Rapa, *E. meyeri* is easily distinguished from *E. rapense* by its much smaller general size, much narrower fronds, thinner rhizomes and petiole scales, which are spreading, subulate acicular and entire.

Distribution and habitat: Austral Islands, endemic to Rapa. Terrestrial or saxicolous, from 240 to 450 m, spreading on rocks and forming large populations.

Other specimens examined: RAPA: Sommet du Mt. Morongouta, 27°37'S, 144°21'W, 260 m, 2.ii.1984, saxicole sur parois rocheuse, Florence 6398 (P); Crête sud du Mt. Mamuere, 27°36'S, 144°22'W, 450 m, 6.ii.1984, terrestre et saxicole, Florence 6507 (P, PAP); Mt. Taga, rock outcropping, 240 m, 4.vii.1934, Fosberg 11385 (BISH, NY, P, UC); Kaukauamoo, shaded earth bank, perpendicular, 350 m, 18.vii.1934, Fosberg 11563 (BISH, NY, US); Mur du fort Morongouta, 258 m, 2.ii.1984, Hallé 7516 (P); summit ridge N Mt. Taga, on Pa (fortress), on muddy bank, 114°19'00"W, 27°335'45"S, 210 m, 19.iii.2002, Motley 2608 (NY); Mt. Ruatara, southern slopes, 27°35′45″S, 144°19'00"W, 300 m, 10.v.2002, Motley & Fenstemacher 2875 (NY); Morongouta, crevices of basalt rock wall, 275 m, 8.vii.1934, St John & Maireau 15438 (BISH, P, UC, US); Maungaaiai, upper forested slopes of Anatakuri, 27°S, 144°W, 600-1000 ft, 23.iv.2002, Wood 9708 (NY, PTBG).

6. ELAPHOGLOSSUM RAPENSE COPEL.

Occas. Pap. Bernice P. Bishop Mus. 14(5): 70, fig. 21 (1938). TYPE: Rapa, Kaimaru, S ridge of Mt. Perahu, on ground or fallen logs in rain forest, 475 m, 13.viii.1934, *St. John & Maireau 15529* (holotype BISH!; isotypes K!, NY!, P!, UC). Figures 5, 14, 31F-K.



Figure 31. A–E, *Elaphoglossum samoense (Ranker 1961*, NY): A, habit; B, rhizome scale; C, petiole scale; D, adaxial blade surface showing hydathodes; E, scale from adaxial surface of the blade. F–H, J, K, *Elaphoglossum rapense (St. John & Maireau 15529*, NY [isotype]): F, habit of rhizome, petioles and blades; G, rhizome scales; H, petiole scale; J, adaxial surface of blade; K, abaxial surface of blade. All scale bars 1 mm unless otherwise indicated. Drawing by H. Fukuda.

Etymology: The specific epithet '*rapense*' refers to the island of Rapa, where the species is endemic.

Description: RHIZOMES erect, 8–14 mm in diameter (excluding the dense covering of scales), unbranched, bearing erect, caespitose fronds; rhizome scales $10-19 \times 0.5-1.25$ mm, narrowly ovate to linear, bases cordate to auriculate, apices attenuate and sinuate, reddish brown, lustrous, papyraceous, margins with numerous short teeth, cells fusiform. PHYLLOPODIA indistinct, covered by a dense layer of scales similar to those of the rhizomes. STERILE FRONDS simple,

 $29-55 \times 5.0-9.8$ cm; petioles 3/5-6/5 the sterile blade length, 1.5–3.5 mm wide, with dense, reddish brown to pale reddish brown, dull scales, $4-8 \times 0.25-0.5$ mm, bases flat or somewhat inrolled or cochleariform, margins distinctly serrulate over the entire length with teeth directed acroscopically. BLADES widely ovate to elliptic, bases rounded to obtuse, apices acute, subcoriaceous, both surfaces of blades covered by a dense (but glabrescent) layer of imbricated, pale yellowish to reddish brown scales, $(2)3-8 \times 0.25-$ 0.5 mm, papyraceous, subulate and acicular, margins serrulate from the base to the apex: the scales form a distinct fringe along the margins of the blades; costae rounded to flattened abaxially, canaliculate adaxially. VEINS prominent but usually hidden by the scales, free, simple to twice bifurcate. HYDATHODES present. FERTILE FRONDS shorter and much narrower than the sterile; petioles approximately three times longer than the fertile blade length, fertile blades similar in shape to the sterile, 1.5-2.0 cm wide; intersporangial scales absent. SPORES $29-34 \ \mu m \times 20-25 \ \mu m$, perispores with discontinuous folds or low cristae. perforate, surfaces between folds smooth to sparsely perforate with scattered tubercles, margins entire (Fig. 26).

Discussion: Based on the subulate scales on the leaf blades, *E. rapense* belongs to the *Subulata* group sensu Rouhan et al. (2004). Within the group, it belongs to subsection *Setosa* because of the presence of hydathodes.

In the Pacific, the species most similar to E. rapense are E. samoense and E. meyeri, because all of these species have similar blade scales: subulate, acicular and spreading. Nevertheless, E. rapense is distinguished by erect rhizomes and large and erect leaves (29–55 cm long). Also, E. rapense differs by its terrestrial habit.

Distribution and habitat: Austral Islands, endemic to Rapa. Terrestrial in wet summit forests, from 440 to 620 m.

Other specimens examined: RAPA: Crête ventée et très humide à forêt dense, touffe au sol, 440 m, 6.ii.1984, *N.Hallé* 7637 (P); Taratika, E side of Mt. Perahu, 620 m, St. John, Fosberg & Maireau 15644 (BISH, P); Mt. Perau, and ridge line to NE of peak, 144°21′25″W, 27°34′55″S, 530 m, 28–29.iii.2002, Motley & Fenstemacher 2677 (NY); Perau, summit and adjacent drainage just below, 144°W, 27°S, 1900 ft, 28.iii.2002, Wood et al. 9478 (NY, PTBG); Perau-Namuere summit, eastern peaks, 27°S, 144°W, 1900–2000 ft, 8.v.2002, Wood 9776 (NY, PTBG).

7. ELAPHOGLOSSUM SAMOENSE BRACK.

U.S. Expl. Exped., Filic. 16: 68, fig. 9(1) (1854). Acrostichum samoense (Brack.) Baker, Syn. Fil. 407 (1868). TYPE: Samoan Islands, Tutuila, in the vicinity of Pago-Pago Bay, in mountain forests, on trees, 1838–1842, Wilkes s.n. (holotype US!). Figures 7, 15, 31A–E.

Synonyms: Elaphoglossum societarum Copel., Bernice P. Bishop Mus. Bull. 93: 12, 67, fig. 13 (1932). TYPE: Tahaa, Ohiri, 1260 ft, 25.i.1931, *M. L. Grant 5156* (holotype BISH!; isotypes BISH!, MICH!, UC).

Elaphoglossum societarum Copel. var. minus J.W.Moore, Bernice P. Bishop Mus. Bull. 102: 12 (1933). TYPE: Raiatea, in moist holes of rock, south-facing slope, Mt. Temehani, 7.x.1926, 400 m, J. W. Moore 186 [holotype BISH!; isotypes BISH (3 sheets)!].

Elaphoglossum squamosum sensu Drake, Fl. Polynésie Franç. 319 (1892); sensu Nadeaud, Enum. Pl. Tahiti 28 (1873), non *E. squamosum* J.Sm, J. Bot. (Hooker) 4: 148 (1841), non *E. squamosum* Sw, J. Bot. (Schrader) 1800(2): 11 (1801).

Elaphoglossum splendens sensu Drake, non (Bory ex Willd.) Brack., U. S. Expl. Exped., Filic. 16: 68 (1854).

Etymology: The specific epithet 'samoense' refers to the Samoan Archipelago, although this species does not occur on these islands as stated by Christensen (in litt.) on the holotype specimen: 'this species is not found in any of the many collections of Samoan ferns [revised by him], and as the present type perfectly matches specimens from Tahiti, [we are] convinced that the locality of the label is false and that the type was collected in Tahiti'.

Description: RHIZOMES short-creeping, 4-8 mm in diameter (excluding the dense covering of scales), unbranched, bearing erect, caespitose fronds; rhizome scales $10-20 \times 0.25-0.75$ mm, linear, bases cordate, apices long-attenuate, dark reddish brown, lustrous, papyraceous, entire or with rare short teeth, cells fusiform. PHYLLOPODIA indistinct, covered by a dense layer of scales similar to those of the rhizomes. STERILE FRONDS simple, $13-43 \times 1.3-3.5$ (7.0) cm; petioles 1/5-3/5 the sterile blade length, 1-2 mm wide, with dense, light reddish brown, dull, subulate and acicular scales, spreading perpendicularly to the petioles, 5-8 mm long, enlarged at the bases, tubular and closed, 0.25-0.5 mm wide, apices attenuate, margins subentire or with few short teeth toward bases, petioles also bearing simple, short capitate trichomes. BLADES narrowly ovate to narrowly elliptic, bases cuneate to acute (more rarely obtuse), apices long-acute to long-attenuate (rarely rounded),

blade margins sometimes sinuate in particular towards the apices, chartaceous to subcoriaceous, both surfaces of blades and costae bearing scattered, subulate and acicular scales, like those on the petioles but shorter, 3-5 mm long, sometimes blades bearing also reddish, resinous dots after scales fall; costae rounded abaxially, canaliculate adaxially. VEINS distinct, free, simple to once bifurcate, tips thickened and rounded forming distinct HYDATHODES. FERTILE FRONDS shorter and narrower than the sterile; petioles 1/2-3/2 the fertile blade length, fertile blades similar in shape to the sterile, 1.3-2.5(3.2) cm wide; intersporangial scales absent. SPORES $32-43 \times 21-$ 28 µm, perispores with discontinuous folds to continuous cristae, perforate, small tubercles on surfaces between folds, margins with scattered spines (Fig. 23).

Discussion: Because it has subulate scales, *E. samoense* belongs to the *Subulata* group *sensu* Rouhan *et al.* (2004). Within this group, it belongs to subsection *Setosa* based on the presence of hydathodes.

Elaphoglossum samoense may be confused with E. meyeri, because both have similar scales on all parts of the blades and rhizomes. However, E. samoense differs by its petiolar and laminar scales that are longer, wider and distinctly subulate, and by being epiphytic rather that sciaphilous and not forming large populations. It differs from E. florencei by the thicker rhizomes, larger rhizome scales and petiole scales subulate, acicular and spreading perpendicularly to the petioles.

Isotypes of *E. societarum* Copel. housed in BISH do not bear any label with Grant's collecting number '5156' that was referenced in the protologue. Nevertheless, all other information, especially that concerning the localities and collecting dates, is in agreement with that described in the protologue.

Distribution and habitat: Society Islands: Huahine, Moorea, Raiatea Tahaa and Tahiti. Also present in Rarotonga, in the Cook Islands (Brownlie & Philipson, 1971; McCormack, 2007). Epiphyte in mist forests, from 400 to 1300 m.

Other specimens examined: HUAHINE: Fare, Mont Mato Ereere, sommet, 16°43'S, 151°1'W, 595 m, 30.x.1992, Florence & Tahuaitu 11607 (P, PAP); Fare, Matoereere, 1640 ft, 7.ii.1931, Grant 5281 (BISH, UC); Mou'a Turi, 18.ix.2005, Jacq et al. 502 (PAP); Mt. Matoereere, north ridge, 550 m, 1.x.1934, St. John 17163 (BISH, UC).

MOOREA: Sur la crête, Mou'a puta, 28.viii.2005, Jacq et al. 438 (PAP); Taiarabu, Lépine 150 (P), Lépine 108 (P, 2 sheets); trail up Mt. Mouaputa, along trail between GPS readings 17°32'09.2"S, 149°47'48.1"W, 291 m & 17°31'42.0"S, 149°48'00.5", 291–751 m, 26.xii.2003, *Ranker & Trapp 1961* (NY, PAP).

TAHITI: Haute vallée de Faatautia, bord de rivière, 17°37'S, 149°21'W, 800 m, 19.x.1988, Birnbaum 131 (PAP); Pic Vert, chemin du Mt. Marau, 2.xi.1988, Chaine 20 (P, PAP); Mt. Marau, haute Tipaerui, sentier Psychotria, 17°37'S, 149°33'W, 1180 m, 28.i.1982, Florence 2354 (P, PAP); Crête ouest de la Papenoo, sentier de l'Orohena, 17°33'S, 149°26'W, 950 m, 3.viii.1982, Florence 3643 (PAP); Mahina, vallée de Tuauru, captage des 1000 sources, 16°34'S, 149°28'W, 920 m, 17.x.1983, Florence 5387 (P, PAP); Mahina, Pihaahateta, The Ahonu, en forêt hygrophile de vallon, 17°36'S, 149°28'W, 1560 m, 18.x.1983, Florence 5414 (P); Papeete, Pic vert, sentier du Mt. Marau, 17°35'S, 149°33'W, 950 m, 27.xi.1986, Florence 8056 (PAP); FAAA, route du Mt. Marau, km 4.2, 17°36'S, 149°34'W, 840 m, 8.x.1987, Florence 8657 (PAP); Tiarei, moyenne Onoheha, branche centrale, 17°35'S, 149°24'W, 400 m, 10.xi.1989, Florence & Birnbaum 9938 (P, PAP); Vallée de la Faatautia, branche gauche, 17°38'S, 149°21'W, 765 m, 3.vii.1990, Florence & Meyer 10695 (P, PAP); Teahupoo, Ronui, 1890 ft, 2.vii.1930, Grant 3928 (BISH [sterile juvenile]); Papenoo, Orofena, 4060 ft, 23.ix.1930, Grant 4263 (BISH, UC); Ivirairai, 20.viii.2005, Jacq & Butaud 424 (PAP); Lépine s.n. (P), Lépine in 1847 (P); S. of Orohena, on tree trunks, 1300 m, 16.v.1927, *MacDaniels* 1547 (BISH), 1500 m, 16.v.1927, MacDaniels 1549 (BISH, UC); Nadeaud s.n. (P); Nadeaud in 1896 (P); 1200 m, Nadeaud 191 (P, 2 sheets); sur les arbres, sur les hauts sommets de l'intérieur, 900 m, Nadeaud 191 (P); sur les arbres, vers 1200 m, Nadeaud s.n. (P); along road to summit of Mt. Marau, 17°36'21.8"S, 149°32'19.3"W, 1000-1303 m, 21.xii.2003, Ranker & Trapp 1907 (PAP, UC); Orofena, south ridge, 1500 m, 20.ix.1934, St. John & Fosberg 16992 (BISH); Orofena east side of south ridge, 1220 m, 20.ix.1934, St. John & Fosberg 17028 (BISH), St. John & Fosberg 17051 (BISH); Orofena, east ridge, moist thicket on divide, 1570 m, 24.ix.1934, St. John & Fosberg 17069 (BISH) [blades atypically wide (to 7 cm) and obtuse at base]; Vesco s.n. (P), Vesco in 1847 (P, 4 sheets); dans les lieux boisés élevés, 800 m au moins, 1847, Vesco s.n. (P); Vesco s.n. (P); Vieillard s.n. (P); 800-1000 m, Vieillard & Panchet 2 (P); 1855, Vieillard & Panchet s.n. ex Herb. Lenormand (P, 2 sheets); collector unknown 1431 (K).

8. *ELAPHOGLOSSUM SAVAIENSE* (BAKER) DIELS

Nat. Pflanzenfam. 1(4): 332 (1899). Aconiopteris savaiense Baker, Ann. Bot. 5: 494 (1891). TYPE:



Figure 32. *Elaphoglossum savaiense (Ranker 1962*, NY): A, habit; B, rhizome scales; C, petiole scale; D, abaxial surface of blade; E, scale from abaxial surface of costa; F, scales from abaxial surface of blade. All scale bars 1 mm unless otherwise indicated. Drawing by H. Fukuda.

Samoa, Mountains of Savaii, 4600 ft, x.1874, *Powell* 197 (holotype K!). Figures 19, 32.

Synonyms: Elaphoglossum gorgoneum sensu auctt., non (Kaulf.) Brack., U.S. Expl. Exped., Filic. 16: 74 (1854). Acrostichum gorgoneum sensu auctt., non Kaulf., Enum. Filic.: 63 (1824).

Etymology: The specific epithet 'savaiense' refers to the island of Savaii in the Samoan Archipelago. The type specimen was collected on Savaii.

Description: RHIZOMES moderately creeping, (3.0)6.5-11.0 mm in diameter (excluding the dense covering of scales), unbranched, bearing erect fronds, borne in two ranks, spaced 3-18 mm; rhizome scales $10-20 \times 1-2.5(4.0)$ mm, narrowly ovate, bases cordate to auriculate with lobes overlapping, apices attenuate, yellowish to light reddish brown, papyraceous, margins subentire with rare glandular-tipped cilia, cells short to elongated. PHYLLOPODIA distinct, 7-25 mm long, dark brown to black, somewhat swollen distally, bearing scales similar to those of the rhizomes, but sparser. STERILE FRONDS simple, $13-88 \times (2.5)3.2-8.2$ cm; petioles 1/5-7/10 the sterile blade length, 1–4 mm wide, subglabrous even in the lower half. BLADES elliptic, commonly undulate, bases cuneate, apices acute to shortly attenuate, subcoriaceous to coriaceous, adaxially lustrous and abaxially dull, margins distinct, cartilaginous and clearer, both surfaces of blades bearing scattered minute scales but adaxial surfaces usually glabrescent; laminae scales brown, appressed, substellate, 0.25-0.5 mm in diameter, margins with bulbous-tipped cilia; costae prominent on both faces, rounded abaxially, canaliculate adaxially, glabrous or with few substellate scales from the blades. VEINS indistinct, free, simple or bifurcate, uniting apically into a continuous intramarginal vein. HYDATHODES absent. FERTILE FRONDS longer or shorter than the sterile; petioles 1/2-3/2 the fertile blade length, fertile blades narrowly elliptic, 2.0-6.4 cm wide; intersporangial scales absent. SPORES $41-46 \times 28-34 \,\mu m$, perispores with continuous cristae, perforate, surfaces between cristae with low ridges and tubercles, margins with scattered spines (Fig. 27).

Discussion: Elaphoglossum savaiense belongs to section Elaphoglossum, a section characterized by nearly glabrous blades. Molecular phylogenetic results (Rouhan *et al.*, 2004) place this species in subsection *Pachyglossa*.

Elaphoglossum savaiense resembles E. marquisearum in overall morphology, and especially by the presence of a continuous intramarginal vein, but E. savaiense can be distinguished by the minute scales on the blades, petioles subglabrous, even in the basal portion, and terrestrial habit (vs. epiphytic). In addition, E. savaiense occurs in the Society Islands, whereas E. marquisearum is endemic to the Marquesas Islands. In the Society Islands, E. savaiense resembles E. feejeense, but only E. savaiense has the continuous intramarginal vein.

The name *Elaphoglossum gorgoneum sensu auctt.* has been widely misapplied. According to Anderson & Crosby (1966), the name *E. gorgoneum* (Kaulf.) Brack., U.S. Expl. Exped., Filic. 16: 74 (1854) is a synonym of *E. aemulum* (Kaulf.) Brack., a species endemic to the Hawaiian Islands. *Elaphoglossum* savaiense is distinct from *E. aemulum* by the intramarginal connecting vein and moderately creeping rhizomes (vs. short-creeping). Two taxon names, *E.* savaiense (Baker) Diels var. grantii and *E. nadeaudii*, were proposed by Krajina, but were never published. They have been widely used in French Polynesia; both refer to *E. savaiense*.

Distribution and habitat: Society Islands (Bora Bora, Huahine, Moorea, Raiatea, Tahaa, and Tahiti) and Austral Islands (Rapa). Also present in the Cook and Samoan Islands. Usually terrestrial on organic soils, or sometimes as a low epiphyte, in summit forests of *Metrosideros* and *Weinmania*, often abundant, from 290 to 2080 m; when terrestrial, it forms large populations in sunny as well as shady habitats.

Other specimens examined: BORA BORA: Faanui, crête entre les monts Otemanu et Pahia, 16°3'S, 151°44'W, 620 m, 6.xii.1993, *Florence 12133* (P); Tevaiitapu, Turapaia, among ridge shrub, 2035 ft, 3.i.1931, *Grant* 4984 (BISH, UC).

HUAHINE: Taiamanu summit, ridge crest, $16^{\circ}43'8''S$, $151^{\circ}0'19''W$, 540 m, 24.xi.2004, Dunn 516 (BISH, MO, P, PAP, UC, US); Fare, Mont Mato Ereere, sommet, $16^{\circ}43'S$, $151^{\circ}1'W$, 595 m, 30.x.1992, *Florence & Tahuaitu 11608* (BISH, P); Maeva, Matoereere, 1710 ft, 7.ii.1931, *Grant 5318* (BISH); *Jacq et al. 506* (PAP); Matoereere, north ridge, 650 m, 1.x.1934, *St John 17160* (BISH, K, P, UC).

MOOREA: Crête, 400 m, 28.vii.2006, *Florence* 7.06 (P, PAP); Haumi, crête SE du Mt. Tohiea, 17°33'S, 149°49'W, 1000 m, 22.x.1986, *Florence* 7956 (P); Maharepa, piton, 23.v.2004, *Jacq et al.* 272 (PAP); Montagnes, 400–600 m, 1847, *Lépine s.n.* (P, 2 sheets); *Lépine* 111 (P); Trail up Mt. Mouaputa along trail between GPS readings 17°32'09.2"S, 149°47'48.1"W and 17°31'42.0"S, 149°48'00.5"S, 291– 751 m, 26.xii.2003, *Ranker & Trapp* 1962 (PAP).

Tetooroa à Pueu, Crête RAIATEA: 700 m, 18.xii.2004, Butaud et al. 842 (PAP); Flanc NW du sommet du Temehani Rahi, 16°47'S, 151°27'W, 740 m, 25.viii.1982, Florence 3755 (PAP); Tevaitoa contreforts NW du Mt. Toomaru, 16°49'S, 151°27'W, 440 m, 26.xi.1987, Florence 8866 (P); Tevaitoa, crête sommitale N du Mt. Toomaru, 16°50'S, 151°27'W, 950 m, 27.xi.1987, Florence 8938 (PAP, 2 sheets); Tevaitoa, environs du sommet du Mt. Toomaru, 16°50'S, 151°27'W, 1015 m, 27.xi.1987, Florence 8961 (PAP, 2 sheets); Tevaitoa, plateau de Temehani Ute, secteur central, 16°47'S, 151°28'W, 660 m, 27.xi.1993, Florence 11931 (P); Temehani Rahi plateau, 650 m, 5.vii.1982, Fosberg & Sachet 63290 (PTBG, US); To'omaru, 860 m, 9.ix.2005, Jacq et al. 458 (PAP), Jacq et al. 459 (PAP), Jacq et al. 462 (PAP); Temehani

Rahi, 12.xi.2004, *Jacq et al.* 395 (PAP); Mt. Temehani, 450 m, 1.i.1927, *Moore 481* (BISH, two sheets); Temehani Plateau 500 m, 5.x.1934, *St John 17270* (BISH, P, UC).

RAPA: Maii, below rim near Pokumaru, 27°S, 144°W, 357 ft, 29.iv.2002, *Wood 9726* (NY); Pokumaru summit region, upper windswept slopes of Maii, 27°S, 144°W, 1450 ft, 21.iv.2002, *Wood 9693* [PTBG (two sheets), NY].

TAHAA: Patio, Mont Ohiri, sommet, 16°37'S, 151°31'W, 590 m, 5.ix.1992, *Florence & Tahuaitu* 11827 (P, two sheets).

TAHITI: Haute vallée de la Faatautia, 17°38'S, 149°22′W, 900 m, 20.ix.1988, Birnbaum 55 (PAP); Montée du Mont Mauru, pluvio de l'affluent gauche de la Faatautia, 17°38'S, 149°22'W, 10.x.1988, 960 m, Birnbaum 93 (PAP); Mt. Marau, crête sommitale, 17°37'S 149°32'W, 1450 m, 4.ii.1982, Florence 2424 (BISH, P, PAP); Sentier de l'Aorai, au-dessus du Rocher du Diable, 17°36'S, 149°30'W, 1530 m, 14.ii.1983, Florence 4517 (BISH, P); Plateau de taravao, piste du captage de l'Hamao, 17°47'S, 149°15′W, 745 m, 9.iii.1983, Florence 4589 (PAP); Crête W de la Papenoo, sentier de l'Orohena, 17°34'S, 149°27′W. 950 m. 8.ix.1983. Florence 5129 (P): Mahina, crête Est de la Tuauru, sentier de l'Orohena, 1560 m, 18.x.1983, Florence 5400 (P); Mahina, crête Est de la Tuauru, sentier de l'Orohena, 1605 m, 3.xi.1987, Florence 8727 (P); Tautira, col entre la Vaitepiha et la Vaiarava, 17°49'S, 149°12'W, 450 m, 21.xi.1987, Florence 8821 (PAP); Mahina, flanc W du sommet du Mt. Pitohiti, 17°37'S, 149°28'W, 2080 m, 1.iv.1988, Florence 9137 (BISH, P); Tiarei, moyenne onoheha, branche centrale, 17°34'S, 149°24'W, 360 m, 15.xi.1988, Florence et al. 9869 (PAP, 2 sheets); Hitiaa, vallée de la Faatautia, branche gauche, 17°38'S, 149°21'W, 775 m, 3.vii.1990, Florence & Meyer 10696 (PAP, two sheets); Afaahiti, planèze d'Afaahiti, 17°43'S, 149°20'W, 290 m, 17.ii.1991, Florence & Jourdan 10722 (BISH, P); Toahotu, vallée de la rivière Paho, crête sud, 17°47'S, 149°15'W, 745 m, 14.vi.1992, Florence & Jourdan 11459 (P, PAP); road from Faaa to Mt. Marau, headwaters, Matatia Tihiure River, 1400 m, 19.vii.1981, Fosberg 61091 (PTBG, US); above Ia, 9.vi.1982, Fosberg 62844 (PTBG, US); NW ridge of Pic Vert, above Papeete, headwaters of lower branch of Tipaerui river, 950-1000 m, 7.vi.1982, Fosberg 62967 (P, PTBG, US); Mt. Orohena, 2240 m, 11.ix.1988, Gagné & Montgomery 2258 (BISH), Gagné & Montgomery 2260 (BISH); Mahina, ridge to Aorai, 3800 ft, 4.vi.1930, Grant 3726 (BISH); Mahina, ridge to Aorai, 4440 ft, 6.vi.1930, Grant 3773 (BISH); 'Oahaniuatea', Mahina, Aorai, summit, 6700 ft, 7.vi.1930, Grant 3804 (BISH); Teahupoo, Ronui, 3240 ft, 3.vii.1930, Grant 3930 (BISH); Tautira, Tarui, 860 ft, 5.viii.1930, Grant 3983 (BISH,

2 sheets); Papenoo, Orofena, 3950 ft, 22.ix.1930, Grant 4238 (BISH); Mahina, Ahonu-Tuauru, with motuu and pua, 2860 ft, Grant 4398 (BISH, UC, US); Hitiaa, Puunui, 1290 ft, 15.xi.1930, Grant 4497 (BISH); Pitohiti, sur une crête en montant, 28.viii.2004, Jacq 342 (PAP, two sheets), Jacq 341 (PAP); 1847, Lépine 112 (P); S of Orohena, top of ridge, 17.v.1927, MacDaniels 1482 (BISH); Mt. Aorai trail, sides of ridges, 1848 m, 23.ix.1921, Quayle 46 (BISH); Orofena, east side of south ridge, 1220 m, 20.ix.1934, St. John & Fosberg 17048 (BISH); 1847, Vesco s.n. (P); Croît sur les crêtes élevées de près de 1000 m, 1847, Vesco s.n. (P).

9. ELAPHOGLOSSUM TOVII E.D.BR.

Bernice P. Bishop Mus. Bull. 89(21): 95, fig. 18, 19A (1931). TYPE: Marquesas Islands, Nukuhiva, Tovii, near Mokuautoto, 1000 m, 15.vii.1921, *Brown 498A* (holotype BISH!). Figures 9, 12, 30E–J.

Etymology: From the locality of the holotype, the Tovii plateau.

Description: RHIZOMES short-creeping, 4-15 mm in diameter (excluding the dense covering of scales), unbranched, bearing erect fronds borne in 2(-3)ranks, spaced 2-8 mm; rhizome scales $6-13 \times 1-$ 2 mm, occasionally twisted, narrowly ovate, bases cordate, apices attenuate and sinuate, dark reddish brown, lustrous, chartaceous, margins subentire with few short teeth, cells short to elongate. PHYLLOPODIA 6-18 mm long, dark brown to black, sometimes slightly swollen distally, bearing scales as on rhizomes. Sterile FRONDS simple, (12.5)36.0- $77.0 \times (1.2)3.5 - 5.4$ cm; petioles 2/5 - 4/5 the sterile blade length, 1.5–2.5 mm wide, with dense, spreading reddish brown to pale reddish brown scales, similar to those on the rhizomes but the margins with longer hair-teeth. BLADES narrowly elliptic to oblong, bases cuneiform, apices acute, subcoriaceous to coriaceous, both surfaces of blades covered by a dense layer of imbricated, light reddish brown scales, scale bodies $2-6 \times 0.5-1$ mm, ovate to narrowly ovate, bases auriculate with lobes being overlapped or not, apices acute, margins fringed with long erect-spreading hair-teeth (up to 1–1.5 the width of the body scales); the scales form a distinct fringe along the margins of the blades; costae rounded to flattened abaxially, slightly canaliculate adaxially. VEINS free, simple or once bifurcate. HYDATHODES absent. FERTILE FRONDS as long as sterile fronds, blades similar in shape but narrower, (1.2)1.5-2.5 mm wide; intersporangial scales absent. SPORES $41-49 \times 31-36 \,\mu\text{m}$, perispores

with broad continuous folds and scattered tubercles between folds, lacking perforations and spines, margins smooth (Fig. 21).

Discussion: Based on its morphological characters, especially the fronds covered by a dense layer of scales and scales with acicular marginal cells, *E. tovii* belongs to section *Lepidoglossa*.

The species most similar to E. tovii is E. austromarquesense, which also belongs to section Lepidoglossa. Elaphoglossum tovii can be distinguished by its larger and broader fronds and by its blades that are much more densely scaly (at least when young) with longer, narrowly ovate scales; as a result, in E. tovii, the abundant laminar scales form a distinct red-brown fringe along the margins of the blades, whereas this is never observed in E. austromarquesense.

Elaphoglossum tovii and E. austromarquesense are endemic to the Marquesas, but apparently never occur together on the same island: E. austromarquesense is restricted to the southern islands, whereas E. tovii occurs only in the northern islands of Nuku Hiva, Ua Pou and Ua Huka.

Distribution and habitat: Marquesas Islands, in the northern islands only: Nuku Hiva, Ua Huka, Ua Pou. Epiphyte, rare, in wet forests with *Hernandia*, *Cyathea*, *Metrosideros*, *Crossostylis*, *Weinmannia*, *Ilex* and Pandanaceae abundant, from 686 to 1020 m.

Other specimens examined: NUKU HIVA: Tovii, vallon du réservoir, 8°52'S, 140°09'W, 830-860 m, 26.v.1984, Florence 6722 (PAP), Florence 6748 (PAP 2 sheets), Florence 6766 (PAP); Tovii, croupe au-dessus du captage du SER, 8°51'S, 140°08'W, 30.xi.1982, Florence 4203 (P); Tovii, épaulement SE du Mt. Tekao, 8°51'S, 140°10'W, 985 m, 28.v.1984, Florence 6802 (PAP); Tovii, épaulement S du Mt. Ooumu, 8°50'S, 140°09'W, 1020 m, 6.iii.1986, Florence 7466 (P, PAP); Toovii Plateau, spur of Mt. Ooumu, 790 m, 16.vii.1977, Gagné 1040 (US); Toovii Valley, ridge above Tapuaooa shelter, 800-950 m, 3.vii.1970, Gillett 2148 (BISH, UC, US); Tovii, 1000 m, vi.1921, Herbier S.F.I.M. 110 (P); Tovii, flanc sud du Mt. Ooumu, 8°51'S, 140°09'W, 1000 m, 28.vii.1987, Florence 8397 (PAP); Tovii, forêt galerie du plateau, 1.iii.1963, Hallé 2051 (P, US); xi.1922, Quayle 1311 (BISH, two sheets); Tovii, Ooumu area, top of Tapueahu valley, 8°51'S, 140°19'W, 20-22.ix.1995, Wood & Perlman 4594 (BISH, PAP, PTBG, US).

UA HUKA: Hitikau to Matokuhoa ridge trail, 8°54'223"S, 139°31'794"W, 686 m, 16.vi.2004, Perlman 19025 (BISH, P, PAP, PTBG, UC, US); Hane, crête menant au Mt. Hitikau, 8°55'S, 139°32'W, 840 m, 20.ii.1986, Florence 7282 (PAP); Hannay, 700 m, 10.xi.1922, *Jones 1687* (BISH). Hitikau summit area, large bowl-like plateau with wind-swept ridges, 8°54'22"S, 139°31'66"W, 2700–2900 ft, 28.vi.1997, *Wood 6398* (PAP, PTBG, US).

UA POU: Upper Pepehitoua River valley south of Hakahetou, on ridge just west of base of Pou Maka, 650 m, 9°23'41"S, 140°5'15"W, 22.vii.2003, *Lorence et al. 9150* (PTBG); Mt. Tekahoipu, 1000 m, 1922, *Quayle 1144* (BISH); forested ridge and slopes up to Teava haakiti, NW side, 914 m, 24.xi.2003, *Wood 10441* (PTBG).

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APPENDIX 1

INDEX TO SPECIES

- 1. E. austromarquesense.
- 2. E. feejeense.
- 3. E. florencei.
- 4. E. marquisearum.
- 5. E. meyeri.
- 6. E. rapense.
- 7. E. samoense.
- 8. E. savaiense.
- 9. E. tovii.

APPENDIX 2

INDEX TO EXSICCATAE

The numbers in parentheses refer to the corresponding species in Appendix 1. Specimens are listed in alphabetical order by first collector. Collection numbers in bold type indicate type specimens.

Birnbaum 55 (8), 93 (8), 113 (2), 131 (7), 147 (2); Brown 14 (4), **498A** (9), 1021A (4), 1100 (4); Brown 1021a (1); Butaud 842 (8).

Chaine 16 (2), 20 (7); Cherrier in McKee 44691 (4).

Dunn 516 (8).

Florence 7.06 (8), 2354 (7), 2424 (8), 3643 (7), 3755 (8), 4203 (9), 4217 (4), 4517 (8), 4589 (8), 5129 (8), 5387 (7), 5400 (8), 5414 (7), 6398 (5), **6507** (5), 6507 (5), 6722 (9), 6748 (9), 6766 (9), 6801 (4), 6802 (9), 7282 (9), 7339 (4), 7359 (1), 7466 (9), 7829 (2), 7956 (8), 8010 (2), 8056 (7), 8121 (2), **8348** (3), 8396 (4), 8397 (9), 8657 (7), 8727 (8), 8811 (2), 8821 (8), 8845 (2), 8866 (8), 8938 (8), 8961 (8), 9137 (8), 9538 (1), 9539 (4), 9616 (4), 9631 (1), 9647 (1), 9782 (2), 9807 (2), 9869 (8), 9871 (2), 9936 (2), 9938 (7), 10695 (7), 10696 (8), 10722 (8), 11459 (8), 11607 (7), 11608 (8), 11827 (8), 11931 (8), 12133 (8); Fosberg 11385 (5), 11563 (5), 61091 (8), 62844 (8), 62967 (8), 63290 (8).

Gagné 1040 (9), 2330 (4), 2258 (8), 2260 (8); Gillett 2148 (9); Grant 3726 (8), 3773 (8), 3804 (8), 3888 (2),

3928 (7), 3930 (8), 3983 (8), 4238 (8), 4263 (7), 4398 (8), 4497 (8), 4498 (2), 4984 (8), **5156 (7)**, 5174 (8), 5281 (7), 5318 (8).

Hallé 2051 (9), 2174 (4), 7516 (5).

Jacq 222 (2), 272 (8), 314 (3), 337 (2), 341 (8), 342 (8), 395 (8), 413 (3), 424 (7), 438 (7), 458 (8), 459 (8), 462 (8), 463 (3), 502 (7), 506 (8), 521 (2); Jones 1607 (4), 1687 (9), **1792** (4), 1842 (4).

Lépine 108 (7), 111 (8), 112 (8), 150 (7); Lorence 6090 (4), 6151 (4), 6172 (1), 6244 (1), 8934 (4), 8937 (1), 8938 (1), 9004 (1), **9011** (1), 9020 (4), 9150 (9).

MacDaniels 1482 (8), 1547 (7), 1549 (7); Moore 186 (7), 481 (8); Motley 2608 (5), 2677 (6), 2875 (5); Mumford 39 (4), 474 (1).

Nadeaud 191 (7).

Oliver 3112 (1).

Pacific Entomol. Surv. Ex 39 (4); Perlman 19021 (4), 19025 (9); Powell **197** (8).

Quayle 46 (8), 1144 (9), 1311 (9).

Ranker 1907 (7), 1961 (7), 1962 (8).

Sachet 1136 (1), 2122 (4); Schäfer 5802 (1); Smith **675** (2); St John 10728 (7), 15438 (5), **15529 (6)**, 15644 (6), 16992 (7), 17028 (7), 17048 (8), 17051 (7), 17069 (7), 17160 (8), 17163 (7), 17270 (8).

Vieillard 2 (7).

Wagner 6113 (4); Wood 4351 (1), 4434 (1), 4593 (4), 4594 (9), 6390 (4), 6398 (9), 9478 (6), 9693 (8), 9708 (5), 9726 (8), 9776 (6), 10040 (1), 10042 (4), 10088 (1), 10141 (1), 10304 (4), 10441 (9), 10445 (4), 10503 (4).