# Polyphyly and hidden species among Hawaiʻi's dominant mesophotic coral genera, *Leptoseris* and *Pavona* (Scleractinia: Agarciidae)

Widespread polyphyly in stony corals (order Scleractinia) has prompted efforts to revise their systematics through approaches that integrate molecular and micromorphological evidence. To date, these approaches have not been comprehensively applied to the dominant genera in mesophotic coral ecosystems (MCEs) because several species in these genera occur primarily at depths that are poorly explored and from which sample collections are limited. This study is the first integrated morphological and molecular systematic analysis of the genera *Leptoseris* and *Pavona* to examine material both from shallow-water reefs (< 30 m) and from mid- to lower-MCEs (> 60 m). Skeletal and tissue samples were collected throughout the Hawaiian Archipelago between 2-127 m. A novel mitochondrial marker (*cox*1-1-rRNA intron) was sequenced for 70 colonies, and the micromorphologies of 94 skeletons, plus selected type material, were analyzed. The *cox*1-1-rRNA intron resolved 8 clades, yet *Leptoseris* and *Pavona* were polyphyletic. Skeletal micromorphology, especially costal ornamentation, showed strong correspondence and discrete differences between mitochondrial groups. One putative new *Leptoseris* species was identified and the global depth range of the genus *Pavona* was extended to 89 m, suggesting that the diversity of mesophotic scleractinians has been underestimated. Examination of species' depth distributions revealed a pattern of depth zonation: Species common in shallow-water were absent or rare > 40 m, whereas others occurred only > 60 m. These patterns emphasize the importance of integrated systematic analyses and more comprehensive sampling by depth in assessing the connectivity and diversity of MCEs.

1  Daniel G. Luck[1*], Zac H. Forsman[2], Robert J. Toonen[2], Sarah J. Leicht[1] and Samuel

2  E. Kahng[1]

3  [1]Hawai'i Pacific University, Marine Science Program, Waimanalo, HI, USA

4  [2]University of Hawai'i, Hawai'i Institute of Marine Biology, Kane'ohe, HI, USA

5  *Corresponding author: Daniel G. Luck, Hawai'i Pacific University, Marine
6  Science Program Office, 41-202 Kalaniana'ole Highway, Waimanalo, HI 96795
7  USA. Email: dluck@my.hpu.edu. Phone: +1 (808) 931-0447

## 1. INTRODUCTION

Within the past two decades, molecular studies have shown that traditional classification systems

for stony corals (Cnidaria: Anthozoa: Scleractinia), which are based on macromorphological

characters, do not accurately reflect the evolutionary relationships of many taxa (Romano &

Palumbi 1996; Romano & Cairns 2000; Fukami et al. 2004; Fukami et al. 2008; Huang et al.

2009; Budd et al. 2010; Kitahara et al. 2010). As recently as 2008, mitochondrial and nuclear

DNA revealed that a majority of scleractinian families with reef-building genera are potentially

polyphyletic (Fukami et al. 2008; Huang et al. 2009). The macromorphological characters that

underpin traditional scleractinian taxonomy are notoriously variable between reef habitats and

biogeographic regions (Veron 2000; Todd 2008), leading to phenotypic overlap between distantly

related taxa (i.e. homoplasy) that confounds phylogenetic analyses. However, recent studies that

have integrated molecular and micromorphological/structural evidence (hereafter referred to as

integrated systematic studies) have found correspondence between molecular-based and

morphologically-based taxa (Fukami et al. 2004; Benzoni et al. 2010; Budd et al. 2010; Benzoni

et al. 2012; Kitahara et al. 2012). Integrated systematics have resolved outstanding problems in

coral taxonomy from the family-level (Budd & Stolarski 2009) to the species-level (Forsman et

al. 2010).

To date, most integrated systematic studies of hermatypic corals have focused on

easily-accessible shallow-water (< 30 m) species. Few species that occur primarily in mesophotic

coral ecosystems (MCEs), which are coral habitats from ~30-40 m to the deepest limits of

obligate zooxanthellate corals (see Hinderstein et al. 2010), have been included in such studies.

In particular, the agariciid genus *Leptoseris* Milne-Edwards & Haime, 1849, has not been

comprehensively examined using an integrated approach despite the fact that it dominates many

31   Indo-Pacific MCEs (Wells 1954; Fricke & Knauer 1986; Kahng & Kelley 2007; Rooney et al.

32   2010). The most recent revision of *Leptoseris* by Dinesen (1980) was based largely on

33   shallow-water material and occurred prior to the widespread use of molecular techniques in coral

34   systematics. Since then, the genus has been included in several molecular studies (Romano &

35   Cairns 2000; Cuif et al. 2003; Le Goff-Vitry, Rogers & Baglow 2004; Fukami et al. 2008;

36   Kitahara et al. 2010), but in each case only one or two shallow-water species were used and just

37   four of 18 described species have been studied genetically. The results of these studies have

38   challenged the monophyly of the family Agariciidae Gray, 1847(Fukami et al. 2008) and of the

39   genus *Pavona* Lamarck, 1801 (Le Goff-Vitry, Rogers & Baglow 2004), but none have tested the

40   monophyly of the genus *Leptoseris* using more than two species. While Benzoni et al. (2012)

41   recently provided an integrated systematic treatment of *L. foliosa* Dinesen, 1980, no study has

42   applied such an approach to multiple species within the genus. Moreover, none of the species

43   with the deepest distributions (> 100 m, e.g. *L. fragilis* Milne-Edwards & Haime, 1849, *L.*

44   *hawaiiensis* Vaughan, 1907and *L. scabra* Vaughan, 1907) have been examined using an

45   integrated approach. These species are particularly interesting to marine ecologists because they

46   may have unique adaptations for efficiently capturing light (Kahng et al. 2012), allowing them to

47   survive deeper than other photoautotrophic corals (Maragos & Jokiel 1986; Kahng & Maragos

48   2006).

49      While MCEs are hypothesized refugia for some reef-building species (Riegl & Piller 2003;

50   Bak, Nieuwland & Meesters 2005; Bongaerts et al. 2010a), there have been few integrated

51   systematic studies comparing shallow and mesophotic reef-building corals. The lack of studies

52   arises from the logistical difficulties of accessing MCEs, but such studies are essential for

53   understanding the diversity and connectivity of MCEs and assessing their conservation value.

54   The few studies that have collected samples from MCEs have found previously unknown

55    morphologies (Kahng & Maragos 2006), cryptic diversity (Chan et al. 2009) and high taxonomic

56    richness (Bridge et al. 2012). These results suggest that the global diversity of mesophotic

57    scleractinians has been underestimated and/or the biogeographic ranges of mesophotic species are

58    not fully explored.

59        The purpose of this study is to provide an integrated systematic analysis for the agariciid

60    genera that dominate Hawaiian MCEs, namely *Leptoseris* and *Pavona*. The monophyly of these

61    genera is tested using molecular methods, and micromorphological characters with diagnostic

62    value are identified and evaluated in terms of their correspondence to a molecular phylogeny and

63    traditional taxonomic designations. More reliable diagnostic characters will facilitate

64    identification of *Leptoseris* and *Pavona* spp. in Hawaiʻi, which will enhance understanding of the

65    ecological processes and biodiversity of Hawaiian MCEs. Accurate identification will help

66    determine the degree of overlap between shallow-water and mesophotic species, which will

67    facilitate investigations of the physiological adaptations that allow these corals to thrive in

68    extreme low-light conditions.

69        Here, we focus on comparisons between a single novel, rapidly evolving mitochondrial

70    marker (*cox*1-1-rRNA intron) and micromorphological traits.  Although mitochondrial genes are

71    often uninformative in reef-building corals (Shearer et al. 2002; Hellberg 2006; Shearer &

72    Coffroth 2008), recently discovered, highly variable mitochondrial markers in Pocilloporidae

73    (Flot & Tillier 2007) have revealed the strongest evolutionary and biogeographical patterns (e.g.

74    Pinzon & LaJeunesse 2011; Keshavmurthy et al. 2013; Pinzón et al. 2013), while remaining

75    consistent with other genetic markers. Although multiple molecular markers are often desirable in

76    phylogenetic studies (Funk & Omland 2003), we show here that the *cox*1-1-rRNA intron provides

77    high resolution for the genera *Leptoseris* and *Pavona* with strong concordance between

78    mitochondrial groups and discrete micromorphological characters.

## 2. MATERIALS AND METHODS

*(a) Sample collections*

Skeletal and tissue samples of *Leptoseris* and *Pavona* spp. were collected throughout the

Hawaiian Archipelago (*n* = 109) and Line Islands (*n* = 3) (Supplemental Table S1). Collections

were authorized via special activity permits by the State of Hawaiʻi Board of Land and Natural

Resources. Although this study focused on species from mid- to lower MCEs (i.e. > 60 m),

shallow-water samples (< 30 m) were also collected for comparative purposes. Most samples

came from MCEs in the Auʻau Channel, located between Maui and Lanaʻi, and along the

nearshore shallow-water reefs off Oʻahu. Collections were made using the Hawaiʻi Undersea

Research Laboratory (HURL) *Pisces* submersibles, technical diving or traditional SCUBA,

depending on the depth. This effort included 14 submersible dives and one remotely controlled

vehicle dive ranging from 49-216 m, 14 technical dives from 40-78 m, and eight shore dives from

5-24 m. Collected samples included all six *Leptoseris* spp. known from Hawaiʻi and ranged from

2-127 m depth, encompassing most of the accepted bathymetric range for the genus (Dinesen

1980). (Vaughan's (1907) record of *L. hawaiiensis* to 470 m is likely erroneous, see Kahng et al.

2010.) Some samples were too small for morphological analyses (*n* = 18); others lacked

preserved tissue and were not included in molecular analyses (*n* = 42). The remaining 52 samples

were included in both molecular and morphological analyses.

 The *Leptoseris* type collections of the U.S. National History Museum (USNM) and the

Natural History Museum, London, UK (BNHM) were also examined (Supplemental Table S2).

Type specimens for a majority of *Leptoseris* spp. and all species previously known from Hawaiʻi

were analyzed morphologically (tissues for molecular analyses were unavailable). *Pavona* types

101    were not examined because at the time of museum visits *Pavona* was not thought to be abundant

102    in Hawaiian MCEs.

103    *(b)* **Molecular analyses**

104    Phylogenetic relationships were determined by analyzing sequences from the *cox*1-1-rRNA

105    intron, a novel, rapidly evolving mitochondrial intergenic spacer. Preliminary analyses of

106    *cox*1-1-rRNA showed that it gave much higher resolution between *Leptoseris* spp. than either the

107    NAD5 5'-intron or the ITS region (D.G. Luck, unpublished data).

108        Host genomic DNA was extracted using the E.Z.N.A.® Tissue DNA Kit (Omega Bio-tek,

109    Norcross, GA, U.S.). The *cox*1-1-rRNA intron was amplified using Biomix Red (Bioline,

110    Taunton, MA, U.S.), a high-density PCR reaction mix, and the following primers: ZFCOXIF

111    (5'-TCT GGT GAG CTC TTT GGG CTC T-3'**)** and ZFtrnar (5'-CGA ACC CGC TTC TTC

112    GGG GC-3'). Primers were designed based on *Agaricia* Lamarck, [1801] and *Pavona*

113    mitochondrial genomes acquired from GenBank (NC_008160,5). Each PCR totaled 12.5 µl and

114    included reagents in the following proportions: 7.5 µl Biomix Red; 6.51 µl nanopure® (Thermo

115    Fisher Scientific) $H_2O$; 0.195 µl of each primer; and 0.6 µl extracted genomic DNA. The

116    thermocycler protocol was as follows: one cycle at 95°C for 2 min; 35 cycles beginning with

117    95°C for 30 sec, followed by 52°C for 30 sec, followed by 72°C for 1 min; and one extension

118    cycle at 72°C for 10 min.  PCR products were cleaned using shrimp alkaline phosphatase and

119    Sanger sequenced using the forward primer. Only the forward primer was necessary since it

120    produced sufficiently long sequences (up to 900 bp) with many informative sites.

121        In order to provide higher resolution and to root the mtDNA phylogeny, *cox*1-1-rRNA

122    sequences were obtained for *Agaricia humilis* Verrill, [1901], *Pavona clavus* (Dana, [1846]) and

123    *Siderastrea radians* (Pallas, [1766]) from whole mitochondrial genomes available on GenBank

124    (accession numbers: DQ643831, DQ643836, DQ643838). These three taxa were included in all

125    phylogenetic analyses.

126        Sequence data were manually cleaned with BioEdit version 7.1.3 (Hall 1999) and imported

127    into MEGA 5.10 for alignment (Tamura et al. 2011). Separate alignments were performed using

128    ClustalW and Muscle algorithms, first using default settings and then with reduced gap opening

129    and extension penalties. The ClustalW alignment (with default parameters) was chosen for final

130    analysis because it produced trees with slightly higher bootstrap support.

131        Maximum Likelihood (ML) and Bayesian phylogenies were constructed using evolutionary

132    models selected by jModelTest 2.1.1 (Darriba et al. 2012). ML analysis was performed in

133    PhylML (Guindon & Gascuel 2003) using a transversional model with a gamma distribution of

134    substitution rates across sites and 1000 bootstrap replicates. Bayesian analysis was performed in

135    MrBayes 3.2.1 (Ronquist et al. 2012) using a three-parameter model with unequal base

136    frequencies and a gamma distribution of substitution rates across sites. The Bayesian model was

137    run over 1.75 million generations at which point the standard deviation of split frequencies fell

138    below 0.01.

139    *(c)  Taxonomy, sample identification, and morphological terminology*

140    With respect to the taxonomy of the genus *Leptoseris*, the synonymies of Dinesen (1980) were

141    followed except that *L. tubulifera* Vaughan, 1907 was treated as a valid species based on

142    molecular and micromorphological evidence. Following the suggestion of Dai & Lin (1992),

143    *Pavona yabei* Pillai and Scheer, 1976 was kept in the genus *Pavona* (rather than reassigned to

144    *Leptoseris* as proposed by Veron & Pichon 1980).  The septal and corallite morphologies of *P.*

145    *yabei* are more similar to those of other *Pavona* spp. (e.g. septocostae that always alternate in

146    length, rows of granules rather than continuous meninae on the lateral faces of septocostae, high

147    corallite density, predominance of radial collines, etc.) and there is no molecular evidence that it

148    should be grouped with *Leptoseris* spp. All samples included in this study were identified to the

149    species-level by comparison to type material and by consultation with taxonomists Z.D. Dinesen

150    and J.E. Maragos.

151        In reference to the features of the coral skeleton, the terminology of Dinesen (1980) was

152    employed except that 'meninaes' (Gill & Russo 1980) was used rather than 'lateral ridges' for the

153    paired lists or ridges along the lateral surfaces of septocostae. For detailed definitions of skeletal

154    terms, consult Wells (1956) and Budd & Stolarski (2009).

155    *(d) **Morphological analyses***

156    Skeletal morphological analyses were conducted on 94 samples (52 with paired tissue vouchers)

157    in order to (1) provide additional support for molecular-based species groups (2) and to identify

158    diagnostic characters for species identification when molecular analyses are not possible.

159    Emphasis was placed on identifying discrete characters because they are easily mapped onto

160    phylogenies.

161        Consistent with other integrated systematic studies of scleractinians (Budd & Stolarski 2009;

162    Benzoni et al. 2010; Budd et al. 2010), morphological analyses focused on septocostal and costal

163    micromorphology, although macromorphological observations of the corallum and corallites

164    were also made. Where samples had free growth margins, costal ornamentation ('costae' being

165    extensions of septocostae on the non-calicinal surface and 'ornamentation' being the

166    granules/spines on costae) were also analyzed. Because of their small size (typically < 100 µm in

167    diameter) and location on the non-photosynthetic side (i.e. the underside) of the corallum, costal

168    granules/spines were selected for closer examination since they may be subject to reduced

169    environmental selection and therefore show less ecotypic variation within a given species.

170        In order to identify diagnostic characters, skeletal samples were examined under a Nikon

171    SMZ 800 light microscope. Skeletons were bleached with sodium hypochlorite to remove tissue,

172    rinsed and then air dried. Examinations were made first with each skeleton intact. Visible features

173    were recorded and digital photographs of the corallites, septocostae and costae were taken using a

174    Nikon P-6000 camera mounted to the microscope. When samples were large enough (n = 40),

175    longitudinal sections were cut throughout the coenosteum using a Dremel® tool or wet saw to

176    investigate the arrangement of meninaes. A subset of skeletons was also analyzed using scanning

177    electron microscopy (SEM). Longitudinal sections or chips of these samples were mounted on

178    metal stubs using carbon glue or tape, sputter-coated with gold-palladium for approximately 2

179    min, and then viewed with a Hitachi S-4800 SEM.

180    **3. RESULTS**

181    (a) *Phylogenetic results*

182    Sequence data from the *cox*1-1-rRNA intron were obtained from 70 coral colonies (Supplemental

183    Table S1) and three sequences were obtained from previously published mitochondrial genomes.

184    The final alignment of 73 sequences was 743 bp long and included 517 variable sites, 321 of

185    which were parsimony informative. Bayesian and ML trees had similar topologies and placed

186    most taxa in well-supported clades (Fig. 1; only Bayesian tree shown). Pairwise nucleotide

187    distances between significant clades were always an order of magnitude higher than within group

188    distances (mean uncorrected p-distance of $0.193 \pm 0.025$ vs. $0.015 \pm 0.008$).

189         The Bayesian phylogeny shows that the genus *Leptoseris*, as currently defined, is

190    polyphyletic (Fig. 1). A majority of Hawaiian *Leptoseris* spp. belong to clades I-II including *L.*

191    *hawaiiensis*, *L. incrustans* (Quelch, [1886]), *L. papyracea* (Dana, [1846]), *L. tubulifera* and *L.* sp. 1.

192    However, *L. scabra*, which forms the sister clade (VII) to *Agaricia humilis*, is distantly related to

193    clades I-II. The mean pairwise nucleotide distances between clade VII and clades I-II were

194    among the highest distances between all groups compared (uncorrected p-distances: I vs. VII =

195    $0.294 \pm 0.018$; II vs. VII = $0.284 \pm 0.018$). Three haplotypes of *L. mycetoseroides* Wells, [1954] are

196    scattered throughout the phylogeny, but all three clearly fall outside the group formed by clades

197    I-II.

198        The genus *Pavona* is also polyphyletic at the *cox*1-1-rRNA intron and consists of at least two

199    clades (V and VIII). Clade V is sister to the group formed by *A. humilis* and *L. scabra*, whereas

200    clade VIII is more closely related to the *Leptoseris* spp. of clades I-II.

201    (b) ***Morphological results***

202    Morphological analyses revealed that most molecular-based species groups could be

203    independently identified using skeletal characters (Fig. 2; Supplemental Table S3). Although no

204    single character could distinguish between all *Leptoseris* or *Pavona* spp., combinations of

205    discrete characters were effective in pairwise comparisons. Among the more important characters

206    were the costal ornamentation, the shape and continuity of the upper septocostal margin, the

207    development of meninaes, and species-specific macro-projections.

208        Several *Leptoseris* spp. had clear diagnostic characters. For example, *L. incrustans*

209    consistently had meninaes four to five times wider than the upper septocostal margin, which was

210    always a narrow and continuous ridge (Fig. 2B). This width ratio was constant throughout the

211    corallum (mean = 0.19, standard deviation = 0.09) except in the vicinity of corallites or where

212    insertions occurred. *L. tubulifera* was clearly diagnosed by the presence of corallites on tubes, a

213    characteristic absent from *Pavona*? sp. 2, which may also form tubes

214        In cases where a species lacked a single diagnostic character, it could usually be distinguished

215    from species with similar gross morphologies by analyzing combinations of discrete

216    micromorphological characters. For example, *L. hawaiiensis* and *L. scabra* both grow as thin

217    plates in lower MCEs (Figs. 3D, J).  The costal ornamentation of the two species, however, is

218    clearly different (Figs. 2C-D). *L. hawaiiensis* has conical spines predominantly aligned in a single

219    row down the center of each costa, whereas *L. scabra* has cylindrical or beady granulations in

220   three rows, one central row and one row on each margin. Similarly, *Pavona* sp.1 and *L.*

221   *papyracea,* both of which form branching colonies (Figs. 3E, H), are easily distinguished by their

222   costal ornamentation. *L. papyracea* has exsert, conical spines arranged in a single row down the

223   center of each costa while *P*. sp. 1 has triangular or bead-like granulations scattered along costae.

224   A final example is that of *L. scabra* versus *L*. sp. 1. Both species grow as crateriform vases with

225   irregular, bumpy surfaces in mid-mesophotic depths (~60-80 m), but the two differ in their

226   development of septal teeth (Figs. 2A, D). *L. scabra* has peg-like teeth formed by discontinuities

227   of the septocostae, including their meninaes. In *L*. sp. 1, teeth are absent or visible only as

228   discontinuities of the upper septocostal margin above the meninaes. *L*. sp. 1 also has septocostae

229   that form numerous abortive branches at proximal cushions, with some branches turning

230   antiparallel from their parent septocosta. In fact, *L*. sp. 1 is distinct from any species described in

231   the literature and is putatively a new species in need of formal description.

232       Some aspects of micromorphology were also concordant with generic differences at the

233   *cox*1-1-rRNA region. For example, members of the "*Leptoseris*" clades (I-II) had more or less

234   continuous meninae, whereas most *Pavona* spp. had granules arranged in rows along their lateral

235   surfaces but lacked continuous meninae. The position of *L. mycetoseroides* outside of the clades

236   I-II is also supported by micromorphology as all three haplotypes of *L. mycetoseroides* have rows

237   of granules rather than continuous meninae. Continuous meninae, however, are apparently not

238   synapomorphic as they are sometimes found in *L. scabra* (clade VII). In fact, while

239   morphological analyses revealed many useful characters, few synapomorphies were found. Most

240   of the patterns of costal ornamentation that differentiate between *Leptoseris* spp. can also be

241   found in *Pavona* spp. (Fig. 2: B vs. E) and *L. scabra* (Fig. 2: A vs. D).

242   (c)  ***Depth distribution of Hawaiian* Leptoseris *and* Pavona**

243    *Leptoseris* and *Pavona* clades sorted into two major groups according to their depth distributions

244    (Fig. 4). Most clades occurred in shallow-water (< 30 m) down to mid-mesophotic depths (60-80

245    m). Only clades Ib (*L. hawaiiensis*) and VII (*L. scabra*) were restricted to depths > 60 m. These

246    two clades were observed deeper than any others, with colonies of *L. hawaiiensis* observed at 141

247    m and *L. scabra* observed to 127 m. One *Leptoseris* species, *L. incrustans*, was never observed in

248    mesophotic depths but was among the more common agariciids observed in dimly-lit,

249    shallow-water caves and undercuts. Of the nominal *Pavona* spp., only *P.* sp. 1 (clade V) was

250    observed from lower MCEs (89 m); all other *Pavona* spp. were restricted to depths < 80 m.

251    **4. DISCUSSION**

252    Although a previous study found polyphyly with a few samples of *Pavona* and *Leptoseris* (Le

253    Goff-Vitry, Rogers & Baglow 2004), this study confirms this finding with more adequate

254    taxonomic sampling. This polyphyly can be attributed to the inclusion of *L. mycetoseroides* and

255    *L. scabra* within the genus since both are distantly related to other *Leptoseris* spp. (Fig. 1) and

256    probably in need of generic reassignment. The remaining Hawaiian *Leptoseris* spp. form a

257    monophyletic group (clades I-II) that could potentially retain the name *Leptoseris*, depending on

258    the phylogenetic position of the type species, *L. fragilis*.

259        This study is also the first to use the *cox*1-l-rRNA intron as a phylogenetic marker for

260    scleractinians. In *Leptoseris* and *Pavona*, this intron is highly variable and capable of

261    distinguishing between closely related species. Such variability is atypical of anthozoan mtDNA,

262    which normally evolves too slowly to distinguish between congenerics (Shearer et al. 2002;

263    Hellberg 2006).  Since the *cox*1-l-rRNA intron gave high resolution across several agariciid

264    genera, it may be useful for resolving species-level relationships throughout the family

265    Agariciidae.

266    Because mtDNA-based trees may not accurately reflect phylogenetic descent (Funk &

267    Omland 2003; McGuire et al. 2007), many phylogenetic studies use nuclear-DNA (nDNA) to

268    corroborate mtDNA-based trees (Romano & Cairns 2000; van Oppen, Koolmes & Veron 2001;

269    Fukami et al. 2008). However, analysis of several nuclear markers is often necessary to achieve

270    the same level of confidence that gene and species trees are congruent that could be achieved

271    with a single mitochondrial marker (Moore 1995). Morphological characters, provided they are

272    rigorously defined (e.g. discrete), can provide an alternative data set for corroborating

273    phylogenies inferred from mtDNA (Puorto et al. 2001; Wiens & Penkrot 2002; Rubinoff &

274    Holland 2005). The strong correspondence found here between mitochondrial *cox*1-1-rRNA

275    groups and discrete skeletal characters suggests that the mtDNA tree accurately reflects the

276    species trees for these genera.

277    In *Leptoseris* and *Pavona*, micromorphology (*sensu* Budd & Stolarski 2009) generally

278    showed higher correspondence with molecular data than macromorphology, which was highly

279    convergent. The colony form of *L. scabra*, for instance, resembles that of both *L. hawaiiensis* and

280    *L.* sp. 1 at their respective depths yet *L. scabra* is not closely related to either species (Fig. 1). In

281    both cases, *L. scabra* is easily distinguished using micromorphological characters. The

282    correspondence between micromorphological and molecular evidence is consistent with the

283    results of recent works in scleractinian systematics. Benzoni et al. (2012) found that *Craterastrea*

284    *levis*, which had been synonymized with *L. foliosa* based on affinities in corallum morphology,

285    differed from *L. foliosa* in micromorphology, microstructure and at several molecular markers.

286    Kitahara et al. (2012) found that the microstructure of *Dactylotrochus cervicornis* (Moseley,

287    1881) agreed with *cox*1 data that had, surprisingly, placed it within the Agariciidae.

288    Of the micromorphological characters explored in this study, costal ornamentation is of

289    particular diagnostic importance for *Leptoseris* and *Pavona* spp. Differences in septal

290    ornamentation (e.g. granule shape) have been found  to be effective at distinguishing between

291    Atlantic and Pacific faviids and mussids (Budd & Stolarski 2009). The diagnostic utility of costal

292    ornamentation for unifacial agariciids is consistent with those results because costal and septal

293    ornamentation are homologous; like interspecific differences in septal ornamentation, differences

294    in costal ornamentation reflect differences in the development and arrangement of calcification

295    zones (i.e. rapid accretion front vs. thickening deposits, see Stolarski 2003). For corals growing in

296    the lower mesophotic where useable light is unidirectional (Kirk 1994), costal ornamentation (on

297    the shaded side of a colony) theoretically does not affect colony photophysiology and should

298    show less ecotypic variation than septal ornamentation (on the side of the colony exposed to

299    light), potentially enhancing the diagnostic value of costal relative to septal ornamentation.

300        In contrast to micromorphological characters, many macromorphological (i.e. gross,

301    colony-level appearance) characters in *Leptoseris* and *Pavona* are not concordant with molecular

302    results. The three haplotypes of *L*. *mycetoseroides*, for example, all have the collines (protuberant

303    ridges between corallites) that ostensibly define the species (Wells 1954; Dinesen 1980), yet these

304    haplotypes are scattered throughout the mtDNA phylogeny. Another example is that of *Pavona*

305    sp. 1 versus *L*. *papyracea*, two species that clearly differ in their costal ornamentation (see results

306    section). *P*. sp. 1 is common in museum collections but is almost always misidentified as *L*.

307    *papyracea* because it also has a branching growth form. Mitochondrial data, however, agree

308    with the observed differences in costal ornamentation and confirm that the two species are

309    distinct (Fig. 1).

310        The ambiguous boundaries between *Leptoseris* and *Pavona* in traditional taxonomic systems

311    may have contributed to the narrative that *Leptoseris* spp. dominate lower MCEs in the

312    Indo-Pacific (Vaughan 1907; Wells 1954; Rooney et al. 2010). The results of this study show that

313   in Hawaiʻi *Leptoseris* spp. coexist with *Pavona* spp. and at least one other clade (which contains

314   *L. scabra*) at depths > 80 m. The collection of *P.* sp. 1 from 89 m surpasses the previous global

315   depth record for the genus *Pavona* (73 m, Gardiner 1905), and the collection of *P. varians* from

316   73 m in the Auʻau Channel extends the Hawaiian depth record for the species from a previous

317   mark of 48-53 m (Vaughan 1907). These new depth records for *Pavona* spp., along with the

318   discovery of one putative new *Leptoseris* sp. and several undescribed morphologies

319   (Supplemental Table S3), indicate that scleractinian diversity in lower Hawaiian MCEs has been

320   underestimated (e.g. Kahng & Kelley 2007; Rooney et al. 2010). As the most remote archipelago

321   in the world, Hawaiʻi is characterized as a low diversity region and Hawaiian coral fauna are

322   depauperate relative to that of the Indo-West Pacific (IWP) (Grigg 1983; Grigg 1988). The

323   discovery of putative new species and expanded vertical distributions of Hawaiian mesophotic

324   corals suggests that the diversity of IWP MCEs, which are relatively unexplored (Kahng et al.

325   2010) but occur in a region of high shallow-water diversity, may be substantially greater than

326   previously estimated.

327       The zonation of *Leptoseris* and *Pavona* spp. from shallow (2 m) to deep-water (≥ 153 m, see

328   Kahng & Maragos 2006) in Hawaiʻi offers the opportunity to study the processes of niche

329   diversification, speciation and possibly adaptive radiation within a group of sympatric marine

330   species. Adaptive radiations can occur when a group of organisms acquires a key innovation that

331   allows them to use an underutilized set of resources (Schluter 2000). For some *Leptoseris* and

332   *Pavona* spp., highly efficient light absorption (see Kahng et al. 2012) may have enabled

333   colonization of deeper habitats (i.e. different niches) where lower levels of useable light

334   previously prevented other species from surviving or competing for space. Divergent selection

335   between habitats could have eventually led to reproductive isolation and then speciation (Schluter

336   2000). Divergence in habitat depth seems to have driven speciation in Hawaiian limpets (*Cellana*

337   spp.)  (Bird et al. 2011) and in eastern Pacific rockfishes (Ingram 2011). In scleractinian corals, a

338   growing number of studies have pointed to ecological divergence as an explanation for

339   partitioning of species or genotypes by depth (Carlon & Budd 2002; Vermeij & Bak 2003;

340   Bongaerts et al. 2010b). Divergent selection between shallow and mesophotic habitats may have

341   contributed to the diversification of Hawaiian *Leptoseris* and *Pavona* and could explain their

342   zonation along depth gradients.

343     Molecular data at two mitochondrial markers now suggest that taxonomic revisions of the

344   genera *Leptoseris* and *Pavona* are warranted (Le Goff-Vitry, Rogers & Baglow 2004; this study).

345   The strong correspondence between mtDNA and micromorphology found here suggests that

346   these revisions should focus on micromorphological characters. The development of more

347   reliable diagnostic characters for Hawaiian agariciids will enable comparative studies along depth

348   gradients. Accurate species identification will facilitate comparisons between mesophotic

349   communities in Hawaiʻi versus other regions and help determine if the pattern of depth zonation

350   observed in Hawaiʻi exists in higher diversity systems such as the IWP.

351   **ACKNOWLEDGEMENTS**

352   Hawaiʻi Undersea Research Laboratory provided the submersibles and crew used to collect a

353   majority of samples; D. Wagner and J.E. Maragos provided additional material. S.D. Cairns

354   supervised a visit to USNM to view the type collections stored there. BMNH loaned type

355   material for examination. Z.D. Dinesen and J.E. Maragos gave taxonomic consultation on the

356   genus *Leptoseris*. D. Wagner provided feedback on the manuscript. K. McClanahan and M.M.

357   Mocaer helped collect morphometric data and analyze skeletons.

358   **REFERENCES**

359  Bak RPM, Nieuwland G, and Meesters EH. 2005. Coral reef crisis in deep and shallow reefs: 30

360       years of constancy and change in reefs of Curaçao and Bonaire. *Coral Reefs*, 24: 475-479.

361  Benzoni F, Arrigoni R, Stefani F, and Stolarski J. 2012. Systematics of the coral genus

362       *Craterastrea* (Cnidaria, Anthozoa, Scleractinia) and description of a new family through

363       combined morphological and molecular analyses. *Systemetics and Biodiversity*, 10: 417-433.

364  Benzoni F, Stefani F, Pichon M, and Galli P. 2010. The name game: morpho-molecular species

365       boundaries in the genus *Psammocora* (Cnidaria, Scleractinia). *Zoological Journal of the*

366       *Linnean Society*, 160: 421-456.

367  Bird CE, Holland BS, Bowen BW, and Toonen RJ. 2011. Diversification of sympatric

368       broadcast-spawning limpets (*Cellana* spp.) within the Hawaiian archipelago. *Molecular*

369       *Ecology*, 20: 2128-2141.

370  Bongaerts P, Ridgway T, Sampayo EM, and Hoegh-Guldberg O. 2010a. Assessing the 'deep reef

371       refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs*, 29: 309-327.

372  Bongaerts P, Riginos C, Ridgway T, Sampayo EM, van Oppen MJ, Englebert N, Vermeulen F,

373       and Hoegh-Guldberg O. 2010b. Genetic divergence across habitats in the widespread coral

374       *Seriatopora hystrix* and its associated *Symbiodinium*. *PloS one*, 5: e10871.

375  Bridge TCL, Fabricius KE, Bongaerts P, Wallace CC, Muir PR, Done TJ, and Webster JM. 2012.

376       Diversity of Scleractinia and Octocorallia in the mesophotic zone of the Great Barrier Reef,

377       Australia. *Coral Reefs*, 31: 179-189.

378  Budd AF, Romano SL, Smith ND, and Barbeitos MS. 2010. Rethinking the phylogeny of

379       scleractinian corals: a review of morphological and molecular data. *Integrative and*

380       *Comparative Biology*, 50: 411-427.

381   Budd AF, and Stolarski J. 2009. Searching for new morphological characters in the systematics of

382      scleractinian reef corals: comparison of septal teeth and granules between Atlantic and Pacific

383      Mussidae. *Acta Zoologica*, 90: 142-165.

384   Carlon DB, and Budd AF. 2002. Incipient speciation across a depth gradient in a scleractinian

385      coral? *Evolution*, 56: 2227-2242.

386   Chan YL, Pochon X, Fisher MA, Wagner D, Concepcion GT, Kahng SE, Toonen RJ, and Gates

387      RD. 2009. Generalist dinoflagellate endosymbionts and host genotype diversity detected from

388      mesophotic (67-100 m depths) coral *Leptoseris*. *BMC ecology*, 9: 21.

389   Cuif JP, Lecointre G, Perrin C, Tillier A, and Tillier S. 2003. Patterns of septal biomineralization

390      in Scleractinia compared with their 28S rRNA phylogeny: a dual approach for a new

391      taxonomic framework. *Zoologica Scripta*, 32: 459-473.

392   Dai CF, and Lin CH. 1992. Scleractinia of Taiwan. Part III. Family Agariciidae. *Acta

393      Oceanographica Taiwanica*, 28: 80-101.

394   Dana J. 1846. Zoophytes. *US Exploring expeditions during the years 1838-1842*, 7: 1-740.

395   Darriba D, Taboada GL, Doallo R, and Posada D. 2012. jModelTest 2: more models, new

396      heuristics and parallel computing. *Nature Methods*, 9: 772-772.

397   Dinesen ZD. 1980. A revision of the coral genus *Leptoseris* (Scleractinia: Fungiina: Agariciidae).

398      *Memoirs of the Queensland Museum*, 20: 181-235.

399   Flot J-F, and Tillier S. 2007. The mitochondrial genome of *Pocillopora* (Cnidaria: Scleractinia)

400      contains two variable regions: The putative D-loop and a novel ORF of unknown function.

401      *Gene*, 401: 80-87.

402   Forsman Z, Martinez JA, Maragos J, and Toonen RJ. 2010. Resurrection of *Porites hawaiiensis*

403      Vaughan, 1907; a Hawaiian coral obscured by small size, cryptic habitat, and confused

404      taxonomy. *Zootaxa*, 2624: 67-68.

405    Fricke HW, and Knauer B. 1986. Diversity and spatial pattern of coral communities in the Red

406        Sea upper twilight zone. *Oecologia*, 71: 29-37.

407    Fukami H, Budd AF, Paulay G, Solé-Cava A, Chen CA, Iwao K, and Knowlton N. 2004.

408        Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals.

409        *Nature*, 427: 832-835.

410    Fukami H, Chen CA, Budd AF, Collins A, Wallace C, Chuang YY, Chen C, Dai CF, Iwao K, and

411        Sheppard C. 2008. Mitochondrial and nuclear genes suggest that stony corals are

412        monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa,

413        Phylum Cnidaria). *PloS one*, 3: e3222.

414    Funk DJ, and Omland KE. 2003. Species-level paraphyly and polyphyly: frequency, causes, and

415        consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology,*

416        *Evolution, and Systematics*, 34: 397-423.

417    Gardiner J. 1905. Madreporaria. III Fungida. IV Turbinolidae. In: Gardiner JS, ed. *The fauna and*

418        *geography of the Maldive and Laccadive Archipelagoes: being an account of the work*

419        *carried on and of the collections made by an expedition during the years 1899 and 1900*.

420        Cambridge: Cambridge University Press, 933-956.

421    Gill GA, and Russo A. 1980. Recognition of pennular structures typical of Mesozoic corals in

422        *Discotrochus orbignyanus* from the Eocene of the Gulf States. *Journal of Paleontology*, 54:

423        1108-1112.

424    Gray J. 1847. An outline of an arrangement of stony corals. *The Annals and Magazine of Natural*

425        *History*, 19: 120-128.

426    Grigg R. 1988. Paleoceanography of coral reefs in the Hawaiian-Emperor Chain. *Science*, 240:

427        1737-1743.

428    Grigg RW. 1983. Community structure, succession and development of coral reefs in. *Marine*

429        *Ecological Progress Series*, 11: 1-14.

430    Guindon S, and Gascuel O. 2003. A simple, fast, and accurate algorithm to estimate large

431        phylogenies by maximum likelihood. *Systematic biology*, 52: 696-704.

432    Hall TA. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis

433        program for Windows 95/98/NT. *Nucleic Acids Symposium*, 41: 95-98.

434    Hellberg ME. 2006. No variation and low synonymous substitution rates in coral mtDNA despite

435        high nuclear variation. *BMC evolutionary biology*, 6: 24.

436    Hinderstein LM, Marr JCA, Martinez FA, Dowgiallo MJ, Puglise KA, Pyle RL, Zawada DG, and

437        Appeldoorn R. 2010. Theme section on "Mesophotic Coral Ecosystems: Characterization,

438        Ecology, and Management". *Coral Reefs*, 29: 247-251.

439    Huang D, Meier R, Todd PA, and Chou LM. 2009. More evidence for pervasive paraphyly in

440        scleractinian corals: systematic study of Southeast Asian Faviidae (Cnidaria; Scleractinia)

441        based on molecular and morphological data. *Molecular Phylogenetics and Evolution*, 50:

442        102-116.

443    Ingram T. 2011. Speciation along a depth gradient in a marine adaptive radiation. *Proceedings of*

444        *the Royal Society B*, 278: 613-618.

445    Kahng SE, Garcia-Sais JR, Spalding HL, Brokovich E, Wagner D, Weil E, Hinderstein L, and

446        Toonen RJ. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs*, 29:

447        255-275.

448    Kahng SE, Hochberg EJ, Apprill A, Wagner D, Luck DG, Perez D, and Bidigare RR. 2012.

449        Efficient light harvesting in deep-water zooxanthellate corals. *Marine Ecological Progress*

450        *Series*, 455: 65-77.

451   Kahng SE, and Kelley CD. 2007. Vertical zonation of megabenthic taxa on deep photosynthetic

452       reef (50-140 m) in the Au'au Channel, Hawaii. *Coral Reefs*, 26: 679-687.

453   Kahng SE, and Maragos JE. 2006. The deepest, zooxanthellate scleractinian corals in the world?

454       *Coral Reefs*, 25: 254-254.

455   Keshavmurthy S, Yang S-Y, Alamaru A, Chuang Y-Y, Pichon M, Obura D, Fontana S, De Palmas

456       S, Stefani F, and Benzoni F. 2013. DNA barcoding reveals the coral "laboratory-rat",

457       *Stylophora pistillata* encompasses multiple identities. *Scientific reports*, 3.

458   Kirk J. 1994. *Light and photosynthesis in aquatic ecosystems*. New York: Cambridge Univ Press.

459   Kitahara MV, Cairns SD, Stolarski J, Blair D, and Miller DJ. 2010. A comprehensive

460       phylogenetic analysis of the Scleractinia (Cnidaria, Anthozoa) based on mitochondrial CO1

461       sequence data. *PloS one*, 5: e11490.

462   Kitahara MV, Stolarski J, Cairns SD, Benzoni F, Stake JL, and Miller DJ. 2012. The first modern

463       solitary Agariciidae (Anthozoa, Scleractinia) revealed by molecular and microstructural

464       analysis. *Invertebrate Systematics*, 26: 303-315.

465   Lamarck J-B. 1801. *Système des animaux sans vertèbres*. Paris: Deterville.

466   Le Goff-Vitry MC, Rogers AD, and Baglow D. 2004. A deep-sea slant on the molecular

467       phylogeny of the Scleractinia. *Molecular Phylogenetics and Evolution*, 30: 167-177.

468   Maragos JE, and Jokiel PL. 1986. Reef corals of Johnston Atoll: one of the world's most isolated

469       reefs. *Coral Reefs*, 4: 141-150.

470   McGuire JA, Linkem CW, Koo MS, Hutchison DW, Lappin AK, Orange DI, Lemos-Espinal J,

471       Riddle BR, and Jaeger JR. 2007. Mitochondrial introgression and incomplete lineage sorting

472       through space and time: phylogenetics of crotaphytid lizards. *Evolution*, 61: 2879-2897.

473   Milne-Edwards H, and Haime J. 1849. Mémoire sur les polypiers appartenant à la famille des

474       oculinides, au groupe intermédiaire des Pseudoastréides et à la famille des Fongides.

475    *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences de Paris*, 29:

476    67-73.

477    Moore WS. 1995. Inferring phylogenies from mtDNA variation: mitochondrial-gene trees versus

478    nuclear-gene trees. *Evolution*, 49: 718-726.

479    Moseley HN. 1881. Report on certain hydroid, alcyonarian and madreporarian corals procured

480    during the voyage of H.M.S. Challenger, in the years 1873-1876. *Report on the scientific*

481    *results of the voyage of the HMS Challenger during the years 1873-76, Zoology 2*.

482    Pallas P. 1766. *Miscellanea zoologica*. Hague Comitum.

483    Pillai CG, and Scheer G. 1976. Report on the stony corals from the Maldive Archipelago.

484    *Zoologica*, 126: 1-83.

485    Pinzon JH, and LaJeunesse T. 2011. Species delimitation of common reef corals in the genus

486    *Pocillopora* using nucleotide sequence phylogenies, population genetics and symbiosis

487    ecology. *Molecular Ecology*, 20: 311-325.

488    Pinzón JH, Sampayo E, Cox E, Chauka LJ, Chen CA, Voolstra CR, and LaJeunesse TC. 2013.

489    Blind to morphology: genetics identifies several widespread ecologically common species

490    and few endemics among Indo-Pacific cauliflower corals (*Pocillopora*, Scleractinia). *Journal*

491    *of Biogeography*, 40: 1595-1608.

492    Puorto G, da Graça Salomão M, Theakston RDG, Thorpe RS, Warrell DA, and Wüster W. 2001.

493    Combining mitochondrial DNA sequences and morphological data to infer species

494    boundaries: phylogeography of lanceheaded pitvipers in the Brazilian Atlantic forest, and the

495    status of *Bothrops pradoi* (Squamata: Serpentes: Viperidae). *Journal of Evolutionary Biology*,

496    14: 527-538.

497   Quelch JJ. 1886. Report on the reef corals collected by the H.M.S. Challenger during the years

498      1873-76. *Report on the scientific results of the voyage of HMS Challenger during the years*

499      *1873-76, Zoology*.

500   Riegl B, and Piller WE. 2003. Possible refugia for reefs in times of environmental stress.

501      *International Journal of Earth Sciences*, 92: 520-531.

502   Romano SL, and Cairns SD. 2000. Molecular and phylogenetic hypotheses for the evolution of

503      scleractinian corals. *Bulletin of Marine Science*, 67: 1043-1068.

504   Romano SL, and Palumbi SR. 1996. Evolution of scleractinian corals inferred from molecular

505      systematics. *Science*, 271: 640-642.

506   Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L,

507      Suchard MA, and Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic

508      inference and model choice across a large model space. *Systematic biology*, 61: 539-542.

509   Rooney J, Donham E, Montgomery A, Spalding H, Parrish F, Boland R, Fenner D, Gove J, and

510      Vetter O. 2010. Mesophotic coral ecosystems in the Hawaiian Archipelago. *Coral Reefs*, 29:

511      361-367.

512   Rubinoff D, and Holland BS. 2005. Between two extremes: mitochondrial DNA is neither the

513      panacea nor the nemesis of phylogenetic and taxonomic inference. *Systematic biology*, 54:

514      952-961.

515   Schluter D. 2000. *The ecology of adaptive radiation*. New York: Oxford University Press.

516   Shearer T, and Coffroth M. 2008. DNA BARCODING: Barcoding corals: limited by interspecific

517      divergence, not intraspecific variation. *Molecular Ecology Resources*, 8: 247-255.

518   Shearer TL, Van Oppen MJH, Romano SL, and Wörheide G. 2002. Slow mitochondrial DNA

519      sequence evolution in the Anthozoa (Cnidaria). *Molecular Ecology*, 11: 2475-2487.

520   Stolarski J. 2003. Three-dimensional micro- and nanostructural characteristics of the scleractinian

521      coral skeleton: a biocalcification proxy. *Acta Palaeontologica Polonica*, 48: 497-530.

522   Tamura K, Peterson D, Peterson N, Stecher G, Nei M, and Kumar S. 2011. MEGA5: molecular

523      evolutionary genetics analysis using maximum likelihood, evolutionary distance, and

524      maximum parsimony methods. *Molecular Biology and Evolution*, 28: 2731-2739.

525   Todd PA. 2008. Morphological plasticity in scleractinian corals. *Biological Reviews*, 83: 315-337.

526   van Oppen MJH, Koolmes EM, and Veron J. 2001. The evolutionary history of the coral genus

527      *Acropora* (Scleractinia, Cnidaria) based on a mitochondrial and a nuclear marker:

528      reticulation, incomplete lineage sorting, or morphological convergence? *Molecular Biology

529      and Evolution*, 18: 1315-1329.

530   Vaughan TW. 1907. Recent Madreporaria of the Hawaiian Islands and Laysan. *United States

531      National Museum Bulletin*, 59: 1-427.

532   Vermeij M, and Bak R. 2003. Species-specific population structure of closely related coral

533      morphospecies along a depth gradient (5-60 M) over a Caribbean reef slope. *Bulletin of

534      Marine Science*, 73: 725-744.

535   Veron JEN. 2000. *Corals of the World*. Townsville: Australian Institute of Marine Science.

536   Veron JEN, and Pichon MM. 1980. *Scleractinia of Eastern Australia. Part III. Families

537      Agariciidae, Siderastreidae, Fungiidae, Oculinidae, Merulinidae, Mussidae, Pectiniidae,

538      Caryophylliidae, Dendrophylliidae*. Townsville, Queensland: Australian Institute of Marine

539      Science.

540   Verrill AE. 1901. Variations and nomenclature of Bermudian, West Indian, and Brazilian reef

541      corals: with notes on various Indo-Pacific corals. *Transactions of the Connecticut Academy of

542      Arts and Sciences*, 11: 631-668.

543    Wells JW. 1954. Recent corals of the Marshall Islands. *US Geological Survey Professional*

544         *Paper,* 260: 285-186.

545    Wells JW. 1956. Scleractinia. In *Treatise on Invertebrate Paleontology*, part F: Coelenterata. In:

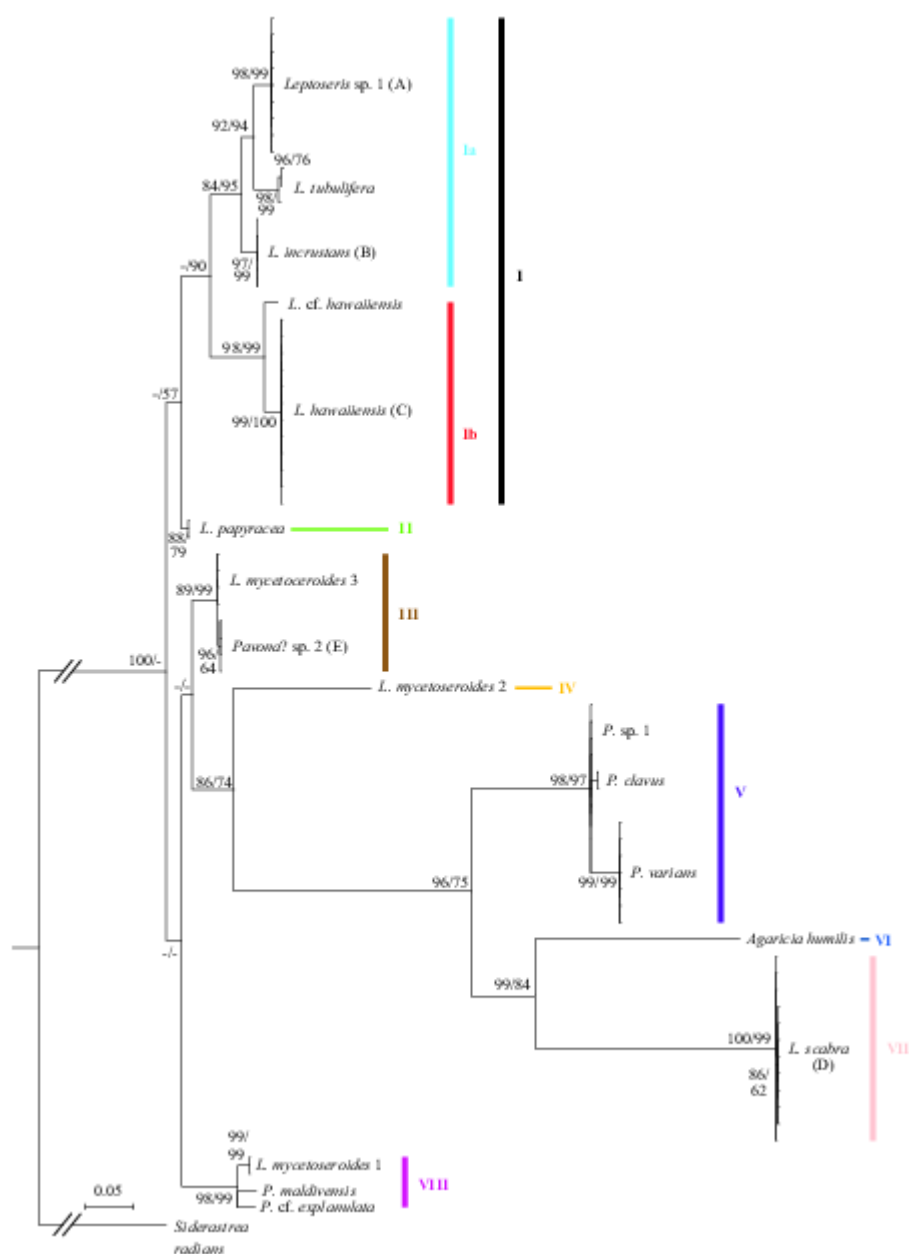
546         Moore RC, ed. Lawrence: University of Kansas Press, F328-F444

547    Wiens JJ, and Penkrot TA. 2002. Delimiting species using DNA and morphological variation and

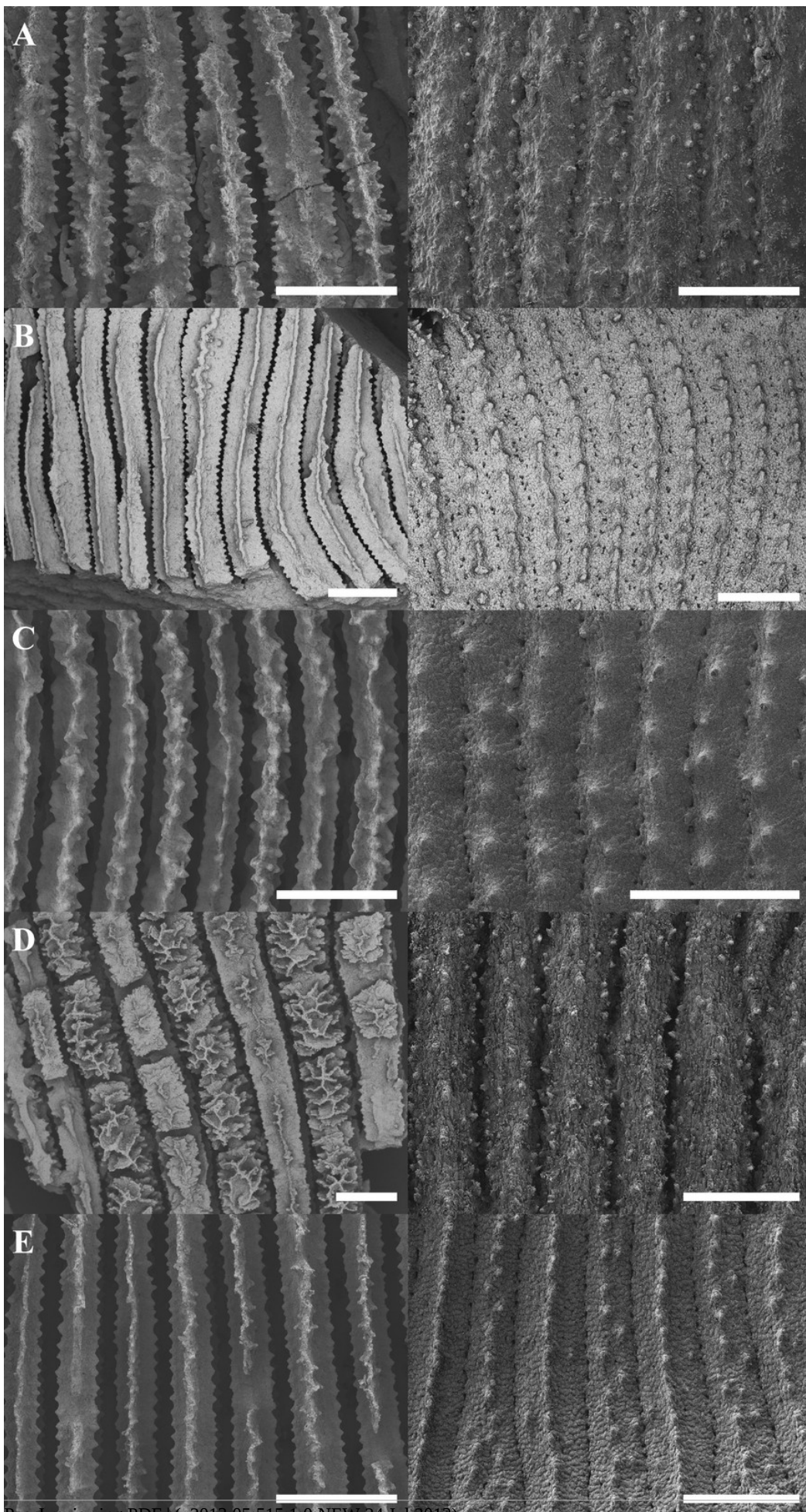
548    discordant species limits in spiny lizards (*Sceloporus*). *Systematic biology*, 51: 69-91.

# Figure 1

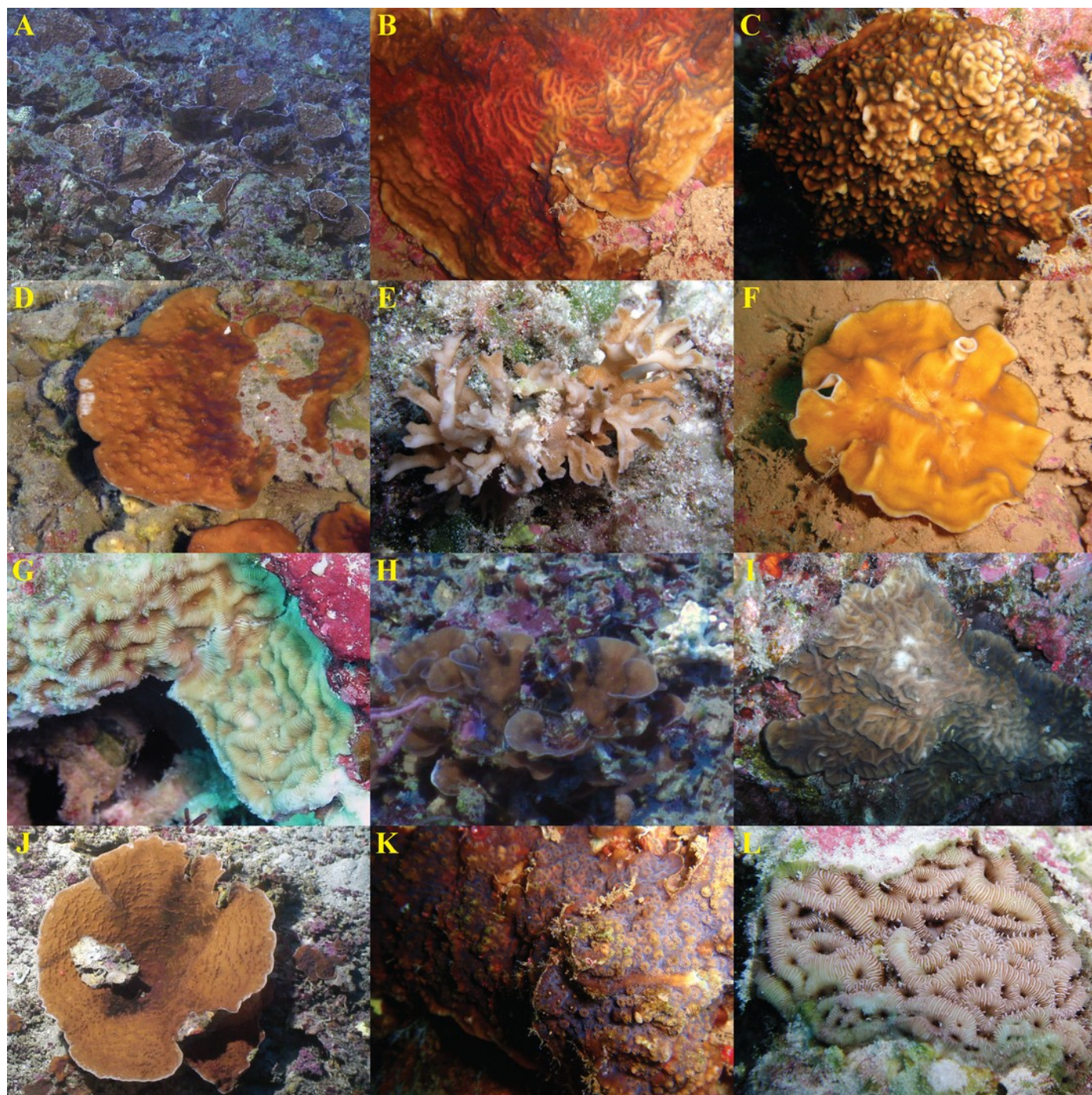
Bayesian phylogeny of Hawaiian *Leptoseris* and *Pavona* spp. using the mitochondrial *cox*1-1-rRNA intron.

Bayesian posterior probabilities (> 70%) followed by maximum likelihood (ML) bootstrap support (> 50%, ML tree not shown) are given at the nodes. Dashes (-) indicate statistically unsupported nodes. Roman numerals indicate clade numbers. Taxa with letters in parentheses have their micromorphologies pictured in Fig. 2.

# Figure 2

Scanning electron micrographs showing representative septocostal and costal micromorphologies for selected *Leptoseris* and *Pavona* spp.

The left-hand column gives a top-down view of the septocostae while the right-hand column shows the arrangement of the costal granulations and spines. The micrographs correspond to the taxa labeled in Fig. 1: (A) *Leptoseris* sp. 1; (B) *L. incrustans*; (C) *L. hawaiiensis*; (D) *L. scabra*; (E) *Pavona*? sp. 2. Scale bars are 500 µm.

# Figure 3

*In situ* images of *Leptoseris* and *Pavona* spp. from Hawaiʻi.

Species are presented in the order they appear (from top to bottom) in Fig. 1: (A) *Leptoseris* sp. 1; (B) *L. tubulifera*; (C) *L. incrustans*; (D) *L. hawaiiensis*; (E) *L. papyracea*; (F) *Pavona*? sp. 2; (G) *L. mycetoseroides* (haplotype III); (H) *P*. sp. 1; (I) *P. varians*; (J) *L. scabra*; (K) *P. maldivensis*; (L) *L. mycetoseroides* (haplotype I). Photo credits: D. Francke (B, F, K); Hawaiʻi Undersea Research Laboratory Archives, P.I. S.E. Kahng (A, D, H, J); R. Knapstein (I); J.E. Maragos (C,E,G,L).

# Figure 4

Depth distributions of major clades of the genera *Leptoseris* and *Pavona* in Hawaiʻi.

Clade coloring corresponds to that shown in Fig. 1.