

The Southwestern Indian Ocean as a potential marine evolutionary hotspot: perspectives from comparative phylogeography of reef brittle-stars

Hoareau Thierry B.^{1*}, Boissin Emilie^{2,3}, Paulay Gustav⁴, Bruggemann J.Henrich⁵

¹ African Coelacanth Ecosystem Programme, Department of Genetics, University of Pretoria, Pretoria, RSA

² Molecular Ecology and Evolution Programme, Department of Genetics, University of Pretoria, Pretoria, RSA

³ current address : USR3278-CRIOBE-CNRS-EPHE, Laboratoire d'excellence "CORAIL", Université de Perpignan-CBETM, 58 Rue Paul Alduy, 66860 Perpignan CEDEX, France

⁴ Florida Museum of Natural History, Gainesville, FL 32611-7800 USA

⁵ ECOMAR – FRE CNRS 3560, Université de La Réunion, CS 92003, 97744 Saint-Denis, La Réunion, France

* **corresponding author:** Thierry B. Hoareau, Department of Genetics, University of Pretoria, Private bag X20, Hatfield, 0028, Rep. South Africa; Fax: +27 12 362 53 27; E-mail: thoareau@gmail.com;

Running title: The SWIO, a peripheral reef evolutionary hotspot

Word count: Text: 6911; approximately 4 pages for Tables and Figures

ABSTRACT.

Aim The global biodiversity crisis requires identifying regions with high evolutionary potential, *i.e.* Evolutionary Hotspots (Evospots). We created an analytical framework based on comparative phylogeography and coalescent methods to assess the dynamics of diversification and population persistence in the reef ecosystem of a little studied region: the Southwestern Indian Ocean (SWIO).

Location Coral reefs of the SWIO, with comparative data from the Pacific Ocean.

Methods We generated sequences of mitochondrial DNA for 10 widespread brittle-stars (345 specimens) from 21 localities (8 in the SWIO). We analysed them by combining comparative phylogeography approaches, coalescent-based methods, molecular clock and the concept of Evolutionary Significant Units to draw conclusions about the drivers of biodiversity in the region.

Results Cryptic diversity was prevalent, increasing lineage diversity within the 10 nominal species by 70% within the SWIO and by 200% across the Indo-west Pacific. All seven new SWIO lineages meet the

criteria for evolutionary significant units (ESUs) and at least six are biological species. We detected likely intraregional diversifications dating to the Plio-Pleistocene, supporting the SWIO as a generator of biodiversity. Geographic restriction of ESUs, long coalescent times (>80 ka) and old (>1 Ma) *in situ* diversification point to persistence of populations over multiple glacio-eustatic cycles. We provide data suggesting demographic expansion during sea-level high stands. Regional connectivity was lower, and cryptic differentiation higher in lecithotrophs than planktotrophs.

Main conclusions The analytical framework based on a biodiversity survey makes it possible to identify Evospots by assessing the potential of a region to maintain and generate biodiversity and evaluating the evolutionary processes and potential drivers at play.

Key words: Barcoding, connectivity, conservation biogeography, coral reef biodiversity, demographic expansion, evospots, Ophiuroidea, palaeoclimates, refuges, speciation.

INTRODUCTION

Coral reefs harbour a large fraction of marine biodiversity and represent an invaluable ecosystem for tropical coastal communities (Moberg & Folke, 1999), but are facing major global and local threats (Riegl *et al.*, 2009). Given financial limitations it is important to focus conservation efforts on key areas that ensure the long term persistence of the greatest fraction of global biodiversity. “Biodiversity Hotspots” were originally defined in terrestrial ecosystems as areas of high diversity and endemism facing high levels of threats (Myers, 1988), but have also been used to denote areas of high species richness (Reid, 1998). Using the diversity patterns and level of threats of thousands of reef fishes and invertebrates, Roberts *et al.* (2002) similarly identified several marine Biodiversity Hotspots within the Indo-west Pacific (IWP), some at the periphery of the region. Because peripheral zones are usually understudied and tend to be both areas of endemism and engines of diversification (Malay & Paulay, 2010), there is a clear need to further evaluate their role as sources and reservoirs of biodiversity (Bellwood & Meyer, 2009).

For long-term persistence of biodiversity, it is important to also identify areas holding key ecological and evolutionary processes in addition to diversity (Moritz, 2002; Briggs, 2005). Vandergast *et al.* (2008) proposed “Evolutionary Hotspots” (herein referred to as Evospots) for areas where multiple taxa show

high genetic divergence and diversity, reflecting high evolutionary potential. In this context, the impact of profound environmental changes during the Pleistocene, that caused extinctions, distributional and demographic change (Hewitt, 2000) is especially important to evaluate. To assess the recent evolutionary history of taxa and potential Evospots, it is necessary to develop an analytical framework combining coalescence and evolutionary significant units (ESUs) across co-occurring species with contrasting life history traits.

Such a framework enables assessing how a region generates and maintains biodiversity. First, it allows for identifying time periods, locations and biological traits involved in intraregional diversification. Second, it permits assessing whether the region can maintain biodiversity, by revealing the long-term persistence of populations and the presence of regional refuges. Regional survival of species through several glacial periods can be identified using the coalescent to retrace demographic histories in the light of palaeoclimates (Provan & Bennett, 2008). This approach more clearly demonstrates maintenance of biodiversity than the commonly used measure of intraspecific genetic diversity (e.g. Vandergast *et al.*, 2008). Furthermore, it is important to assess the connectivity among populations, since high levels suggest resilience at the metapopulation scale (Botsford *et al.*, 2009).

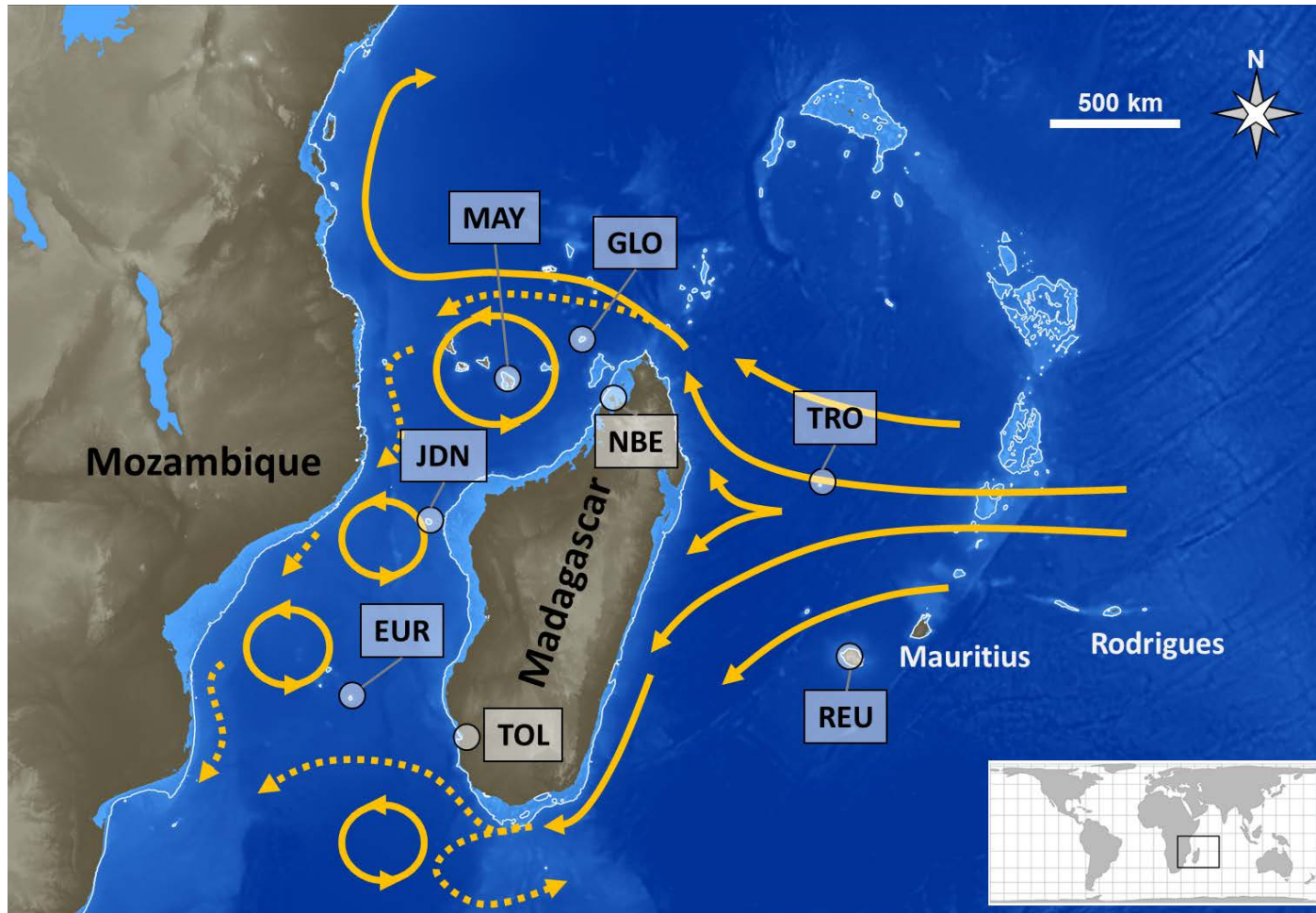
In this pilot study, we test the utility and limitations of our framework to identify Evospots for brittle-stars (Echinodermata: Ophiuroidea) in the Southwestern Indian Ocean (SWIO), a relatively little studied area (Wafar *et al.*, 2011). Using this framework, we evaluate diversification, survival of lineages, and connectivity of populations.

MATERIALS AND METHODS

Sampling and DNA sequencing

We utilised collections from a large-scale biodiversity survey, selecting 10 locally common, widespread, reef-associated brittle-star species with contrasting dispersal abilities. Specimens were collected with scuba and snorkelling in shallow reefs at La Reunion Island (REU), Tromelin Island (TRO), Mayotte Island (MAY), Glorieuse Island (GLO), Europa Island (EUR), Juan De Nova (JDN), and two areas in Madagascar: Nosy-Be Island (NBE) and Toliara (TOL) (Fig. 1). All specimens were identified to the species (Clark & Rowe, 1971; Cherbonnier & Guille, 1978; Boissin *et al.*, in revision), or subspecies level (*O. cincta cincta* Müller & Troschel, 1842 and *O. c. garretti* Sloan, 1979) using the appropriate nomenclature (Stöhr &

Figure 1. Sampling locations and sample sizes in the SWIO. Oceanic circulation shown schematically after Schott & McCreary (2001); the -120 m isobaths, representing late Pleistocene glacial low stand, is marked by the white line. EUR, Europa Island (n=5); GLO, Glorieuse Island (n=17); JDN, Juan De Nova (n=4); MAY, Mayotte Island (n=21); NBE, Nosy-Be Island (n=59); REU, Reunion Island (n=150); TOL, Toliara (n=49); TRO, Tromelin Island (n=3).



O'Hara, 2013). Species represented by >10 specimens from ≥ 2 SWIO locations are included. Additional samples from outside the SWIO were included when available in the Florida Museum of Natural History (University of Florida) collection. We analysed 345 specimens of 10 nominal species from four families (see Appendix S1, S2 in Supporting Information), including a new species of *Ophiocoma* (Boissin *et al.*, in revision; Stöhr *et al.*, in prep).

Total genomic DNA was extracted from a piece of arm following the DNeasy kit protocol (Qiagen, Hilden, Germany). Genetic diversity was assessed using cytochrome c oxidase subunit I (COI), because this marker is effective for assessing species limits (Ward *et al.*, 2008; Hoareau & Boissin, 2010) and phylogeographic patterns in echinoderms (Boissin *et al.*, 2011; Vogler *et al.*, 2012). We amplified a 655 bp portion of the 5' region of this gene using echinoderm-specific hybrid primers (Hoareau & Boissin, 2010). For a subset of samples, we amplified 500 bp of the 16S ribosomal gene using universal primers (Palumbi, 1996), to check for potential artefacts linked to co-amplification of nuclear pseudogenes of COI. PCR conditions and cycling parameters were as described in these studies. PCR products were sequenced using BigDyeTerminator (Applied Biosystems, Foster City, California, USA) cycle sequencing reactions, and an ABI-3730-XL for electrophoresis at the Interdisciplinary Center for Biotechnology Research (University of Florida). Sequences were aligned using MAFFT v6 online (<http://mafft.cbrc.jp/alignment/server/>) and the FFT-NS-i setting (Slow; iterative refinement method), a gap-opening penalty of 1.53, and the default substitution matrix BLOSUM62. Sequences are available in GenBank (KC759737- KC760145, see Appendix S1).

Evolutionary significant units and phylogenetic species concept

Our assessment of diversity pattern focuses on genetically distinct ESUs (Waples, 1991) that satisfy the phylogenetic species concept (Nixon & Wheeler, 1990). We will consider two populations as distinct ESUs if they are 1) reciprocally monophyletic at COI, and 2) further distinguished by colour pattern, distribution range and/or morphology. Furthermore, when genetically distinct groups co-exist in sympatry, reproductive barriers between them are required and they can be considered distinct biological species (Coyne & Orr, 2004). Consequently, when ESUs occur sympatrically and have the potential for encounters and interbreeding, the lack of gene flow indicated by covarying independent characters implies that they meet the criteria for the biological species concept.

Larval developmental modes and dispersal potential

Most brittle-stars have pelagic larvae. Planktotrophic larvae are pelagic feeders, typically take weeks to develop, and are usually capable of substantially delaying settlement and metamorphosis. In contrast lecithotrophic larvae do not feed, often complete development within days in tropical waters, and their capacity to delay settlement may be limited by energy reserves (Emler, 1990). These life history traits may correlate with dispersal capacity (Young *et al.*, 1997; Richards *et al.*, 2007). Larval development has been documented for four of the species studied: *Ophiarachnella gorgonia* (Müller & Troschel, 1842) and *Ophiolepis cincta* are lecithotrophic and can settle after a few days (Mortensen, 1938; Cisternas & Byrne, 2005), while *Ophiocoma erinaceus* Müller & Troschel, 1842 and *O. scolopendrina* (Lamarck, 1816) are planktotrophic (Mortensen, 1938), and some *Ophiocoma* can stay in the plankton for up to three months (Mladenov, 1985). Because there is substantial phylogenetic constraint on the mode of development at the genus level (Selvakumaraswamy & Byrne, 2004), it is likely that *Ophiocoma brevipes* Peters, 1851, *O. nov. sp.* and *O. cynthiae* Benavides-Serrato & O'Hara, 2008 are planktotrophic (Mortensen, 1938), while *Ophioplocus imbricatus* (Müller & Troschel, 1842) (Hendler, 1975; Komatsu & Shosaku, 1993), *Ophionereis porrecta* Lyman, 1860 (Selvakumaraswamy & Byrne, 2004) and *Ophiopeza fallax* Lütken, 1869 (Byrne *et al.*, 2008) are lecithotrophic.

Genetic diversity and phylogenetic analyses

For each nominal species and lineage, we estimated number of haplotypes (H), haplotype diversity (Hd) and nucleotide diversity (π) and two estimates of the mutational parameter θ that are proxies for effective population size ($\theta=2N_e\mu$; N_e : effective population size; μ : mutation rate): Watterson's θ_s and Tajima's θ_π , using ARLEQUIN v3.1 (Excoffier *et al.*, 2005). Relationships were assessed with a neighbor-joining (NJ) tree using the program MEGA v5.01 (Tamura *et al.*, 2011) with 1,000 permutations and applying the K2P model (no difference observed with the best fitting model: TN93). K2P patristic distances were calculated between and within lineages.

Time to the most recent common ancestor (T_{mrca})

We estimated T_{mrca} for groups of haplotypes using the program BEAST v.1.6.1 (Drummond & Rambaut, 2007). For each nominal species, we identified the best model of evolution using MEGA v5: HKY (*O. brevipes*, *O. cynthiae*, *O. erinaceus*, *O. fallax*, *O. porrecta*) and TN93 (*O. nov. sp.*, *O. scolopendrina*, *O.*

imbricatus, *O. gorgonia*). Each run started with a randomly generated tree and several priors were tested using a Bayes-factor approach available in BEAST: two tree priors (constant growth, exponential growth) and four molecular clock models (strict clock, relaxed uncorrelated lognormal and exponential clocks, and random local clock). As no molecular clocks have been calibrated for ophiuroids, we applied a COI-based echinoid clock of 3.7% Ma⁻¹ (HPD95: 2.9 – 4.5% Ma⁻¹) based on divergence across the Isthmus of Panama (Lessios, 2008). Chain lengths were varied between 20 – 1000 million among species to ensure good chain mixing (effective sample size or ESS>200). A total of 10,000 phylogenetic trees and parameters were recovered after discarding the first 25% as burn-in. Three replicates were completed for each lineage, combined, and re-sampled using the program LOGCOMBINER v1.6.1. Then, the program TRACER v1.5 provided the highest posterior density region at 95% (HPD95) as confidence interval for T_{mrca}.

Tests for demographic changes

We used three parameters to test for departure from a constant population size and neutrality: Tajima's D, Fu's Fs and Ramos-Onsins & Rozas' R2. These parameters were estimated and compared to a null distribution obtained from coalescent simulations using the program DNASP v5.10 (Librado & Rozas, 2009). Significant negative Tajima's D, large negative Fs and small positive R2 indicate demographic expansion. Demographic expansion was also assessed using observed and expected (under sudden expansion model) mismatch distributions available in ARLEQUIN. Demographic expansion and stability would produce unimodal and multimodal distributions respectively. For taxa that fit the model of demographic expansion, we estimated time since expansion using the approximate intra-population coalescent time τ ($\tau=2\mu T_{\text{exp}}$; μ = mutation rate per year per locus; T_{exp} = start of expansion) in ARLEQUIN. We used BEAST to reconstruct changes in N_e by generating Bayesian Skyline Plots (BSPs; Drummond *et al.*, 2005). The program generates a posterior probability distribution for N_e backward in time from the distribution of coalescence events in gene genealogies using Markov Chain Monte Carlo (MCMC) samplings. We used the same substitution models, clock models, divergence rates, and sampling scheme as for T_{mrca}. We set the number of groups to 10 and ensured that all the ESSs were above 200. We then used TRACER v1.6.1 to generate the evolution of $N_e T$ (with T = generation time) over time together with confidence intervals. Association between demographic evolution and environmental change were illustrated by overlying changes in N_e with sea-levels (Waelbroeck *et al.*, 2002) and Marine Isotopic Stages (MIS, cool and warm periods deduced from oxygen isotope data; Lisiecki & Raymo, 2005).

Tests for spatial genetic variation

The AMOVA framework was used to search for overall (overall Φ_{st}) and between localities (pairwise Φ_{st}) spatial differentiation excluding small sample sizes ($N < 5$). Location effects were tested by comparison of pairwise Φ_{st} obtained by including/excluding major locations (GLO, MAY, NBE, REU, TOL) using Mann-Whitney U -tests (STATEXT v1.4.2, <http://www.statext.com/>). Effect of dispersal capacity on connectivity was tested (Mann-Whitney U test) by comparing frequency distributions of pairwise Φ_{st} values of species with presumed lecithotrophic versus species with presumed planktotrophic development.

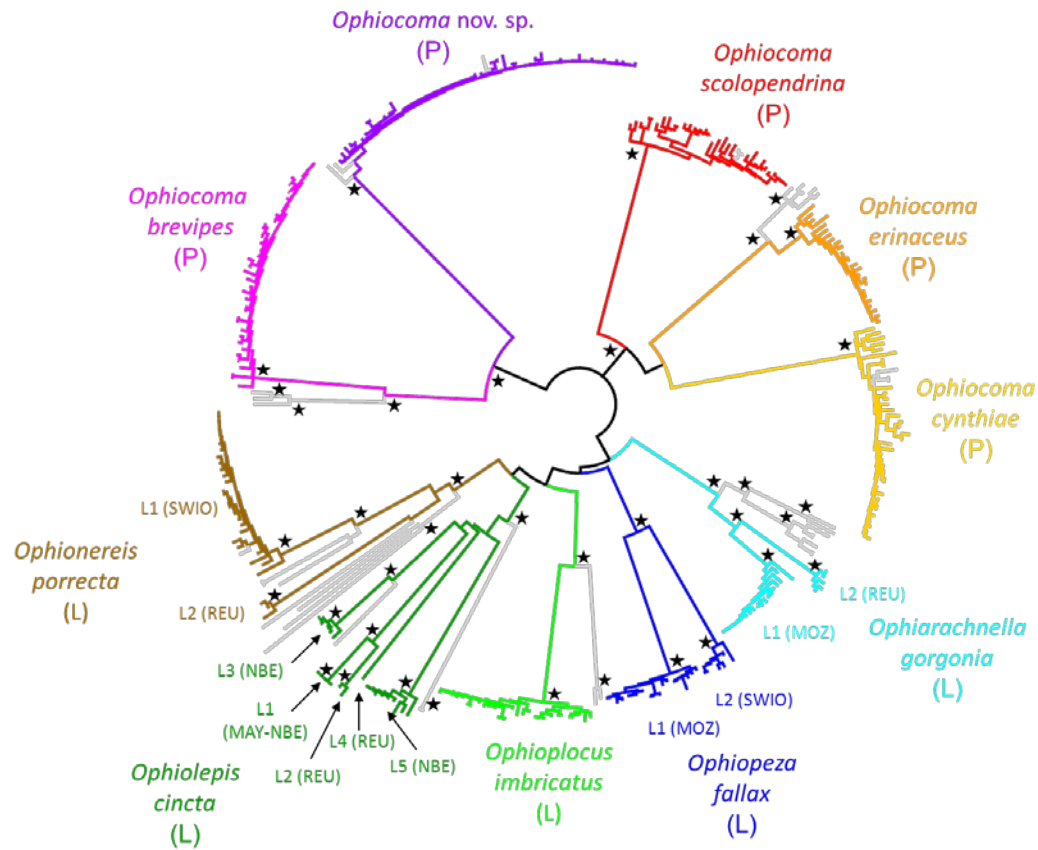
Phylogeny-trait correlations (PTC) were used as a complementary method to test for association between locality (spatial character) and genetic variation (phylogeny) using the program BATS v2.0 (Parker *et al.*, 2008). The method is based on a Bayesian Markov Chain Monte Carlo approach and accounts for uncertainty arising from phylogenetic errors. It thus provides a statistical framework to test the null hypothesis that localities are randomly associated at the tips of the phylogeny. First, the parsimony score statistic (PS) represents the most parsimonious number of character changes in the phylogeny. The PS of the phylogeny is compared against the null distribution of PS obtained from the randomised tip-character associations on the tree (significantly lower PS values indicate phylogeny-trait association). Second, the association index statistic (AI) compares the distribution of characters for all internal nodes of the phylogeny against random distributions. Finally, the monophyletic clade statistic (MC) quantifies the association between the phylogeny and a specific character (one locality). A specific locality strongly associated with the phylogeny will display larger monophyletic clades than expected under random association. For each lineage, we used 10,000 BEAST-generated phylogenetic trees as input and tested each parameter by generating a null distribution from 1000 replicates. These approaches allowed us to test (1) for a restriction of gene flow between the localities (AI and PS statistics) and (2) whether all the localities respond equally to spatial genetic variation (MC statistic).

RESULTS

Evidence for cryptic species

Of the 10 nominal species four included eleven deeply-divergent lineages in the SWIO (Fig. 2 and 3; see Appendix S2): five in *O. cincta*, two each in *O. gorgonia*, *O. fallax*, and *O. porrecta*. Several criteria show that all these genetic lineages are phylogenetically distinct (Fig. 3): 1) reciprocal monophyly with COI

Figure 2. Neighbour-joining phylogenetic reconstruction (K2P distances) for 345 specimens based on COI. MAY, Mayotte Island; MOZ, Mozambique Channel; NBE, Nosy-Be Island; REU, Reunion Island; SWIO, Southwestern Indian Ocean. Larval developmental modes are indicated for each nominal species (L: lecithotrophic larvae; P: planktotrophic larvae); light grey colour indicates samples and lineages from outside the SWIO; stars indicate a support value of 100%.



(concordance of 16S); 2) mean 14.3% K2P divergences (Table 1a), thus in the range observed among echinoderm species (Ward *et al.*, 2008; Hoareau & Boissin, 2010), representing an estimated divergence time of 1.6-3.8 Ma (Table 1a); 3) each lineage is strongly supported (100% bootstrap), with COI sequence variation <1.6% K2P (Table 1b), thus in the range observed within echinoderm species (Ward *et al.*, 2008; Hoareau & Boissin, 2010), representing estimated ages of 0.06-0.53 Ma (Table 1b); 4) The differences in genetic diversity between and within lineages suggest a clear barcoding gap (Meyer & Paulay, 2005).

Each also is distinguishable by colour pattern. In *O. cincta*, L1 (lineage 1) and L2 correspond to *O. cincta cincta* but have distinct colouration: L1 is pale brown with scattered white patches on the disc, while L2 is bright red-brown with one conspicuous central white patch (Fig. 3). The colour pattern of the single L3 specimen was not documented. L4 and L5 concur with *O. cincta garretti* but have distinct colouration: L4 is mottled dark grey, while L5 is uniformly dark brown (Fig. 3a). In *O. gorgonia*, L2 is conspicuously dark grey with paler, banded arms, while L1 is white and green with red patches, as typical for the nominal species elsewhere (Fig. 3b). In *O. fallax*, L1 is yellow and brown with dark banded arms, while L2 has a disc with pink and dark patches and a conspicuous, red, proximal dorsal arm plate (Fig. 3c). In *O. porrecta*, L1 presents the usual colouration of the species, light beige with brown irregular markings on the disc and brown arms, while L2 is white with bright orange patches both on disc and arms (Fig. 3d). Several lineages within nominal species co-occurred sympatrically (Fig. 3). Allopatric distributions occurred in two lineages of *O. gorgonia* (Fig. 3b), sister lineages L1 vs. L2 of *O. cincta*, and lineage L4 vs. lineages L1, L3, L5 of *O. cincta* (Fig. 3a). Four lineages (*O. gorgonia* L2, *O. cincta* L2 and L4, and *O. porrecta* L2) were encountered only on Reunion.

When specimens from outside the SWIO are included for the 10 nominal species, 30 distinct lineages are recovered based on the above criteria (Fig. 2). Most of these lineages are found within the four species complexes that show cryptic diversification within the SWIO (N=21), only three are in species that are monomorphic in the SWIO (*O. brevipes*, *O. erinaceus*, *O. imbricatus*). Only one lineage (*O. porrecta* L1) among 11 in the four species complexes was encountered among the samples taken outside the SWIO. Three species remain phylogenetically homogeneous even with the inclusion of Pacific samples (*O. nov. sp.*, *O. scolopendrina*, *O. cynthiae*).

Figure 3. Colour morphs, distribution, and phylogenetic considerations for assessment of ESUs in the four nominal species of brittle-stars with multiple lineages in the

SWIO. No photo of live specimen for L3 was available.

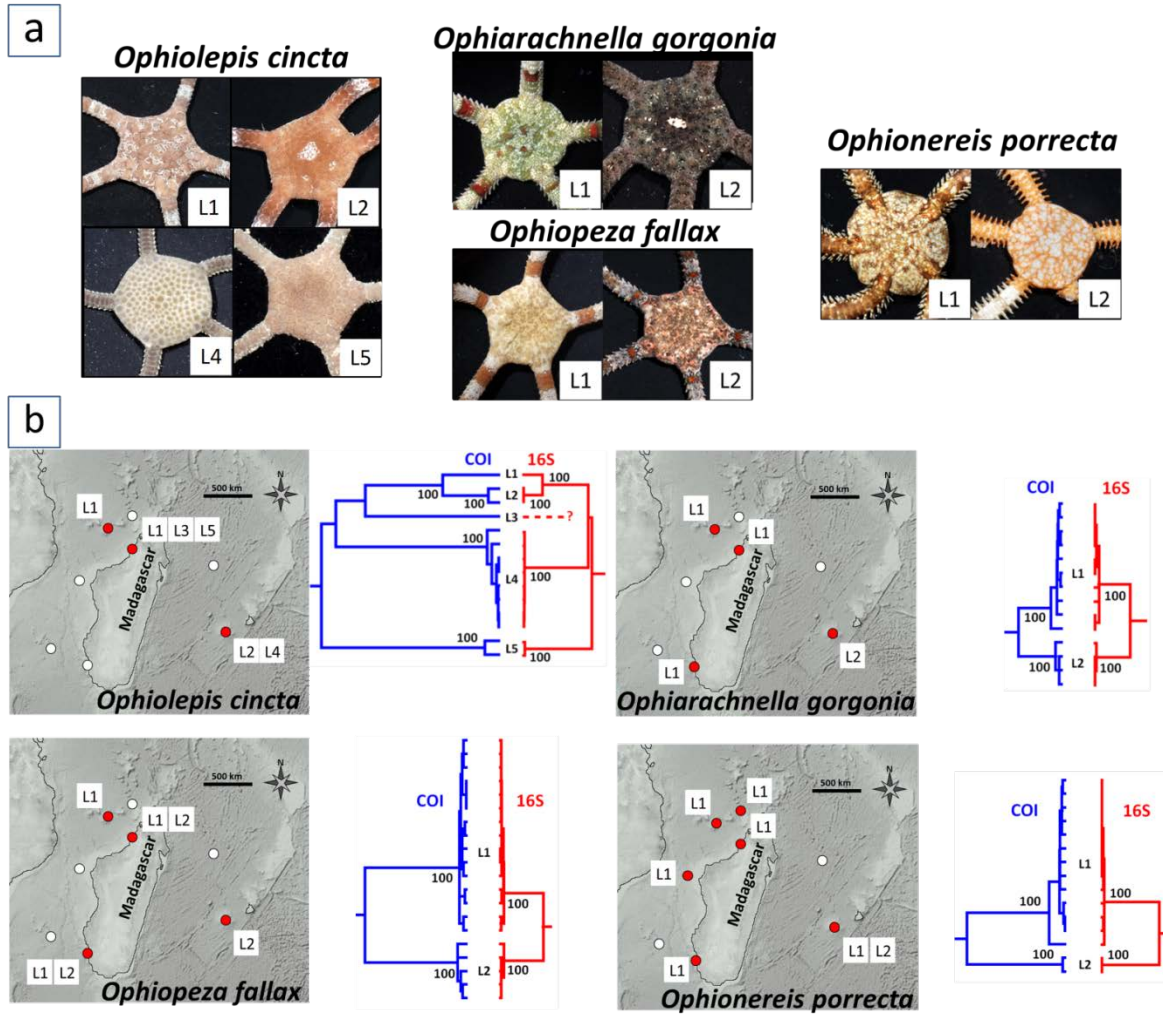


Figure 4. Evolution of female effective population sizes (NeT) reconstructed from the Bayesian skyline plot method over the past 0.42 Ma and sea-level variations over the last 11 MISs (data from Waelbroeck *et al.*, 2002) for the eight species/ESUs displaying departure from mutation-drift equilibrium (Appendix S2): *Ophiocoma brevipes*, n=42; *Ophiocoma* nov. sp., n=55; *Ophiocoma cynthiae*, n=39; *Ophiocoma erinaceus*, n=30; *Ophiocoma scolopendrina*, n=33; *Ophioplocus imbricatus*, n=30; *Ophiarachnella gorgonia*, n=19; *Ophiopeza fallax*, n=19. Upper and lower yellow lines on the skyline plot represent the limits of 95% highest posterior density intervals; the MIS corresponding to sea-level low stands are shaded.

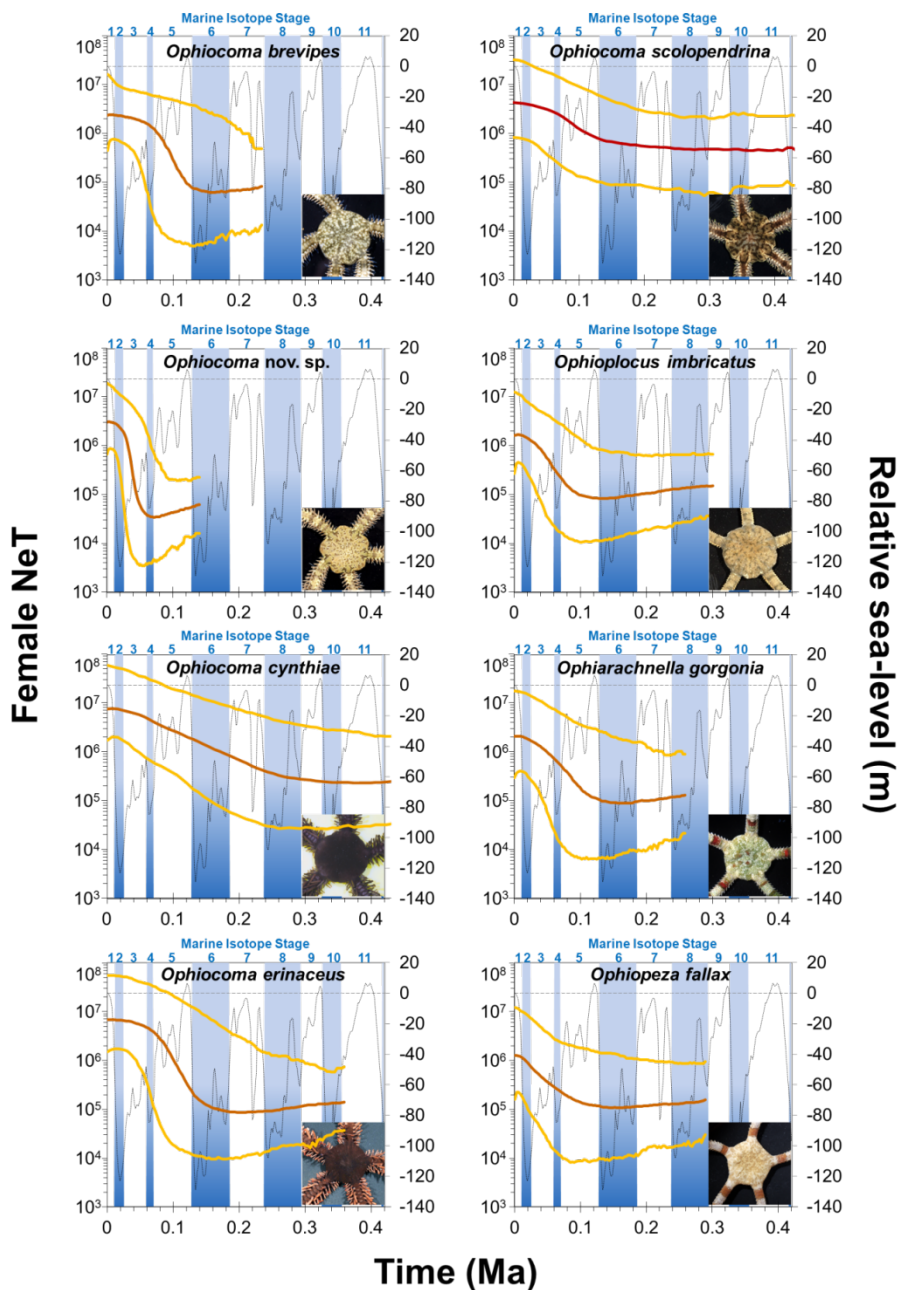
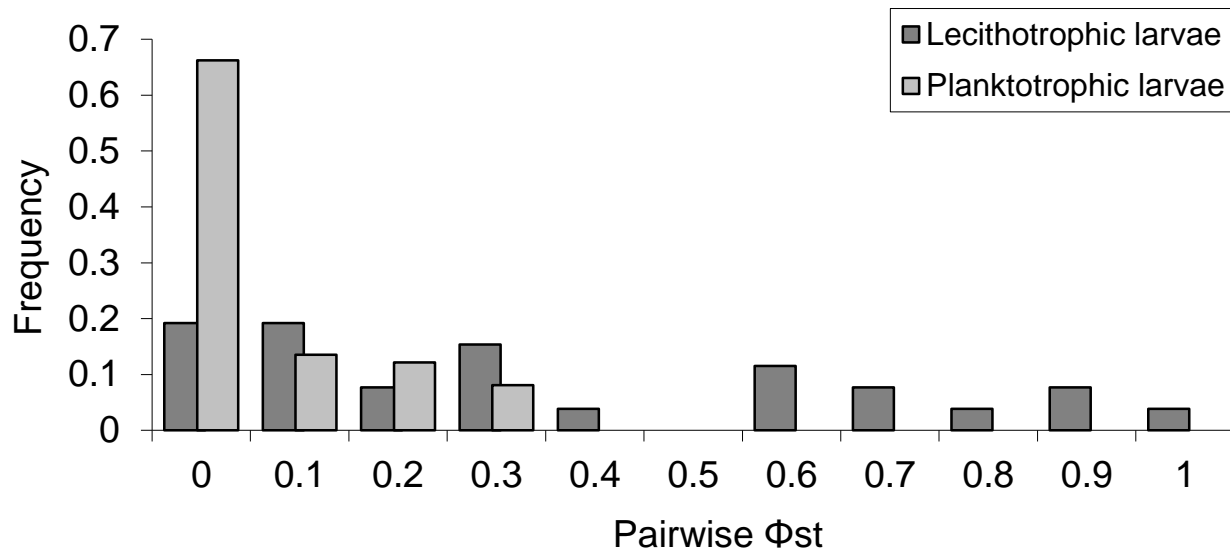


Figure 5. Comparison of the frequency-distribution of the pairwise Φ_{st} values between populations in lecithotrophic and planktotrophic species, excluding small sample sizes ($n < 5$); the two distributions are significantly different (Mann-Whitney U -test, $P < 0.001$).



The correlation of two independent characters (mtDNA and colour) that define these lineages implies lack of gene flow, thus all lineages meet the criteria of ESUs or phylogenetic species. Below, all analyses treat these lineages as distinct ESUs.

Demographic changes

The neutrality tests suggest demographic expansion in eight of 17 SWIO ESUs (see Appendix S2): *O. brevipes*, *O. nov. sp.*, *O. cynthiae*, *O. erinaceus*, *O. scolopendrina*, *O. imbricatus*, *O. gorgonia* L1 and *O. fallax* L1. In other ESUs, the lack of significance in the neutrality tests may be related to small sample size (see Appendix S2). No difference was detected (sum of squared deviation and the Harpending raggedness index; $P > 0.05$) between the observed mismatch distributions and the model of sudden expansion for these eight ESUs (see Appendix S3). The estimated mean times of expansion of six ESUs were between 80 and 110 ka (Table 1c), the expansion time of *O. nov. sp.* was younger (58 ka), while that of *O. scolopendrina* older (238 ka). These expansion dates coincided with MIS 3, 5 and 7. BSP results further confirmed demographic expansion in these eight ESUs, and indicated an onset consistently >100 ka (Fig. 4), except for *O. nov. sp.* which displayed a more recent expansion.

Spatial distribution of diversity

Nine ESUs were present in at least two localities and provided sufficient sample sizes for AMOVA analyses: *O. brevipes*, *O. cynthiae*, *O. erinaceus*, *O. scolopendrina*, *O. imbricatus*, *O. gorgonia* L1, *O. fallax* L1 and L2, and *O. porrecta* L1. AMOVA identified significant spatial genetic subdivision in four (44%): *O. cynthiae*, *O. scolopendrina*, *O. imbricatus* and *O. fallax* L2, with Φ_{st} between 0.11 – 0.31 (Table 2). Considering the PTC results obtained from all three parameters (PS, AI, MC), a significant geographic structure was found in eight of these nine (89%). The MC-statistic further identified TOL as the location most commonly influencing genetic structure, as did tests including/excluding different locations (see Appendix S2). Lecithotrophs had higher Φ_{st} (0.35 ± 0.33) than planktotrophs (0.10 ± 0.12 ; $U = 309$, $P < 0.001$; Fig. 5).

DISCUSSION

High cryptic diversity in reef brittle-stars

Even with the limited sampling employed, the diversity of ESU increased by 70% within the SWIO and by 200% across the IWP with genetic scrutiny, supporting evidence that brittle-star diversity is substantially underestimated (Boissin *et al.*, 2008a, 2011; Hoareau & Boissin, 2010). Given the high species richness of IWP brittle-stars (Stöhr *et al.*, 2012), a large fraction of this diversity has yet to be discovered.

The seven novel lineages in the SWIO satisfy the criteria for ESUs (Waples, 1991; Meyer & Paulay, 2005; Malay & Paulay, 2010; O’Loughlin *et al.*, 2011), because they could be distinguished by several independent characters (mtDNA, colour pattern, and distribution range; Fig. 3). The limited samples obtained from outside the SWIO represent lineages that are similarly deeply divergent (mostly >10%; Fig. 2) and thus likely represent distinct ESUs. Seven of the 10 SWIO ESUs occur sympatrically (Fig. 3), suggesting that despite their co-occurrence they are unable to interbreed and they can be considered to represent full, biological species (cf. method section on ESUs). These ESUs, including the sympatric “subspecies” *O. cincta cincta* and *O. cincta garretti* should be elevated to the rank of species.

Diversification within the SWIO

The multiple divergences observed offer an opportunity to investigate drivers of diversification. Geographic isolation has long been recognized as one of the main drivers of speciation (Mayr, 1954; Coyne and Orr 2004). However, identifying geographic speciation in oceans is challenging because of the lack of obvious physical barriers (but see Quenouille *et al.*, 2011), the dynamic nature of the environment (Norris & Hull, 2012), broad time range of speciation events (few to millions of generations; Jablonski, 2008; Reznick & Ricklefs, 2009) and difficulty of assessing extinctions (Quental & Marshall, 2010; Morlon *et al.*, 2011). Because these biases are exacerbated by passing time, recent speciation events provide the best evidence for the geographic setting of diversification (Lynch, 1989). As a result, young ESUs are useful models for understanding speciation in the sea.

We found six cases of reciprocal monophyly between Indian and Pacific Ocean populations (Fig. 2), suggesting that isolation is an important driver of diversification between the two basins. These results support previous studies showing the importance of this barrier in marine diversification (reviewed in Gaither *et al.*, 2010). Three pairs of sister ESUs – in each of *O. gorgonia*, *O. garretti* and the SWIO

endemic *O. fallax* (Stöhr, 2012) – are known only from the SWIO and show allopatric divergence, suggestive of *in situ* diversification.

The estimated mean divergence times between sister-ESUs within the SWIO ranged from 1.6 – 3.9 Ma (Table 1a). However, caution in interpretation is required as the accuracy of these dates might be affected by small sample sizes (significant underestimation; Heled & Drummond, 2010) and the use of non-specific molecular clocks (Ho *et al.*, 2008). The estimated dates are associated with the late Pliocene/early Pleistocene a period characterised by increasing intensity of glacio-eustatic cycles beginning ~3 million years ago (Pillans *et al.*, 1998). This process is well known to have affected marine diversification in both temperate (Hewitt, 2000) and tropical regions (Paulay, 1990; Barber *et al.*, 2006). Vicariance is excluded as sea-ways remained open in the SWIO even at the lowest sea-level stands (-130 m; Fig. 1), leaving founder speciation (long distance colonisation) and soft-vicariance (interruption of gene flow caused by oceanography) (Paulay & Meyer, 2002; Hickerson & Meyer, 2008) as likely drivers.

Different dispersal capacities lead to different levels of connectivity, which in turn should lead to contrasting diversification patterns. The overall differences in diversification between lecithotrophic and planktotrophic species observed in our data (Fig. 2) support this assumption. The three species phylogenetically homogeneous across the IWP are all planktotrophic. None of the five planktotrophic species have cryptic intra-SWIO lineages, but four of the five lecithotrophic species do. Moreover, all taxa showing allopatric diversification within the Indian basin are lecithotrophic.

Regional maintenance of diversity

Pleistocene sea-level fluctuations and associated environmental changes strongly affected marine populations, causing range fragmentation, contraction, expansion, or extinction (Paulay, 1990; Hewitt, 2000; Provan & Bennett, 2008). Marine regional communities are therefore composed of species that either survived *in situ* or colonized subsequently to these changes. The relative proportion of species in these two categories informs on the ability of a region to allow persistence of a community. Because the last glacial period (80 – 10 ka) broadly impacted the demography of organisms (Provan & Bennett, 2008), including those in the SWIO (Visram *et al.*, 2010; Hoareau *et al.*, 2012), persistence of regional marine biodiversity can be evaluated from the survival of ESUs older than 80 ka. The presence of genetically divergent populations across the IWP barrier in several species suggests limited inter-basin

migration (Fig. 2). Furthermore, the *in situ* divergence between the SWIO ESUs of *O. fallax*, *O. porrecta*, and *O. garretti* are older than 1 Ma (Table 1a). Finally, the ages of each SWIO-endemic ESUs (Table 1b) are older than several sea-level low stands (MIS 2 to 12), implying their local persistence. Here as well, caution in interpretation is required because accuracy of intraspecific evolutionary inferences is affected by small sample sizes ($N < 8$; Heled & Drummond, 2008); however these errors are modest compare to interspecific inferences (Heled & Drummond, 2010).

Environmental forcing of brittle-star demography

In spite of small sample sizes, all analyses are consistent with demographic expansions, and the expansion dates concur with periods of sea-level high stands (Table 1c; Fig. 4), although with a broad credibility interval. These results need to be interpreted cautiously, because of the use of a general, echinoid-based molecular clock, rate heterogeneity among lineages, small sample sizes, and the use of a single gene. Nonetheless, the association observed between demography and sea-levels fits expectations of the contraction-expansion model, identified in both temperate (Provan & Bennett, 2008; Marko *et al.*, 2010) and tropical taxa (Paulay, 1996; Crandall *et al.*, 2008; Hoareau *et al.*, 2012). During glacial regressions, large portions of continental shelf and coral reefs became emergent (Paulay, 1990; Voris, 2000), leading to a severe reduction of habitat area and diversity, even within the SWIO (Visram *et al.*, 2010). Population expansions of brittle-stars during interglacial periods are expected because of concomitant increases in shallow reef habitats. Improvements in accuracy and precision will help refine the time frame of these demographic expansions.

All species studied have pelagic larvae and experienced recent demographic expansions, two features supposed to reduce spatial genetic differentiation among marine populations (Paulay & Meyer, 2006; Kelly & Palumbi, 2010; McGovern *et al.*, 2010; Selkoe & Toonen, 2011). Yet, we found support for restricted connectivity in the SWIO, with 89% of the widespread ESUs displaying some level of spatial genetic differentiation (Table 2), and some ESUs encountered only in a subset of the surveyed areas. Toliara (TOL), southern Mozambique Channel, had the most divergent populations (Table 2, see Appendix S2). The result is consistent with a recent genetic study (Muths *et al.*, 2011) that

Table 1. Dating of demographic events in the SWIO brittle-stars applying a divergence rate of 2.9–4.5% Ma⁻¹. A) Dates of divergence (stem T_{mrca}) and K2P distances of lineages within species; B) Age (crown T_{mrca}) of each supported lineage and K2P distances; C) Time since demographic expansion (T_{exp} derived from τ) in species/ESUs displaying departure from mutation-drift equilibrium. Ni and Nii: sample size of the two haplogroups analysed; HPD95: highest posterior density interval at 95% (lower bound from 4.5% and higher bound from 2.9%); τ : approximate intra-population coalescent time; CI: confidence interval obtained from the lower bound from 4.5% and higher bound from 2.9%.

a						
Family	Nominal species	ESUs	Ni	Nii	K2P	Tmrca (HPD95) in Ma
Ophiolepididae	<i>Ophiolepis cincta</i>	ALL	21	-	0.1184 ± 0.0658	3.8906 (1.5425 - 7.1682)
Ophiolepididae	<i>Ophiolepis cincta</i>	L1 x L2	4	2	0.0475 ± 0.0035	2.4372 (0.9063 - 4.5901)
Ophiolepididae	<i>Ophiolepis cincta</i>	L1 x L3	4	1	0.1681 ± 0.0000	3.5585 (1.2667 - 6.6943)
Ophiolepididae	<i>Ophiolepis cincta</i>	L1 x L4	4	9	0.1638 ± 0.0034	3.7987 (1.3322 - 7.0021)
Ophiolepididae	<i>Ophiolepis cincta</i>	L1 x L5	4	5	0.1656 ± 0.0010	3.7022 (1.3396 - 6.9011)
Ophiolepididae	<i>Ophiolepis cincta</i>	L2 x L3	2	1	0.1437 ± 0.0041	3.5585 (1.2667 - 6.6943)
Ophiolepididae	<i>Ophiolepis cincta</i>	L2 x L4	2	9	0.1564 ± 0.0018	3.7987 (1.3322 - 7.0021)
Ophiolepididae	<i>Ophiolepis cincta</i>	L2 x L5	2	5	0.1574 ± 0.0031	3.7022 (1.3396 - 6.9011)
Ophiolepididae	<i>Ophiolepis cincta</i>	L3 x L4	1	9	0.1585 ± 0.0027	3.3591 (1.2223 - 6.3612)
Ophiolepididae	<i>Ophiolepis cincta</i>	L3 x L5	1	5	0.1681 ± 0.0024	3.8397 (1.4417 - 7.1378)
Ophiolepididae	<i>Ophiolepis cincta</i>	L4 x L5	9	5	0.1582 ± 0.0019	3.7590 (1.3452 - 7.0418)
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1 x L2	19	5	0.0729 ± 0.0027	1.5990 (0.5238 - 3.0518)
Ophiodermatidae	<i>Ophiopeza fallax</i>	L1 x L2	19	7	0.1261 ± 0.0041	2.1921 (0.8365 - 4.0022)
Ophionereididae	<i>Ophionereis porrecta</i>	L1 x L2	26	3	0.1321 ± 0.0056	2.6029 (0.9806 - 4.9360)

b						
Family	Nominal species	ESU	N	H	K2P	Tmrca (HPD95) in Ma
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	39	31	0.0118 ± 0.0198	0.1371 (0.7124 - 0.2149)
Ophiocomidae	<i>Ophiocoma</i> nov. sp.	-	52	29	0.0045 ± 0.0040	0.0606 (0.0327 - 0.0923)
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	35	33	0.0131 ± 0.0065	0.3293 (0.1699 - 0.5238)
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	25	24	0.0122 ± 0.0099	0.1620 (0.0922 - 0.2498)
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	31	27	0.0156 ± 0.0056	0.3148 (0.1648 - 0.4993)
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	28	22	0.0147 ± 0.0270	0.1288 (0.0626 - 0.2142)
Ophiolepididae	<i>Ophiolepis cincta</i>	L1	4	1	0.0000 ± 0.0000	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L2	2	2	0.0061	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L3	1	1	-	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	9	8	0.0084 ± 0.0057	0.4139 (0.1113 - 0.8218)
Ophiolepididae	<i>Ophiolepis cincta</i>	L5	5	5	0.0052 ± 0.0032	0.2501 (0.0481 - 0.5610)
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	19	14	0.0063 ± 0.0047	0.3384 (0.0995 - 0.6739)
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L2	5	5	0.0058 ± 0.0028	0.2017 (0.0325 - 0.4869)
Ophiodermatidae	<i>Ophiopeza fallax</i>	L1	19	14	0.0065 ± 0.0035	0.2974 (0.0888 - 0.6079)
Ophiodermatidae	<i>Ophiopeza fallax</i>	L2	7	6	0.0079 ± 0.0048	0.2860 (0.0760 - 0.6189)
Ophionereididae	<i>Ophionereis porrecta</i>	L1	26	20	0.0078 ± 0.0056	0.5277 (0.1706 - 1.0645)
Ophionereididae	<i>Ophionereis porrecta</i>	L2	3	3	0.0071 ± 0.0035	0.1733 (0.0167 - 0.4490)

c						
Family	Nominal species	ESU	N	H	τ	Start of expansion (CI) in Ma
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	39	31	4.930	0.1011 (0.1290 - 0.0831)
Ophiocomidae	<i>Ophiocoma</i> nov. sp.	-	52	29	2.848	0.0584 (0.0745 - 0.0480)

Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	35	33	5.352	0.1097 (0.1400 - 0.0902)
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	25	24	4.086	0.0838 (0.1069 - 0.0689)
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	31	27	11.600	0.2380 (0.3037 - 0.1957)
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	28	22	4.979	0.1021 (0.1303 - 0.0839)
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	19	14	3.848	0.0789 (0.1007 - 0.0649)
Ophiodermatidae	<i>Ophiopeza fallax</i>	L1	19	14	5.016	0.1029 (0.1312 - 0.0846)

highlighted the effect of oceanography on fish connectivity in the region. Our data show that lecithotrophic species have, on average, more limited connectivity than planktotrophic species, confirming previous correlations between dispersal capacity and genetic structure in other marine invertebrates (Goldson *et al.*, 2001; Paulay & Meyer, 2006; Boissin *et al.*, 2008b). Moreover, unlike planktotrophic species, six of the 12 lecithotrophic ESUs were found only in a single location (Fig. 3). Like diversification, the genetic structure of brittle-stars in the SWIO is probably also affected by both regional oceanography and dispersal capacity. These results suggest that long-term persistence of biota and their resilience to climatic changes are not dependent on high population connectivity.

SWIO as an “Evolutionary Hotspot”

Using an integrative analytical framework, we identified intra-regional speciation, examples of population persistence through Milankovitch cycles, and demographic changes in reef brittle-stars of the SWIO. These results support the SWIO reefs as a potential Evospot, but further investigations are required. More samples and additional loci are needed to improve accuracy and precision of the inferences (e.g. T_{mrc} , AMOVA and BSP). Moreover, thorough evaluation of the SWIO Evospot will be obtained by using more taxa and broadening the biodiversity surveys to the whole distribution range of the species. It will then be possible to identify the evolutionary role and importance of the SWIO relative to the four additional marine biodiversity hotspots identified in the Indian Ocean (Roberts *et al.*, 2002). Nonetheless, several additional lines of evidence support the SWIO as an Evospot: 1) the region includes five operational geographical units (Samyn & Tallon, 2005); 2) two biodiversity hotspots have been identified within the region (Roberts *et al.*, 2002) and an additional one was recently identified in the northern Mozambique Channel (Obura, 2012); 3) a recent study identified multiple potential SWIO endemic lineages in eight IWP reef fishes (Hubert *et al.*, 2012). Because large marine biodiversity conservation programs start with the identification of regions of importance for biodiversity persistence (Briggs, 2005), we believe that this analytical framework represent an efficient and rapid way to assess

Table 2. Results of spatial genetic analyses obtained using phylogeny-trait correlation with BaTS (AI, PS, MC) and Analyses of Molecular Variance (AMOVA) performed on the nine ESUs present in more than one location. AI: association index statistic; PS: parsimony score statistic; MC: locations with significant genetic signal using the monophyletic clade signal; HPD95: highest posterior density confidence interval at 95%; Significance levels: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The locality codes are presented in Appendix S1.

ESU	BaTS			AMOVA
	AI (HPD95)	PS (HPD95)	MC	Φ_{st} (pairwise dist)
<i>Ophiocoma brevipes</i>	3.06 (2.51 - 3.58)	18.76 (17.00 - 20.00)	TOL	0.01847
<i>Ophiocoma cynthiae</i>	1.76 (1.28 - 2.25)**	12.46 (11.00 - 13.00)	TOL	0.14020*
<i>Ophiocoma erinaceus</i>	2.76 (2.23 - 3.21)	16.90 (15.00 - 18.00)	-	0.07006
<i>Ophiocoma scolopendrina</i>	1.68 (1.20 - 2.10)**	11.90 (11.00 - 13.00)**	NBE, REU, TOL	0.10851*
<i>Ophioplocus imbricatus</i>	0.03 (0.00 - 0.12)***	1.76 (1.00 - 3.00)***	REU, TOL	0.31463***
<i>Ophiarachnella gorgonia</i> L1	1.07 (0.64 - 1.47)	7.78 (6.00 - 9.00)	-	-0.05653
<i>Ophiopeza fallax</i> L1	0.44 (0.17 - 0.75)**	4.19 (3.00 - 5.00)**	NBE	0.10647
<i>Ophiopeza fallax</i> L2	0.09 (0.08 - 0.12)***	2.00 (2.00 - 2.00)***	NBE, TOL	0.29123*
<i>Ophionereis porrecta</i> L1	1.42 (0.96 - 1.88)***	10.51 (10.00 - 12.00)***	REU, TOL	0.10055

the evolutionary potential of other peripheral regions, regions still overlooked despite a growing number of studies highlighting their importance (Bellwood & Meyer, 2009).

ACKNOWLEDGEMENTS

Funding was provided by the French *Agence Nationale de Recherche* (program BIOTAS, no. ANR-06-BDIV-002) and the National Science Foundation (NSF DEB-0529724). We acknowledge the *Centre National de Recherches Océanographiques* (Madagascar), les *Territoires Australes et Antarctiques Françaises* and the *Marine Nationale* and *Forces armées de la zone Sud de l'Océan Indien* for their logistic support during our field works. We thank J Maharavo (CNRO), MW Rabenavanana (IHSM), the *Affaires Maritimes* and the *Réserve Naturelle Marine de la Réunion* for sampling permits. Field assistance was provided by G Bakara (CNRO), F Ramahatratra, F Rasoamanendrika (IHSM), V Denis (ECOMAR) and M Malay (FLMNH). We thank D DaSilva and L Humeau for providing laboratory facilities in the UMR PBVMT at Université de La Réunion. We wish to thank Michael Dawson, Tim O'Hara and two anonymous reviewers for their insightful comments. TBH is a postdoctoral research fellow funded by the African Coelacanth Ecosystem Programme II and University of Pretoria. EB is a postdoctoral research fellow funded by the University of Pretoria.

REFERENCES

- Barber, P.H., Erdmann, M.V. & Palumbi, S.R. (2006) Comparative phylogeography of three codistributed stomatopods: Origins and timing of regional lineage diversification in the coral triangle. *Evolution*, **60**, 1825-1839.
- Bellwood, D.R. & Meyer, C.P. (2009) Searching for heat in a marine biodiversity hotspot. *Journal of Biogeography*, **36**, 569-576.
- Boissin, E., Feral, J.P. & Chenuil, A. (2008a) Defining reproductively isolated units in a cryptic and syntopic species complex using mitochondrial and nuclear markers: the brooding brittle star, *Amphipholis squamata* (Ophiuroidea). *Molecular Ecology*, **17**, 1732-1744.
- Boissin, E., Stohr, S. & Chenuil, A. (2011) Did vicariance and adaptation drive cryptic speciation and evolution of brooding in *Ophioderma longicauda* (Echinodermata: Ophiuroidea), a common Atlanto-Mediterranean ophiuroid? *Molecular Ecology*, **20**, 4737-4755.

- Boissin, E., Hoareau, T., Feral, J. & Chenuil, A. (2008b) Extreme selfing rates in the cosmopolitan brittle star species complex *Amphipholis squamata*: data from progeny-array and heterozygote deficiency. *Marine Ecology Progress Series*, **361**, 151-159.
- Botsford, L.W., White, J.W., Coffroth, M.A., Paris, C.B., Planes, S., Shearer, T.L., Thorrold, S.R. & Jones, G.P. (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. *Coral Reefs*, **28**, 327-337.
- Briggs, J.C. (2005) Coral reefs: Conserving the evolutionary sources. *Biological Conservation*, **126**, 297-305.
- Byrne, M., Cisternas, P. & O'Hara, T. (2008) Brooding of pelagic-type larvae in *Ophiopeza spinosa*: reproduction and development in a tropical ophiidermatid brittlestar. *Invertebrate Biology*, **127**, 98-107.
- Cherbonnier, G. & Guille, A. (1978) *Echinodermes: Ophiurides*. Faune de Madagascar, 48, 1-272.
- Cisternas, P.A. & Byrne, M. (2005) Evolution of abbreviated development in the ophiuroid *Ophiarachnella gorgonia* involves heterochronies and deletions. *Canadian Journal of Zoology- Revue Canadienne De Zoologie*, **83**, 1067-1078.
- Clark, A.M. & Rowe F.W.E. (1971) *Monograph of Shallow-water Indo-West Pacific Echinoderms*. Trustees of the British Museum (Natural History), London.
- Coyne, J.A. & Orr, H.A. (2004) *Speciation*. Sinauer Associates, Sunderland, MA.
- Crandall, E.D., Frey, M.A., Grosberg, R.K. & Barber, P.H. (2008) Contrasting demographic history and phylogeographical patterns in two Indo-Pacific gastropods. *Molecular Ecology*, **17**, 611-626.
- Drummond, A.J. & Rambaut, A. (2007) BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, **7**, 214.
- Drummond, A.J., Rambaut, A., Shapiro, B. & Pybus, O.G. (2005) Bayesian coalescent inference of past population dynamics from molecular sequences. *Molecular Biology and Evolution*, **22**, 1185-1192.
- Emler, R.B. (1990) Flow-fields around ciliated larvae – The effect of natural and artificial tethers. *Marine*

Ecology Progress Series, **63**, 211-225.

- Excoffier, L., Laval, G. & Schneider, S. (2005) Arlequin (version 3.0): An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics*, **1**, 47-50.
- Gaither, M.R., Toonen, R.J., Robertson, D.R., Planes, S. & Bowen, B.W. (2010) Genetic evaluation of marine biogeographical barriers: perspectives from two widespread Indo-Pacific snappers (*Lutjanus kasmira* and *Lutjanus fulvus*). *Journal of Biogeography*, **37**, 133-147.
- Goldson, A.J., Hughes, R.N. & Gliddon, C.J. (2001) Population genetic consequences of larval dispersal mode and hydrography: a case study with bryozoans. *Marine Biology*, **138**, 1037-1042.
- Heled, J. & Drummond, A.J. (2008) Bayesian inference of population size history from multiple loci. *BMC Evolutionary Biology*, **8**, 289.
- Heled, J. & Drummond, A.J. (2010) Bayesian Inference of Species Trees from Multilocus Data. *Molecular Biology and Evolution*, **27**, 570-580.
- Hendler, G. (1975) Adaptational significance of patterns of ophiuroid development. *American Zoologist*, **15**, 691-715.
- Hewitt, G. (2000) The genetic legacy of the Quaternary ice ages. *Nature*, **405**, 907-913.
- Hickerson, M.J. & Meyer, C.P. (2008) Testing comparative phylogeographic models of marine vicariance and dispersal using a hierarchical Bayesian approach. *BMC Evolutionary Biology*, **8**, 322.
- Ho, S.Y.W., Saarma, U., Barnett, R., Haile, J. & Shapiro, B. (2008) The Effect of Inappropriate Calibration: Three Case Studies in Molecular Ecology. *Plos One*, **3**, e1615.
- Hoareau, T.B. & Boissin, E. (2010) Design of phylum-specific hybrid primers for DNA barcoding: addressing the need for efficient COI amplification in the Echinodermata. *Molecular Ecology Resources*, **10**, 960-967.
- Hoareau, T.B., Boissin, E. & Berrebi, P. (2012) Evolutionary history of a widespread Indo-Pacific goby: The role of Pleistocene sea-level changes on demographic contraction/expansion dynamics. *Molecular phylogenetics and evolution*, **62**, 566-72.
- Hubert, N., Meyer, C.P., Bruggemann, H.J., Guerin, F., Komeno, R.J.L., Espiau, B., Causse, R., Williams, J.T.

- & Planes, S. (2012) Cryptic Diversity in Indo-Pacific Coral-Reef Fishes Revealed by DNA-Barcoding Provides New Support to the Centre-of-Overlap Hypothesis. *Plos One*, **7**, e28987.
- Jablonski, D. (2008) Biotic interactions and macroevolution: Extensions and mismatches across scales and levels. *Evolution*, **62**, 715-739.
- Kelly, R.P. & Palumbi, S.R. (2010) Genetic Structure Among 50 Species of the Northeastern Pacific Rocky Intertidal Community. *Plos One*, **5**, e8594.
- Komatsu, M. & Shosaku, T. (1993) Development of the brittle star, *Ophioplocus japonicus* Clark, H.L. 1. *Zoological Science*, **10**, 295-306.
- Lessios, H.A. (2008) The Great American Schism: Divergence of Marine Organisms After the Rise of the Central American Isthmus. *Annual Review of Ecology Evolution and Systematics*, **39**, 63-91.
- Librado, P. & Rozas, J. (2009) DnaSP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, **25**, 1451-1452.
- Lisiecki, L.E. & Raymo, M.E. (2005) A Pliocene-Pleistocene stack of 57 globally distributed benthic $\delta^{18}\text{O}$ records. *Paleoceanography*, **20**, PA1003. doi:10.1029/2004PA001071
- Lynch, J.D. (1989) The gauge of speciation: on the frequencies of modes of speciation. *Speciation and its consequences* (ed. by D. Otte and J.A. Endler), pp. 527-553. Sinauer, Sunderland, MA.
- Malay, M.C.D. & Paulay, G. (2010) Peripatric speciation drives diversification and distributional pattern of reef hermit crabs (Decapoda: Diogenidae: Calcinus). *Evolution*, **64**, 634-662.
- Marko, P.B., Hoffman, J.M., Emme, S.A., McGovern, T.M., Keever, C.C. & Cox, L.N. (2010) The 'Expansion-Contraction' model of Pleistocene biogeography: rocky shores suffer a sea change? *Molecular Ecology*, **19**, 146-169.
- Mayr, E. (1954) Change of genetic environment and evolution. *Evolution as a process* (ed. by J. Huxley, A.C. Hardy and E.B. Ford), pp. 157-180. Allen and Unwin, London.
- McGovern, T.M., Keever, C.C., Sasaki, C.A., Hart, M.W. & Marko, P.B. (2010) Divergence genetics analysis reveals historical population genetic processes leading to contrasting phylogeographic patterns in co-distributed species. *Molecular Ecology*, **19**, 5043-60.

- Meyer, C.P. & Paulay, G. (2005) DNA barcoding: Error rates based on comprehensive sampling. *Plos Biology*, **3**, 2229-2238.
- Mladenov, P.V. (1985) Development and metamorphosis of the brittle star *Ophiocoma pumilla* – evolutionary and ecological implications. *Biological Bulletin*, **168**, 285-295.
- Moberg, F. & Folke, C. (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics*, **29**, 215-233.
- Moritz, C. (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, **51**, 238-254.
- Morlon, H., Parsons, T.L. & Plotkin, J.B. (2011) Reconciling molecular phylogenies with the fossil record. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 16327-16332.
- Mortensen, T. (1938) Contributions to the study of the development and larval forms of echinoderms. IV. Det Kongelige Danske Videnskabsnæst Selskabs Skrifter, naturvidenskabelig og matematisk afdeling, pp. 1-59. Høst & Søn, København.
- Muths, D., Tessier, E., Gouws, G., Craig, M., Mwale, M., Mwaluma, J., Mwandya, A. & Bourjea, J. (2011) Restricted dispersal of the reef fish *Myripristis berndti* at the scale of the SW Indian Ocean. *Marine Ecology Progress Series*, **443**, 167-180.
- Myers, N. (1988) Threatened biotas: "hot spots" in tropical forests. *The Environmentalist*, **8**, 187-208.
- Nixon, K.C. & Wheeler, Q.D. (1990) An amplification of the phylogenetic species concept. *Cladistics-the International Journal of the Willi Hennig Society*, **6**, 211-223.
- Norris, R.D. & Hull, P.M. (2012) The temporal dimension of marine speciation. *Evolutionary Ecology*, **26**, 393-415.
- O'Loughlin, P.M., Paulay, G., Davey, N. & Michonneau, F. (2011) The Antarctic region as a marine biodiversity hotspot for echinoderms: Diversity and diversification of sea cucumbers. *Deep-Sea Research Part II-Topical Studies in Oceanography*, **58**, 264-275.
- Obura, D. (2012) The Diversity and Biogeography of Western Indian Ocean Reef-Building Corals. *Plos*

One, **7**, e45013.

- Palumbi, S.R. (1996) Nucleic acids II: The polymerase chain reaction. *Molecular Systematics* (ed. by D. Hillis and C. Moritz), pp. 205-247. Sinauer Associates Inc., Sunderland, MA.
- Parker, J., Rambaut, A. & Pybus, O.G. (2008) Correlating viral phenotypes with phylogeny: Accounting for phylogenetic uncertainty. *Infection Genetics and Evolution*, **8**, 239-246.
- Paulay, G. (1990) Effects of late Cenozoic sea-level fluctuations on the bivalve faunas of tropical oceanic islands. *Paleobiology*, **16**, 415-434.
- Paulay, G. (1996) Dynamic clams: Changes in the bivalve fauna of Pacific islands as a result of sea-level fluctuations. *American Malacological Bulletin*, **12**, 45-57.
- Paulay, G. & Meyer, C. (2002) Diversification in the tropical pacific: Comparisons between marine and terrestrial systems and the importance of founder speciation. *Integrative and Comparative Biology*, **42**, 922-934.
- Paulay, G. & Meyer, C. (2006) Dispersal and divergence across the greatest ocean region: Do larvae matter? *Integrative and Comparative Biology*, **46**, 269-281.
- Pillans, B., Chappell, J. & Naish, T.R. (1998) A review of the Milankovitch climatic beat: template for Plio-Pleistocene sea-level changes and sequence stratigraphy. *Sedimentary Geology*, **122**, 5-21.
- Provan, J. & Bennett, K.D. (2008) Phylogeographic insights into cryptic glacial refugia. *Trends in Ecology and Evolution*, **23**, 564-571.
- Quenouille, B., Hubert, N., Bermingham, E. & Planes, S. (2011) Speciation in tropical seas: Allopatry followed by range change. *Molecular Phylogenetics and Evolution*, **58**, 546-552.
- Quental, T.B. & Marshall, C.R. (2010) Diversity dynamics: molecular phylogenies need the fossil record. *Trends in Ecology and Evolution*, **25**, 434-441.
- Reid, W.V. (1998) Biodiversity hotspots. *Trends in Ecology and Evolution*, **13**, 275-280.
- Reznick, D.N. & Ricklefs, R.E. (2009) Darwin's bridge between microevolution and macroevolution. *Nature*, **457**, 837-842.
- Richards, V.P., Thomas, J.D., Stanhope, M.J. & Shivji, M.S. (2007) Genetic connectivity in the Florida reef

system: comparative phylogeography of commensal invertebrates with contrasting reproductive strategies. *Molecular Ecology*, **16**, 139-157.

Riegl, B., Bruckner, A., Coles, S.L., Renaud, P. & Dodge, R.E. (2009) Coral Reefs Threats and Conservation in an Era of Global Change. *Year in Ecology and Conservation Biology 2009*, **1162**, 136-186.

Roberts, C.M., McClean, C.J., Veron, J.E.N., Hawkins, J.P., Allen, G.R., McAllister, D.E., Mittermeier, C.G., Schueler, F.W., Spalding, M., Wells, F., Vynne, C. & Werner, T.B. (2002) Marine biodiversity hotspots and conservation priorities for tropical reefs. *Science*, **295**, 1280-1284.

Samyn, Y. & Tallon, I. (2005) Zoogeography of the shallow-water holothuroids of the western Indian Ocean. *Journal of Biogeography*, **32**, 1523-1538.

Schott, F.A. & McCreary, J.P. (2001) The monsoon circulation of the Indian Ocean. *Progress in Oceanography*, **51**, 1-123.

Selkoe, K.A., & Toonen, R.J. (2011) Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Marine Ecology Progress Series*, **436**, 291-305.

Selvakumaraswamy, P. & Byrne, M. (2004) Metamorphosis and developmental evolution in Ophioureis (Echinodermata : Ophiuroidea). *Marine Biology*, **145**, 87-99.

Sloan, N.A. (1979) Microhabitat and resource utilization in cryptic rocky inter-tidal echinoderms at Aldabra atoll, Seychelles. *Marine Biology*, **54**, 269-279.

Stöhr, S. (2012). *Ophiopeza fallax fallax* Peters, 1851. In: Stöhr, S., O'Hara, T. (Eds) (2012). World Ophiuroidea database. Accessed through: Stöhr, S., O'Hara, T. (Eds) (2012). World Ophiuroidea database at <http://www.marinespecies.org/ophiuroidea/aphia.php?p=taxdetails&id=245136> on 2013-02-07

Stöhr, S., O'Hara, T. (Eds) (2013). World Ophiuroidea database. Accessed at <http://www.marinespecies.org/ophiuroidea> on 2013-02-07

Stöhr, S., O'Hara, T.D. & Thuy, B. (2012) Global Diversity of Brittle Stars (Echinodermata: Ophiuroidea). *PLoS One*, **7**, e31940.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular

Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution*, **28**, 2731-2739.

- Vandergast, A.G., Bohonak, A.J., Hathaway, S.A., Boys, J. & Fisher, R.N. (2008) Are hotspots of evolutionary potential adequately protected in southern California? *Biological Conservation*, **141**, 1648-1664.
- Visram, S., Yang, M.-C., Pillay, R.M., Said, S., Henriksson, O., Grahn, M. & Chen, C.A. (2010) Genetic connectivity and historical demography of the blue barred parrotfish (*Scarus ghobban*) in the western Indian Ocean. *Marine Biology*, **157**, 1475-1487.
- Vogler, C., Benzie, J., Barber, P.H., Erdmann, M.V., Ambariyanto, Sheppard, C., Tenggardjaja, K., Gerard, K. & Woerheide, G. (2012) Phylogeography of the Crown-of-Thorns Starfish in the Indian Ocean. *Plos One*, **7**, e43499.
- Voris, H.K. (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. *Journal of Biogeography*, **27**, 1153-1167.
- Waelbroeck, C., Labeyrie, L., Michel, E., Duplessy, J.C., McManus, J.F., Lambeck, K., Balbon, E. & Labracherie, M. (2002) Sea-level and deep water temperature changes derived from benthic foraminifera isotopic records. *Quaternary Science Reviews*, **21**, 295-305.
- Wafar, M., Venkataraman, K., Ingole, B., Khan, S.A. & LokaBharathi, P. (2011) State of Knowledge of Coastal and Marine Biodiversity of Indian Ocean Countries. *Plos One*, **6**, e14613.
- Waples, R.S. (1991) Pacific salmon, *Oncorhynchus* spp., and the definition of species under the Endangered Species Act. *Marine Fisheries Review*, **53**, 11-22.
- Ward, R.D., Holmes, B.H. & O'Hara, T.D. (2008) DNA barcoding discriminates echinoderm species. *Molecular Ecology Resources*, **8**, 1202-1211.
- Young, C.M., Sewell, M.A., Tyler, P.A. & Metaxas, A. (1997) Biogeographic and bathymetric ranges of Atlantic deep-sea echinoderms and ascidians: the role of larval dispersal. *Biodiversity and Conservation*, **6**, 1507-1522.

BIOSKETCH

Thierry B Hoareau is a postdoctoral fellow at University of Pretoria. His research focuses on the evolution of widespread organisms. The data presented here were generated during a previous project based at Université de la Reunion.

Author contributions: TBH conceived the ideas and led the writing; EB, GP, JHB and TBH collected the samples; TBH and EB performed the lab work and analysed the data. All the authors read and improved the manuscript.

Editor: Michael Dawson

SUPPORTING INFORMATION

Appendix S1 Characteristics of the brittle-star specimens used in the analyses, including the nominal species name, evolutionarily significant unit (ESU), haplotype, collection location, and GenBank IDs for both *COI* and *16S* sequences.

Family	Species	ESU	Haplotype	Field ID number	Specimen voucher	Locality	Locality code	<i>COI</i> GenBank no.	<i>16S</i> GenBank no.
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H001	MEPA-9320	URUN2009-09320	Glorieuses Islands	GLO	KC759737	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H001	NBE-1749	URUN2008-05819	Nosy-Be	NBE	KC759738	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H002	MEPA-9323	URUN2009-09323	Glorieuses Islands	GLO	KC759739	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H003	REU-3706	URUN2009-11094	Réunion	REU	KC759740	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H004	MAY-7044	UF7044	Mayotte Is	MAY	KC759741	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H004	NBE-0704	URUN2008-04774	Nosy-Be	NBE	KC759742	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H004	REU-0202-1	URUN2007-00270	Réunion	REU	KC759743	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H004	REU-3702	URUN2009-11090	Réunion	REU	KC759744	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H005	MGTU-0110-5	URUN2013-11166	Toliara	TUL	KC759745	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H006	MGTU-0110-4	URUN2013-11165	Toliara	TUL	KC759746	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H007	MAY-7044-1	UF7044-1	Mayotte Is	MAY	KC759747	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H008	MEPA-9391	URUN2009-09391	Tromelin	TRO	KC759748	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H009	REU-0032-1	URUN2007-00047	Réunion	REU	KC759749	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H010	REU-0841	URUN2007-01322	Réunion	REU	KC759750	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H010	REU-0847	UF6547	Réunion	REU	KC759751	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H011	MAY-7056	UF7056	Mayotte Is	MAY	KC759752	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H012	NBE-0692	URUN2008-04762	Nosy-Be	NBE	KC759753	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H012	MGTU-0124	URUN2008-07705	Toliara	TUL	KC759754	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H013	MGTU-0110-2	URUN2013-11163	Toliara	TUL	KC759755	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H014	REU-3646	URUN2009-11034	Réunion	REU	KC759756	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H015	MGTU-0127	URUN2008-07708	Toliara	TUL	KC759757	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H016	MAY-7103	UF7103	Mayotte Is	MAY	KC759758	-

Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H016	NBE-0681	URUN2008-04751	Nosy-Be	NBE	KC759759	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H017	REU-3704	URUN2009-11092	Réunion	REU	KC759760	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H018	REU-0646	UF6523	Réunion	REU	KC759761	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H019	MGTU-0110	URUN2008-07691	Toliara	TUL	KC759762	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H019	MGTU-0110-1	URUN2013-11162	Toliara	TUL	KC759763	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H020	REU-3640	URUN2009-11028	Réunion	REU	KC759764	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H021	REU-0282	UF6451	Réunion	REU	KC759765	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H022	REU-0282-1	URUN2013-11151	Réunion	REU	KC759766	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H023	REU-3641	URUN2009-11029	Réunion	REU	KC759767	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H024	MGTU-0110-3	URUN2013-11164	Toliara	TUL	KC759768	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H025	NBE-0735-1	URUN2013-11153	Nosy-Be	NBE	KC759769	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H026	REU-3705	URUN2009-11093	Réunion	REU	KC759770	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H027	REU-3701	URUN2009-11089	Réunion	REU	KC759771	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H028	REU-3703	URUN2009-11091	Réunion	REU	KC759772	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H029	NBE-0735-2	URUN2013-11154	Nosy-Be	NBE	KC759773	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H030	REU-3639	URUN2009-11027	Réunion	REU	KC759774	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H031	NBE-0692-1	URUN2013-11152	Nosy-Be	NBE	KC759775	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H032	GUA4739	UF4739	Guam	GUA	KC759776	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H033	HAW2114	UF2114	Hawaii	HAW	KC759777	-
Ophiocomidae	<i>Ophiocoma brevipes</i>	-	H034	HER16111	UF16111	Heron Island	HER	KC759778	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-0033-1	URUN2007-00048	Réunion	REU	KC759779	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3608	URUN2009-10996	Réunion	REU	KC759780	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3635	URUN2009-11023	Réunion	REU	KC759781	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3636	URUN2009-11024	Réunion	REU	KC759782	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3670	URUN2009-11058	Réunion	REU	KC759783	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3680	URUN2009-11068	Réunion	REU	KC759784	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3708	URUN2009-11096	Réunion	REU	KC759785	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3712	URUN2009-11100	Réunion	REU	KC759786	-
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	-	H035	REU-3713	URUN2009-11101	Réunion	REU	KC759787	-

Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H035	REU-3714	URUN2009-11102	Réunion	REU	KC759788	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H035	REU-3715	URUN2009-11103	Réunion	REU	KC759789	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H035	REU-3717	URUN2009-11105	Réunion	REU	KC759790	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H035	REU-3719	URUN2009-11107	Réunion	REU	KC759791	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3609	URUN2009-10997	Réunion	REU	KC759792	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3637	URUN2009-11025	Réunion	REU	KC759793	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3660	URUN2009-11048	Réunion	REU	KC759794	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3664	URUN2009-11052	Réunion	REU	KC759795	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3674	URUN2009-11062	Réunion	REU	KC759796	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3675	URUN2009-11063	Réunion	REU	KC759797	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3676	URUN2009-11064	Réunion	REU	KC759798	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3679	URUN2009-11067	Réunion	REU	KC759799	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-3710	URUN2009-11098	Réunion	REU	KC759800	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H036	REU-0355	UF6597	Réunion	REU	KC759801	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H037	REU-0285	UF6454	Réunion	REU	KC759802	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H037	REU-3668	URUN2009-11056	Réunion	REU	KC759803	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H038	REU-3625	URUN2009-11013	Réunion	REU	KC759804	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H039	REU-3630	URUN2009-11018	Réunion	REU	KC759805	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H040	REU-3633	URUN2009-11021	Réunion	REU	KC759806	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H041	REU-3647	URUN2009-11035	Réunion	REU	KC759807	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H042	REU-3671	URUN2009-11059	Réunion	REU	KC759808	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H043	REU-3666	URUN2009-11054	Réunion	REU	KC759809	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H044	REU-3711	URUN2009-11099	Réunion	REU	KC759810	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H045	REU-3721	URUN2009-11109	Réunion	REU	KC759811	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H046	MEPA-9398	URUN2009-09398	Tromelin	TRO	KC759812	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H047	REU-3632	URUN2009-11020	Réunion	REU	KC759813	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H048	REU-3678	URUN2009-11066	Réunion	REU	KC759814	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H049	REU-3667	URUN2009-11055	Réunion	REU	KC759815	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H050	REU-3677	URUN2009-11065	Réunion	REU	KC759816	-

Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H051	REU-3607	URUN2009-10995	Réunion	REU	KC759817	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H052	REU-3673	URUN2009-11061	Réunion	REU	KC759818	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H053	REU-3634	URUN2009-11022	Réunion	REU	KC759819	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H054	REU-3669	URUN2009-11057	Réunion	REU	KC759820	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H055	REU-3638	URUN2009-11026	Réunion	REU	KC759821	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H056	REU-3629	URUN2009-11017	Réunion	REU	KC759822	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H057	REU-3716	URUN2009-11104	Réunion	REU	KC759823	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H058	REU-3631	URUN2009-11019	Réunion	REU	KC759824	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H058	REU-3718	URUN2009-11106	Réunion	REU	KC759825	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H059	REU-3672	URUN2009-11060	Réunion	REU	KC759826	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H060	REU-3628	URUN2009-11016	Réunion	REU	KC759827	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H061	REU-3707	URUN2009-11095	Réunion	REU	KC759828	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H062	REU-3627	URUN2009-11015	Réunion	REU	KC759829	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H063	REU-3626	URUN2009-11014	Réunion	REU	KC759830	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H064	LIZ3283	UF3283	Lizard Island	LIZ	KC759831	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H065	MOO5231	UF5231	Moorea	MOO	KC759832	-
Ophiocomidae	<i>Ophiocoma</i> sp. nov.	-	H066	'MAR2762	UF2762	Marshall Is	MAR	KC759833	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H067	MEPA-9178	URUN2009-09178	Europa Island	EUR	KC759834	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H068	MEPA-9317	URUN2009-09317	Glorieuses Islands	GLO	KC759835	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H069	REU-3616	URUN2009-11004	Réunion	REU	KC759836	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H070	REU-9003	Specimen released	Réunion	REU	KC759837	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H071	MEPA-9329	URUN2009-09329	Glorieuses Islands	GLO	KC759838	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H072	MGTU-0118-1	URUN2013-11172	Toliara	TUL	KC759839	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H073	MAY-7047	UF7047	Mayotte Is	MAY	KC759840	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H074	REU-3618	URUN2009-11006	Réunion	REU	KC759841	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H074	REU-3623	URUN2009-11011	Réunion	REU	KC759842	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H075	REU-3621	URUN2009-11009	Réunion	REU	KC759843	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H076	MGTU-0118-2	URUN2013-11173	Toliara	TUL	KC759844	-

Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H077	NBE-3386	URUN2008-07253	Nosy-Be	NBE	KC759845	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H078	REU-3643	URUN2009-11031	Réunion	REU	KC759846	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H079	REU-3606	URUN2009-10994	Réunion	REU	KC759847	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H079	REU-3662	URUN2009-11050	Réunion	REU	KC759848	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H080	REU-3617	URUN2009-11005	Réunion	REU	KC759849	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H081	MAY-7053-1	URUN7053-1	Mayotte Is	MAY	KC759850	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H082	NBE-0679	URUN2008-04749	Nosy-Be	NBE	KC759851	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H083	REU-3624	URUN2009-11012	Réunion	REU	KC759852	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H084	REU-3619	URUN2009-11007	Réunion	REU	KC759853	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H085	MGTU-0118-3	URUN2013-11174	Toliara	TUL	KC759854	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H086	REU-3644	URUN2009-11032	Réunion	REU	KC759855	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H087	REU-0178	UF6417	Réunion	REU	KC759856	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H088	REU-3663	URUN2009-11051	Réunion	REU	KC759857	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H089	REU-9004	Specimen released	Réunion	REU	KC759858	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H090	REU-3620	URUN2009-11008	Réunion	REU	KC759859	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H091	REU-3665	URUN2009-11053	Réunion	REU	KC759860	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H092	MGTU-0136	URUN2008-07717	Toliara	TUL	KC759861	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H093	MGTU-0136-1	URUN2013-11185	Toliara	TUL	KC759862	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H094	MAY-7053-2	UF7053-2	Mayotte Is	MAY	KC759863	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H095	MOO5278	UF5278	Moorea	MOO	KC759864	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H096	MAY-7069	UF7069	Mayotte Is	MAY	KC759865	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H097	REU-3622	URUN2009-11010	Réunion	REU	KC759866	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H098	REU-0162-1	UF6335	Réunion	REU	KC759867	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H099	REU-3661	URUN2009-11049	Réunion	REU	KC759868	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H100	REU-9005	Specimen released	Réunion	REU	KC759869	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H101	WAU8838	UF8838	West Australia	WAU	KC759870	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H095	MOO5278-1	UF5278-1	Moorea	MOO	KC759871	-
Ophiocomidae	<i>Ophiocoma cynthiae</i>	-	H102	HAW6133	UF6133	Hawaii	HAW	KC759872	-

Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H103	MEPA-9169	URUN2009-09169	Europa Island	EUR	KC759873	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H104	NBE-0176	URUN2008-04244	Nosy-Be	NBE	KC759874	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H105	MEPA-9354	URUN2009-09354	Glorieuses Islands	GLO	KC759875	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H106	MGTU-0136-2	URUN2013-11186	Toliara	TUL	KC759876	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H107	MGTU-0139	URUN2008-07720	Toliara	TUL	KC759877	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H108	OMA4178	UF4178	Oman	OMA	KC759878	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H109	REU-3724	URUN2009-11112	Réunion	REU	KC759879	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H109	MGTU-0134	URUN2008-07715	Toliara	TUL	KC759880	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H110	MGTU-0139-1	URUN2013-11187	Toliara	TUL	KC759881	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H111	MEPA-9362	URUN2009-09362	Glorieuses Islands	GLO	KC759882	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H112	MEPA-9256	URUN2009-09256	Juan de Nova	JDN	KC759883	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H113	MEPA-9197	URUN2009-09197	Europa Island	EUR	KC759884	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H114	OMA4175	UF4175	Oman	OMA	KC759885	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H115	MEPA-9371	URUN2009-09371	Glorieuses Islands	GLO	KC759886	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H116	MEPA-9370	URUN2009-09370	Glorieuses Islands	GLO	KC759887	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H117	REU-0075-2	URUN2013-11150	Réunion	REU	KC759888	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H118	MAY-7060	UF7060	Mayotte Is	MAY	KC759889	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H119	MEPA-9279	URUN2009-09279	Glorieuses Islands	GLO	KC759890	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H120	MAY-7053-2	UF7053	Mayotte Is	MAY	KC759891	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H121	MEPA-9283	URUN2009-09283	Glorieuses Islands	GLO	KC759892	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H122	MEPA-9270	URUN2009-09270	Juan de Nova	JDN	KC759893	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H123	MEPA-1894	URUN2009-01894	Tromelin	TRO	KC759894	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H124	REU-0075-1	URUN2007-00110	Réunion	REU	KC759895	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H125	MAY-7060-1	UF7060-1	Mayotte Is	MAY	KC759896	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H126	MEPA-9232	URUN2009-09232	Juan de Nova	JDN	KC759897	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H127	LIZ8570	URUN8570	Lizard Island	LIZ	KC759898	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H128	HER10088	URUN10088	Heron Island	HER	KC759899	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H129	MOO5201	URUN5201	Moorea	MOO	KC759900	-
Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H130	WAU8860	URUN8860	West Australia	WAU	KC759901	-

Ophiocomidae	<i>Ophiocoma erinaceus</i>	-	H131	LIZ8495	URUN8495	Lizard Island	LIZ	KC759902	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H132	MEPA-9160	URUN2009-09160	Europa Island	EUR	KC759903	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H133	MEPA-9177	URUN2009-09177	Europa Island	EUR	KC759904	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H134	NBE-0701	UF7337	Nosy-Be	NBE	KC759905	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H135	NBE-0742	URUN2008-04812	Nosy-Be	NBE	KC759906	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H136	REU-0088-1	URUN2007-00126	Réunion	REU	KC759907	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H137	NBE-0679	URUN2008-04749-1	Nosy-Be	NBE	KC759908	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H138	MGTU-0125	URUN2008-07706	Toliara	TUL	KC759909	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H139	MEPA-9318	URUN2009-09318	Glorieuses Islands	GLO	KC759910	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H140	MEPA-9324	URUN2009-09324	Glorieuses Islands	GLO	KC759911	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H141	MAY-7040	UF7040	Mayotte Is	MAY	KC759912	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H142	REU-3652	URUN2009-11040	Réunion	REU	KC759913	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H143	MADA-3362	URUN2008-07229	Nosy-Be	NBE	KC759914	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H144	NBE-0703	UF7338	Nosy-Be	NBE	KC759915	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H144	NBE-0703	UF7338-1	Nosy-Be	NBE	KC759916	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H144	NBE-0715	UF7343	Nosy-Be	NBE	KC759917	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H145	MADA-3364	URUN2008-07231	Nosy-Be	NBE	KC759918	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H146	NBE-1580	URUN2008-05650	Nosy-Be	NBE	KC759919	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H147	NBE-0743	URUN2008-04813	Nosy-Be	NBE	KC759920	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H148	REU-3645	URUN2009-11033	Réunion	REU	KC759921	-

Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H149	NBE-0724	URUN2008-04794	Nosy-Be	NBE	KC759922	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H150	REU-3653	URUN2009-11041	Réunion	REU	KC759923	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H150	REU-3657	URUN2009-11045	Réunion	REU	KC759924	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H151	REU-3654	URUN2009-11042	Réunion	REU	KC759925	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H152	REU-3656	URUN2009-11044	Réunion	REU	KC759926	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H153	MOO5234	UF5234	Moorea	MOO	KC759927	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H154	REU-3655	URUN2009-11043	Réunion	REU	KC759928	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H155	MADA-3363	URUN2008-07230	Nosy-Be	NBE	KC759929	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H156	NBE-0715-1	UF7343-1	Nosy-Be	NBE	KC759930	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H157	NBE-1579	URUN2008-05649	Nosy-Be	NBE	KC759931	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H158	MGTU-0120	URUN2008-07701	Toliara	TUL	KC759932	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H158	MGTU-0133	URUN2008-07714	Toliara	TUL	KC759933	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H159	MGTU-0126	URUN2008-07707	Toliara	TUL	KC759934	-
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	-	H160	MOO5236	UF5236	Moorea	MOO	KC759935	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H161	REU-0055-1	URUN2007-00081	Réunion	REU	KC759936	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H162	REU-3611	URUN2009-10999	Réunion	REU	KC759937	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H163	REU-0133-1	URUN2007-00176	Réunion	REU	KC759938	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H164	REU-0261	UF6439	Réunion	REU	KC759939	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H164	REU-3612	URUN2009-11000	Réunion	REU	KC759940	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H165	REU-0179	UF6418	Réunion	REU	KC759941	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H166	REU-0183	UF6429	Réunion	REU	KC759942	-
Ophiopodidae	<i>Ophioplocus imbricatus</i>	-	H167	REU-3689	URUN2009-11077	Réunion	REU	KC759943	-

Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H168	REU-0439	UF6489	Réunion	REU	KC759944	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H168	REU-3684	URUN2009-11072	Réunion	REU	KC759945	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H169	REU-3685	URUN2009-11073	Réunion	REU	KC759946	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H170	REU-3695	URUN2009-11083	Réunion	REU	KC759947	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H171	REU-3688	URUN2009-11076	Réunion	REU	KC759948	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H172	REU-3691	URUN2009-11079	Réunion	REU	KC759949	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H173	REU-3687	URUN2009-11075	Réunion	REU	KC759950	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H174	REU-3693	URUN2009-11081	Réunion	REU	KC759951	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H175	REU-3613	URUN2009-11001	Réunion	REU	KC759952	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H176	REU-3690	URUN2009-11078	Réunion	REU	KC759953	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H176	REU-3692	URUN2009-11080	Réunion	REU	KC759954	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H177	REU-3694	URUN2009-11082	Réunion	REU	KC759955	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H178	REU-3696	URUN2009-11084	Réunion	REU	KC759956	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H179	MGTU-0117	URUN2008-07698	Toliara	TUL	KC759957	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H179	MGTU-0117-1	URUN2013-11170	Toliara	TUL	KC759958	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H179	MGTU-0122-2	URUN2013-11182	Toliara	TUL	KC759959	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H180	MGTU-0117-3	URUN2013-11171	Toliara	TUL	KC759960	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H181	MGTU-0122	URUN2008-07703	Toliara	TUL	KC759961	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H181	MGTU-0122-1	URUN2013-11181	Toliara	TUL	KC759962	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H182	REU-3642	URUN2009-11030	Réunion	REU	KC759963	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H183	WAUST8898	UF8898	West Australia	WAU	KC759964	-
Ophiolepididae	<i>Ophioplocus imbricatus</i>	-	H184	NGL9415	UF9415	Ningaloo	NGL	KC759965	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L1	H185	MAY-7035	UF7035	Mayotte Is	MAY	KC759966	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L1	H185	MAY-7067	UF7067	Mayotte Is	MAY	KC759967	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L1	H185	NBE-1434	URUN2008-05503	Nosy-Be	NBE	KC759968	KC760082
Ophiolepididae	<i>Ophiolepis cincta</i>	L1	H185	NBE-1971	URUN2008-06042	Nosy-Be	NBE	KC759969	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L2	H186	REU-0453	UF6496	Réunion	REU	KC759970	KC760083
Ophiolepididae	<i>Ophiolepis cincta</i>	L2	H187	REU-1290	UF6581	Réunion	REU	KC759971	KC760084
Ophiolepididae	<i>Ophiolepis cincta</i>	L3	H188	NBE-7227	UF7227	Nosy-Be	NBE	KC759972	-

Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H189	REU-0176	UF6416	Réunion	REU	KC759973	KC760085
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H190	REU-0180	UF6419	Réunion	REU	KC759974	KC760086
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H191	REU-0248-1	URUN2007-00328	Réunion	REU	KC759975	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H192	REU-3610	URUN2009-10998	Réunion	REU	KC759976	KC760092
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H192	REU-3650	URUN2009-11038	Réunion	REU	KC759977	KC760089
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H193	REU-3651	URUN2009-11039	Réunion	REU	KC759978	KC760091
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H194	REU-3709	URUN2009-11097	Réunion	REU	KC759979	KC760090
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H195	REU-3649	URUN2009-11037	Réunion	REU	KC759980	KC760088
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	H196	REU-3648	URUN2009-11036	Réunion	REU	KC759981	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L5	H197	NBE-0773	URUN2008-04843	Nosy-Be	NBE	KC759982	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L5	H198	NBE-1744	URUN2008-05814	Nosy-Be	NBE	KC759983	KC760094
Ophiolepididae	<i>Ophiolepis cincta</i>	L5	H199	NBE-1435	URUN2008-05504	Nosy-Be	NBE	KC759984	KC760093
Ophiolepididae	<i>Ophiolepis cincta</i>	L5	H200	MADA-3342	URUN2008-07209	Nosy-Be	NBE	KC759985	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L5	H201	MADA-3346	URUN2008-07213	Nosy-Be	NBE	KC759986	-
Ophiolepididae	<i>Ophiolepis cincta</i>	LX	H202	GUAM4762	UF7462	Guam	GUA	KC759987	-
Ophiolepididae	<i>Ophiolepis cincta</i>	LX	H203	NWC8649	UF8649	New Caledonia	NWC	KC759988	-
Ophiolepididae	<i>Ophiolepis cincta</i>	LX	H203	MOO8048	UF8048	Moorea	MOO	KC759989	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H204	MEPA-9309	URUN2009-09309	Glorieuses Islands	GLO	KC759990	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H204	MAY-7045	UF7045	Mayotte Is	MAY	KC759991	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H204	MAY-7054	UF7054	Mayotte Is	MAY	KC759992	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H204	MAY-7063	UF7063	Mayotte Is	MAY	KC759993	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H204	NBE-0627	URUN2008-04697	Nosy-Be	NBE	KC759994	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H204	NBE-1412	URUN2008-05481	Nosy-Be	NBE	KC759995	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H205	MGTU-0107	URUN2008-07688	Toliara	TUL	KC759996	-
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	H206	NBE-0717	URUN2008-04787	Nosy-Be	NBE	KC759997	KC760136

Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H207	NBE-0714	URUN2008-04784	Nosy-Be	NBE	KC759998	KC760139
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H208	NBE-0727	URUN2008-04797	Nosy-Be	NBE	KC759999	KC760140
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H209	MGTU-0123	URUN2008-07704	Toliara	TUL	KC760000	-
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H210	MGTU-0132	URUN2008-07713	Toliara	TUL	KC760001	KC760135
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H211	MGTU-0107-1	URUN2013-11159	Toliara	TUL	KC760002	KC760133
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H212	MGTU-0107-2	URUN2013-11160	Toliara	TUL	KC760003	KC760134
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H213	MGTU-0123-1	URUN2013-11183	Toliara	TUL	KC760004	KC760138
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H214	MGTU-0123-2	URUN2013-11184	Toliara	TUL	KC760005	KC760137
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H215	NBE-0712	URUN2008-04782	Nosy-Be	NBE	KC760006	KC760132
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H216	NBE-0708	URUN2008-04778	Nosy-Be	NBE	KC760007	-
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L1	H217	MGTU-0107-3	URUN2013-11161	Toliara	TUL	KC760008	KC760141
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L2	H218	REU-0354	UF6474	Réunion	REU	KC760009	KC760142
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L2	H219	REU-3723	URUN2009-11111	Réunion	REU	KC760010	-
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L2	H220	REU-0822	UF6537	Réunion	REU	KC760011	KC760145
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L2	H221	REU-1291	UF6578	Réunion	REU	KC760012	KC760144
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	L2	H222	REU-0641	UF6519	Réunion	REU	KC760013	KC760143
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	LX	H223	PNG2091	UF2091	Papua-New Guinea	PNG	KC760014	-
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	LX	H224	VAN4332	UF4332	Vanuatu	VAN	KC760015	-
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	LX	H225	LIZ3303	UF3303	Lizard Island	LIZ	KC760016	-
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	LX	H226	NWC8664	UF8664	New Caledonia	NWC	KC760017	-

Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	LX	H227	NGL9508	UF9508	Ningaloo	NGL	KC760018	-
Ophiidermatidae	<i>Ophiarachnella gorgonia</i>	LX	H228	IND4655	UF4655	Indonesia	IND	KC760019	-
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H229	MAY-7037	UF7037	Mayotte Is	MAY	KC760020	-
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H230	NBE-1351-2	URUN2013-11156	Nosy-Be	NBE	KC760021	KC760104
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H230	MGTU-0119-3	URUN2013-11177	Toliara	TUL	KC760022	KC760115
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H230	MGTU-0131	URUN2008-07712	Toliara	TUL	KC760023	KC760105
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H231	NBE-0967	URUN2008-05036	Nosy-Be	NBE	KC760024	KC760101
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H232	NBE-1433	URUN2008-05502	Nosy-Be	NBE	KC760025	KC760107
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H232	NBE-9999-1	UF9999-1	Nosy-Be	NBE	KC760026	-
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H233	NBE-1351-3	URUN2013-11157	Nosy-Be	NBE	KC760027	KC760106
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H233	MGTU-0119	URUN2008-07700	Toliara	TUL	KC760028	-
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H234	MGTU-0119-5	URUN2013-11179	Toliara	TUL	KC760029	KC760114
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H235	MGTU-0119-2	URUN2013-11176	Toliara	TUL	KC760030	KC760109
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H236	MGTU-0119-6	URUN2013-11180	Toliara	TUL	KC760031	KC760110
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H237	MADA-3381	URUN2008-07248	Nosy-Be	NBE	KC760032	KC760112
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H238	MGTU-0119-4	URUN2013-11178	Toliara	TUL	KC760033	KC760113
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H239	NBE-1351-4	URUN2013-11158	Nosy-Be	NBE	KC760034	KC760111
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H240	NBE-1351-1	URUN2013-11155	Nosy-Be	NBE	KC760035	KC760102
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H241	MADA-3382	URUN2008-07249	Nosy-Be	NBE	KC760036	KC760103
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H241	NBE-9999	UF9999	Nosy-Be	NBE	KC760037	-
Ophiidermatidae	<i>Ophiopeza fallax</i>	L1	H242	MGTU-0119-1	URUN2013-11175	Toliara	TUL	KC760038	KC760108
Ophiidermatidae	<i>Ophiopeza fallax</i>	L2	H243	MADA-3388	URUN2008-07255	Nosy-Be	NBE	KC760039	KC760099
Ophiidermatidae	<i>Ophiopeza fallax</i>	L2	H243	MADA-3349	URUN2008-07216	Nosy-Be	NBE	KC760040	-
Ophiidermatidae	<i>Ophiopeza fallax</i>	L2	H244	MGTU-0115	URUN2008-07696	Toliara	TUL	KC760041	KC760095/KC760097
Ophiidermatidae	<i>Ophiopeza fallax</i>	L2	H245	MGTU-0115-1	URUN2013-11169	Toliara	TUL	KC760042	-
Ophiidermatidae	<i>Ophiopeza fallax</i>	L2	H246	REU-0199-1	URUN2007-00266	Réunion	REU	KC760043	KC760098
Ophiidermatidae	<i>Ophiopeza fallax</i>	L2	H247	REU-0199-2	URUN2007-00267	Réunion	REU	KC760044	KC760096

Ophiodermatidae	<i>Ophiopeza fallax</i>	L2	H248	REU-0644	UF6521	Réunion	REU	KC760045	KC760100
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H249	MEPA-9280	URUN2009-09280	Glorieuses Islands	GLO	KC760046	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H250	MEPA-9289	URUN2009-09289	Glorieuses Islands	GLO	KC760047	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H251	MEPA-9299	URUN2009-09299	Glorieuses Islands	GLO	KC760048	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H251	MAY-7101-1	UF7101-1	Mayotte Is	MAY	KC760049	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H251	NBE-0733	URUN2008-04803	Nosy-Be	NBE	KC760050	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H251	MADA-3373	URUN2008-07240	Nosy-Be	NBE	KC760051	KC760118
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H251	NBE-7442	UF7442	Nosy-Be	NBE	KC760052	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H252	MEPA-9229	URUN2009-09229	Juan de Nova	JDN	KC760053	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H253	MAY-7102	UF7102	Mayotte Is	MAY	KC760054	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H254	MEPA-9349	URUN2009-09349	Glorieuses Islands	GLO	KC760055	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H255	MGTU-0111	URUN2008-07692	Toliara	TUL	KC760056	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H255	MGTU-0111-1	URUN2013-11167	Toliara	TUL	KC760057	KC760120
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H256	MGTU-0111-2	URUN2013-11168	Toliara	TUL	KC760058	KC760121
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H256	MGTU-0135	URUN2008-07716	Toliara	TUL	KC760059	KC760122
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H257	MADA-3372	URUN2008-07239	Nosy-Be	NBE	KC760060	KC760129
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H258	REU-0269	UF6447	Réunion	REU	KC760061	KC760128
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H259	REU-0026-1	URUN2007-00037	Réunion	REU	KC760062	KC760126
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H260	REU-0258	UF6437	Réunion	REU	KC760063	KC760127
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H261	NBE-7150-2	UF7150-2	Nosy-Be	NBE	KC760064	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H262	REU-0283	UF6452	Réunion	REU	KC760065	KC760119
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H263	REU-0846	UF6546	Réunion	REU	KC760066	KC760124
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H264	NBE-0780	URUN2008-04849	Nosy-Be	NBE	KC760067	KC760116/KC760123
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H265	NBE-0969	URUN2008-05038	Nosy-Be	NBE	KC760068	KC760117
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H266	MAY-7101	UF7101	Mayotte Is	MAY	KC760069	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H267	NBE-7150-1	UF7150-1	Nosy-Be	NBE	KC760070	-
Ophionereidae	<i>Ophionereis porrecta</i>	L1	H268	REU-0848	UF6550	Réunion	REU	KC760071	KC760125
Ophionereidae	<i>Ophionereis porrecta</i>	L2	H269	REU-0054-1	URUN2007-00080	Réunion	REU	KC760072	KC760130

Ophionereidae	<i>Ophionereis porrecta</i>	L2	H270	REU-0257	UF6436	Réunion	REU	KC760073	KC760131
Ophionereidae	<i>Ophionereis porrecta</i>	L2	H271	REU-0269-1	UF6447-1	Réunion	REU	KC760074	KC760087
Ophionereidae	<i>Ophionereis porrecta</i>	LX	H272	WAU15310	UF15310	West Australia	WAU	KC760075	-
Ophionereidae	<i>Ophionereis porrecta</i>	LX	H273	HAW6089	UF6089	Hawaii	HAW	KC760076	-
Ophionereidae	<i>Ophionereis porrecta</i>	LX	H274	LIZ8380	UF8380	Lizard Island	LIZ	KC760077	-
Ophionereidae	<i>Ophionereis porrecta</i>	LX	H275	LIZ3339	UF3339	Lizard Island	LIZ	KC760078	-
Ophionereidae	<i>Ophionereis porrecta</i>	LX	H276	LIZ3308	UF3308	Lizard Island	LIZ	KC760079	-
Ophionereidae	<i>Ophionereis porrecta</i>	LX	H277	WAU8952	UF8952	West Australia	WAU	KC760080	-
Ophionereidae	<i>Ophionereis porrecta</i>	LX	H278	HER15494	UF15494	Heron Island	HER	KC760081	-

Appendix S2 Summary statistics and demographic parameters of reef brittle-star nominal species in the Southwestern Indian Ocean.

Appendix S2a Summary statistics of mtDNA *COI* in (a) reef brittle-star nominal species surveyed in the Southwestern Indian Ocean (SWIO); and (b) divergent lineages (evolutionarily significant units, ESUs) observed in the SWIO. Larval developmental mode (LDM), total sample size (*n*), number of haplotypes (*H*), haplotype diversity (*Hd*), nucleotide diversity (π), mutational parameters θ_s and θ_π , Fu's F_s , Ramos-Onsins and Rozas' R_2 ; planktotrophic (P) and lecithotrophic species (L).

(a)											
Family	Nominal species	LDM	<i>n</i>	<i>H</i>	<i>Hd</i> (\pm SD)	π (\pm SD)	θ_s (\pm SD)	θ_π (\pm SD)	Tajima's <i>D</i>	F_s	R_2
Ophiocomidae	<i>Ophiocoma brevipes</i>	P	39	31	0.9852 (\pm 0.0104)	0.00721 (\pm 0.00400)	9.934 (\pm 3.217)	4.753 (\pm 2.639)	-1.9287**	-28.1834***	0.0502**
Ophiocomidae	<i>Ophiocoma sp. nov.</i>	P	52	29	0.9057 (\pm 0.0295)	0.00391 (\pm 0.00236)	7.967 (\pm 2.513)	2.577 (\pm 1.558)	-2.3701***	-28.791***	0.0318***
Ophiocomidae	<i>Ophiocoma cynthiae</i>	P	35	33	0.9966 (\pm 0.0078)	0.01266 (\pm 0.00668)	12.870 (\pm 4.155)	8.343 (\pm 4.400)	-1.567*	-27.756***	0.0673*
Ophiocomidae	<i>Ophiocoma erinaceus</i>	P	25	24	0.9967 (\pm 0.0125)	0.00964 (\pm 0.00527)	12.712 (\pm 4.401)	6.350 (\pm 3.471)	-2.0417*	-20.3733***	0.0499***
Ophiocomidae	<i>Ophiocoma scolopendrina</i>	P	31	27	0.9892 (\pm 0.0119)	0.01541 (\pm 0.00805)	14.018 (\pm 4.606)	10.157 (\pm 5.305)	-1.746	-13.9369***	0.0784
Ophiolepididae	<i>Ophioplocus imbricatus</i>	L	28	22	0.9815 (\pm 0.0147)	0.00734 (\pm 0.00411)	8.223 (\pm 2.899)	4.836 (\pm 2.708)	-1.5143*	-15.0325***	0.0631**
Ophiolepididae	<i>Ophiolepis cincta</i>	L	21	17	0.9667 (\pm 0.0301)	0.10535 (\pm 0.05282)	45.862 (\pm 15.564)	69.429 (\pm 34.805)	0.7797	2.2467	0.2031*
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L	24	19	0.9457 (\pm 0.0401)	0.02780 (\pm 0.01425)	15.800 (\pm 5.433)	18.322 (\pm 9.388)	0.2706	-2.2836	0.1486
Ophiodermatidae	<i>Ophiopeza fallax</i>	L	26	20	0.9785 (\pm 0.0166)	0.05115 (\pm 0.02566)	24.109 (\pm 7.964)	33.711 (\pm 16.913)	1.2751	0.0448	0.1786*
Ophionereididae	<i>Ophionereis porrecta</i>	L	29	23	0.9704 (\pm 0.0223)	0.02927 (\pm 0.01485)	25.209 (\pm 8.116)	19.288 (\pm 9.786)	-1.1989	-3.4679	0.0902
(b)											
Family	Nominal species	ESU	<i>n</i>	<i>H</i>	<i>Hd</i> (\pm SD)	π (\pm SD)	θ_s (\pm SD)	θ_π (\pm SD)	Tajima's <i>D</i>	F_s	R_2
Ophiolepididae	<i>Ophiolepis cincta</i>	L1	4	1	-	-	-	-	-	-	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L2	2	2	1.0000 (\pm 0.5000)	0.00607 (\pm 0.00679)	4.000 (\pm 3.162)	4.000 (\pm 4.472)	-	-	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L3	1	1	-	-	-	-	-	-	-
Ophiolepididae	<i>Ophiolepis cincta</i>	L4	9	8	0.9722 (\pm 0.0640)	0.00835 (\pm 0.00503)	6.991 (\pm 3.241)	5.500 (\pm 3.313)	-1.0455	-2.4592	0.1229
Ophiolepididae	<i>Ophiolepis cincta</i>	L5	5	5	1.0000 (\pm 0.1265)	0.00516 (\pm 0.00370)	3.360 (\pm 2.001)	3.400 (\pm 2.437)	0.0830	-2.0043*	0.2623
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L1	19	14	0.9123 (\pm 0.0605)	0.00625 (\pm 0.00364)	6.867 (\pm 2.678)	4.117 (\pm 2.396)	-1.6625*	-6.7838**	0.0963
Ophiodermatidae	<i>Ophiarachnella gorgonia</i>	L2	5	5	1.0000 (\pm 0.1265)	0.00577 (\pm 0.00407)	3.840 (\pm 2.243)	3.800 (\pm 2.682)	-0.0734	-1.8053	0.1772
Ophiodermatidae	<i>Ophiopeza fallax</i>	L1	19	14	0.9649 (\pm 0.0276)	0.00643 (\pm 0.00373)	5.150 (\pm 2.088)	4.240 (\pm 2.458)	-0.8428	-6.5897**	0.1092
Ophiodermatidae	<i>Ophiopeza fallax</i>	L2	7	6	0.9524 (\pm 0.0955)	0.00780 (\pm 0.00493)	5.714 (\pm 2.893)	5.143 (\pm 3.247)	-0.5504	-1.0734	0.1729
Ophionereididae	<i>Ophionereis porrecta</i>	L1	11	9	0.9636 (\pm 0.0510)	0.00770 (\pm 0.00456)	6.828 (\pm 3.018)	5.073 (\pm 3.008)	-1.3293	-2.7400	0.162
Ophionereididae	<i>Ophionereis porrecta</i>	L2	3	3	1.0000 (\pm 0.2722)	0.00708 (\pm 0.00592)	4.667 (\pm 3.127)	4.667 (\pm 3.900)	-	-	-

Significance levels: ns $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Appendix S2b Influence of localities on the genetic structure of nine species/ESUs of brittle-stars in the SWIO using the monophyletic clade (MC) statistic that quantifies the association between the phylogeny and a specific character (one locality) from the phylogeny–trait correlation analysis. The highest posterior density intervals at 95% are given in brackets. The locality codes are presented in Appendix S1.

ESU	EUR	GLO	JDN	MAY	NBE	REU	TRO	TOL
<i>Ophiocoma brevipes</i>	-	NA	-	NA	1.10 (1.00 - 2.00)	3.12 (2.00 - 4.00)	NA	2.55 (2.00 - 3.00)**
<i>Ophiocoma cynthiae</i>	NA	NA	-	1.13 (1.00 - 2.00)	NA	4.28 (3.00 - 7.00)	-	2.02 (2.00 - 2.00)*
<i>Ophiocoma erinaceus</i>	NA	1.33 (1.00 - 2.00)	1.14 (1.00 - 2.00)	1.09 (1.00 - 2.00)	NA	NA	NA	1.18 (1.00 - 2.00)
<i>Ophiocoma scolopendrina</i>	NA	1.18 (1.00 - 2.00)	-	NA	5.07 (5.00 - 6.00)**	3.62 (3.00 - 4.00)**	-	3.00 (3.00 - 3.00)**
<i>Ophioplocus imbricatus</i>	-	-	-	-	-	11.64 (9 - 20)*	-	4.43 (2.00 - 6.00)**
<i>Ophiarachnella gorgonia</i> L1	-	NA	-	1.43 (1.00 - 2.00)	2.02 (1.00 - 3.00)	-	-	3.12 (3.00 - 4.00)
<i>Ophiopeza fallax</i> L1	-	-	-	NA	5.06 (3.00 - 6.00)**	-	-	3.38 (2.00 - 5.00)
<i>Ophiopeza fallax</i> L2	-	-	-	-	1.99 (2.00 - 2.00)**	1.96 (1.00 - 2.00)	-	2.00 (2.00 - 2.00)**
<i>Ophionereis porrecta</i> L1	-	1.09 (1.00 - 2.00)	NA	NA	1.97 (1.00 - 3.00)	4.73 (3.00 - 5.00)**	-	1.92 (1.00 - 2.00)*

Appendix S2c Influence of the major locations on the global genetic structure (Φ_{ST}) for the community of brittle-stars within the SWIO. The average Φ_{ST} values are computed when including/excluding the location of interest. The Mann–Whitney U -test and its significance for each Φ_{ST} comparison are reported. The locality codes are presented in Appendix S1.

Location	Average Φ_{ST} values (\pm standard deviation)		Mann–Whitney U -test	P -value
	Only involving location	Excluding location		
GLO	0.144 \pm 0.231	0.102 \pm 0.301	988.0	0.643
MAY	0.121 \pm 0.253	0.103 \pm 0.293	855.5	0.201
NBE	0.124 \pm 0.343	0.105 \pm 0.259	855.0	0.403
REU	0.160 \pm 0.310	0.121 \pm 0.282	1080.5	0.760
TOL	0.230 \pm 0.225	0.084 \pm 0.310	648.0	0.001

Appendix S3 Mismatch distributions for the eight species/evolutionarily significant units of brittle-stars from the Southwestern Indian Ocean displaying departure from mutation-drift equilibrium (Appendix S2). Solid lines represent the expected distribution for a population under expansion and bars represent the observed distribution.

