

Biogeography of the terrestrial and freshwater biota of the Seychelles islands

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Abstract: The biodiversity of the Seychelles islands has long been considered to include a notable component of species isolated on the islands following the final fragmentation of Gondwanaland 65 million years ago. A review of the biogeography of all non-marine multicellular organisms recorded on the 115 islands is presented. The southern coral atolls of the group have a small biota descended from colonists arriving on the atolls as a result of rafting, mainly from Madagascar and Africa. A much smaller dispersive element is also present in the granitic islands, but these include fewer species of African origin. Few species can be confidently identified as having a Gondwanan origin. Detailed molecular phylogenetic studies are needed for a wide range of taxa to evaluate the true origins of the biota of these interesting islands.

Biogeographical patterns have long been of interest as indicators of past distributions and evolutionary processes. Wallace (1880) first drew attention to the extreme significance of islands as exemplars of biodiversity and since then they have been the subject of intense study at multiple levels. These include distribution patterns as indicators of dispersal or vicariance processes, and equilibrium dynamics as described by Island Biogeography Theory (McArthur & Wilson 1967). In all studies of island biogeography it is apparent that different organisms have different dispersal mechanisms which dramatically alter their biogeography. Highly motile species such as flies or birds tend to have relatively low endemic diversity levels and wider ranges except on the most isolated of islands. This often makes them less useful in biogeographic studies than less motile groups such as amphibians and molluscs. These latter two groups are of particular significance due to their relatively limited dispersal abilities over large areas of ocean.

High levels of endemism in the amphibian fauna of the Seychelles islands (90%) was one of the early pieces of evidence indicating an ancient continental origin for the islands (Wallace 1880). However, the low diversity of the group (only 12 species in the islands) and the restriction of most species to four islands (50% restricted to two islands) makes detailed biogeographical analysis impossible. The biogeography of Seychelles molluscs also has a long history, being mentioned by Wallace (1880) and Gardiner (1936). However, the first serious consideration of their biogeography was given by Bruggen (1967, 1986) who discussed the affinities of the Aldabran Streptaxidae. He noted the short geological history of the atoll and the close affinity of the streptaxids to African species, with a greater Asian influence in the granitic islands. Peake (1971) gave some examples of biogeographical patterns in molluscs but these were based only on literature and include several misidentifications. He considered the origin of the fauna to be primarily due to dispersal, accounting for the widely distributed coral island species but also the endemic genera such as *Stylodonta*, more usually

considered to be Gondwana relics. Gerlach & Bruggen (1999) noted that the mollusc fauna could be divided into two groups: the widespread recent colonists (introductions, cosmopolitan species and colonists from Africa) predominant in the low-lying coral atolls and cays and the more ancient species (largely of Gondwanan origin) of the high islands. The biogeography of only one genus has been analysed in detail within the islands; the cerastuid *Pachnodus* (Gerlach 1999). This genus is a Gondwanaland relict and shows a largely vicariant pattern with diversity being promoted by isolation and habitat specialisation.

In the 20th century other groups received some consideration (insects in general – Scott 1936; Cogan 1984), plants (Summerhayes 1931) and lizards (Cheke 1984). These studies concluded that oriental affinities dominated for the plants (Christensen 1912; Summerhayes 1931) in the granitic islands but with a higher pantropical or Indo-Pacific component in the coral islands (Procter 1984). Similarly, granitic Seychelles insects have been largely considered to be oriental (Holdhaus 1928; Scott 1933), as have the land snails (Nevill 1869).

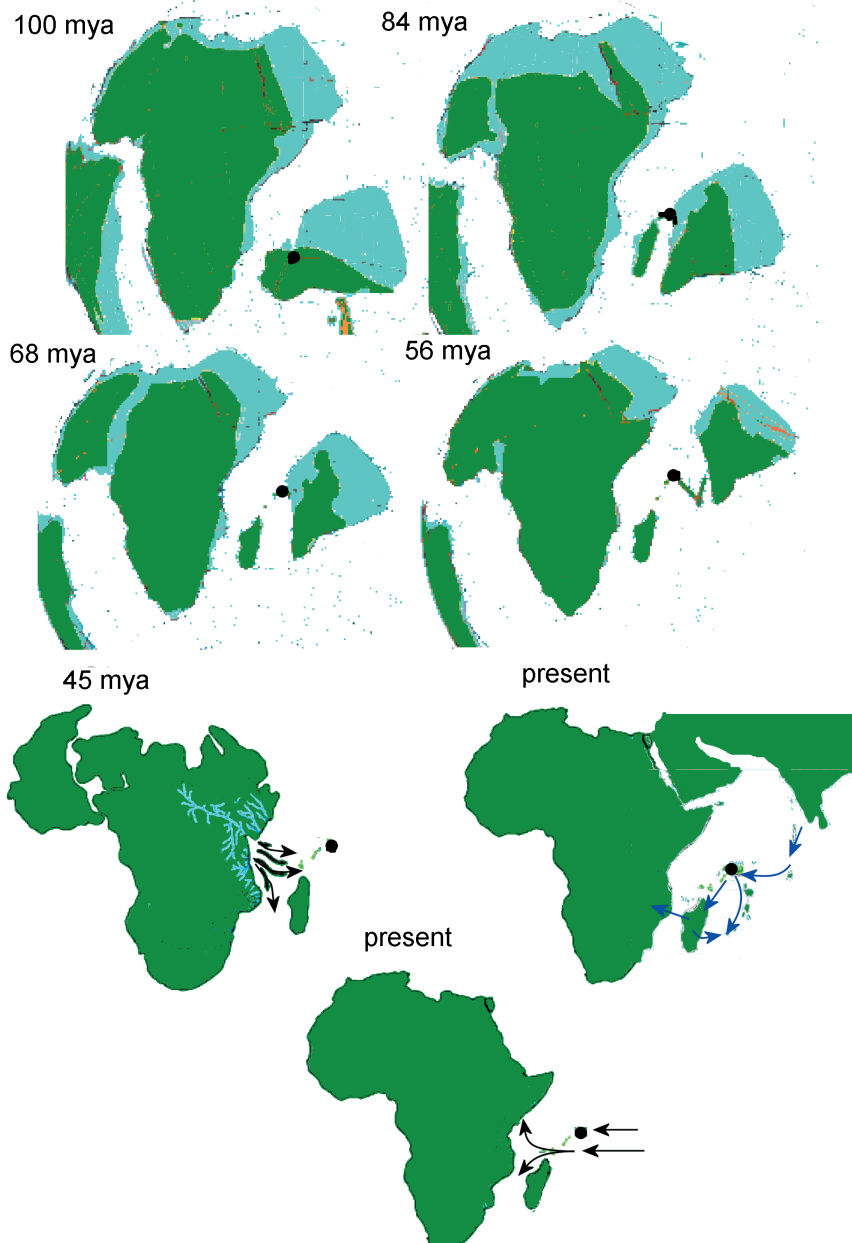
In investigating the origins of taxa based simply on distributions particular problems are found in distinguishing indigenous species from invasive ones. The difficulty of distinguishing successful colonist from invasives is exemplified by the nemertean ribbon worm *Geonemertes pelaensis*. This species was first described from south-east Asia (1863), followed by Seychelles (1905) and the west Pacific (1927). Records from other localities are more recent: Mascarenes (1975) and Caribbean and Florida (1982), suggesting a recent range expansion from an originally Indo-Pacific distribution. Caribbean populations can be considered introductions based on dating and biogeography, but its natural distribution within the Indo-Pacific remains conjectural. It is noteworthy that the only other members of the genus are the extinct Mascarene *G. rodericana* and the Phillipine species *G. philippinensis*.

In the past 10 years there has been a significant increase in biogeographical research, particularly using molecular techniques e.g. (Rocha *et al.* 2010a-d, 2011, 2013; Lima *et al.* 2013; Rouhan *et al.* 2007; Townsend *et al.* 2010). Western Indian Ocean biogeography studies were synthesised by Agnarrson & Kuntner (2012). In this synthesis they erroneously claimed that most of the granitic Seychelles islands had been submerged at times and that the biota was therefore largely of dispersive origin. They cited in support of this the fact that freshwater crabs had colonised by transoceanic dispersal (Daniels *et al.* 2006; Cumberlidge 2008; Daniels 2011) but noted that this did not apply to caecilians (Zhang & Wake 2009), sooglossid frogs (Biju & Bossuyt 2003) and some ferns (Lehtonen *et al.* 2010). This apparent contradiction was not resolved. A more detailed synthesis is presented here specifically for the Seychelles islands.

Geological background

The origin of the Seychelles islands as a whole is well established following numerous studies of Madagascar-Seychelles-India ('Greater India') geology. The islands are a remnant of the progressive fragmentation of Gondwanaland starting some 180 million years ago (mya). 100-90 mya Greater India split from Africa, followed by the movement of India-Seychelles and the Mascarene Plateau northwards, away from

Fig. 1. Position of Seychelles relative to nearby landmasses over the past 100 million years (after Ali & Aitchison 2008), and present day position with 100 m lower sea levels showing island stepping-stones scenario – blue arrows (after Warren *et al.* 2010), and prevailing ocean currents – black arrows.



Madagascar 89-85 mya (Storey *et al.* 1995). There is a recent suggestion that Mauritius overlies a fragment of ancient continent, being called 'Mauritia' (Torsvik *et al.* 2013). This appears to have broken off from the Madagascan part of Greater India, and to have been isolated from around 70 mya.

At this time extensive areas of magma surfaced to the east of Madagascar, giving rise to the Mascarene Ridge (Mukhopadhyay *et al.* 2012). Seychelles can first be considered to have existed 62 mya when the Seychelles microcontinent split from India as a result of intense activity in the Carlsberg ridge which started 64 mya (Mukhopadhyay *et al.* 2012). This suggests that Gondwanan affinities may be found in taxa showing a close relationship to India, Madagascar and, to a much lesser extent, Africa.

64 mya the area that became the Seychelles microcontinent would probably have been volcanically active, with traces of such activity on Silhouette and North islands. A large part of the microcontinent was, however, probably stable and volcanic activity may have been geographically very restricted. There is no evidence of volcanic activity on the Seychelles microcontinent (or plateau) since that date. Volcanic activity probably occurred to the south-west of the microcontinent, giving rise to the Amirantes and southern atolls. Whether these were ever exposed volcanoes or remained submarine sea mounts is not known. The coral islands have been dated back to 2.5 mya (in the case of Aldabra) but have been submerged repeatedly since then, most recently 125,000 years ago (Braithwaite *et al.* 1973).

Between 50 mya and the Ice Ages of the past 5 million years the land-masses in the Seychelles area would have been subject to erosive process and subsidence as the Amirante trench formed by subduction (Mukhopadhyay *et al.* 2012). The original topography of the Seychelles microcontinent is unknown; by the start of the Ice Ages it may have been similar to the present day and principally affected by fluctuating sea levels.

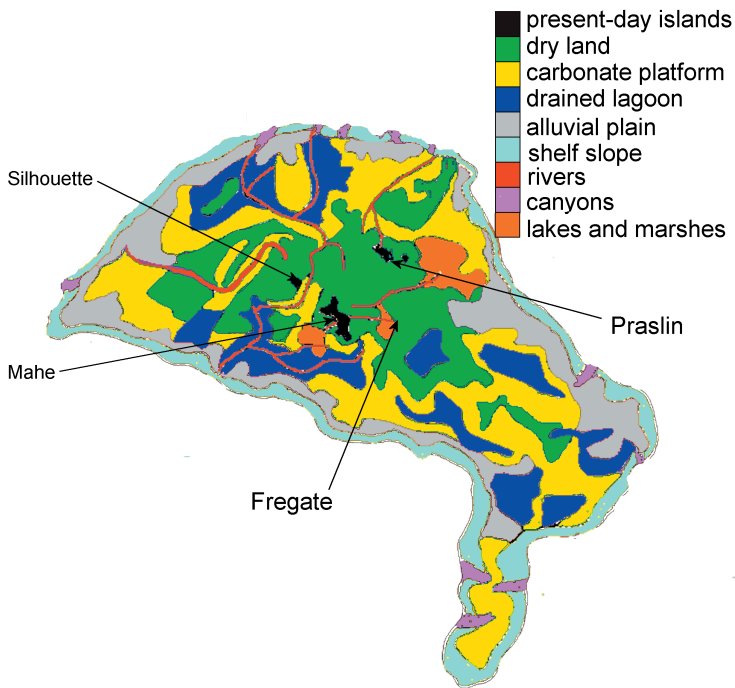
During the Ice Ages the Seychelles Bank would have been subject to repeated periods of exposure and extensive submergence. At times of extreme low sea-level all of the Bank would have been exposed as largely dry land. Lowland organisms would have been able to spread across much of this area, and at least some of the higher altitude species. Conversely, during high sea-levels the lowlands would have been flooded, isolating species on separate islands, drastically reducing the area of some of today's islands and completely flooding the lower ones. At the same time the coral islands of the Amirantes and the southern atolls, and the Salha de Maya bank would have been repeatedly exposed and completely submerged.

There are no detailed reconstructions of the exposed Seychelles Bank but a crude interpretation of a variety of data sources was carried out in 1986 (Badyukov *et al.* 1988). This is simplified here (Fig. 2), showing the unification of the islands by dry land at extreme low sea levels. There would have been rivers creating partial barriers between Silhouette, Fregate and the other islands.

Dispersal routes

The isolation of the islands as indicated by the geological reconstructions may not have been incomplete as chains of islands may have allowed some organisms

Fig. 2 Reconstruction of the main habitats of the exposed Seychelles plateau (modified from Badyukov *et al.* 1988). Black – present day islands; green – dry land; yellow – sea-level plateau of exposed carbonate platform; blue – tidal lagoon and estuaries; pale green - marsh; grey – reef rim, tidally exposed; pale blue – reef



to move between the apparently isolated land masses. These island chains have been described as the “Lemurian stepping-stones” (Schatz 1996; Steenis 1962) and are supposed to have been created by a drop in global sea levels 56-34mya exposing the Seychelles bank and Mascarene plateau (Rage 2003).

Ocean currents may have been favourable for colonisation from Africa to Madagascar and the Seychelle microcontinent initially until 50 mya (Masters *et al.* 2006), or occasionally until 20 mya (Ali & Huber 2010). Since then present-day current patterns have predominated, with a general east-west transport. This makes oceanic dispersal from Asia to Seychelles and from Seychelles towards northern Madagascar and east Africa most likely. Local current patterns around Aldabra are predominantly from the direction of Madagascar. It has been hypothesized that during periods of extreme low sea levels the exposure of the Seychelles Bank and the Mascarene Plateau would have altered the currents, specifically by blocking most of the east-west currents. This may have facilitated movement of organisms in a reverse direction, from Madagascar north-eastwards along the Amirante chain, which would have been exposed as a chain of stepping-stones up to the Seychelles Bank.

Lemurian stepping stones

The putative colonisation route between Africa/Madagascar and Asia via Seychelles was termed the ‘Lemurian stepping-stones’ by Van Steenis (1962) who proposed that a land-bridge (‘Lemuria’) had existed between Madagascar and Sri Lanka. Schatz (1996) proposed that Seychelles or the Mascarenes may have acted as these stepping stones.

Van Steenis (1962) included *Pyrostria* in the Rubiaceae as an example of a genus that used this route in the Eocene-Oligocene. However, a recent phylogeny of the Vanguerieae (Rubiaceae) (Wikstrom *et al.* 2010) failed to support this route, with no evidence of progression from Asia to Africa, via the Indian Ocean.

Broad geographical patterns

The comprehensive enumeration of the biodiversity of the islands (Table 1) shows that different taxonomic groups show differing broad geographical patterns (Fig. 3). These differ too much to allow any broad generalisations to be made. Even within major taxonomic groups there are notable differences, such as in the Myriapoda where the Diplopoda (millipedes) are Pantropical (60%) or Western Indian Ocean

Table 1. Numbers of species of different taxonomic groups identified in the Seychelles islands. Note Fungi and Nematoda are still insufficiently investigated and that Bryophyta collections have not been completely identified. Number of angiosperms are restricted to species established in the wild, excluding cultivated species.

	endemic	indigenous	introduced	uncertain	total
Lichens	0	305	0	100	405
Fungi	0	11	0	0	405
Bryophyta	14	161	0	0	175
Pteridophyta	17	66	7	2	92
Angiospermae	109	533	873	119	1,634
Platyhelminthes	2	0	7	9	18
Nematoda	18	20	1	12	54
Nemertea	0	0	0	1	1
Rotifera	0	0	0	36	36
Annelida	4	1	9	0	14
Mollusca	51	1	13	1	89
Tardigrada	19	14	0	0	33
Crustacea	24	48	4	4	82
Hexapoda	1,606	1,366	126	33	3,081
Chelicerata	201	127	16	15	359
Myriapoda	40	35	4	10	88
Vertebrates	54	39	24	3	120
TOTAL	2,169	2,727	1,084	345	6,586

(20%), whereas the Chilopoda (centipedes) are Asian (45%) or African (19%). The current estimates of origins for angiosperms are 14-35% endemic depending on what proportion of species are considered to be native. Procter (1984) considered the affinities to be mainly Asian but gave no comprehensive analysis for this. Scott (1933) considered 57% of the 2,426 species known at the time to be endemic and considered the majority to have affinities in the Oriental zoogeographical region. In Cogan's (1984) review the number of species was estimated to be 3,500 and from a selected group (Phasmopeta, Dermaptera, Blattidae, Odonmata and some Diptera) 51% were thought to be endemic, and the non-endemics predominately Afrotropical, followed by Oriental. The present analysis also gives 51% endemism for a total of 3,120 species and 25% of non-endemics are thought to be African in origin and only 13% Oriental.

Fungi have not been adequately sampled, the more inconspicuous forms in particular have been rarely studied (e.g. Sparrow 1975; Tedersoo *et al.* 2007; Suvi *et al.* 2010; Piątek & Vánky 2012) only one paper on macrofungi has been published (Watling & Seaward 2004). Lichens have been more extensively studied although new records are still being made (Sipman 2010).

The flying vertebrates (birds and mammals) have very high Western Indian Ocean affinities, with a strong Asian connection in the birds; it has been proposed that Seychelles acted as a steppingstone in the colonisation of Madagascar by Asian birds (Warren *et al.* 2005).

Comparison of the diversity of taxa with different biogeographical origins and their ranges shows that the southern atolls are occupied exclusively by recent colonists (in accordance with the islands having been exposed for only 120,000 years), with the majority from Madagascar (55% of native snail species). The granitic islands support a mainly ancient fauna (67% for snails: 44% having Gondwana affinities, 23% Asian possibly reflecting continental drift), although there is also a significant proportion of recent colonists from the Malagasy region (21% of snails). The dominance of the Malagasy origin within the recent colonists is more apparent in the granitic islands than in the coral islands (69% of snails compared to 55%). Most ancient taxa have smaller ranges than those of recent origin.

Vicariance or dispersal: the evidence

Table 2 summarises the studies that have discussed the origins of the Seychelles fauna and flora. In the molecular studies a molecular clock has sometimes been used to provide dating estimate. This is based on the assumption that the mutation rate within the genes studied remain constant, this mutation rate should be calibrated to the phylogeny produced, which requires some accurately dated points. Such calibration points are very rare, for the Western Indian Ocean the dating of emergence of the volcanic islands provide maximum ages for some lineages and these have been used in some studies (e.g. Warren *et al.* 2005). Studies that use assumed rates of mutation, without calibration should be considered cautiously (see Heads 2005 for a detailed criticism of examples of the use of uncalibrated clocks).

Table 2. Origins of genera and families in Seychelles. Dating is noted as E – estimate, C – calculated, (c) – calculated but without independent calibration.

Taxon	Origin	Route	Date (mya)	Data type	Source
Pteridophyta	<i>Nesolindsaea</i>				
	<i>Elaphoglossum</i>	long-range dispersal		molecular	Rouhan <i>et al.</i> 2004
Palmeae	<i>Deckenia</i>				Baker <i>et al.</i> 2011
	<i>Lodoicea</i>	vicariant			Baker <i>et al.</i> 2011
	Versaffeltiinae				
	(<i>Roscheria</i> + <i>Verschaffeltia</i> , <i>Nephrosperma</i> + <i>Phoenicophorium</i>)	long-range dispersal			Baker <i>et al.</i> 2011
Araceae	<i>Pistia</i>				
Medusagynaceae	<i>Medusagyne</i>	vicariant			Renner & Zhang 2004
					Fay <i>et al.</i> 1996
Dipterocarpaceae	<i>Vatieropsis</i>		25 C - but ancestor in Greater India early Eocene		Gunasekara 2004; Gamage <i>et al.</i> 2006
Nepenthaceae	<i>Nepenthes</i>	vicariant		morphology	Danser 1928; Clarke 1997
		land bridges		molecular	Meimberg <i>et al.</i> 2001
Rubiaceae	<i>Ixora</i> (<i>Pavettoides</i>)				B r e m e k a m p 1937b; Smith & Darwin 1988; De Block 1998
	<i>Ixora</i> (<i>Microixora</i>)				
Araliaceae	<i>Pyrostria bibracteata</i>				Wikstrom <i>et al</i> 2010
	<i>Canthium carinatum</i>				Wikstrom <i>et al</i> 2010
	<i>Polyscias</i>	vicariant		molecular	Lowry & Plunkett 2010

Taxon		Origin	Route	Date (mya)	Data type	Source
Annelida - Haemadipsidae	terrestrial leeches (<i>Idiobdella</i> and <i>Mahebdella</i> spp.)	Post-Gondwanan relics, closest to Madagascar	vicariant		morphology	Borda <i>et al.</i> 2007
Annelida - Oligocha	<i>Maheina</i>	Gondwana?, endemic Madagascar ?	?		morphology	
Mollusca - Pomatissidae	<i>Tropidophora pulchra</i>	Asia ?			morphology	
Mollusca - Hydrobiidae	<i>Moominia willii</i>	Gondwana	vicariant		morphology	
Mollusca - Acavidae	<i>Sylodonta</i>	Gondwana (west Africa)	vicariant		morphology, molecular	Mordan 1991, 1992 Bruggen 1975, 1978; Gerlach & Bruggen 1999)
Mollusca - Cerastidae	<i>Pachnodus</i>	Gondwana	vicariant		morphology	Rowson et al. 2011
	A) <i>Augustula</i>	molecular phylogeny origin ?	dispersal ?	C - Early Tertiary ?	molecular	Rowson et al. 2011
	B) <i>Priodiscus</i>	Molecular Origin ?	dispersal ?	C - Early Tertiary ?	molecular	Rowson et al. 2011
	C) other endemic genera	Mascarenes, origin ?	dispersal ?		molecular	Rowson et al. 2011
Mollusca - Gastrodon- toidea	<i>Nesokaliella</i>	basal		ancient ?	morphology	Gerlach 2001a
Crustacea - Talitridae	<i>Talitroides</i>	Greater India or alien?	?		morphology	Bousfield 1984
	<i>Syecheillum</i>	Africa	dispersal	8.7 (5.8-11.8)	molecular	Daniels 2011
Araneae	<i>Nephila inaurata</i>	Western Indian Ocean				Kuntner & Agnarsson 2011 & Kuntner
	<i>Nephylengys</i>	Western Indian Ocean				Agnarsson 2011 Wesener & Van
Myriapoda	<i>Seychellonema</i>	allied to Thereuopoda from south, east, south-east Asia and Australia	vicariant		morphology	den Spiegel 2009; Butler et al. 2010
Insecta - Drosophilidae	<i>Zaphrotius</i>	Asia to Africa by stepping stones				Yassin <i>et al.</i> 2008
Pisces	<i>Pachypanchax</i>	Madagascar	vicariant		molecular	Hedges et al.
Amphibia - Caeciliidae		Gondwana	vicariant		molecular	
Amphibia - Sooglossidae		Gondwana	dispersal			
Amphibia - Hyperoliidae	<i>Tachycinemis</i>	Madagascar	(rafting) vicariant?		molecular	
Reptilia	<i>Pamelaescincus</i>	Afro-Malagasy				Brandley et al. 2005

Taxon	Origin	Route	Date (mya)	Data type	Source
	<i>Janetaescincus</i>	Afro-Malagasy			Brandley et al. 2005
	<i>Lycognathophis</i>	Ethiopian & Oriental			Dowling 1990;
	<i>Archiaus tigris</i>	Africa	48.5-28.7 C	molecular	Vidal et al. 2008
	<i>Ailuronyx</i>	Afro-Malagasy	Cretaceous ?		Townsend et al. 2011
	<i>Urocyon ledon</i>	Afro-Malagasy	Cretaceous ?		A. Bauer pers. comm.
	<i>Trachylepis</i>	Asian	Cretaceous ?		A. Bauer pers. comm.
	<i>Phelsuma</i>	Africa - Comores	24-48 C		Lima et al. 2013
	<i>Pelusios</i>	Madagascar	30 C		Rocha thesis
	<i>Aldabrachelys</i>	Madagascar		molecular	Fritz et al. 2012
	<i>Zosterops</i>	Madagascar			Gerlach & Riux-Paquette 2013
		Asia			Warren et al. 2006
	<i>Dicrurus</i>	Madagascar	-	molecular, Aldabra as calibration	Pasquet et la. 2007
	<i>Hypsipetes</i>				Warren 2005
	<i>Nectarinia</i>	Africa	1-1.9 C	molecular, calibrated	Warren et al. 2003
Mammalia	<i>Electroenas</i>	Asia			Warren et al. 2010
	<i>Otus insularis</i>	Indo-Malaya, or Africa to Asia	3.6 C		Fuchs et al. 2008
	<i>Pteropus</i>	Asia to Africa to Seychelles			O'Brien et al. 2009
		Madagascar		dispersal	Chan et al. 2011
	<i>Coleura</i>	Madagascar		dispersal	Goodman et al. 2012

For vicariant Gondwanan origins to be identifiable, the group must have little, or no, ability to cross open ocean. Soft bodied animals lacking waterproofing could be good candidates for this; worms, snails and amphibians being the most likely. Leeches have no waterproofing and would not tolerate contact with salt-water; today they are restricted to the dampest high-forest habitats of Mahé and Silhouette islands. This suggests that they have been present on the islands since their formation and are true Gondwana relics, although no dating has been provided for their separation. The coco-de-mer *Lodoicea maldivica* is found in the otherwise Asian group Corylophoideae. This species has a gigantic seed that cannot undergo oceanic dispersal as a viable seed due to its weight. This lack of dispersal ability and Asian affinity suggests that it is a vicariant relict. Some flying species have been suggested to have Gondwanan origins (e.g. the chironomid midges *Tanytus complanatus*, *Larsia pallidissima*, *Gymnometriocnemus* (G.) *mahensis*, *Smittia megalochirus* and *Lepidopus nigratipes* – Sæther 2004), however, these taxa need more detailed investigation.

Dispersal is strongly indicated in the origin of the tiger chameleon *Archiaus*. The ancestral chameleon is thought to have been carried by a freshwater plume from rivers draining the central eastern African coast (Townsend *et al.* 2011). This drainage and its eastward plume would have facilitated rafting along the eastward ocean current of the Palaeogene (Ali & Huber 2010). This outflow would have remained effective until the Mioocene East African rifting forced the rivers into the Nile drainage, northwards.

Vences *et al.* (2003) considered the tree-frog *Tachycnemis* to fall into the group of recent dispersers, in this case from Madagascar although they did not estimate a date for this. However, Heads (2005) criticised the assumptions of their explanation, suggesting that a vicariant origin might be possible.

Probable recent colonists include *Hemidactylus mercatorius* with an endemic genetic group in the southern atolls, where colonisation must have occurred since the islands emerged from the sea 100,000 years ago.

The difficulty of determining origins is exemplified by the Streptaxidae family of carnivorous snails. Three lineages are present in the granitic islands of Seychelles, these all diverged during a major radiation of the family coincidental with the fragmentation of Gondwanaland. The dating for the relevant points is too imprecise to determine whether the groups diverged before or after the fragmentation of Greater India, it is therefore unclear whether they originated vicariantly or by early dispersal. The main Seychelles radiation forms a sister-group to the Mascarene streptaxid genera which may indicate that members of this group were distributed across the Mascarene plateau linking Seychelles and the Mascarenes. A major part of the plateau is the Sala de Maya bank which when it was formed some 31 million years ago would have been a substantial island close to, or linked to, the Seychelles plateau. The bank would have eroded progressively over millions of years but may have been in existence until sea-level rise some 10,000 years ago would have flooded it. This leaves several million years for Seychelles streptaxids to colonise the shrinking island before rafting between the islands of the Mascarene group.

Diversification within the islands

Within the islands the Cerastuidae *Pachnodus* snails show a clear vicariance pattern to speciation, with initial divergence into sympatric subgenera (*Pachnodus* and *Nesiocerastus*) and allopatric speciation of populations isolated on different islands as a result of post-glacial sea-level rise, with some degree of habitat specialisation leading to further speciation (Gerlach 1999). This analysis predates the discovery of the extinct species *P. curiosus*. Inclusion of this poorly known species into the phylogeny places it at the same node as *P. ladiguensis*, which is plausible biogeographically (Fig. 3). This study does not include any dating, studies of which are restricted to the reptiles and the endemic freshwater crab *Seychellum alluaudi* (Table 3).

Fig. 3. Evolution of *Pachnodus* species showing the possible distribution of forms at different times over the past 250,000 years. Dry land shaded, 50m submarine contours shown. a) 250,000 years ago – two subgenera widely distributed; b) 100,000 years ago – isolation of *P. lionneti* and habitat specialisation within the *Nesiocerastus* subgenus; c) 50,000 years ago – isolation of different island forms; d) present day – isolation of *Pachnodus* forms within Mahé and specialisation of the high altitude *Nesiocerastus* species.

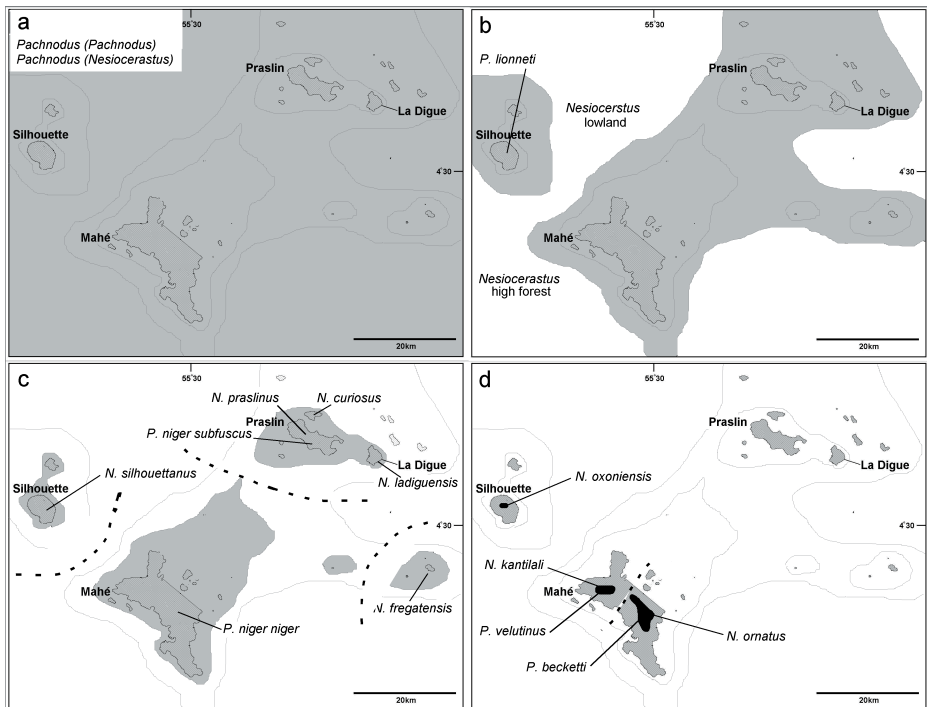


Table 3. Dates for division into island groups based on molecular studies of three reptile genera and the crab *Seychellum*. Splits are between the North (Praslin-La Digue) and South (Mahé-Silhouette groups)

Taxon	Split	Date (mya)	Source
<i>Phelsuma</i>	<i>astriata</i> – <i>sundbergi</i> split	6.4 (4.3-8.4) or 4	Rocha <i>et al.</i> 2013
<i>Phelsuma astriata</i>	North-South	0.5	Rocha <i>et al.</i> 2013
<i>Phelsuma sundbergi</i>	North-South	0.5	Rocha <i>et al.</i> 2013
<i>Urocytyledon inexpectata</i>	North-South	6.24 (3.4-13.9)	Rocha <i>et al.</i> 2011
	Within North	1.6	Rocha <i>et al.</i> 2011
	Within South	0.47	Rocha <i>et al.</i> 2011
<i>Seychellum</i>	Silhouette – others	2.73 (1.8-3.8)	Daniels 2011
	Mahé - Praslin	1.18 (0.8-1.7)	Daniels 2011
	Praslin – La Digue	0.41 (0.2-0.6)	Daniels 2011
	Fregate colonised	0.21 (0.1-0.4)	Daniels 2011

In lizards (data from Rocha *et al.* 2011, 2013) speciation appears to have occurred within the past 6 million years, and mostly within the past million years. Where there is geographical separation of species or genetic groups these can be dated to less than 0.8 mya for most species. The exception is *Urocytyledon inexpectata* which shows a north-south division at least 3.4 million years old and also relatively early divergence within those groups. The *Phelsuma* species show much more recent divergence, indicative of extensive dispersal until recently. In this genus *P. astriata* seems to have diverged into northern, southern and Fregate forms simultaneously (with Fregate being most similar to the norther group, but only weakly so). For *Urocytyledon* however, Fregate groups with the southern forms. In the case of the *Mabuya* skinks the ancestral form seems to have diverged more than 0.8 mya, giving rise to northern and southern clades of *M. sechellensis*. The southern clade seems to have hybridised with *M. wrightii* and also to have given rise to the Fregate population, although with some gene flow from the northern population a well and from Fregate to Mahé. Of all the reptiles this genus appears to have dispersed most frequently.

Synthesis

There thus seem to be four major events in Seychelles biogeography. Firstly the fragmentation of Gondwana as indicated by the vicariant species of Greater India aged around 64 mya. These comprise the caecilians and the sooglossid frogs and probably *Lodoicea*, *Nepenthes* and *Vateriopsis*. The second group are African migrants from the Palaeogene (65-23 mya) when rivers dispersed organisms eastwards, as exemplified by the chameleon and the freshwater crab. The third group dispersed from Asia into Seychelles and on to Madagascar using the stepping stones, the identified species are mainly volant vertebrates: birds and bats (Warren *et al.* 2006, 2010; O'Brien *et al.* 2009). The fourth category colonised from Madagascar by dispersal over the exposed land areas during periods of glaciation, this probably includes many of the lizard species. The exposed Seychelles and Saya de Malha banks would have altered ocean surface currents in the region, facilitating the south-west to north-east dispersal. Since the rise in sea-level 100,000 years ago ocean currents have been predominantly easterly to north-easterly, reducing colonisation potential from nearby land masses.

Within the islands two further events are identifiable: sea-level rise and current

patterns. Vicariant fragmentation has occurred in the granitic islands as the Seychelles bank has been submerged. In general this may be assumed to have been a broadly homogenous land mass, although with notable altitude variation. However, the present day distribution of some species suggests some patchiness of the habitat on the continental fragment. The restriction of *Lodoicea* to Praslin, Curieuse and St. Pierre suggests that the northern fringe was lower-lying, dryer (possibly fire-prone) habitat suited to palm forests, whereas the southern areas may have been wetter, in association with the high mountains of Mahé and Silhouette. In turn this suggests that *Lodoicea* may have originally been spread across the northern fringe, making a historical presence on La Digue probable. Although there is no direct evidence for this the presence of subfossils of the *Lodoicea*-associated snail *Styldonota studeriana* on La Digue suggest that such a distribution is possible. One other aspect of distribution suggests a notable change in habitats: that of the isolated cloud forest adapted species. Mahé and Silhouette share many biogeographical similarities due to the restriction of cloud forest species on the two islands. This is not surprising given their altitudes, but some of these species have very restricted dispersal abilities. Most notable is the terrestrial dytiscid diving beetle *Labourdonnaisia mahensis* which is restricted to the water film between leaves above 650 m altitude. This is flightless and so its presence on the two islands requires either extreme dispersal events, or a continuous area of habitat in the past. Extreme dispersal would require a storm of such intensity that waterlogged *Northea* leaves could be blown from one island to the other, which may seem implausible. Alternatively cloud forest must have been present from Mahé to Silhouette, accounting for the close similarity of the fauna of the two main habitat patches. For this to have eroded away into the present-day relatively deep marine channel between the islands would require a considerable passage of time. A molecular comparison of the Mahé and Silhouette populations is required to give an indication of the timing of the separation of the *Labourdonnaisia* populations. At present these remain unanswerable enigmas.

As the sea-levels rose Silhouette and North would have been isolated first, followed by a three-way split between Mahé, Praslin and Fregate. This is reflected in snail distributions. Ocean current mediated dispersal gives a different pattern with a north – south split, Silhouette now grouping with Mahé. This is reflected in the reptiles in particular. With dispersal Fregate is anomalous, being at the junction of the northern and southern groups, in most cases it falls into the latter. In the case of the crab *Seychellum* it has been proposed that a freshwater plume from Mahé to Fregate allowed colonisation of the island, this could also have transported rafting animals in that direction, around 210,000 years ago (Daniels 2011). It is notable that the reconstruction of the Seychelles bank exposed during low sea levels indicates that a river may have run from central Mahé to a marsh near Fregate island (Fig. 2), providing a dispersal route from Mahé to Fregate. This may make a more plausible colonisation route for *Seychellum* on Fregate.

Within Mahé there are three haplotype clusters in *Seychellum*, corresponding to the south, the north and La Gogue, La Misere and North Mahé, South Mahé (Daniels 2011). This is in agreement with biogeographical analyses of snails which find a division between north and south Mahé in *Edenutlina*, *Pachnodus*, *Nesokaliella* and *Styldonota*

(Gerlach & Bruggen 1999; Gerlach 2001, 2007). In the case of the crab this appears to relate to river drainages, for the snails it has been interpreted to be due to seal-level changes altering habitats around a topographical division in the La Misere area of Mahé. A similar pattern is thought to occur in sooglossid frogs (pers. obs.).

Overall the biogeography of the Seychelles islands shows a mixture of vicariant and dispersal patterns. This is clearest in recently radiating species groups (e.g. some of the snails) and well studied taxa (reptiles and birds). However, the significance of the original Gondwanan component remains largely speculative after 100 years of biogeographical research. This is unlikely to change until a wide range of taxa have been studied in detail using molecular phylogenies with calibrated dating estimates. The author did propose the organisation of a comprehensive molecular phylogenetic research programme with representative coverage of different groups, however, this proposal was rejected by the Seychelles government (D. Dogley *in litt.*) and research on this topic remains restricted to a piecemeal approach relying on the interests of individual researchers.

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Appendix: Emendations to the Seychelles fauna monographs

Corrected names are shown in bold.

Mollusca

Euconulidae

Dupontia sp. = ***Microcystina minima*** (H. Adams, 19867) (Rowson *et al.* 2010).

Subulinidae

Subulina striatella = ***Striosubulina striatella*** (Rang, 1831)

Cerastidae

Edouardia conulina = ***Gittenedouardia conulina*** (von Martens, 1869)

Myriapoda

Chilopoda

Scutigerae

Scutigera coleoptera Linnaeus, 1758 – introduced: Praslin (K. Joliffe pers. comm.).

Chelicerata

Araneae

Nephilengys borbonica Saaristo, 2010 = ***Nephilengys livida*** (Vinson, 1863) removed from synonymy of *N. borbonica* (Kuntner & Agnarsson 2011).

Aridella bowleri Saaristo, 2002 = ***Brignolia bowleri*** (Saaristo, 2002) (Platnick *et al.* 2011).

Lisa trichinalis (Benoit, 1979) = ***Brignolia trichinalis*** (Benoit, 1979) (Platnick *et al.* 2011), a Mauritian species.

Matyotia tetraspinosus Saaristo, 2001 = ***Heteroonops spinimanus*** (Simon, 1891) (Platnick & Dupérré 2009), an introduced pantropical species.

Pelecinus mahei Saaristo, 2010 = ***Pelecinus marmoratus*** Simon, 1891 (Platnick *et al.* 2012) a pantropical species.

Pholcus longiventris Saaristo, 2010 = ***Uthina luzonica*** Simon, 1893 (Huber 2011).

Cenemus squamata Saaristo, 2010 (misidentified) = ***Cenemus lami*** Berry, Beatty & Prószyński, 1997 (Zabka & Waldock, 2012).

Brignolia cubana Saaristo, 2010 = ***Brignolia parumpunctata*** (Simon, 1893) (Platnick *et al.* 2011).

Silhouettella assumptia Saaristo, 2001 = ***Noidiatella assumptia*** (Saaristo, 2001) Madagascar, Assumption, Farquar.

Hexapoda

Diptera

Culicidae (Le Goff *et al.* 2012)

Aedes seychellensis = junior synonym of *Aedes (Aedimorphus) albocephalus*

Culex antennatus – new record Aldabra

Culex sunyaniensis – new record Praslin

Clusiidae

Heteromeringia nigrifrons Lamb, 1914 = *Heteromeringia tephros* Lonsdale & Marshall, 2007

Cecidomyiidae

Megommata seychellensis was recorded on Mahé in 1940 as a species commonly feeding on *Pulvinaria* sp. (Vesey-Fitzgerald 1940, 1941)

Syrphidae

Figures of Syrphidae (p. 238) were mislabelled and should be: Fig. 12.1a - *Ischiodon aegyptiacus*, 12.1b - *Eristalinus seychellarum*. *Melanostoma annulipes* is not figured.

Two species were omitted:

Allograpta nasuta (Macquart, 1842) widespread in Africa and the western Indian Ocean (see www.syrphidae.com) and *Syritta nigrofemorata* Macquart - Aldabra 1968 (Lyneborg & Barkemeyer 2005).

Coleoptera

Curculionidae

Cratopus roberti Galman *et al.*, 2012 – Praslin

C. griseovittatus Linell, 1897 = *Cratopus griseovestitus* Linell, 1887. Galman *et al.* 2012 describe several subspecies despite probable movement of this species between islands. *C. g. griseovestitus* is known from the Mahé and Praslin groups and Silhouette. *C. g. northilandensis* from North and *C. g. fregata* from Fregate.

Cratopus venustus Galman *et al.* 2012 – Praslin

Galman *et al.* 2012 recognise the *C. segregatus* subspecies as valid: *C. s. segregatus* from Silhouette, *C. segregatus subcinctus* from Praslin and Round

Nitidulidae

Cybocephalinae

Cybocephalus blandus Endrody-Younga, 1964

C. compressus Endrody-Younga, 1964

C. grouvillei Endrody-Younga, 1964

C. mahensis Endrody-Younga, 1964

C. minimus Grouvelle, 1913 = *C. brevis* Grouvelle, 1913

C. rugatus Endrody-Younga, 1964

C. seychellensis Endrody-Younga, 1964

Eupraeinae

Eupraea (Haptoncuria) motschulskyi Reitter, 1873 – introduced. Kirejtshuk 2005