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an exclusively to predominantly herbivorous diet^{23,24}. In overall morphology the dentition most closely resembles that of some ornithischian dinosaurs, particularly stegosaurs and ankylosaurs, which are also generally regarded as herbivores^{25,26}. Still, there are no modern crocodylian analogues with which to compare the potential function of *Simosuchus'* unique skull and dentition, and the suggestion of an herbivorous diet is speculatively based on dental comparisons with non-crocodylian reptiles. Given the cranial and dental specializations as well as the small size of the adult *Simosuchus*, it can be assumed that *Simosuchus* did not bring down large prey. It is still plausible, however, that the diet may have consisted of arthropods, other invertebrates and potentially small vertebrates such as frogs.

Similarities with ankylosaurid dinosaurs are not limited to dentition. Other features of *Simosuchus* appear to be convergent with those of ankylosaurs, such as the broad compact body, extensive dorsal and ventral shielding, bony protection of the skull above the supratemporal fenestrae and orbits, and a deep cranium with a broad, short snout. A crocodyliform convergent upon an ornithischian dinosaur is intriguing in light of the apparent absence of the latter from the Late Cretaceous of Madagascar.

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Diversity and endemism of the benthic seamount fauna in the southwest Pacific

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Seamounts comprise a unique deep-sea environment, characterized by substantially enhanced currents and a fauna that is dominated by suspension feeders, such as corals¹⁻⁴. The potential importance of these steep-sided undersea mountains, which are generally of volcanic origin, to ocean biogeography and diversity was recognized over 40 years ago⁵, but this environment has remained very poorly explored. A review³ of seamount biota and biogeography reported a total of 597 invertebrate species recorded from seamounts worldwide since the Challenger expedition of 1872. Most reports, based on a single taxonomic group, were extremely limited: 5 seamounts of the estimated more than 30,000 seamounts in the world's oceans^{4,6} accounted for 72% of the species recorded. Only 15% of the species occurring on seamounts were considered potential seamount endemics. Here we report the discovery of more than 850 macro- and megafaunal species from seamounts in the Tasman Sea and southeast Coral Sea, of which 29-34% are new to science and potential seamount endemics. Low species overlap between seamounts in different portions of the region indicates that the seamounts in clusters or along ridge systems function as 'island groups' or 'chains,' leading to highly localized species distributions and apparent speciation between groups or ridge systems that is exceptional for the deep sea. These results have substantial implications for the conservation of this fauna, which is threatened by fishing activity⁷.

Whereas previous studies of the seamount fauna have often focused on particular taxa, the present study sought to describe the benthic community as a whole and enlisted broad taxonomic support (see Acknowledgements). In all, 516 species of fish and macro-invertebrates were obtained from 6 seamounts along the Norfolk Ridge, 108 from 4 seamounts on the Lord Howe Rise, and 297 from 14 seamounts south of Tasmania (Table 1, Fig. 1). Thirtysix per cent of species from the Norfolk Ridge seamounts were new to science and not known from sampling of the open seafloor and are therefore potential endemic species, along with 31% of species from the Lord Howe seamounts and between 16 and 33% from the Tasmanian seamounts.

- Over the range of sampling carried out on Norfolk and Lord Howe Ridges, we found a linear relationship between number of species recorded from each seamount and the number of samples obtained there (Fig. 2). This relationship implies that the greater number of species obtained from seamounts on Norfolk Ridge is

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Figure 2 Relationship between the number of species recorded at each seamount site and the number of samples obtained from that site.

Figure 1 Location of seamount sampling sites (triangles) and topographic and oceanographic features mentioned in the text. Depths are given in fathoms (1 fathom = 1.83 m).

owing to greater sampling effort there rather than greater species richness. The lack of an asymptote in the relationship implies that the number of species present on these seamounts is far greater than the number currently recorded. Species richness on the Tasmanian seamounts appears to be significantly greater, but it is unclear whether this is due to greater diversity or is an artifact of sampling over a greater number of seamounts, albeit within a limited area. Although sampling on the Tasmanian seamounts extended deeper than on Lord Howe Ridge and the Norfolk Rise, sampling in the northern Tasman Sea extended into shallower depths (Table 1). Most species on the Tasmanian seamounts exhibited a broad depth distribution and few were found only at the greatest depths sampled⁷. High species diversity has been previously noted off southeastern Australia^{8,9}.

The coefficient of community (C) between seamounts decreased significantly from a median value of 0.21 (range 0.08–0.49) for adjacent seamounts on the same ridge to a median of 0.04 (range 0–0.17) for seamounts on different ridge systems within the northern sector of the Tasman Sea and southeast Coral Sea (that is, the Norfolk Ridge and Lord Howe Rise) (analysis of variance (ANOVA), $F_{1,43}$ (C) = 46.56, P < 0.001) (Fig. 3). Just four species from the Tasmanian seamounts are known from the seafloor around New Caledonia (the bryozoan Haswelliporina multiaviculata, the bivalve Acesta sp., the barnacle Hexelasma sp., and the hydroid Symplectoscyphus commensalis), but none of these was found on

seamounts in that region (C = 0). Thus there are significant differences in species composition of the seamount communities between ridge systems at a similar latitude and separated by ~1,000 km across the northern Tasman Sea and southeast Coral Sea, and a complete changeover of species between the northern and southern sectors of the Tasman Sea. C did not decline significantly with distance on smaller scales (tens to several hundred kilometres) (Fig. 3).

Although the region around southern Australia and New Caledonia is noted for its relatively isolated faunas^{10,11}, the complete lack of affinity between the seamount communities across this area appears remarkable. For comparison, about 60% of the 93 species of non-mesopelagic decapod crustaceans (Anomura, Caridea, Palinura, Brachyura and Astacidea) recorded from depths greater than 200 m on the continental slope off southeastern Australia (south of \sim 35° S latitude) are recorded from the Indo-West Pacific region as well (G.C.B.P., unpublished data). This mirrors the general pattern for decapods on the continental shelf in this region, although isopod affinities are mostly with Antarctic and deep-sea faunas⁹. Thus, the isolation of the seamount faunas between the southern and northern Tasman Sea contrasts markedly with the generally strong affinity displayed by the soft-sediment slope fauna between these two regions.

It was also striking to find such little overlap in community composition in the deep sea between sites sharing the same habitat

Table 1 Location and depth range of seamounts sampled					
Seamount	Latitude	. Longitude	Seamount depth range (m)	Sampling depth range (m)	Number of samples
Norfolk Ridge			· · · · ·		
Aztec ·	24° 07'	168° 45'	55-1.000	57-800	16
Sponge	24° 55'	168° 20'	450-2.000	494-920	84
Jumeau East	23° 42′	168° 17′	250-1.500	380-950	30
Jumeau West	23° 40′	168° 00'	200-1.000	230-730	51
Kaimon Maru	23° 26'	168° 05'	400-2.000	223-600	58
Stylaster	23° 40′	167° 40'	400-1.000	418-970	29
Lord Howe		•			
Argo	23° 13'	159° 35′	150-2.000	178-300	6
Kelso	23° 51′	159° 24′	150-2.000	160-840	12
Nova	22° 28'	159° 15'	250-2.000	277-930	9
Capel	24° 50'	159° 35′	200-2.000	223-540	8
Tasmanian*	44° 12′ - 44° 24′	146° 59' - 147° 23'	660-2,000	660-1.700	34

* The Tasmanian seamounts are aggregated owing to limited sampling on 14 individual seamounts.

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Figure 3 The coefficient of community (*C*) in relation to distance. *C* is shown between seamount sites (inverted solid diamonds), hydrothermal vent sites from the East Pacific Rise in the North and South Pacific and Galapagos Rift (open circles), and vent sites from disjunct ridges in the northeast Pacific at $41-49^{\circ}$ N (crossed circles).

type, at similar latitude and depth, and only \sim 1,000 kilometres apart. This distribution pattern is consistent with Johannesson's hypothesis that many taxa adapted to seamount conditions limit their dispersal to maintain their populations, because of the generally small size of seamounts, the considerable distance between them and their unique oceanographic environment^{12,13}. Circulation cells in the vicinity of seamounts and along seamount chains have been shown to facilitate recruitment to seamounts within relatively close proximity of each other and along ridge systems^{14,15}.

Endemicity of the benthic fauna on southwest Pacific seamount groups/chains appears to be greater than that of deep-sea vent communities, another specialized deep-sea habitat. For comparison, we calculated C on the basis of available data for vent sites from the Explorer, Juan de Fuca and Gorda Ridges in the northeast Pacific at 41-49° N latitude, several sites along the northern East Pacific Rise (9-13°, 21° and 27° N latitude), the Galapagos Rift on the equator and 17–18° S'latitude on the southern East Pacific Rise¹⁶. In contrast to the seamounts, there was substantial similarity in community composition, even at distances of 3,000-4,000 km (Fig. 3). There was some indication that similarity might be reduced between disjunct ridge systems (for example, between the Juan de Fuca and East Pacific Rise) but these differences were not significant (analysis of covariance (ANCOVA), $F_{1,12} = 3.02$, P = 0.11), and the similarity of vent communities between disjunct ridge systems was still clearly greater than between seamounts in the northern and southern Tasman Sea (Fig. 3). Vents are relatively ephemeral environments, whereas seamounts are typically millions to tens of millions of years in age, so dispersal between vent sites is essential to the continuance of these communities. Cold seeps, on the other hand, appear to have higher levels of endemicity: most species are apparently restricted to single regions¹⁷, which has been related to the stability and isolation of these habitats. However, direct comparison with cold seep communities would be premature, as most cold seeps are poorly explored with only a few species recorded per site.

Wilson and Kaufmann³ estimated the endemism of fishes and invertebrates on seamounts as 12 and 15%, respectively, but half of the reports that they cited from reasonably well-studied regions (that is, the Hawaiian Ridge, Mid-Pacific Mountains, Kyushu-Palau Ridge, Vema seamount) indicated levels of endemism of 22–36%, consistent with our results. Citing Hubb's 'stepping-stone' hypothesis⁵, Wilson and Kaufmann³ emphasized the faunistic links among seamount chains extending around the rim of the North Pacific, along the East Pacific Rise into the southeast Pacific and through the Emperor Chain and Hawaiian Ridge into the central North Pacific. The apparently distinct seamount chains of the southwest Pacific, Indian and Southern Oceans and much of the Indo-West Pacific¹⁸ were, however, virtually unexplored at that time. Seventeen new genera were obtained from the Norfolk Ridge samples, four from the Lord Howe Ridge and seven or eight from the Tasmanian samples. Some appear to be relicts of groups earlier believed to have disappeared in the Mesozoic^{19–23}. These seamounts thus appear to be isolated marine systems and provide an exceptional opportunity to examine evolution and speciation in the deep sea.

The highly localized distribution of many seamount species has profound implications for their conservation. Seamount communities are extremely vulnerable to the impacts of fishing: their limited fixed habitat, the extreme longevity of many species (of the order of 100 years and more^{22–24}), and the apparently limited recruitment between seamounts, all compound the uncertainty of recovery from trawling, which sweeps away the benthic epifaunal communities is unknown; however, the localized distribution of many benthic seamount species greatly increases the threat of extinction and may require that conservation and protection of seamount communities be undertaken on a local scale.

Methods

Our study is based on 23 cruises that the Muséum National d'Histoire naturelle and the Institut François de Recherche Scientifique pour le Développement en Coopération (MUSORSTOM) carried out since 1984 to study the fauna of the seamounts, ridges and adjacent seafloor within the EEZ of New Caledonia at the northern edge of the Tasman Sea, 11 of which focused on seamounts, primarily along the Norfolk and Lord Howe Ridges¹⁶, a single cruise carried out by the Commonwealth Scientific and Industrial Research Organization (CSIRO) in 1998 to study the benthic fauna of 14 small seamounts off southern Tasmania at the southern extreme of the Tasman Sea⁷; and surveys by the Museum of Victoria of the soft-bottom fauna of the continental slope off southeastern Australia based cruises in 1984, 1986 and 1994 (ref. 9) (Table 1, Fig. 1). ORSTOM carried out 462 travlis and 748 dredge hauls using a cod end with 10 mm mesh²²; many results are presented in the 21 volumes of *Resultats des campagnes MUSORSTOM*²⁶. On the CSIRO cruise, so far as was possible, each seamount was sampled on its summit, slope and base using a dredge with a cod end of 25 mm of stretched mesh; 34 samples were obtained in all.

To compare the similarity in fauna between two seamounts, we used the coefficient of community (variously referred to as Sorensen's, Dice's or the Bray-Curtis similarity statistic for binary data): C = 2a/(b+c), where *a* is the number of species in common to both sites and *b* and *c* are the total number of species found at each site. *C* is commonly assumed to vary between 0 and 1 (ref. 25), but in fact the maximum value is sensitive to the relative number of species present at the two sites³⁷ and is conservatively biased when the sampling and number of species at two sites differs significantly. The proportion of species at the less well-sampled site in common to the two sites (that is, C' = a/b, where b < c) is biased in the opposite direction and was used as an upper limit to the coefficient of community between two sites, where there were large differences of sampling intensity; however, use of *C'* did not materially affect any of our conclusions.

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Digital selection and analogue amplification coexist in a cortex-inspired silicon circuit

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Digital circuits such as the flip-flop use feedback to achieve multistability and nonlinearity to restore signals to logical levels, for example 0 and 1. Analogue feedback circuits are generally designed to operate linearly, so that signals are over a range, and the response is unique. By contrast, the response of cortical circuits to sensory stimulation can be both multistable and graded¹⁻⁴. We propose that the neocortex combines digital selection of an active set of neurons with analogue response by dynamically varying the positive feedback inherent in its recurrent connections. Strong positive feedback causes differential instabilities that drive the selection of a set of active neurons under the constraints embedded in the synaptic weights. Once selected, the active neurons generate weaker, stable feedback that provides analogue amplification of the input. Here we present our model of cortical processing as an electronic circuit that emulates this hybrid operation, and so is able to perform computations that are similar to stimulus selection, gain modulation and spatiotemporal pattern generation in the neocortex.

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The multistability of digital circuits and the linear amplification achieved in analogue circuits are generally seen as incompatible functions and are separated into two classes of electronic technology. However, the neuronal circuits of the neocortex do not respect this distinction. There, multistability coexists with analogue response. For example, when a visual stimulus is attended at the expense of other visual stimuli—the subject is concentrating on one object in a field of vision—then many cortical neurons tend to respond in a graded way to the sensory attributes of the attended stimulus, as if it were presented alone².

We have designed a simple electronic circuit that emulates this hybrid behaviour. The circuit comprises a ring of 16 excitatory neurons, each of which makes synaptic connections of variable strength onto itself and onto its nearest and next nearest neighbours. These localized excitatory interactions reflect the preference for local connections observed in neocortex. At the centre of the ring is a single inhibitory neuron that receives synaptic input from all the



Figure 1 Silicon implementation of a recurrent network with a ring architecture. The synaptic connections are consistently coloured in the **a**–**c**. **a**, Each excitatory neuron E makes connections (blue) with itself and four neighbours on the ring, of strength α_r . The inhibitory neuron I makes global recurrent connections on the ring of strength β . Green, presynaptic connections; red, postsynaptic connections. **b**, The core of the excitatory neuron is the current mirror labelled rectification which contains a large capacitance. **c**, The core of the inhibitory neuron is the bipolar current mirror that sets the gain of inhibition (see Methods).

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