precipitation as sulphide and carbonate decrease the Fe^{2+} activity[5] such that redox potentials around −0.53 V are realistic. Proton reduction to H_2 ($E^0_{pH7} = -0.41$ V) on metallic iron in such surroundings would thus be far from the thermodynamic equilibrium.

Equation (1) is based on the equations for sulphate reduction with the organic compound ($2[CH_2O] + SO_4^{2-} \rightarrow 2HCO_3^- + H_2S$) and hydrogen ($4H_2 + SO_4^{2-} + 2H^+ \rightarrow H_2S + 4H_2O$). If SRB reduce 1 mol SO_4^{2-} with an organic compound to 1 mol H_2S, the latter yields 1 mol H_2 upon chemical reaction with Fe to FeS. Use of H_2 for further sulphate reduction yields $^1/_4$ mol H_2S which leads to $^1/_4$ mol H_2. Continuation ad infinitum leads to a total of $1^1/_3$ (sum of infinite row $1 + {}^1/_4 + {}^1/_{16}$ etc.) mol H_2S that attacks the iron. (For other remarks on reactions in corrosion see Supplementary Information.)

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Correspondence and requests for materials should be addressed to F.W. (fwiddel@mpi-bremen.de). The nucleotide sequences have been deposited at EMBL GenBank under accession numbers AY274444 (strain HS2) AY274449 (strain IS5), AY274450 (strain IS4) and AY274451 (strain IM1).

Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals

Hironobu Fukami[1,2], Ann F. Budd[3], Gustav Paulay[4], Antonio Solé-Cava[5], Chaolun Allen Chen[6], Kenji Iwao[7] & Nancy Knowlton[1,2]

[1]*Smithsonian Tropical Research Institute, Naos Marine Laboratory, Box 2072, Balboa, Republic of Panama*
[2]*Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, University of California San Diego, La Jolla, California 92093-0202, USA*
[3]*Department of Geoscience, University of Iowa, Iowa City, Iowa 52242, USA*
[4]*Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611-7800, USA*
[5]*Department of Genetics, Federal University of Rio de Janeiro, Rio de Janeiro, RJ, Brazil*
[6]*Institute of Zoology, Academia Sinica, Nankang, Taipei 115, Taiwan*
[7]*Akajima Marine Science Laboratory, Zamami-son, Okinawa 901-3311, Japan*

Only 17% of 111 reef-building coral genera and none of the 18 coral families with reef-builders are considered endemic to the Atlantic, whereas the corresponding percentages for the Indo-west Pacific are 76% and 39%[1,2]. These figures depend on the assumption that genera and families spanning the two provinces belong to the same lineages (that is, they are monophyletic). Here we show that this assumption is incorrect on the basis of analyses of mitochondrial and nuclear genes. Pervasive morphological convergence at the family level has obscured the evolutionary distinctiveness of Atlantic corals. Some Atlantic genera conventionally assigned to different families are more closely related to each other than they are to their respective Pacific 'congeners'. Nine of the 27 genera of reef-building Atlantic corals belong to this previously unrecognized lineage, which probably diverged over 34 million years ago. Although Pacific reefs have larger numbers of more narrowly distributed species, and therefore rank higher in biodiversity hotspot analyses[3], the deep evolutionary distinctiveness of many Atlantic corals should also be considered when setting conservation priorities.

We tested the assumption of inter-oceanic monophyly by examining the relationships of Atlantic and Pacific members of the Faviidae and Mussidae, ecologically dominant families that comprise one-third of all reef-building or zooxanthella-containing coral genera[1,2]. We analysed mitochondrial cytochrome B (*cytB*) and cytochrome oxidase I (*COI*) genes as well as parts of two exons from a nuclear β-tubulin gene. We sequenced representatives of more than half the genera in both families, including most of the Caribbean species, as well as taxa in related families.

Unexpectedly, most Atlantic lineages conventionally assigned to the Faviidae and Mussidae are not distributed within the more numerous Pacific lineages of these 'families', but instead represent a well-defined clade (Fig. 1). Notably, the Atlantic 'faviid' *Favia* and the Atlantic 'mussid' *Scolymia* are more closely related to each other than they are to their respective 'congeners' in the Pacific (taxa in bold in Fig. 1). The only Atlantic corals closely related to the group containing Pacific 'faviids' belong to the clearly polyphyletic 'genus' *Montastraea*; seven other genera in this group that are now restricted to the Pacific once had Atlantic representatives (on the basis of conventional taxonomy)[4].

Moreover, the distinctiveness of this previously unrecognized Atlantic clade is greater than that of several conventionally recognized families that are restricted to the Indo-west Pacific. Specifically, the Merulinidae and Pectiniidae (which in our analyses are polyphyletic), as well as the monotypic Trachyphylliidae, are nested within and are more closely related to Pacific 'faviids' and 'mussids'

than the Atlantic clade is related to any of these taxa. In other words, the Atlantic clade clearly deserves recognition at the family level (Mussidae Ortmann 1890 is the senior available family name), whereas several currently recognized Pacific families probably do not.

These two conclusions are supported by mitochondrial and nuclear genes analysed by a variety of methods (Fig. 1, and Supplementary Information). Previous molecular analyses of corals[5–8] did not come to comparable conclusions, either because they did not simultaneously analyse large numbers of Pacific and Atlantic corals in these groups or did not have adequate resolution to detect these patterns.

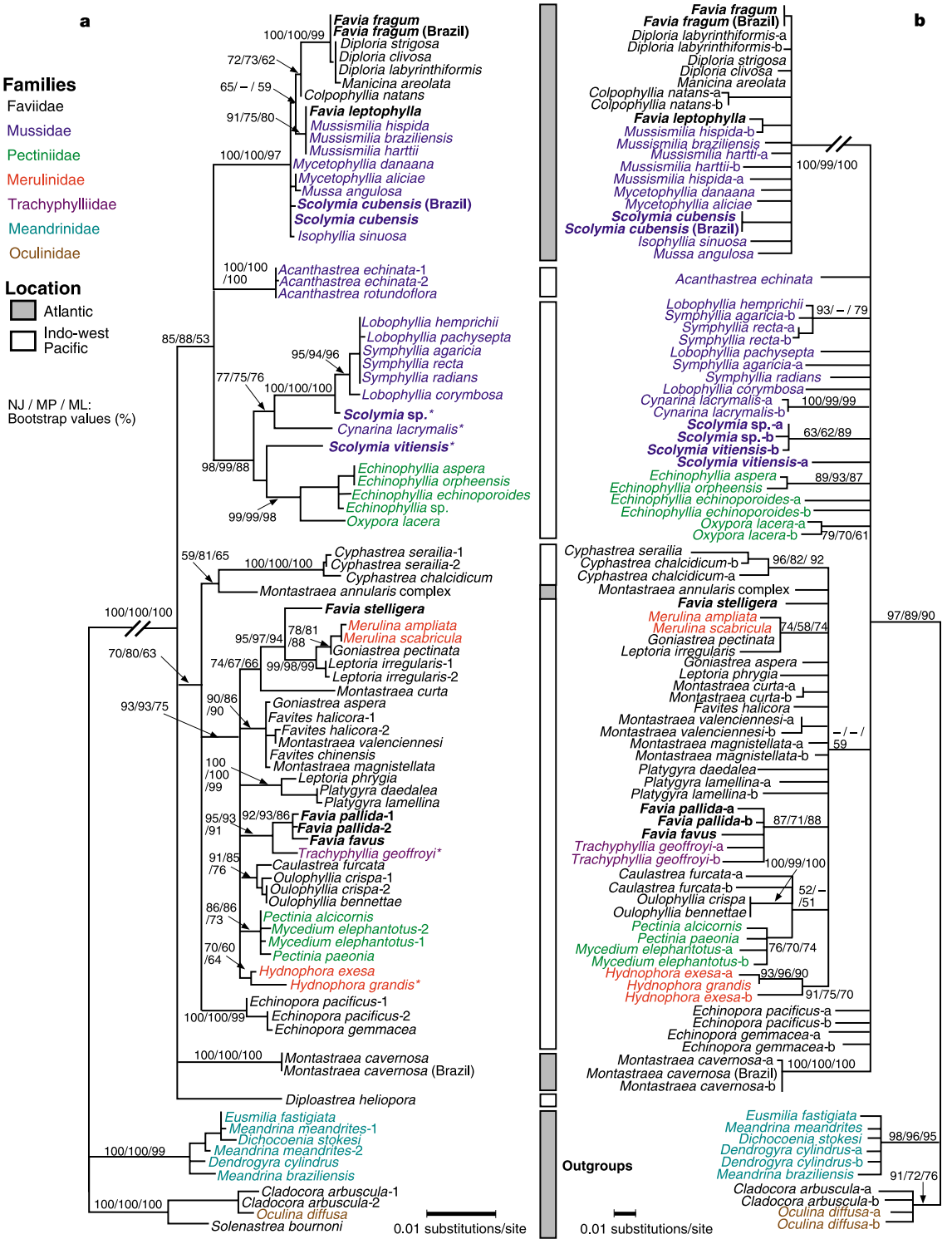

Figure 1 Phylogenies for corals in the suborder Faviina and related families (Oculinidae, Meandrinidae). **a**, ML tree for *cytB* and *COI* genes. When different colonies had distinct sequences they are indicated by numbers (1, 2) after species; asterisks indicate that only one colony was analysed. **b**, ML tree for β-tubulin gene. Letters (a, b) distinguish sequences of different clones from the same colony. Branches with less than 50% bootstrap values were collapsed; values for major nodes are indicated. Four species in **a** are missing in **b** (see Methods).

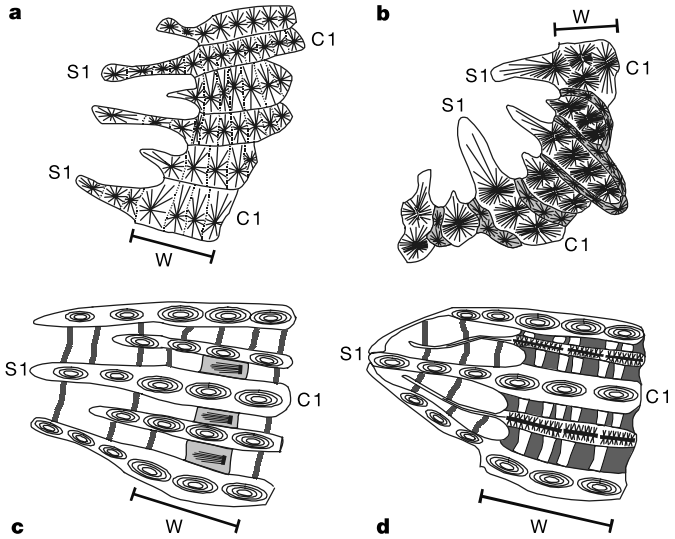

Figure 2 Illustrations of wall structures based on thin sections. **a**, *Favia fragum*, walls formed by septal thickening (septothecal). **b**, *Favia stelligera*, walls formed by insertion of skeletal structures with trabecular centres (trabeculothecal). **c**, *Mycetophyllia aliciae*, walls composed mostly of dissepiments (parathecal) with some trabeculothecal elements. **d**, *Symphyllia recta*, walls composed of dissepiments thickened by sclerenchyme. Abbreviations: W, wall; S1, primary septum; C1, primary costa. Trabecular centres are points completely surrounded by radiating spokes (concentric ellipses represent trabecular fans). Trabeculothecal elements (**b**, **c**) are lightly shaded; dissepiments (**c**, **d**) are dark.

Our results are unexpected given the long-term taxonomic stability of zooxanthellate/reef-building scleractinian coral families. Of the 18 families currently recognized[2], all except three had been described by 1902, and the biogeographic coherence of the Mussidae and Faviidae has never previously been questioned[1,2,9]. This suggests that new morphological characters and approaches must be identified for both living and fossil taxa[8,10]. A full morphological analysis is beyond the scope of this paper, but several characters largely ignored by previous workers substantiate several aspects of our molecular phylogeny. For example, the corallite walls of Atlantic *Favia fragum* and other examined Atlantic 'faviids' except *Montastraea* are formed by septal thickening (Fig. 2a), whereas the walls of the Pacific *F. stelligera* (Fig. 2b) and other examined relatives are constructed by the insertion of skeletal structures with distinct trabecular centres between the costae. Atlantic 'mussids' have corallite walls formed partly by thin dissepiments and by additional fibrous structures inserted between the costae that lack trabecular centres (Fig. 2c), whereas Pacific 'mussids' have walls composed of dissepiments and thickened by sclerenchyme (Fig. 2d). Pacific members of the 'genus' *Scolymia* are more like other Pacific 'mussids' in having corallite centres with primarily lamellar linkage, whereas Atlantic *Scolymia* resemble Atlantic *Mussa* in having centres with trabecular linkage, a fact noted decades ago[11] but deemed insignificant in later taxonomic treatises.

This Atlantic clade represents one-third of the 27 genera of zooxanthellate or reef-building corals of the region. Its timing is difficult to specify with precision because our results imply that previous generic assignments of fossil taxa need to be re-examined. On the basis of the fossil record of the most morphologically distinctive genera (for example *Colpophyllia*, which dates back to the Eocene epoch (34–55 Myr ago)), the dominant Atlantic and Pacific lineages probably diverged long before the closure of the Tethyan connection between the tropical Indo-west Pacific and Atlantic in the early Miocene epoch (about 16–24 Myr ago), the time traditionally associated with the breakdown of connections between coral communities from these two provinces[4,12,13].

These new phylogenies help to make sense of previously noted discrepancies in patterns of molecular evolution for corals. It had been noted[14] that divergences between *F. fragum* and *Diploria* and among Pacific members of the 'families' Merulinidae, Pectiniidae and Faviidae are lower than that observed between the 'congeners' *M. annularis* and *M. cavernosa*, observations that are completely compatible with molecular phylogenies presented here. Our results also strengthen the case for unusually slow rates of molecular evolution in corals, because species widely separated in our phylogeny exhibit very low levels of genetic divergence (for example, *M. annularis* and *M. cavernosa*, with a *COI* divergence of only 2.4%[14]).

Preservation of evolutionarily distinct lineages is an important aspect of conservation[15], but phylogenies have had little role in marine conservation except in the context of 'living fossils' such as the coelacanth. The evolutionary distinctiveness of these Atlantic corals indicates that factors in addition to diversity and endemicity at the species level[3] need to be considered in planning conservation actions, especially in view of the precarious state of most Caribbean reefs[16,17]. □

Methods

Collections and DNA extraction

We collected 15 cm × 15 cm samples from the following locations: Bocas del Toro, Republic of Panama (Caribbean coast); the Abrolhos Archipelago, Brazil; Aka Island, Okinawa, Japan; Penghu Island, Taiwan; and islands of the Republic of Palau (see Supplementary Information for locations of skeletal vouchers and availability of photographs). Total DNA was extracted from tissue stored in modified guanidine solution (4 M guanidine thiocyanate, 0.1% *N*-lauroyl sarcosine sodium, 10 mM Tris-HCl pH 8, 0.1 M 2-mercaptoethanol) by conventional extraction with phenol/chloroform (1:1) and precipitation with ethanol. Alternatively, tissues were stored in 95% ethanol, and total DNA was extracted with a DNA isolation kit (Gentra Systems) after tissues had been homogenized in liquid nitrogen.

DNA sequencing

Coral-specific primers for mitochondrial *cytB* and *COI* were designed on the basis of the complete mitochondrial genome sequences of members of the *Montastraea annularis* complex (H.F. and N.K., manuscript in preparation). The entire *cytB* gene was amplified by polymerase chain reaction (PCR) with primers MCytbF (5′-GTT GCT AGT AGT AAT TTG GAT TG-3′) and MCytbR (5′-CAA ACC CAC CAA GCT TAA TA-3′). Half the *COI* gene was amplified with primers MCOIF (5′-TCT ACA AAT CAT AAA GAC ATA GG-3′) and MCOIR (5′-GAG AAA TTA TAC CAA AAC CAG G-3′). The protocol for amplifications was 94 °C for 120 s, followed by 30 cycles at 94 °C for 45 s, 60 °C for 45 s and 72 °C for 90 s, ending with a final phase of 72 °C for 5 min. PCR products were then directly

sequenced as described in ref. 18. Internal primers McytbseqF (5′-ATT GAC TAT GGC GAC CGC TTT T-3′) and McytbseqR (5′-GAA TAA AAT TCT CTG CGT CTC C-3′) for *cytB* were used in addition to PCR primers.

Primers to amplify the β-tubulin gene (intron and exon regions), designed on the basis of sequence data of *Montastraea faveolata*[19], were TubulinF (5′-GCA TGG GAA CGC TCC TTA TTT-3′) and TubulinR (5′-ACA TCT GTT GAG TGA GTT CTG-3′). They amplify a region corresponding to amino acid positions 144–299 within exon 4 of the human and *Drosophila* β-tubulin gene; the beginning of the intron corresponds to position 247, and the flanking exons have 99% amino acid similarity to the corresponding vertebrate sequence. Depending on the genus, one, two or three bands of about 600 bases, 1.0–1.5 kilobases (kb) and more than 2.0 kb were amplified by PCR with the above-described protocol. The size difference between bands was due to the length of the intron. Because most genera had a 1.0–1.5-kb band, this was used for phylogenetic analyses. *Diploastrea* and *Solenastrea* had only the 600-base-pair (bp) band, and no bands could be amplified for *Acanthastrea rotundoflora* and *Favites chinensis*; consequently these four taxa were not analysed for β-tubulin. Amplified fragments of the β-tubulin gene were separated by agarose electrophoresis, cloned with the pGEM-T System (Promega) and sequenced for both strands. At least five clones obtained from each of two independent PCRs were analysed. If only one sequence occurred more than once, this sequence was used in the phylogenetic analyses; otherwise the two most abundant sequences were used.

DNA phylogenetic analyses

Only the exon regions of the β-tubulin gene (444 bp) were analysed, because the intron was too variable for alignment. Phylogenetic analyses were performed with PAUP*[20]. DNA sequences of the entire *cytB* gene and the *COI* gene excluding the third codon position (total length 1,557 bases) were combined on the basis of nucleotide saturation analyses and the incongruence length difference test. Phylogenetic trees were constructed on the basis of neighbour-joining (NJ), maximum-parsimony (MP) and maximum-likelihood (ML) methods with the use of PAUP*. The NJ analysis was done with a two-parameter model[21]. In MP and ML analyses, heuristic searches with TBR branch swapping and 25 random additions of taxa were performed. For ML analysis, we used Modeltest[22] to find an appropriate model of evolution. For mitochondrial genes the K81uf model[23] with gamma parameter (*G*) and proportion of invariable positions (*I*) was chosen. For β-tubulin we chose the TrN model[24] with *G* and *I*. Bootstrapping was used to evaluate support for trees (1,000 replicates for NJ and MP; 300 bootstraps with the fast-stepwise heuristic search for ML).

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Correspondence and requests for materials should be addressed to N.K. (nknowlton@ucsd.edu).
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Phylogenetic constraints and adaptation explain food-web structure

Marie-France Cattin[1], Louis-Félix Bersier[1,2], Carolin Banašek-Richter[1], Richard Baltensperger[3] & Jean-Pierre Gabriel[3]

[1]*Institut de Zoologie, University of Neuchâtel, Rue Emile-Argand 11, CP2, CH-2007 Neuchâtel, Switzerland*
[2]*Chair of Statistics, Department of Mathematics, Swiss Federal Institute of Technology, CH 1015 Lausanne, Switzerland*
[3]*Department of Mathematics, Université de Fribourg, Pérolles, CH 1700 Fribourg, Switzerland*

Food webs are descriptions of who eats whom in an ecosystem. Although extremely complex and variable, their structure possesses basic regularities[1–6]. A fascinating question is to find a simple model capturing the underlying processes behind these repeatable patterns. Until now, two models have been devised for the description of trophic interactions within a natural community[7,8]. Both are essentially based on the concept of ecological niche, with the consumers organized along a single niche dimension; for example, prey size[8,9]. Unfortunately, they fail to describe adequately recent and high-quality data. Here, we propose a new model built on the hypothesis that any species' diet is the consequence of phylogenetic constraints and adaptation. Simple rules incorporating both concepts yield food webs whose structure is very close to real data. Consumers are organized in groups forming a nested hierarchy, which better reflects the complexity and multidimensionality of most natural systems.

A central issue in ecology is to uncover the basic determinants of the distribution of trophic interactions among the members of natural communities[9]. The architecture of interactions affects the stability properties of dynamical models of food webs[2,10,11]. Therefore, a full understanding of dynamic ecosystems cannot be achieved at the economy of assuming a static structure of food webs, as was the case in the pioneering works on stability and complexity that considered interactions to be random[12,13]. It has been shown unambiguously that real food webs are different from randomly connected networks, and that such a null-model cannot account for the observed properties of the highest-quality food webs available[6,8]. The structural models of trophic interactions proposed