

# Evolution of corallivory in the gastropod genus *Drupella*

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Received: 25 March 2011 / Accepted: 26 May 2011 / Published online: 18 June 2011  
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**Abstract** Although muricid gastropods in the genus *Drupella* are well-known consumers of Indo-Pacific corals, their evolutionary and ecological history is unclear, as is their relationship to the apparently facultative coral-feeder *Ergalatax margariticola*, which has been reported to feed upon corals in Hong Kong. We use a well resolved molecular phylogeny (reconstructed from one nuclear and two mitochondrial genes) to show that the monophyletic genus *Drupella* falls into the muricid subfamily Ergalataxinae and that the genus includes ‘*E. margariticola*’, which is composed of two cryptic species. We show that genetic structure within the here reassigned ‘*Drupella margariticola*’ species complex does not relate to feeding mode, but instead seems to correspond to broad patterns of habitat ecology found in other gastropod taxa. Our analyses suggest that *Drupella* originated in the late Miocene (approximately 9.6 Ma) and diversified approximately 5.0 Ma, much later than the appearance of modern coral

reefs in the early Cenozoic. Thus, it is possible that corallivory in *Drupella* evolved in response to the major expansion and reorganization of reefs that took place in the early Miocene.

**Keywords** Muricidae · Speciation · Coral feeding · Molecular phylogeny · *Ergalatax margariticola*

## Introduction

Modern, shallow-water coral reefs first appeared in the early Cenozoic (approximately 65 Ma) and most major coral families were extant by the end of the Eocene; these proliferated extensively from the early Miocene onwards (23 Ma; Wood 1999; Crame and Rosen 2002; Hughes et al. 2002; Wallace and Rosen 2006). Similarly, many reef-associated taxa appeared in the Cenozoic and diversification rates in these groups increased markedly in the late Oligocene and early Miocene (Wilson and Rosen 1998; Crame and Rosen 2002; Williams 2007; Williams and Duda 2008). It has thus been suggested that marine diversification may be linked to the appearance and proliferation of the coral-reef habitat (Crame and Rosen 2002; Alfaro et al. 2007; Williams 2007; Bellwood et al. 2010). It might be expected that, among reef-associated groups, corallivory should arise frequently, yet this does not seem to be the case. Although corals are preyed upon by a variety of macro-consumers, including fish, polychaete worms, gastropods, echinoderms and crabs (Robertson 1970; Glynn 1990), coral-feeding behaviour is rare within each group. For example, shallow-water corallivores represent less than 3% of all fish species, and occur in only four families of crustaceans, a few echinoderm genera (e.g., *Acanthaster*) and four currently-recognized families

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Communicated by Biology Editor Dr. Ruth Gates

**Electronic supplementary material** The online version of this article (doi:10.1007/s00338-011-0788-5) contains supplementary material, which is available to authorized users.

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of gastropods (Robertson 1970; Glynn 1990; Barco et al. 2010; Bellwood et al. 2010). Given the otherwise extraordinary diversity of reef-associated taxa, it is unclear why corallivory is so rare, but this rarity emphasizes the importance of investigating coral-feeding behaviour and determining how and when this unusual ecology arose in each group.

Gastropods that feed upon stony corals are found in the families Architectonicidae, Epitoniidae, Pediculariidae and Muricidae (including the Coralliophilinae; Robertson 1970; Lorenz and Fehse 2009; Barco et al. 2010). There have been several independent acquisitions of coral feeding behaviour within the Muricidae, which otherwise feed predominantly by drilling molluscan and barnacle shells. Corallivory occurs only in the genus *Drupella*, in the species *Ergalatax margariticola* and in the muricid subfamily Coralliophilinae (Taylor and Morton 1996; Vermeij and Carlson 2000; Morton et al. 2002; Barco et al. 2010). Coralliophilines are morphologically and genetically distinct from the rest of the Muricidae, lacking the jaws and radula characteristic of most gastropods (Vermeij and Carlson 2000; Barco et al. 2010; Modica and Holford 2010). These snails are typically parasitic on corals, feeding suctorially (Robertson 1970; Modica and Holford 2010). Coralliophiline species first appeared in the fossil record in the middle Eocene and were feeding on corals by the early Oligocene (Lozouet and Renard 1998; Vermeij and Carlson 2000). Their phylogeny has been relatively well investigated (e.g., Oliverio and Mariottini 2001a, 2001b; Massin and Dupont 2003; Gittenberger 2006; Oliverio et al. 2009; Gittenberger and Gittenberger 2011).

The evolutionary and ecological history of the muricid genus *Drupella* is less clear. This genus has been classified either in the subfamily Rapaninae (e.g., Herbert et al. 2007; Houart and Héros 2008) or Ergalataxinae (Vermeij and Carlson 2000; Modica and Holford 2010; Vermeij 2010). Snails in this genus have a radula, unlike the coralliophilines, but the radula is different in structure from all other muricids and may be specialized for corallivory (Thiele 1925; Fujioka 1982, 1985; Vermeij and Carlson 2000). *Drupella* species exhibit several additional adaptations that may aid in coral feeding, including an externally cuticularized proboscis that shields vulnerable tissues from the stings of nematocysts (Robertson 1970; Hadfield 1976; Morton and Blackmore 2009). These snails have been observed to perch on dead coral in order to feed on adjacent live polyps by extending this proboscis (reviewed in Turner 1992; see also Cumming 2009a). Some species of *Drupella* also exhibit aggregation behaviour; during the 1980s and 1990s, such aggregations were reported in Western Australia, Japan and the Red Sea, and in some cases, coral cover was reduced by up to 75% (reviewed in Turner 1992; Cumming 2009b). The destruction caused by these

population explosions has been compared to that caused by *Acanthaster* (see e.g., Turner 1992), although subsequent analyses have not shown a significant correlation between *Drupella* outbreaks and declines in coral cover (Miller and Dolman 2008). Such outbreaks seem to be more common in diseased corals (Antonius and Riegl 1997, 1998).

*Ergalatax margariticola*, in contrast to *Drupella*, has a radula typical of the subfamily Ergalataxinae (Taylor 1976; Fujioka 1985; Tan 1995). It has been observed to feed by drilling, but it is primarily a scavenger (Tan 1995; Ishida 2001, 2004a, b). Although this species is common throughout the Indo-Pacific and its feeding ecology has been well studied (e.g., Taylor 1976; Taylor and Morton 1996; Ishida 2001; Tan 2003), only in Hong Kong has it been reported to include coral in its diet (Taylor 1980; Cumming and McCorry 1998; Morton and Blackmore 2009). In Hong Kong it is rarely observed to be corallivorous in the absence of *Drupella*; it is thought that, lacking specialized coral-feeding adaptations, *E. margariticola* may only be able to feed upon corals when an attack has already been initiated by *Drupella* (Morton and Blackmore 2009, but see Taylor 1980). Why this species is apparently not corallivorous outside Hong Kong is not known.

Although the coral-feeding behaviour of *Drupella* has been relatively well investigated, especially in the context of destructive aggregations (e.g., Turner 1992; Morton et al. 2002; Cumming 2009a, b), its phylogenetic relationships with *E. margariticola* and the rest of the Muricidae remain unknown. Therefore, we constructed a multi-gene phylogeny of the genus, together with several species of muricids already shown to belong to the Ergalataxinae, Rapaninae or Coralliophilinae (Barco et al. 2010). We investigated the composition of the genus using statistical methods for species delimitation. Concurrently, we analysed several species of *Ergalatax*, including corallivorous and non-corallivorous populations of *E. margariticola*, to investigate their relationships with *Drupella*. Finally, we used molecular dating methodologies informed by reliable fossil data to provide a temporal framework within which to interpret the ecology of these corallivorous species.

## Materials and methods

### Specimen identification and outgroup selection

Preliminary analyses (data not shown) suggested that *D. cornus* formed a clade with the Ergalataxinae, but since *Drupella* has previously also been placed in the Rapaninae, we included in our analysis several species already confirmed to be members of the Coralliophilinae, Rapaninae or Ergalataxinae (Barco et al. 2010; Table 1). For dating purposes, members of an additional ergalataxine clade

**Table 1** Specimens used in this study. Vouchers have been deposited in either the Natural History Museum, London (NHMUK), the Australian Museum, Sydney (AM) or the Museum Nationale d’Histoire Naturelle, Paris (MNHN)

Species and/or specimen code	Locality	Voucher	28S	12S	COI
<b>Coralliophilinae outgroups</b>					
<i>Coralliophila erosa</i> (Röding, 1798)	Yaté, New Caledonia	NHMUK 20070626	FR853896	FR853977	FR853815
<i>Coralliophila neritoides</i> (Lamarck, 1816)	Guam	NHMUK 20080819	FR853897	FR853978	FR853816
<b>Rapaninae outgroups</b>					
<i>Drupa morum</i> (Röding, 1798)	Cabo Delgado Prov., Mozambique	NHMUK 20060441	EU391559	FN677375	FN677405
<i>Rapana bezoar</i> (Linnaeus, 1758)	Kochi Pref., Japan	NHMUK 20080038	FN677476	FN677376	FN677421
<b>Ergalataxinae outgroups</b>					
<i>Morula granulata</i> (Duclos, 1832)	Port Boisé, New Caledonia	NHMUK 20070621	FN677469	FN677383	FN677414
<i>Morula musiva</i> (Kiener, 1836)	Langkawi, Malaysia	NHMUK 20080744	FN677472	FN677380	FN677417
<i>Morula mutica</i> (Lamarck, 1816)	Pago Bay, Guam	NHMUK 20080772	FN677473	FN677379	FN677418
<i>Muricodrupa fenestrata</i> (Blainville, 1832)	Port Boisé, New Caledonia	NHMUK 20070620	FN677474	FN677378	FN677419
<i>Muricodrupa fiscella</i> (Gmelin, 1791)	Port Boisé, New Caledonia	NHMUK 20070623	FN677470	FN677382	FN677415
<i>Pascula ochrostoma</i> (Blainville, 1832)	Izu Is, Tokyo, Japan	NHMUK 20100160	FR853920	FR854002	FR853839
<i>Pascula ochrostoma</i> (Blainville, 1832)	Panglao I., Philippines	MNHN IM-2007-18176	FR853921	FR854003	FR853840
<i>Pascula ochrostoma</i> (Blainville, 1832)	Merizo Bay, Guam	NHMUK 20080757	FN677460	FN677393	FN677406
<b>Ergalatax species</b>					
<i>Cronia amygdala</i> (Kiener, 1835)	Queensland, Australia	AM C458326	FR853903	FR853984	FR853822
<i>Cronia aurantiaca</i> (Hombron and Jacquinot, 1852)	Darwin Harbour, Northern Territory, Australia	NHMUK 20100355	FR853902	FR853983	FR853821
<i>Ergalatax contracta</i> (Reeve, 1846)	Chiba Pref., Japan	NHMUK 20080019	FR853963	FR854045	FR853882
<i>Ergalatax contracta</i> (Reeve, 1846)	Langkawi, Malaysia	NHMUK 20080747	FN677462	FN677391	FN677408
<i>Ergalatax junionae</i> Houart, 2008	Abu Dhabi, United Arab Emirates	NHMUK 20080906	FN677463	FN677396	FN677409
<i>Ergalatax junionae</i> Houart, 2008	Ras Ajoza (Kuwait Tower), Kuwait	NHMUK 20100394	FR853964	FR854046	FR853883
<i>Maculotreron serriale</i> (Deshayes, 1834)	Okinawa Pref., Japan	NHMUK 20080022	FR853974	FR854056	FR853893
<i>Maculotreron serriale</i> (Deshayes, 1834)	Panglao I., Philippines	MNHN IM-2007-18197	FR853975	FR854057	FR853894
<b><i>Drupella cornus</i> (Röding, 1798)</b>					
Guam1.1	Merizo Bay, Guam	NHMUK 20080751	FR853922	FR854004	FR853841
Guam2.1	Merizo Bay, Guam	NHMUK 20080754	FR853906	FR853988	FR853825
Guam5.1	Pago Bay, Guam	NHMUK 20080820	FR853907	FR853989	FR853826
Hawaii1.1	Oahu, Hawaii, USA	NHMUK 20100373.1	FR853898	FR853979	FR853817
Hawaii2.1	Oahu, Hawaii, USA	NHMUK 20100374	FR853899	FR853980	FR853818
Hawaii3.1	Hawaii (Big Island), Hawaii, USA	NHMUK 20100378	FR853900	FR853981	FR853819
Japan1.1	Sakihara I., Japan	NHMUK 20100153	FR853901	FR853982	FR853820
NewCaledonia1.1	Yaté, New Caledonia	NHMUK 20070144	FR853923	FR854005	FR853842
Philippines2.1	Panglao I., Philippines	MNHN IM-2007-18181	FR853911	FR853993	FR853830
Philippines3.1	NW Tutuba I., Vanuatu	MNHN IM-2007-18178	FR853924	FR854006	FR853843
<b><i>Drupella fragum</i> (Blainville, 1832)</b>					
Guam3.1	Merizo Bay, Guam	NHMUK 20080755	FR853925	FR854007	FR853844
Japan2.1	Fukushima, Oita Pref., Japan	NHMUK 20090097	FR853926	FR854008	FR853845
Japan3.1	Fukushima, Oita Pref., Japan	NHMUK 20090098	FR853927	FR854009	FR853846
Japan6.1	Fukushima, Oita Pref., Japan	NHMUK 0090111.1	FR853965	FR854047	FR853884
Japan6.2	Fukushima, Oita Pref., Japan	NHMUK 20090111.2	FR853969	FR854051	FR853888
Japan6.3	Fukushima, Oita Pref., Japan	NHMUK 20090111.3	FR853970	FR854052	FR853889

**Table 1** continued

Species and/or specimen code	Locality	Voucher	28S	12S	COI
Japan6.6	Fukushima, Oita Pref., Japan	NHMUK 20090111.6	FR853971	FR854053	FR853890
Japan6.7	Fukushima, Oita Pref., Japan	NHMUK 20090111.7	FR853972	FR854054	FR853891
Japan6.8	Fukushima, Oita Pref., Japan	NHMUK 20090111.8	FR853973	FR854055	FR853892
Japan6.10	Fukushima, Oita Pref., Japan	NHMUK 20090111.10	FR853966	FR854048	FR853885
Japan6.11	Fukushima, Oita Pref., Japan	NHMUK 20090111.11	FR853967	FR854049	FR853886
Japan6.12	Fukushima, Oita Pref., Japan	NHMUK 20090111.12	FR853968	FR854050	FR853887
Japan6.13	Fukushima, Oita Pref., Japan	NHMUK 20090111.13	FR853928	FR854010	FR853847
<i>Drupella eburnea</i> (Küster, 1862)					
Japan7.2	Sakaematsu, Kyushu Is, Japan	NHMUK 20100146.2	FR853909	FR853991	FR853828
<i>Drupella rugosa</i> (Born, 1778)					
Hong Kong2.1	Bluff I., Hong Kong	NHMUK 20080824.1	FR853929	FR854011	FR853848
Hong Kong2.2	Bluff I., Hong Kong	NHMKUK 20080824.2	FR853915	FR853997	FR853834
Hong Kong2.3	Bluff I., Hong Kong	NHMKUK 20080824.3	FR853916	FR853998	FR853835
Hong Kong2.6	Bluff I., Hong Kong	NHMKUK 20080824.6	FR853917	FR853999	FR853836
Hong Kong2.7	Bluff I., Hong Kong	NHMKUK 20080824.7	FR853918	FR854000	FR853837
Hong Kong2.8	Bluff I., Hong Kong	NHMKUK 20080824.8	FR853919	FR854001	FR853838
Hong Kong2.10	Bluff I., Hong Kong	NHMKUK 20080824.10	FR853912	FR853994	FR853831
Hong Kong2.13	Bluff I., Hong Kong	NHMKUK 20080824.13	FR853913	FR853995	FR853832
Hong Kong2.15	Bluff I., Hong Kong	NHMKUK 20080824.15	FR853914	FR853996	FR853833
Japan7.1	Kyushu, Japan	NHMKUK 20100146.1	FR853908	FR853990	FR853827
Japan7.6	Kyushu, Japan	NHMKUK 20100146.6	FR853910	FR853992	FR853829
<i>Ergalatax margaritcola</i> (Broderip, 1833) ‘Continental’					
corallivorous					
Hong Kong1.1	Bluff I., Hong Kong	NHMUK 20080741.1	FR853904	FR853985	FR853823
Hong Kong1.4	Bluff I., Hong Kong	NHMUK 20080741.4	FR853938	FR854020	FR853857
Hong Kong1.5	Bluff I., Hong Kong	NHMUK 20080741.5	FR853939	FR854021	FR853858
Hong Kong1.6	Bluff I., Hong Kong	NHMUK 20080741.6	FR853940	FR854022	FR853859
‘ <i>crassulnata</i> ’					
<i>crassulnata</i> 1.2	Darwin Harbour, Northern Territory, Australia	NHMUK 20100354.2	FR853933	FR854015	FR853852
<i>crassulnata</i> 2.1	Darwin Harbour, Northern Territory, Australia	NHMUK 20100357.1	FR853934	FR854016	FR853853
<i>crassulnata</i> 3.2	Darwin Harbour, Northern Territory, Australia	NHMUK 20100358.2	FR853935	FR854017	FR853854
<i>crassulnata</i> 3.3	Darwin Harbour, Northern Territory, Australia	NHMUK 20100358.3	FR853936	FR854018	FR853855
<i>crassulnata</i> 3.4	Darwin Harbour, Northern Territory, Australia	NHMUK 20100358.4	FR853937	FR854019	FR853856
typical					
Japan5.1	Kyushu, Japan	NHMUK 20100154	FR853941	FR854023	FR853860
Malaysia1.2	Langkawi, Malaysia	NHMUK 20080815.2	FR853944	FR854026	FR853863
Malaysia1.4	Langkawi, Malaysia	NHMUK 20080815.4	FR853945	FR854027	FR853864
Malaysia1.5	Langkawi, Malaysia	NHMUK 20080815.5	FR853946	FR854028	FR853865
Malaysia1.6	Langkawi, Malaysia	NHMUK 20080815.6	FR853947	FR854029	FR853866
Malaysia1.7	Langkawi, Malaysia	NHMUK 20080815.7	FR853948	FR854030	FR853867
Malaysia2.1	Langkawi, Malaysia	NHMUK 20080742.1	FR853949	FR854031	FR853868
Malaysia2.2	Langkawi, Malaysia	NHMUK 20080742.2	FR853950	FR854032	FR853869
Malaysia2.3	Langkawi, Malaysia	NHMUK 20080742.3	FR853951	FR854033	FR853870
Malaysia2.4	Langkawi, Malaysia	NHMUK 20080742.4	FR853952	FR854034	FR853871

**Table 1** continued

Species and/or specimen code	Locality	Voucher	28S	12S	COI
Malaysia2.5	Langkawi, Malaysia	NHMUK 20080742.5	FR853953	FR854035	FR853872
Malaysia2.6	Langkawi, Malaysia	NHMUK 20080742.6	FR853954	FR854036	FR853873
Malaysia3.1	Melaka, Malaysia	NHMUK 20080791.1	FR853955	FR854037	FR853874
Malaysia3.2	Melaka, Malaysia	NHMUK 20080791.2	FR853956	FR854038	FR853875
Malaysia3.3	Melaka, Malaysia	NHMUK 20080791.3	FR853957	FR854039	FR853876
Malaysia3.4	Melaka, Malaysia	NHMUK 20080791.4	FR853958	FR854040	FR853877
Malaysia3.5	Melaka, Malaysia	NHMUK 20080791.5	FR853959	FR854041	FR853878
Malaysia4.1	Melaka, Malaysia	NHMUK 20080790	FR853905	FR853986	FR853824
NewCaledonia2.1	Plage de Foué, New Caledonia	NHMUK 20070630	FR853961	FR854043	FR853880
Philippines5.1	Cavite, Manila Bay, Philippines	MNHN IM-2009-4850	FR853930	FR854012	FR853849
Philippines5.2	Cavite, Manila Bay, Philippines	MNHN IM-2009-4851	FR853931	FR854013	FR853850
Philippines5.5	Cavite, Manila Bay, Philippines	MNHN IM-2009-4854	FR853932	FR854014	FR853851
Thailand1.1	Ko Phi Phi I., Thailand	NHMUK 20100388	FR853962	FR854044	FR853881
<i>Ergalatax margaritcola</i> (Broderip, 1833) ‘Oceanic’					
Japan10.1	Kyushu, Japan	NHMUK 20100143	FR853943	FR854025	FR853862
Japan9.1	Amami Is, Japan	NHMUK 20100157	FR853942	FR854024	FR853861
Mozambique1.1	Cabo Delgado Prov., Mozambique	NHMUK 20060466	EU391552	FR853987	EU391587
NewCaledonia3.1	Isle of Pines, New Caledonia	NHMUK 20070636	FR853976	FR854058	FR853895
NewCaledonia4.1	Isle of Pines, New Caledonia	NHMUK 20070637	FR853960	FR854042	FR853879

Specimen codes match those in Fig. 1a. Sequence accession numbers in the range EU391552–EU391559 were previously published in Claremont et al. (2008); accession numbers in the range FN677375–FN677476 were previously published in Barco et al. (2010)

(three specimens of *Pascuala ochrostoma*; Table 1; identification based on Okutani 2000; Poppe 2008) were also included.

Some taxonomic confusion surrounds the composition of *Drupella* (see Johnson and Cumming 1995 for a brief review) and the identity of the type species, *D. cornus* (discussed in Turner 1992). Although the only genetic study of *Drupella* of which we are aware supported only three species of *Drupella* (*D. cornus*, *D. rugosa* and *D. fragum*; Johnson and Cumming 1995), we follow more recent species lists (Héros et al. 2007; Tröndlé and Boutet 2009), which have recognized four species in the genus: *D. cornus*, *D. fragum*, *D. rugosa* and *D. eburnea*. A fifth species, *D. minuta*, is recognized by some authors (e.g. Fujioka 1984; Houart and Héros 2008; Poppe 2008), but we were unable to obtain samples of this species. We sequenced 10 individuals of *D. cornus*, 13 of *D. fragum*, 11 of *D. rugosa* and one of *D. eburnea* (Table 1; identifications based on Fujioka 1982, 1984; Okutani 2000; Poppe 2008).

Further preliminary analyses indicated a close relationship between *D. cornus* and *E. margaritcola*, so we attempted to sample *E. margaritcola* comprehensively, including both corallivorous and non-corallivorous

specimens. We thus included four specimens from Hong Kong, collected while feeding on corals (Table 1), as well as 28 ‘typical’ specimens from intertidal locations elsewhere in the Indo-Pacific. It has also been suggested (Tan 1995) that the Australian ‘*crassulnata* form’ of *E. margaritcola* should be recognized as a distinct species on morphological grounds. We included five ‘*crassulnata*’ specimens in our analysis to test this hypothesis. To clarify the identity of the genus *Ergalatax*, we included in our analyses the type species, *E. contracta* (Table 1; Tan 1995).

A total of 94 specimens and 282 sequences were used in this study. Sequences for some or all genes of eleven species (32 sequences) have previously been published (Table 1; Claremont et al. 2008; Barco et al. 2010).

#### DNA sequencing and alignment

For all specimens, two mitochondrial genes (cytochrome *c* oxidase subunit I (COI) and 12S rRNA) and one nuclear gene (28S rRNA), known to be informative for phylogenetic analysis in the Muricidae (Claremont et al. 2008; Barco et al. 2010), were sequenced, following the protocols of Claremont et al. (2011). DNA was extracted with the

Qiagen QIAamp DNA mini kit. Polymerase chain reactions (PCR; 200  $\mu$ M of each dNTP, 0.1  $\mu$ M of both forward and reverse PCR primer, 2.5 U Qiagen DNA Taq polymerase) amplified approximately 1,500 bp of 28S, 700 bp of COI and 650 bp of 12S. Primers and PCR conditions were identical to those of Claremont et al. (2011). PCR products were sequenced using a BigDye Terminator v1.1 Cycle Sequencing Kit (Applied Biosystems) and run on an Applied Biosystems 3730 DNA Analyzer automated capillary sequencer. Sequences were assembled and edited with Sequencher (v4.6; GeneCodes Corporation, Ann Arbor, Michigan). Clear heterozygous peaks in both the forward and reverse sequence of 28S were coded as polymorphisms.

Ribosomal (28S and 12S) sequences were aligned using ClustalX (v2.0.9; Thompson et al. 1997; delay divergent sequences: 95%; gap-opening penalty: 20; gap-extension penalty: 5). Gblocks (v.0.91beta; Castresana 2000) was then used to remove poorly aligned sites (minimum number of sequences for a conserved position: 70%; minimum number of sequences for a flanking position: 90%; maximum number of contiguous non-conserved positions: 3; minimum length of a block: 5; all gap positions allowed). COI sequences were aligned by eye in MacClade (v4.06 OSX; Maddison and Maddison 2003). For each gene partition, 24 different models of nucleotide substitution were tested with MrModelTest (v.2.2; Nylander 2004).

Before combining the three gene partitions, we compared posterior probabilities (PP) of all clades among individual Bayesian gene trees. Conflict among strongly supported clades (PP > 95%) can be seen as evidence of genetic incongruence and divergent phylogenetic histories, while conflict among weakly supported clades (PP < 50%) may be due to stochastic error (Wiens 1998; Reeder 2003; Williams and Ozawa 2006). Lack of resolution was not seen as conflict.

### Molecular species delimitation

The three-gene alignment was analysed using Bayesian inference and the Markov Chain Monte Carlo Method (MCMC; MrBayes v.3.1, Huelsenbeck and Ronquist 2001). Model parameters for each gene were set according to the model selected by MrModelTest, and were free to vary among gene partitions. The MCMC analysis ran twice, for 3,500,000 generations each, with a sample frequency of 1,000 and a burn-in of 15,001. Tree convergence was tested by examining the average deviations of split frequencies and the potential scale reduction factor (PSRF). Any branches in the consensus tree supported by <50% posterior probability (PP) were collapsed.

We then used BEAST (v.1.5.4, Drummond and Rambaut 2007) to generate an ultrametric tree for use in species delimitation tests. Site models were again set based on the models chosen by MrModelTest. In this analysis, we were only interested in relative clade ages, so we used a relaxed clock model (uncorrelated log normal; Drummond et al. 2006) without estimating rates. The starting tree was random and the coalescent tree prior was set to a constant population size. Priors were adjusted based on preliminary analyses in order to improve effective sample size (ESS) values. Two identical analyses (one 75,000,000 generations, the other 90,000,000 generations) were sampled every 7,500 and 9,000 generations respectively to generate 10,001 trees each. These treefiles were combined using LogCombiner (v.1.5.4; part of the BEAST package: <http://www.code.google.com/p/beast-mcmc/downloads/list>), with a 0.5% burn-in for both analyses. Length of burn-in was determined by examination of traces in Tracer (v.1.5; Drummond and Rambaut 2007). The final tree was generated from the resulting 19,892 trees and calculated with maximum clade credibility and median node heights.

In order to find significant clusters within the BEAST tree, we applied the GMYC function from the SPLITS package (Ezard et al. 2009) in R (R Development Core Team 2009). This function optimizes the likelihood of genetic clusters, where branching rates between species follow a Yule model, but branching rates within species follow a neutral coalescent model (Pons et al. 2006; Fontaneto et al. 2007). This method has been shown to help identify phylogenetic species and cryptic taxa in other muricids (Claremont et al. 2011). We also estimated the average evolutionary divergence over pairs of COI sequences among and within clusters with the Maximum Composite Likelihood model using MEGA5 (Tamura et al. 2011). Where possible, we re-examined the shell morphology of all specimens in each cluster.

### Time of origin of *Drupella*

We estimated the time of the origin of the genus *Drupella* with Species Tree Ancestral Reconstruction in BEAST (\*BEAST; Heled and Drummond 2010). This extension to BEAST (Drummond and Rambaut 2007) allows the construction of a species tree from population data and the dating of the tree using calibration points.

For calibration, we examined a specimen of *Taurasia sacyi* Cossmann and Peyrot, 1923 from the Stampien de Gaas (Espibos) of France (28.4–33.9 Ma; R. Houart, personal collection). Based on the similarity of this fossil to Recent species in the genus *Pascuala*, we set the minimum age of the stem of the *Pascuala* clade to 28.4 Ma and the maximum age to 37 Ma, because the maximum age of the subfamily is Late Eocene, 34–37 Ma (Vermeij and Carlson

2000; Barco et al. 2010). We then assumed that the entire clade (including outgroup species) could not be older than the earliest Cenozoic (following Claremont et al. 2011), nor younger than the oldest known coralliophiline fossil (Middle Eocene, Clairbonian; 40.4–48.6 Ma; Lozouet and Renard 1998).

We assigned a ‘species’ trait to each sequence based on the species delimitation analyses. Site models were set based on MrModelTest. We used a relaxed, uncorrelated lognormal molecular clock, estimating all rates. Tree models were set to mitochondrial for COI and 12S, and autosomal for 28S, with starting trees randomly generated in all cases. We used the Yule process for the species tree prior and a constant population size coalescent model. BEAST xml files were hand-edited, following McCormack et al. (2011), to apply the fossil dates to the species tree rather than the gene trees and to insert a user-defined starting species tree. Four identical analyses (500,000,000 generations each) were sampled every 50,000 generations to generate 10,001 trees each. These treefiles were combined using LogCombiner (v.1.5.4; part of the BEAST package: <http://www.code.google.com/p/beast-mcmc/downloads/list>), with a 10% burn-in for all analyses. Length of burn-in was determined by examination of traces in Tracer (v.1.5; Drummond and Rambaut 2007).

## Results

### Gene sequences

Each gene alignment consisted of 94 sequences (see Table 1 for sequence accession numbers). After the removal of primer sequences and ambiguous regions in the alignment, the 28S alignment, originally 1,485 bp, was 1,435 bp (96%), while the 12S alignment, initially 554 bp, was unchanged. COI sequences obtained with COIF and COI-MUR (Claremont et al. 2011) were 703 bp; those sequences obtained using universal primers (Folmer et al. 1994) were 658 bp. In the alignment, 79 bp of 28S, 220 bp of 12S, and 264 bp of COI were informative; remaining bases were either constant or parsimony uninformative. The model chosen by MrModelTest was GTR+I+G for 28S and 12S, and HKY+I+G for COI. Inspection of individual gene trees did not reveal any well-supported clades (PP > 95%) in conflict (Electronic Supplemental Material, ESM Fig. S1).

### Phylogeny and species delimitation

PSRF values for all MrBayes analyses were 1.00, while average deviations of split frequencies converged on 0, indicating that all trees had reached stationarity. All

effective sample size (ESS) values for the combined BEAST run were greater than 200. Both the MrBayes and the BEAST analyses recovered a well-supported monophyletic Eragalataxinae, which included all analysed species in the genus *Drupella* (Fig. 1a; PP/Beast posterior probability (BPP) = 100%).

The genus *Eragalatax*, as currently defined, is polyphyletic. The *Drupella* clade includes, with high support, all specimens morphologically identified as *E. margariticola* (Fig. 1a; PP/BPP = 100%). *Eragalatax contracta*, the type species of *Eragalatax*, forms a separate clade with *E. junoniae*, *Cronia aurantiaca*, *C. amygdala* and *Maculotriton serriale* (Fig. 1a; PP/BPP = 100%).

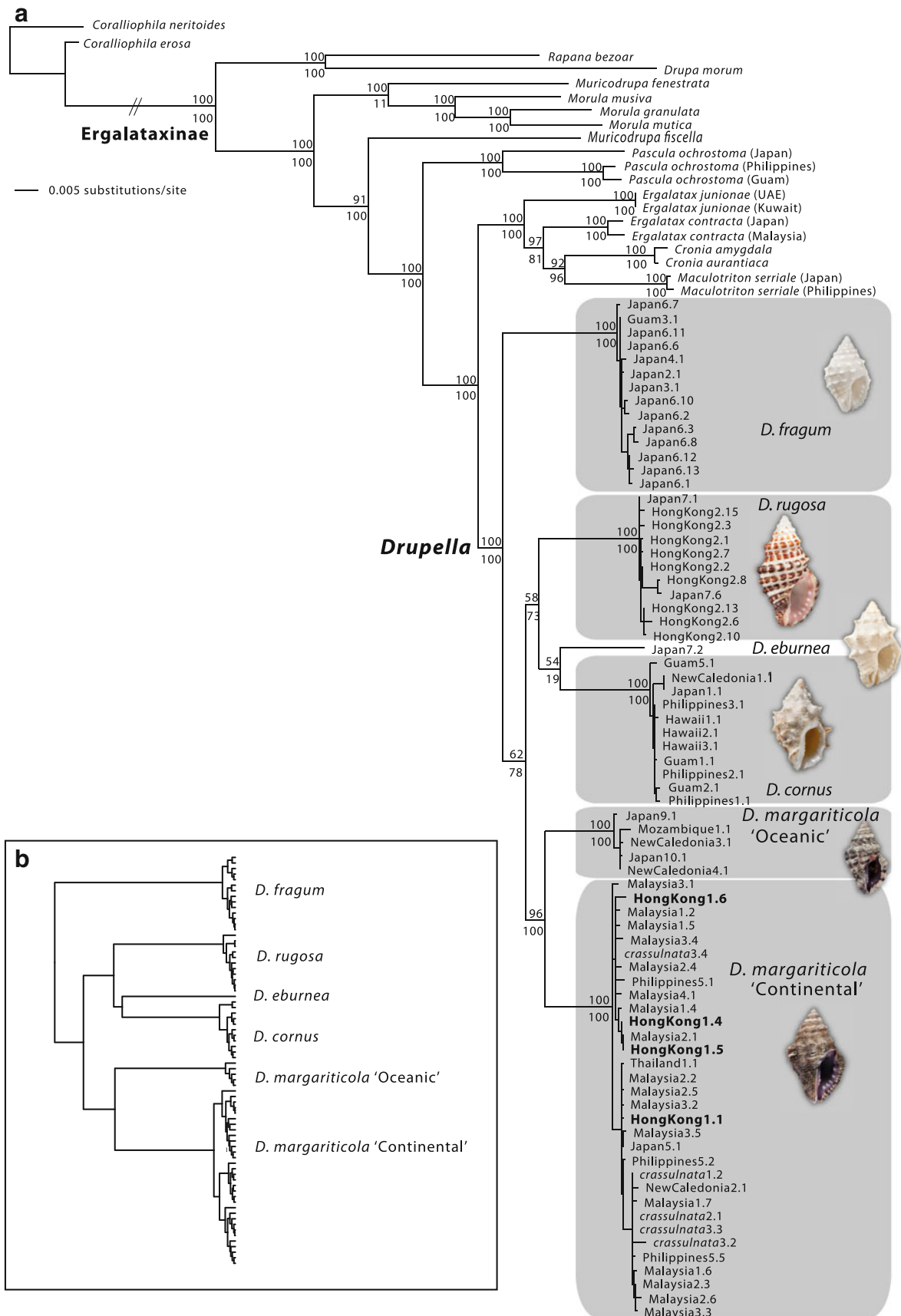
Six significant entities were recovered within *Drupella* by the GMYC analysis (Fig. 1; ML clusters = 5; ML entities = 6; likelihood of null model = 569.778; likelihood of GMYC model = 587.259;  $P < 0.0001$ ). Morphological re-examination of sequenced specimens suggests that four of these entities corresponded to the sampled morphospecies (*D. cornus*, *D. fragum*, *D. rugosa* and *D. eburnea*; PP/BPP for all clusters = 100%). The single specimen of *D. eburnea* did not form a clade with any other species and was recognized as a distinct entity by the GMYC analysis (Fig. 1).

The final two GMYC clusters within *Drupella* were well supported, but morphologically cryptic (Fig. 1; PP/BPP = 100%), and were wholly composed of specimens identified morphologically as *E. margariticola*. We observed no correspondence between these clades and any known morphological character or feeding ecology.

Although much of the molecular support for the clades within *Drupella* comes from the mitochondrial genes, there were several fixed differences in the nuclear gene among the clades (ESM Table S1). In addition, average evolutionary divergence in COI within clades was less than 0.7% across the entire genus, while divergence among clades ranged from 7.8 to 12.3%. Sequence divergence between the two cryptic clades of *E. margariticola* was 7.8%.

### Age of *Drupella*

All ESS values for the combined \*BEAST analyses were greater than 200. This analysis also recovered a monophyletic Eragalataxinae, including all specimens of *Drupella* and *E. margariticola* (BPP = 99%; Fig. 2). A monophyletic *Drupella* was well supported, consisting of *D. eburnea*, *D. cornus*, *D. rugosa*, *D. fragum* and two clades in *E. margariticola* (Fig. 2; BPP = 100%). The median age estimated for the origin of *Drupella* is 9.6 Ma and for the diversification of its extant members, 5.0 Ma (Fig. 2). Relationships among clades within *Drupella* were not well resolved (Fig. 2).





**Fig. 1 a** MrBayes Bayesian phylogeny of *Drupella* and muricid outgroups based on concatenated analysis of 28S, 12S and cytochrome *c* oxidase subunit I (COI). Support values are posterior probabilities; those above the branch are from MrBayes; those below are from BEAST. Intraspecific support values are not shown for the sake of clarity. Codes indicate general localities; detailed information can be found in Table 1. Shaded boxes indicate selections of species-level clades by GMYC analysis. Within the *D. margariticola* species complex, specimens collected from corals are indicated in bold; specimens labeled ‘*crassulnata*’ are the endemic northern Australian form. **b** Simplified ultrametric tree generated by a BEAST molecular phylogeny of *Drupella* based on concatenated analysis of 28S, 12S and COI, indicating the entities supported by GMYC analysis

**Discussion**

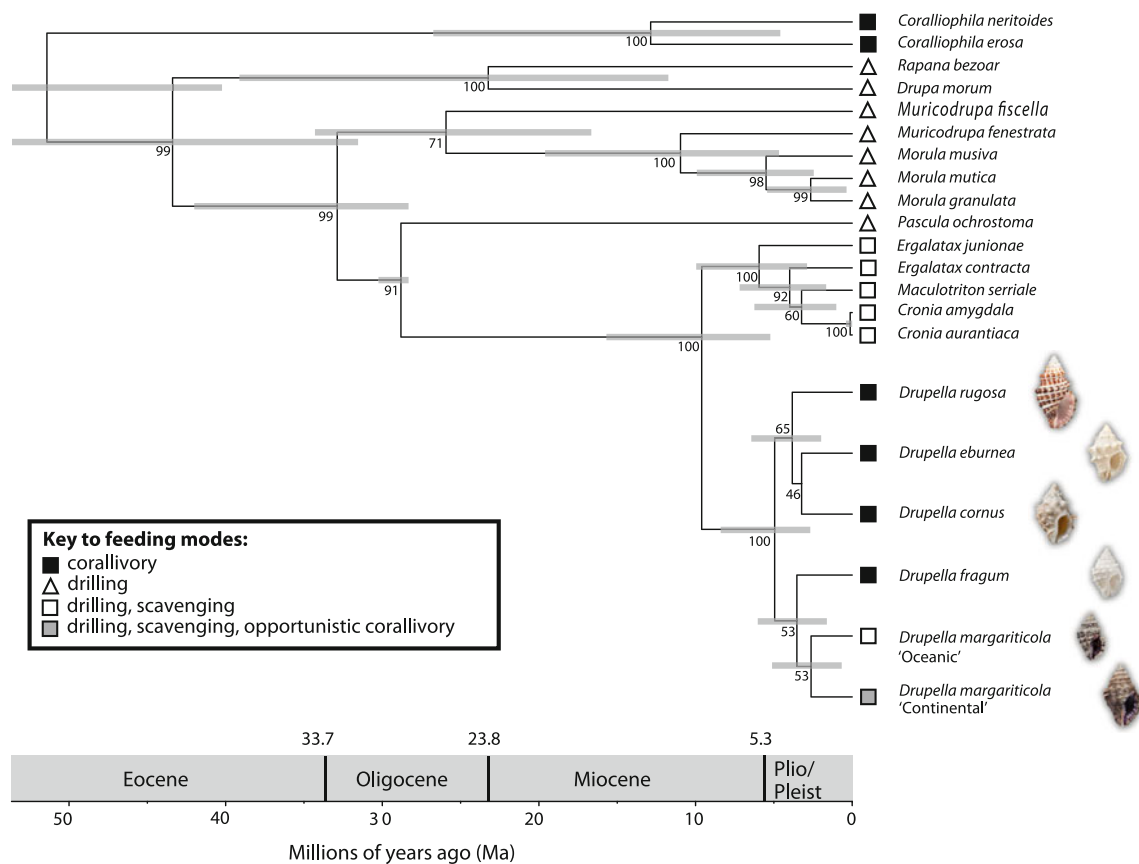
*Drupella* phylogeny and species delimitation

*Drupella* has been recognized as a distinctive genus, defined by its corallivory and apomorphies of its radula (Thiele 1925; Fujioka 1982, 1985). However, it has been unclear to which muricid subfamily the genus should be

assigned (Ergalataxinae: Modica and Holford 2010; Vermeij 2010; Rapaninae: Herbert et al. 2007; Houart and Héros 2008). Our analyses show conclusively that *Drupella* is a clade within the subfamily Ergalataxinae (Fig. 1; PP/BPP = 100%). This subfamily has previously been shown to be monophyletic, distinct from both the Rapaninae and the Coralliophilinae (Claremont et al. 2008; Barco et al. 2010).

The genus *Ergalatax* as previously defined is not monophyletic. Both members of the *E. margariticola* species complex fall within the genus *Drupella* (Figs. 1, 2; PP/BPP = 100%), while the type species of *Ergalatax*, *E. contracta*, belongs to a separate clade including *E. junionae*, *Cronia amygdala*, *C. aurantiaca* and *Maculotriton serriale* (Figs. 1a, 2). Therefore, we reassign the *E. margariticola* species complex to *Drupella*; we will refer to it as such hereafter.

Our BEAST/GMYC analysis recognizes six entities within *Drupella* (five clusters and one distinct sequence; Fig. 1). The five clades are strongly supported by the pattern of variation in COI: nucleotide diversity is much



**Fig. 2** \*BEAST phylogeny of *Drupella* and muricid outgroups, based on combined analysis of 28S, 12S and cytochrome *c* oxidase subunit I (COI). Support values are BEAST posterior probabilities. Grey bars indicate 95% highest posterior density intervals on nodes with more than 50% support. Predicted feeding mode is shown with

symbols next to species name (based on radulae and gut contents analysis from Taylor 1976, 1980, 1993; Tan 2003; Vermeij and Carlson 2000; Modica and Holford 2010; Taylor, *personal communication*)

higher between clades (minimum 7.8%) than within them (maximum 0.7%). Additionally, evolutionary distances among clades compare favourably with those found among species in other gastropod groups (e.g., Reid 2007, 2009; Claremont et al. 2011). Four of the GMYC entities correspond to the morphological species *D. cornus*, *D. fragum*, *D. eburnea* and *D. rugosa*, supporting previous taxonomic hypotheses (Héros et al. 2007; Tröndlé and Boutet 2009). A fifth species, *D. minuta*, was not sampled in this study. Although it is morphologically distinct (Fujioka 1984; Héros et al. 2007; Houart and Héros 2008; Poppe 2008), it has been synonymized with *D. fragum* based on allozyme analysis (Johnson and Cumming 1995); this should be tested in future molecular analyses.

The remaining two clades recovered by the BEAST/GMYC analysis were composed of specimens identified morphologically as *D. margaritica* (Table 1; Fig. 1a). The clades did not correspond to named forms (e.g., *crassulnata*) or known feeding ecologies, and we were unable to identify morphological characters by which to distinguish them. However, we did observe an ecological difference between the clades, which were characterized by collection from continental or oceanic sites (and named accordingly; Fig. 1a). This type of ecological distinction has been recognized before (e.g., Rocha et al. 2005; Reid et al. 2006; Claremont et al. 2011); marine distribution patterns have been classified on a continuum from ‘oceanic’ to ‘continental’, referring to a requirement (or tolerance) for a suite of environmental conditions associated with primary productivity, freshwater influence and turbidity, all of which are greater on continental margins and around high islands. Although most of the molecular support for the clades comes from the mitochondrial genes, the ‘Continental’ clade has a significant insertion and other fixed differences in the nuclear gene with respect to the ‘Oceanic’ clade (ESM Table S1). Therefore, because the clades are differentiated not only genetically (both in the mitochondrial and nuclear genes) but also ecologically, we recognize them both as Evolutionarily Significant Units (ESUs; *sensu* Moritz 1994). We will hereafter refer to them as *D. margaritica* ‘Oceanic’ and *D. margaritica* ‘Continental’. Our samples of these two species are allopatric at the level of sites, but their large-scale ranges show broad overlap. Thus, our evidence strongly suggests that these ESUs correspond to biological species, but we refrain from naming them here. The nomenclature of *D. margaritica* is complicated (see e.g., Tan 1995), and we are unable to assign the available names without diagnostic morphological characters for the two species. We do note that the type locality of *D. margaritica* is Lord Hood Island (Marutea Atoll, Gambier Islands; Broderip 1833), suggesting that our ‘Oceanic’ species may prove to be *D. margaritica sensu stricto*.

## Ecology and phylogeny of coral feeding

All species previously assigned to *Drupella* (*D. cornus*, *D. eburnea*, *D. fragum*, *D. rugosa* and *D. minuta*) are obligate coral feeders (Thiele 1925; Fujioka 1982, 1985; Vermeij and Carlson 2000). In addition, *D. margaritica* ‘Continental’ is corallivorous in Hong Kong (Taylor 1980; Cumming and McCorry 1998; Morton and Blackmore 2009), but it is unclear how such feeding is achieved. It has been presumed that coral feeding in *Drupella* is associated with the unique radular type (characterized by long, slender lateral teeth) and other unusual adaptations (such as the externally cuticularized proboscis) that are present in the species previously assigned to this genus (reviewed by Turner 1992; see also Arakawa 1965; Moyer et al. 1982; Fujioka 1985). *Drupella margaritica sensu lato*, however, has never been observed to possess such adaptations: the proboscis is not cuticularized and the radula resembles those observed in other ergalataxine genera (e.g., *Cronia*, *Muricodrupa*, *Ergalatax*; compare Fujioka 1982, 1984 to Arakawa 1965; Fujioka 1985; Tan 1995). *Drupella margaritica s. l.* is thought to be primarily a scavenger (Taylor 1976; Tan 1995; Ishida 2001, 2004a, b); perhaps feeding on corals that have already been damaged by other species of *Drupella* requires no special adaptations, and is simply an example of opportunism within a generalist feeding behaviour.

This theory may explain why corallivory in the *D. margaritica* species complex has not been observed outside Hong Kong. In this area of high water turbidity, corals must occur much closer to the surface than in most other localities (Cope and Morton 1988), resulting in a unique overlap with the shallow-subtidal range of *D. margaritica s. l.* (Tan 1995; M. C. and D. G. R., *pers obs*).

We found no genetic structure within *D. margaritica* ‘Continental’ that corresponds to known feeding mode: specimens collected from corals and from the intertidal are genetically indistinguishable (Table 1; Fig. 1a). This lack of genetic (and morphological) distinction suggests that *D. margaritica* ‘Continental’ from all localities could have the ability to scavenge coral tissue. Although *D. margaritica* ‘Oceanic’ is genetically and ecologically differentiated from *D. margaritica* ‘Continental’, its feeding morphology is not known to be different. Therefore, it may be that this species also has the ability, if not the opportunity, to feed on coral tissue.

Given sufficient resolution and numbers of taxa, phylogenetic trees can be used to reconstruct the evolution of superimposed characters, but the phylogeny of *Drupella* is not sufficiently resolved to rigorously test hypotheses about the unique or parallel origin of coral feeding (or even its secondary loss in *D. margaritica s.l.*) and the

corresponding morphological adaptations (Figs. 1, 2). However, we suggest that the suite of morphological and behavioural characteristics that permit corallivory is so specialized that a single origin is most likely. Future studies should examine feeding behaviour and radular structure more closely in this genus. In view of the known intraspecific variability of muricid radulae (Fujioka 1985), the possibility of radular plasticity should also be considered (Padilla 1998).

#### Time of origin of corallivory

Our analyses suggest that *Drupella* separated from other ergalataxine species in the late Miocene (approximately 9.6 Ma) and diversified approximately 5.0 Ma (Fig. 2). Although these ages coincide well with previous estimates of the age of the genus based on morphology (e.g., Vermeij and Carlson 2000), they are much more recent than ages estimated for other intertidal and reef-associated gastropod clades (late Oligocene to early Miocene; e.g., Williams and Duda 2008). Despite the ambiguity in the precise phylogenetic reconstruction of corallivory, this behaviour is restricted to *Drupella* and is therefore unlikely to have evolved before the origin of the genus. Corallivory therefore evolved later in *Drupella* than it did in the other coral-feeding muricids, the coralliophilines (by the early Oligocene; Lozouet and Renard 1998; Vermeij and Carlson 2000). Thus, in contrast to the coralliophilines, the origin of corallivory in *Drupella* does not seem to be connected with the appearance of the major coral groups in the Eocene (Wilson and Rosen 1998; Wood 1999; Crame and Rosen 2002; Wallace and Rosen 2006). Instead, the acquisition of coral-feeding behaviour may have been stimulated by the considerable expansion and reorganization of coral reefs in the Miocene (Crame and Rosen 2002; Hughes et al. 2002; Wallace and Rosen 2006). Similar results have been found in the coral-feeding fishes, where corallivory has arisen several times from the early Oligocene to the late Miocene and Pliocene (butterflyfish, 15.7–3.2 Ma, Bellwood et al. 2010; labrids, 29 Ma, Cowman et al. 2009; parrotfish, 12–10 Ma, Robertson et al. 2006).

Specialization on corals from the late Miocene onwards may have been related to the increasing availability of acroporid corals from the middle Eocene (McIlwain and Jones 1997; Morton et al. 2002; Wallace and Rosen 2006; Bellwood et al. 2010), triggering an adaptive radiation in later-evolving corallivores. Consistent with this interpretation is that acroporid corals are the preferred prey of species of *Drupella* (Forde 1992; Morton et al. 2002), whereas the earlier-evolving coralliophilines show a broad spectrum of coral hosts (e.g., Hayes 1990; Baums et al. 2003; Johnston and Miller 2007). The preference for acroporids could be connected with the observation that

*Drupella* species and some corallivorous fish feed preferentially on damaged coral tissues (Forde 1992; Antonius and Riegl 1997, 1998; McIlwain and Jones 1997; Morton et al. 2002) and that fast-growing acroporid corals are prone to damage and fragmentation (Lirman 2000; Johnson et al. 2008). The attraction of predators to damaged corals could be the result of increased release of mucus following damage (Forde 1992; Turner 1992; McIlwain and Jones 1997).

If acroporid corals presented a new ecological niche, the diversification of *Drupella* could be interpreted as a case of ecological release (see e.g., Schluter 1996). Indeed, from the early Miocene, the Indo-West Pacific fauna appears to have been characterized by trophic expansion and specialization across many taxa (Vermeij and Carlson 2000; Vermeij 2001; Bellwood et al. 2010) and this may have taken place in an environment of intense competition. In the face of such competition, it is surprising that there are so few corallivorous marine species, implying that corals are a difficult resource for predators to exploit.

**Acknowledgments** We are indebted to R. Houart for advice and the loan of the fossil *Taurasia sacyi*. We are also very grateful for the assistance and loans provided by the staff of museums and research institutions, especially P. Bouchet, V. Héros, B. Buge and N. Puillandre of Museum nationale d'Histoire naturelle, Paris (MNHN); I. Loch and A. Miller of the Australian Museum, Sydney. We appreciated useful discussions with J. Taylor and B. Rosen. We would also like to thank the many others who provided specimens and assisted us in various ways including L. Alsayegh, C. Bird, T. Haga, T. Hamada, G. Herbert, Y. Ito, R. Jones, Y. Kano, P. Kuklinski, M. V. Modica, T. Nakano, B. Ng, S. Nielson, N. Razalli, K. S. Tan, S. H. Tan, J. D. True, R. C. Willan and Z. Yasin. We would also like to thank the PANGLAO 2004 Marine Biodiversity Project (funded by the Total Foundation and the French Ministry of Foreign Affairs) and the MNHN-IRD-PNI Santo 2006 expedition (made possible by grants, among others, from the Total Foundation and the Stavros Niarchos Foundation) for collecting some of the specimens that we used. M. C. is supported by a studentship from the Natural History Museum, London and by an Imperial College Deputy Rector's studentship. Photography of specimens by H. Taylor, Natural History Museum, London. We thank the editor and two anonymous referees for helpful comments.

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