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Mitochondrial and morphological differentiation in a previously unrecognized radiation of the land snail genus *Parachloritis* Ehrmann, 1912 on Timor (Pulmonata: Camaenidae)

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Abstract

The present work revises the taxonomy of one group of camaenid gastropods from Timor-Leste based on the study of a large number of recently collected ethanol preserved samples as well as historic museum material, including types. By employing comparative analyses of the variation in morphological features (shell, penial anatomy) and the differentiation in mitochondrial DNA sequences of the cytochrome c oxidase subunit 1 gene (COI) and the 16S rDNA (16S), altogether nineteen species are recognized from Timor-Leste and adjacent areas in the Lesser Sunda and Moluccas, such as West-Timor, Adonara, Leti and Sermata Islands (Indonesia). Four of these species were described previously and have mostly been placed within the genus *Chloritis* Beck, 1837 in the few historic treatments available. Fifteen species found to be new are formally described. In contrast to the previous taxonomic treatment, placement in the genus *Parachloritis* Ehrmann, 1912 is proposed on grounds of comparative shell morphology. Molecular phylogenetic analyses revealed that all examined species form a monophyletic group, which encompasses diverse shell forms. While most species have shells of the general chloritid type, which are of little taxonomic utility, highly distinct shell morphs (trochoid shells, dwarf forms) have originated within this radiation in independent lineages. Morphological change has occurred in some taxonomic lineages while the bulk of *Parachloritis* species has maintained an ancestral shell phenotype. This phenotypic stasis is attributed to stabilizing selection in species, which have maintained associations with ancestral habitats, while distinct shell forms have evolved as result of habitat shifts. Consequently, purely shell-based taxonomies are prone to errors due to misjudging the significance of shell characters. While some *Parachloritis* species uncovered here were found to be narrowly endemic, others had wide distributions that include more than one island. Narrow range endemism was predominantly found in dwarf species and in species that live in high altitudes.

Contents

Introduction

Located near the south-western margin of the Wallacea, Timor is the largest of the Lesser Sunda Islands, an archipelago created by the collision of the Australian and the Asian Plate. The Lesser Sunda Islands comprise two arches of different geological origins and ages (Hall, 2002; Sparkman and Hall, 2010). As part of the geologically younger, orogenic southern arc, the island of Timor sits on the Australian plate. Studies suggested the island to have emerged about 3.3 to 2.7 Million years ago (Ma) (Haig and McCartain, 2007; Quigley *et al*., 2012), or even as early as 4.5 Ma (Nguyen *et al*., 2013).

In biogeographical terms, Timor represents a zone of overlap between the Australian and Southeast Asian biotas (Trainor and Andersen, 2010), but it has also been identified as a regional centre of endemism in its own right (Michaux, 2010; Andersen *et al*., 2013). Contemporary studies of Timor's biodiversity are still utterly rare and limited to a small number of taxa (Trainor and Andersen, 2010, Kaiser *et al*., 2011, Simões *et al*., 2011; Andersen *et al*., 2013). Likewise, Timor's land snails have last been studied in the 1930's by Rensch (1931a, 1935), who listed 61 species-level taxa for all of Timor. This figure included historic accounts scattered through the taxonomic literature as well as many new records and several newly described taxa. Historically, in particular the works of Martens (1864, 1867, 1892, 1897) on non-marine molluscs are relevant. Rensch's (1931a, 1935) taxonomic works were largely based on the study of shells with some additions on the radular and genital anatomy of several species. His study material originated entirely from West-Timor (at the time a Dutch colony) while East Timor (then Portuguese; later annexed by Indonesia, now Timor-Leste) has remained a malacological *terra incognita* until this day. The only exceptions to this were taxonomic lists of predominantly marine (Nobre, 1907) and terrestrial gastropods (Nobre, 1937), which were based on collections undertaken by Francis Newton at the end of the 19th century. Newton evidently collected in the eastern, Portuguese part of the island, but Nobre (1907, 1937) generally referred just to 'Timor' as provenance of the taxa. Therefore, the two *Chloritis* species described by Nobre (1917) from 'Dilly' (= Dili, capital of Timor-Leste) have remained the only historic records of non-marine gastropods from Timor-Leste. The short history of the study of Timorese land snails is completely summarised with reference to the works of Haniel (1921), who published a comparative study on shells of *Amphidromus* Albers, 1850 – yet again based exclusively on material from West-Timor, and two short taxonomic papers each containing descriptions of one or two new species or subspecies of *Asperitas* Gray, 1857 and *Amphidromus*, respectively (Dharma, 1999; Severns, 2006).

The first comprehensive field survey of Timor-Leste's land snail fauna was carried out between 2009 and 2012 by Vince Kessner and collaborators. This survey covered most of the country's surface and was the main source of material used in the present work. The collections in the field revealed the Camaenidae Pilsbry, 1895 to be amongst the most abundant and diverse pulmonate families in Timor-Leste. In turn, tree snails of the genus *Amphidromus* and 'chloritid' species (*i.e.*, species traditionally assigned to the genus *Chloritis* Beck, 1837 based in reference to their shell) were the two dominating camaenid genera in terms of their abundance, diversity and biomass. In this respect, the informal term 'chloritids' refers to species with a generally subglobose shell, a height/width ratio below 1.0 and a usually brownish, rather uniform colour. Chloritid lineages represent a non-monophyletic assemblage within the Camaenidae (Hugall and Stanisic, 2011). However, this term is used here to avoid a formal assignment of the Timorese species to the genus *Chloritis*, which has traditionally been employed to contain numerous probably unrelated species from throughout the geographical range of the entire family. The type species of *Chloritis*, *Helix ungulina* Linneaus, 1758, exhibits as a unique shell feature a deeply sunken apex. However, the apical morphology of the Timorese species differs from this unique morphology of the type species and might underpin the systematic distinctiveness of the Timorese species (Solem, 1979). Other generic names for chloritids from the Indo-Australian Archipelago (IAA) are available, such as *Parachloritis* Ehrmann, 1912 and *Trachychloritis* Haas, 1934. Both genera were introduced for species from the Tanimbar Islands of which no preserved material has been available. In absence of a robust phylogenetic framework including species from throughout the entire IAA and for the unavailability of preserved material of key taxa (*i.e.* type species of genera), currently any generic assignment of the Timorese species remains hypothetical. Provisionally, we prefer assigning the Timorese taxa to the second oldest generic name introduced for chloritids from the IAA, *Parachloritis*.

The present work is the first comprehensive taxonomic study of land snails from Timor-Leste incorporating molecular and morphological evidence. By analysing the differentiation in morphological characters (shell, penial anatomy) and mitochondrial sequences (cytochrome oxidase c subunit 1 = COI, 16S rDNA = 16S), we revise the species-level taxonomy of the Timorese chloritids with main focus on Timor-Leste. Three species have previously been described and were mostly assigned to the genus *Chloritis*: *Parachloritis argilacea* (Férussac, 1821) [often misspelled as '*argillacea*'] from Kupang (West-Timor), *P. mariae* (Nobre, 1917) and *P. newtoni* (Nobre, 1917) from Dili (Timor-Leste) (Nobre, 1917; Rensch, 1931a, 1935; Nobre, 1937). A fourth species, *P. mendax* (Martens, 1864), was previously placed within another genus, *Landouria* Godwin-Austen, 1918, for its much smaller shell (Rensch, 1935). Rensch (1931a, 1935) recognised *P. mariae*, *P. newtoni* and *P. mendax* as distinct species for their distinctive shells but subsumed all other material of somewhat similar shell size, shape, sculpture and colour under one species, *P. argilacea*, which he considered to be widespread and polymorphic. In contrast to this consideration, the present work uncovered a diverse radiation of this group in Timor-Leste comprising several newly described species that differ in part vastly in their shell morphology and the extent of their distribution.

Material and methods

Material examined

The study is based on examination of relevant type material of already described species from Timor as well as newly collected ethanol preserved samples and dry shells from throughout Timor-Leste, now deposited at the Australian Museum in Sydney. Collection data of Australian Museum samples can be accessed online on www.ozcam.gov.au.

Repositories

AM, Australian Museum, Sydney; ENA, European Nucleotide Archive; MNHN, Museum National d'Histoire Naturelle, Paris; MNHML, Museu National De Historia Natural, Universidade de Lisboa; FLMNH, Florida Museum of Natural History, Gainesville; SMF, Naturmuseum Senckenberg, Frankfurt/Main; ZMB, Museum für Naturkunde, Berlin.

Molecular methods

DNA was extracted from small pieces of foot muscle from up to four specimens per lot by use of a QIAGEN DNA extraction kit for animal tissue following the standard procedure of the manual. Fragments of the mitochondrial 16S rRNA (16S) and of the cytochrome c oxidase subunit 1 (COI) genes were amplified by PCR using the primer pairs 16Scs1 (Chiba, 1999) and 16Sbd1 (Sutcharit *et al*., 2007) and L1490 and H2198 (Folmer *et al*., 1994), respectively. Reactions were performed with annealing steps of 60 s at 55 °C for 16S and 50 °C for COI and elongation times of 90 s for 16S and 60 s for COI. Both strands of PCR fragments were purified and cycle sequenced by use of the PCR primers. Electropherograms were corrected for misreads and forward and reverse strands were merged into one sequence file using CodonCode Aligner v. 3.6.1 (CodonCode Corporation, Dedham, MA). Sequences have been deposited in the European Nucleotide Archive (ENA; Accession Numbers HG515079-HG515228 [COI], HG515229-HG515373 [16S]). The 16S sequences were aligned by using the online version of MAFFT (available at http://mafft.cbrc.jp/alignment/server/) employing the E-INS-i strategy suitable for thorough alignments of sequences with multiple conserved domains and long gaps (Katoh *et al*., 2002). COI sequences did not require alignment as they had an identical length of 655 bp after trimming of the primer sites. Pair-wise genetic distances were calculated using MEGA5.2.1 (Tamura *et al*., 2011) under the option 'pair-wise deletion of gaps'. For phylogenetic analyses, 16S and COI sequences were concatenated into one partitioned data set. Prior to the model-based phylogenetic analyses, the best-fit model of nucleotide substitution was identified for each gene partition separately by means of the Akaike Information Criterion calculated with MrModeltest (Nylander, 2002). In the following model-based phylogenetic analyses, the data were partitioned to allow each gene fragment to be analysed under the appropriate model of sequence evolution. The BI analyses were performed with four unlinked data partions (16S, each codon position in COI), the parameters being estimated from the data set separately for each partition. Maximum Likelihood (ML) analyses were performed using RaxMLGui (Silvestro and Michalak, 2010). Two-hundred thorough ML bootstrap replicates were performed in order to assess the branch support of the ML tree. Bayesian posterior probabilities of phylogenetic trees were estimated by running a 20,000,000 generations Metropolis-coupled Markov chain Monte Carlo (2 runs with each 4 chains, of which one was heated) as implemented by MrBayes vs. 3.2.1 (Ronquist and Huelsenbeck, 2003). A data partition was applied that allowed parameters to be estimated separately for each gene fragment and for each codon position of the COI gene. Sampling rate of the trees was 1,000 generations. Generations sampled before the chain reached stationary were discarded as burn-in. Stationarity was reached when the average standard deviation of split frequencies shown in MrBayes was less than 0.01 and the log likelihood of sampled trees reached a stationary distribution.

Morphological examinations

Morphological characters of adult shells (dimension, colouration and sculpture) were assessed from adult specimens, which were recognised by having a complete apertural lip. Shells were measured with callipers precise to 0.1 mm. Characters measured were height (H = maximum dimension parallel to axis of coiling, including lip) and diameter (D = maximum dimension perpendicular to H, including lip). The number of whorls (W), including protoconch, was counted precise to 0.1 as shown in Köhler (2011a: fig. 2). Genital anatomy was examined in two to five specimens from each mtDNA clade (= 'molecular operational taxonomic unit') by use of a Leica M8 stereo microscope with drawing mirror.

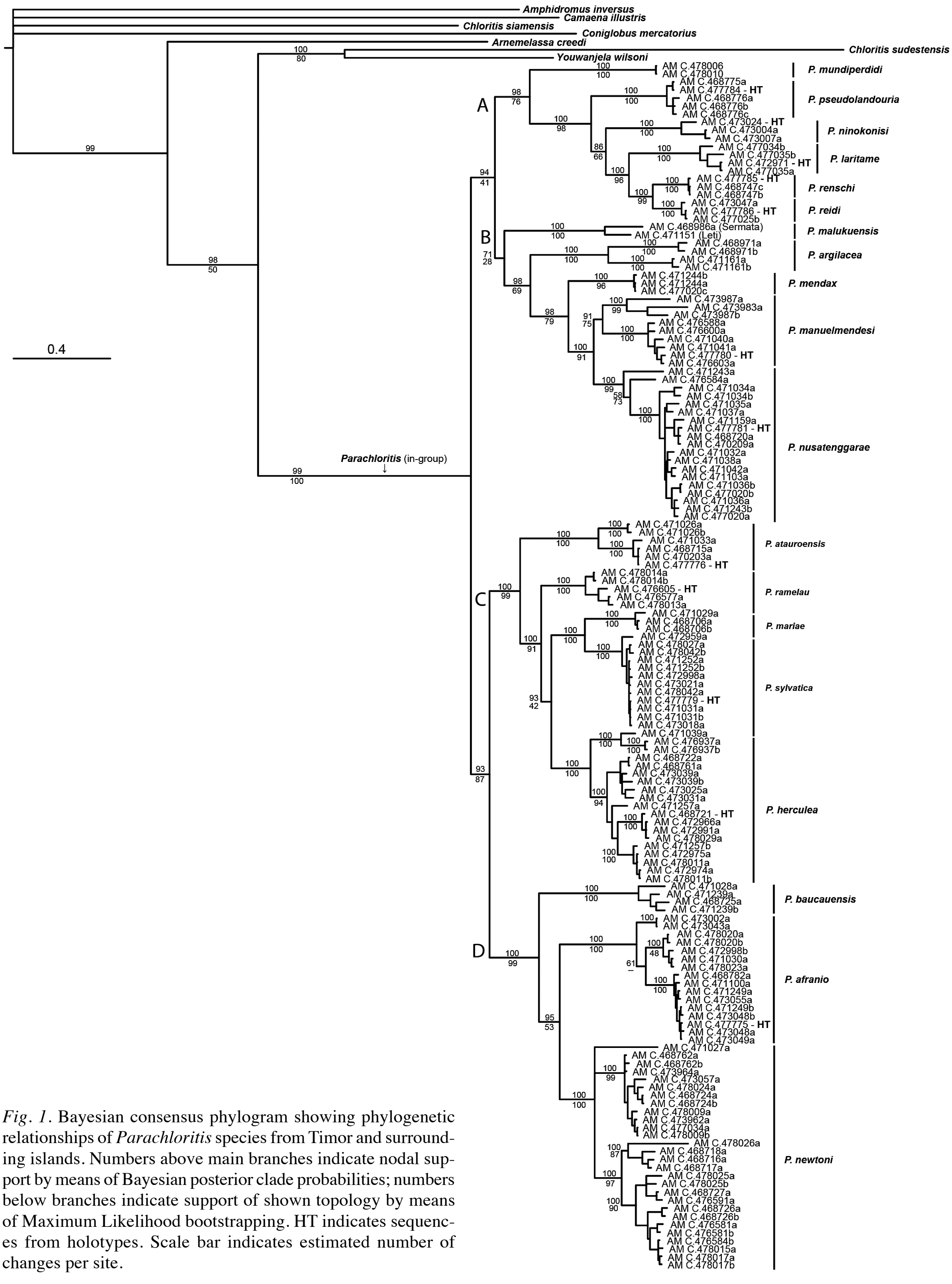

Fig. 1. Bayesian consensus phylogram showing phylogenetic relationships of *Parachloritis* species from Timor and surrounding islands. Numbers above main branches indicate nodal support by means of Bayesian posterior clade probabilities; numbers below branches indicate support of shown topology by means of Maximum Likelihood bootstrapping. HT indicates sequences from holotypes. Scale bar indicates estimated number of changes per site.

Species delimitation

We formally recognized species as distinct when they formed phenotypically and genotypically distinct clusters (Sites and Marshall, 2004). To this end four criteria were employed to delimit species: 1) species formed clades in the mtDNA trees, 2) these clades were comparatively well differentiated from other such clades, 3) the morphology of members of any of these clades differed in at least one feature unlikely to be polymorphic or under environmental control (autapomorphy), 4) no intermediate morphs existed.

Abbreviations used

16S, partial sequence of the 16SrDNA; at, atrium or genital pore; COI, partial sequence of the *cytochrome c oxidase* subunit 1 gene; ct, connective tissue; D, diameter of shell; ef, epiphallic flagellum; el, epiphallic lobe; ep, epiphallus; ew, epiphallic wall; H, height of shell; p, penis; pil, pilasters; rm, retractor muscle; va, vagina; vd, vas deferens; W, number of whorls.
Species codes: afr, *P. afranio*; arg, *P. argilacea*; ata, *P. atauroensis*; bau, *P. baucauensis*; her, *P. herculea*; rei, *P. reidi*; lar, *P. laritame*; mal, *P. malukuensis*; man, *P. manuelmendesi*; mar, *P. mariae*; mdx, *P. mendax*; mun, *P. mundiperdidi*; new, *P. newtoni*; nin, *P. ninokonisi*; nus, *P. nusatenggarae*; pse, *P. pseudolandouria*; ram, *P. ramelau*; ren, *P. renschi*; syl, *P. sylvatica*.

Results

Molecular phylogenetics

The analysed mitochondrial data sets contained sequences representing 150 ingroup specimens and seven outgroup taxa (Table 1), which were used to root the phylogenetic trees. The COI sequences (655 bp) and the aligned 16S sequences (798 bp) were merged into one concatenated sequence data set. Eight specimens (including two outgroup taxa) were represented by only one sequence fragment, either COI or 16S. The missing sequences were coded as unknown. However, every ingroup specimen with one missing sequence fragment was accompanied by additional conspecific individuals with complete sequence data. The General time-reversible model of sequence evolution (Tavaré, 1986), GTR+G+I, was identified as the best-fit model for both mitochondrial datasets by means of the Akaike Information Criterion as well as by a Likelihood ratio test. This model has been employed in all ML and BI analyses of the separate or partitioned sequence datasets.

Table 1. Outgroup sequences of camaenid gastropods used to root the tree.

species	origin	Genbank (*) and ENA (**) accession numbers
Amphidromus inversus	Thailand	16S: AB112400* COI: FJ472655*
Arnemelassa creedi	NW Australia (AM C.462990)	16S: HQ245442* COI: HG515080**
Youwanjela wilsoni	NW Australia (WAM S49583)	16S: HE588141* COI: HG515081**
Chloritis sudestens	New Guinea (FLMNH 339062)	16S: KF833399* COI: HG515079**
Chloritis siamensis	Thailand	16S: AB112390* COI: n/a
Camaena illustris	Thailand	16S: AB112389* COI: n/a
Coniglobus mercatorius	Japan	16S: AF098715* COI: AB480894*

Maximum Likelihood (ML) and Bayesian Inference (BI) trees were calculated independently for each dataset as well as for the concatenated sequences. All phylogenetic analyses produced trees with nearly identical topologies. Most significantly, in all trees the Timorese species formed a well-supported monophyletic group with respect to the outgroup containing several Australian and Southeast Asian camaenids. Secondly, all trees supported the monophyly of each species as delimited herein based on their morphological and mitochondrial differentiation. Moreover, all trees supported the same phylogenetic relationships between these species. Trees differed to a small degree with respect to the branching order amongst tips within phylogenetic clusters (*i.e.*, intraspecific relationships). These differences were deemed to be not relevant for the scope of the present study. Thus, for sake of simplicity, only the BI tree for the concatenated dataset is shown here (Fig. 1).

In this tree, the chosen outgroup is not monophyletic but paraphyletic with respect to the ingroup. Most closely related to the ingroup were two camaenid lineages from north-western Australia (*Arnemelassa* and *Youwanjela*) as well as *Chloritis sudestensis* from Papua New Guinea while all included Asian lineages are more distantly related. A basal bifurcation separates the ingroup, genus *Parachloritis*, into two principal clades. Each of these principal clades has a basal bifurcation as well. Thus, four principal clades (A-D) can be

Table 2. Average evolutionary divergences between species of *Parachloritis* in COI. Shown are average base substitutions per site between species (upper rows: calculated by employing the Maximum Composite Likelihood model, MC; lower rows (in bold), uncorrected p-distances, p). Shaded cells show infraspecific distances.

		arg	afr	ata	bau	her	lar	mal	man	mar	men	mun	new	nin	nus	pse	ram	rei	ren	syl
arg	ML	0.082																		
	p	**0.076**																		
afr	ML	0.180	0.031																	
	p	**0.155**	**0.030**																	
ata	ML	0.195	0.173	0.044																
	p	**0.168**	**0.151**	**0.042**																
bau	ML	0.170	0.127	0.195	0.035															
	p	**0.148**	**0.115**	**0.167**	**0.034**															
her	ML	0.166	0.137	0.145	0.152	0.048														
	p	**0.146**	**0.122**	**0.131**	**0.134**	**0.046**														
lar	ML	0.185	0.193	0.206	0.178	0.184	0.042													
	p	**0.159**	**0.161**	**0.176**	**0.154**	**0.159**	**0.041**													
mal	ML	0.186	0.156	0.183	0.148	0.140	0.187	0.052												
	p	**0.160**	**0.136**	**0.157**	**0.130**	**0.125**	**0.159**	**0.050**												
man	ML	0.180	0.172	0.183	0.194	0.142	0.198	0.161	0.025											
	p	**0.157**	**0.149**	**0.158**	**0.166**	**0.126**	**0.169**	**0.142**	**0.024**											
mar	ML	0.165	0.145	0.144	0.141	0.112	0.183	0.151	0.164	0.010										
	p	**0.146**	**0.129**	**0.129**	**0.125**	**0.104**	**0.158**	**0.133**	**0.145**	**0.010**										
men	ML	0.173	0.161	0.204	0.178	0.144	0.191	0.148	0.137	0.157	0.003									
	p	**0.152**	**0.141**	**0.174**	**0.154**	**0.128**	**0.163**	**0.130**	**0.124**	**0.138**	**0.003**									
mun	ML	0.198	0.183	0.168	0.187	0.165	0.183	0.173	0.189	0.157	0.184	0								
	p	**0.168**	**0.156**	**0.147**	**0.159**	**0.144**	**0.158**	**0.150**	**0.163**	**0.138**	**0.158**	**0**								
new	ML	0.185	0.116	0.167	0.135	0.132	0.178	0.157	0.169	0.148	0.176	0.174	0.063							
	p	**0.159**	**0.106**	**0.147**	**0.122**	**0.118**	**0.155**	**0.137**	**0.147**	**0.131**	**0.153**	**0.150**	**0.060**							
nin	ML	0.203	0.204	0.193	0.190	0.174	0.157	0.178	0.217	0.187	0.214	0.175	0.189	0.033						
	p	**0.173**	**0.173**	**0.164**	**0.163**	**0.151**	**0.139**	**0.153**	**0.183**	**0.161**	**0.180**	**0.152**	**0.163**	**0.033**						
nus	ML	0.174	0.162	0.196	0.174	0.156	0.197	0.157	0.131	0.165	0.148	0.166	0.161	0.185	0.036					
	p	**0.152**	**0.142**	**0.168**	**0.150**	**0.138**	**0.168**	**0.138**	**0.119**	**0.145**	**0.133**	**0.145**	**0.141**	**0.159**	**0.035**					
pse	ML	0.166	0.159	0.178	0.160	0.158	0.139	0.158	0.180	0.153	0.159	0.165	0.164	0.152	0.167	0.010				
	p	**0.144**	**0.139**	**0.153**	**0.139**	**0.138**	**0.125**	**0.137**	**0.156**	**0.135**	**0.139**	**0.144**	**0.142**	**0.136**	**0.146**	**0.010**				
ram	ML	0.166	0.155	0.149	0.157	0.105	0.175	0.149	0.158	0.109	0.158	0.164	0.149	0.177	0.166	0.167	0.024			
	p	**0.146**	**0.138**	**0.134**	**0.138**	**0.098**	**0.152**	**0.132**	**0.141**	**0.101**	**0.139**	**0.143**	**0.133**	**0.153**	**0.146**	**0.145**	**0.023**			
rei	ML	0.187	0.189	0.204	0.169	0.159	0.110	0.173	0.203	0.177	0.178	0.187	0.167	0.143	0.171	0.125	0.170	0.007		
	p	**0.162**	**0.165**	**0.173**	**0.148**	**0.139**	**0.102**	**0.149**	**0.174**	**0.154**	**0.153**	**0.160**	**0.146**	**0.129**	**0.149**	**0.114**	**0.148**	**0.007**		
ren	ML	0.198	0.193	0.219	0.173	0.167	0.122	0.175	0.205	0.175	0.201	0.176	0.180	0.139	0.183	0.123	0.179	0.073	0.001	
	p	**0.170**	**0.165**	**0.185**	**0.151**	**0.146**	**0.112**	**0.151**	**0.175**	**0.153**	**0.171**	**0.152**	**0.156**	**0.125**	**0.158**	**0.112**	**0.155**	**0.070**	**0.001**	
syl	ML	0.172	0.133	0.145	0.140	0.100	0.182	0.127	0.155	0.076	0.150	0.164	0.134	0.171	0.151	0.157	0.106	0.170	0.185	0.007
	p	**0.151**	**0.119**	**0.130**	**0.124**	**0.093**	**0.157**	**0.114**	**0.137**	**0.072**	**0.132**	**0.143**	**0.120**	**0.148**	**0.134**	**0.137**	**0.099**	**0.148**	**0.160**	**0.007**

differentiated, each comprising three to six species.

The shown topology was usually well supported by means of Bayesian posterior clade probabilities and ML bootstrapping. However, exceptionally some nodes were not well supported. Low support was occasionally observed amongst conspecific lineages (*e.g.* within *P. nusatenggarae*, *P. herculea* and *P. afranio*) or basal branches (*e.g.*, relationships between clades A, B, C, D; amongst the outgroup). However, all species clades received high nodal support.

The species delimited here were differentiated by mean uncorrected p-distances of 7.0-18.5% (or 7.3-21.9% Maximum composite likelihood distances; Tamura *et al.*, 2004) in COI and p-distances of 4.5-18.0% (MCL, 4.7-21.0) in 16S. On average, the observed intraspecific distances were considerably smaller (COI: average p-distance = 3.1%; 16S: average p-distance = 2.2%). However, minimal interspecific p-distances (COI, 7.0%; 16S, 4.5%) and maximal intraspecific distances (COI, 8.4%; 16S, 6.4%) overlapped with each other (Tables 2-3).

Table 3. Average evolutionary divergences between species of *Parachloritis* in 16S. Shown are average base substitutions per site between species (upper rows: calculated by employing the Maximum Composite Likelihood model, MC; lower rows (in bold), uncorrected p-distances, p). Shaded cells show infraspecific distances.

		arg	afr	ata	bau	her	lar	mal	man	mar	men	mun	new	nin	nus	pse	ram	rei	ren	syl
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	p	**0.168**	**0.156**	**0.147**	**0.159**	**0.144**	**0.158**	**0.150**	**0.163**	**0.138**	**0.158**	**0**								
new	ML	0.185	0.116	0.167	0.135	0.132	0.178	0.157	0.169	0.148	0.176	0.174	0.063							
	p	**0.159**	**0.106**	**0.147**	**0.122**	**0.118**	**0.155**	**0.137**	**0.147**	**0.131**	**0.153**	**0.150**	**0.060**							
nin	ML	0.203	0.204	0.193	0.190	0.174	0.157	0.178	0.217	0.187	0.214	0.175	0.189	0.033						
	p	**0.173**	**0.173**	**0.164**	**0.163**	**0.151**	**0.139**	**0.153**	**0.183**	**0.161**	**0.180**	**0.152**	**0.163**	**0.033**						
nus	ML	0.174	0.162	0.196	0.174	0.156	0.197	0.157	0.131	0.165	0.148	0.166	0.161	0.185	0.036					
	p	**0.152**	**0.142**	**0.168**	**0.150**	**0.138**	**0.168**	**0.138**	**0.119**	**0.145**	**0.133**	**0.145**	**0.141**	**0.159**	**0.035**					
pse	ML	0.166	0.159	0.178	0.160	0.158	0.139	0.158	0.180	0.153	0.159	0.165	0.164	0.152	0.167	0.010				
	p	**0.144**	**0.139**	**0.153**	**0.139**	**0.138**	**0.125**	**0.137**	**0.156**	**0.135**	**0.139**	**0.144**	**0.142**	**0.136**	**0.146**	**0.010**				
ram	ML	0.166	0.155	0.149	0.157	0.105	0.175	0.149	0.158	0.109	0.158	0.164	0.149	0.177	0.166	0.167	0.024			
	p	**0.146**	**0.138**	**0.134**	**0.138**	**0.098**	**0.152**	**0.132**	**0.141**	**0.101**	**0.139**	**0.143**	**0.133**	**0.153**	**0.146**	**0.145**	**0.023**			
rei	ML	0.187	0.189	0.204	0.169	0.159	0.110	0.173	0.203	0.177	0.178	0.187	0.167	0.143	0.171	0.125	0.170	0.007		
	p	**0.162**	**0.165**	**0.173**	**0.148**	**0.139**	**0.102**	**0.149**	**0.174**	**0.154**	**0.153**	**0.160**	**0.146**	**0.129**	**0.149**	**0.114**	**0.148**	**0.007**		
ren	ML	0.198	0.193	0.219	0.173	0.167	0.122	0.175	0.205	0.175	0.201	0.176	0.180	0.139	0.183	0.123	0.179	0.073	0.001	
	p	**0.170**	**0.165**	**0.185**	**0.151**	**0.146**	**0.112**	**0.151**	**0.175**	**0.153**	**0.171**	**0.152**	**0.156**	**0.125**	**0.158**	**0.112**	**0.155**	**0.070**	**0.001**	
syl	ML	0.172	0.133	0.145	0.140	0.100	0.182	0.127	0.155	0.076	0.150	0.164	0.134	0.171	0.151	0.157	0.106	0.170	0.185	0.007
	p	**0.151**	**0.119**	**0.130**	**0.124**	**0.093**	**0.157**	**0.114**	**0.137**	**0.072**	**0.132**	**0.143**	**0.120**	**0.148**	**0.134**	**0.137**	**0.099**	**0.148**	**0.160**	**0.007**

Morphological examinations

Species of *Parachloritis* from Timor possessed small (D < 5 mm) to large (D > 30 mm) shells with low to moderately elevated spire (see Table 4 for shell size of each species). The species can roughly be grouped into two size groups (small, large). Within these groups, species can usually not readily be differentiated by their shell size (Fig. 2). Shells may be uniform brown in colour, banded, suffused or even vividly red-white marbled. Shell sculpture is generally smooth; microscopic sculpture on the teleoconch varies; it may comprise axial lirae or periostracal protrusions, or both. These elements vary in their development and distribution across the shell surface. The protoconch microsculpture generally consists of a combination of more or less well-developed radial lirae and radially arranged corrugations; exceptionally well-developed pustules may be present. Some species are readily distinguished by unique shell features, such as *P. mundiperdidi* n. sp.

Table 4. Shell measurements, given are averages ± standard deviation (minima – maxima) of n measured shells (in mm).

species	H	D	W	n
P. argilacea	15.9 ± 0.9 (14.7 - 18.0)	21.8 ± 1.1 (20.1 - 23.5)	4.2 ± 0.1 (3.9 - 4.3)	10
P. mariae	16.0 ± 0.8 (14.2 – 17.2)	20.8 ± 1.1 (18.9 – 23.0)	4.3 ± 0.1 (4.2 – 4.5)	21
P. newtoni	14.2 ± 1.5 (11.3 – 17.5)	19.8 ± 1.8 (16.6 – 23.4)	4.2 ± 0.2 (3.7 – 4.6)	64
P. baucauensis	14.8 ± 0.8 (14.0 - 16.6)	20.7 ± 1.0 (19.0 – 23.0)	4.2 ± 0.1 (4.0 – 4.4)	14
P. afranio	16.7 ± 1.3 (14.5 – 19.0)	21.2 ± 0.8 (19.5 – 22.5)	4.3 ± 0.1 (4.1 – 4.4)	14
P. atauroensis	15.8 ± 1.4 (13.5 – 18.6)	21.5 ± 1.7 (18.3 – 24.9)	4.1 ± 0.2 (3.8 – 4.4)	40
P. herculea	20.7 ± (18.5 – 24.4)	29.9 ± (27.6 – 35.6)	4.3 ± (4.0 – 4.8)	17
P. sylvatica	17.8 ± 1.6 (14.0 – 20.0)	24.6 ± 2.1 (20.0 – 27.7)	4.3 ± 0.2 (4.0 – 4.4)	23
P. manuelmendesi	18.5 ± 1.3 (15.6 – 20.5)	26.9 ± 1.7 (24.0 – 29.2)	4.3 ± 0.1 (4.0 – 4.4)	20
P. nusatenggarae	15.7 ± 1.7 (12.4 – 17.9)	20.2 ± 1.8 (16.5 – 23.0)	4.1 ± 0.2 (3.8 – 4.4)	19
P. ramelau	16.5 ± 1.2 (14.9 – 20.0)	23.3 ± 1.8 (20.5 – 26.8)	4.4 ± 0.1 (4.3 – 4.6)	16
P. malukuensis	13.1 ± 2.6 (9.5 – 15.8)	17.0 ± 3.2 (12.5 – 20.0)	4.3 ± 0.2 (4.0 – 4.5)	3
P. mundiperdidi	16.2 ± 0.7 (14.8 – 17.3)	27.5 ± 0.9 (26.4 – 29.0)	4.3 ± 0.1 (4.2 – 4.4)	7
P. mendax	5.2 ± 0.4 (4.7 – 6.0)	8.8 ± 0.2 (8.5 – 9.0)	3.3 ± 0.1 (3.2 – 3.5)	9
P. renschi	5.9 ± 0.1 (5.8 – 6.0)	9.2 ± 0.2 (9.0 – 9.5)	3.7 ± 0.4 (3.4 – 4.2)	3
P. reidi	6.4 ± 0.3 (6.0 – 6.9)	10.1 ± 0.4 (9.5 – 10.8)	3.4 ± 0.1 (3.2 – 3.6)	13
P. laritame	6.3 ± 0.3 (5.8 – 6.5)	9.8 ± 0.6 (9.0 – 10.5)	3.1 ± 0.2 (3.0 – 3.4)	3
P. pseudolandouria	5.5 ± 1.2 (4.0 – 7.3)	9.5 ± 1.3 (7.6 – 11.0)	3.7 ± 0.2 (3.3 – 4.0)	5

(trochoid shape), *P. mariae* (marbled colouration) or *P. ramelau* n. sp. (red-brown colour). Most species are recognizable by a combination of shell characters, such as coloration, size, shape, microsculpture, while several species have rather indistinctive shells and may only be differentiated by combining evidence from mtDNA and penial anatomy (Table 5).

The genital (mainly penial) anatomy of species has been studied and found to be broadly consistent. All species have a penis without penial sheath with a well-developed epiphallus with long epiphallic flagellum and epiphallic lobe. The vas deferens is rather thin. The penial retractor muscle attaches at about the mid-epiphallus. Penis and epiphallus communicate through a pore. Inner penial wall and inner epiphallic wall are sculptured by pilasters of variable thickness and number. Species may also differ in the thickness of these walls as well as in the relative length of penis, epiphallus and flagellum. For detailed descriptions of anatomical features refer to the taxonomic descriptions in the Appendix.

Discussion

Taxonomy and systematics of Timorese chloritids

In the few historic taxonomic accounts available, previously described species were usually assigned to *Chloritis*. However, this procedure was for mere convenience and not based on comparative morphology or even phylogenetic analyses. Solem (1979) first raised doubts whether the genus name *Chloritis* should be employed for the Timorese species *P. argilacea* for differing significantly from the type species in its shell morphology. Irrespectively, many other species with such chloritid shells have been assigned to this genus; often probably incorrectly (*e.g.*, Vermeulen and Whitten, 1998). Instead of continuing this probably ill-advised procedure, we give preference to the second oldest genus name for chloritids from the IAA, *Parachloritis*. This decision is also based on the fact that the Timorese species possess shell characters, which correspond with the original generic diagnosis of *Parachloritis* given by Ehrmann (1912). This provisional treatment requires validation through future phylogenetic studies of chloritids from across the entire IAA.

The earliest described species from Timor is *P. argilacea* from Kupang (West-Timor). Subsequently, this species name has widely been employed for specimens with similar, rather generic shell characters from throughout Timor and neighbouring islands, such as Savu, Sumba, Flores, Adonara, Solor and Alor (*e.g.*, Martens, 1892; van Benthem Jutting, 1928; Rensch, 1931b). However, as shown here, *P. argilacea* is not present in Timor-Leste indicating that it is not as widely distributed and vastly polymorphic as previously thought. Thus, the assignment of samples from outside the currently confirmed range (western West Timor) to this taxon requires confirmation by future comparative studies. The molecular phylogenetic reconstructions produced herein showed that the name *P. argilacea* as previously encompassed represents a complex of shell-wise cryptic species. Thus, a revised delimitation of species and a differentiated appraisal particularly of shell characters for species de-

Table 5. Comparative overview of shell characters in *Parachloritis* species.

species	type	coloration	periphery	protoconch microsculpture	teleoconch microsculpture
P. argilacea	subglobose, medium	rather uniform	rounded	radial lirae, corrugations	periostracal projections, weak axial lirae
P. atauroensis	subglobose, medium	banded or rather uniform	rounded	radial lirae, corrugations	axial lirae
P. baucauensis	subglobose, medium	banded	rounded	radial lirae, corrugations	weak axial lirae
P. herculea	subglobose, large	rather uniform	rounded	radial lirae, corrugations	weak axial lirae
P. malukuensis	subglobose, medium	rather uniform	rounded	radial lirae, corrugations	weak axial lirae
P. manuelmendesi	subglobose, large	rather uniform	rounded	radial lirae, corrugations	weak axial lirae
P. mariae	subglobose, medium	red-white marbled	rounded	radial lirae, corrugations	weak axial lirae
P. newtoni	subglobose, medium	usually banded	rounded	radial lirae, corrugations	weak axial lirae
P. nusatenggarae	subglobose, medium	rather uniform	rounded	radial lirae, corrugations	weak axial lirae
P. ramelau	subglobose, medium	red brown	rounded	radial lirae, corrugations	weak axial lirae
P. sylvatica	subglobose, large	rather uniform	rounded	radial lirae, corrugations	weak axial lirae
P. afranio	subglobose, medium	dark basal suffusion	rounded	strong pustulation	periostracal projections, weak axial lirae
P. mundiperdidi	trochoid, large	rather uniform	angulated	radial lirae, corrugations	sparse periostracal projections
P. reidi	depressed subglobose, small	rather uniform	angulated	dense pustulation	periostracal projections
P. laritame	depressed subglobose, small	rather uniform	angulated	dense pustulation	periostracal projections
P. mendax	depressed subglobose, small	rather uniform	rounded	dense pustulation	periostracal projections
P. ninokonisi	depressed subglobose, small	rather uniform	rounded	sparse, irregular pustulation	periostracal projections
P. pseudolandouria	depressed subglobose, small	rather uniform	keeled	dense pustulation	periostracal projections
P. renschi	depressed subglobose, small	rather uniform	angulated	dense pustulation	periostracal projections

lineation was required (further details below). Accordingly, we are recognising several new species from Timor-Leste, which would have earlier been subsumed under the previous concept of a widely distributed and polymorphic *P. argilacea*.

Another remarkable discovery of the present study is that the evolutionary radiation of *Parachloritis* on Timor contains several species with aberrant shells types. Species with considerably smaller shells than the 'typical' chloritids were found to be members of the same monophyletic group, such as for example *P. mendax* and *P. laritame* n. sp. The phylogenetic trees demonstrate that such 'dwarf forms' have originated at least twice amongst *Parachloritis* in the clades A and B (Figs 1, 3).

Only one taxonomic name for one of these 'dwarf' species is available (*P. mendax*), but had been placed in a different genus, *Landouria* Godwin-Austen, 1918, based on its shell (Rensch, 1935). Although similar indeed, genuine members of *Landouria* in Timor-Leste are phylogenetically distinct from *Parachloritis* (unpubl. data). In addition, *P. mundiperdidi* n. sp. has a trochoid shell shape unlike any other congener.

Summarizing the above, the radiation of *Parachloritis* in Timor-Leste contains species with more or less indistinct shells of a general chloritid type (*i.e.*, uniform brown, subglobose, moderate in size), which were so far subsumed under one species name (*P. argilacea*), as well as several species that are readily distinguished by their shell colour or shape (*e.g.*, *P. newtoni*, *P. mariae*, *P. mundiperdidi* n. sp.). It also contains several 'dwarf' species (*e.g.*, *P. mendax*), which have evolved twice (Fig. 3). These findings corroborate results from other studies that demonstrated that macroscopic shell characters alone are unreliable indicators for phylogenetic relationships within the Camaenidae (*e.g.*, Hugall and Stanisic, 2011; Köhler and Johnson, 2012; Criscione and Köhler, 2013). Even closely related species may have vastly different shells due to divergent morphological evolution while most species have apparently retained a plesiomorphic phenotype. This contrast between relative rapid morphological change in some taxonomic lineages and the long-term phenotypic stasis in the bulk of remaining *Parachloritis* lineages (Fig. 3) probably relates to the presence of stabilizing selection in species, which have maintained associations with ancestral habitats, and selection towards distinct morphotypes in species that colonized new environments. Similar phenotype-habitat correlations in camaenid shells have been documented in various Australian camaenids (*e.g.*, Criscione and Köhler, 2013), most notably though in *Rhagada* Albers, 1850 (Stankowski, 2011).

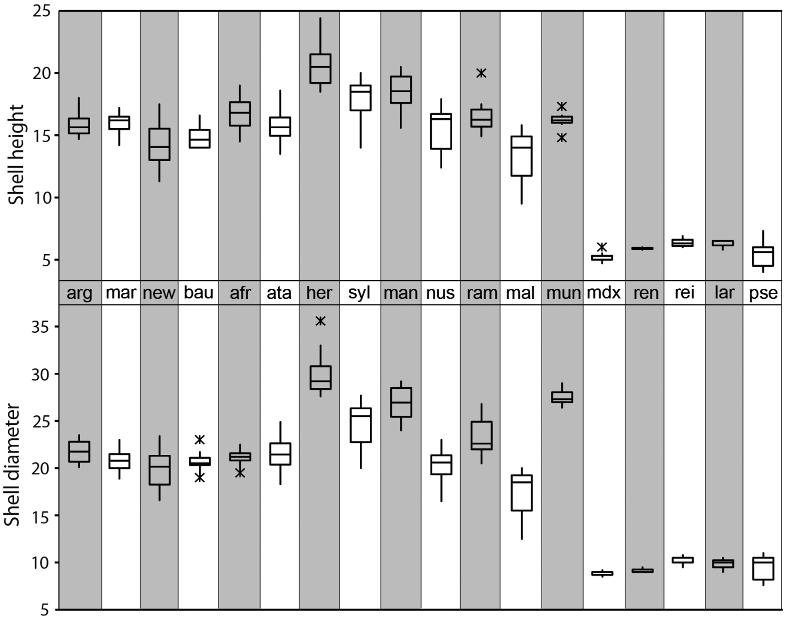

Fig. 2. Comparison of shell dimensions H (above) and D (below) by means of box-and-whisker plots showing means (horizontal line in box), inner upper and lower quartiles (box), outer upper and lower quartiles (whiskers) and outliers (asterisks) in mm.

Species delineation by means of comparative morphology and mitochondrial differentiation

We employed a rather conservative approach in species delimitation and acknowledge that in particular criterion 1 (monophyly in mtDNA-based trees) is very stringent and might not generally be applicable. There is a growing body of studies that suggest that evolutionarily rather young species may not appear as monophyletic clusters in mtDNA-based phylogenies for various reasons (*e.g.*, Funk and Omland, 2003; Köhler and Deein, 2010; Sauer and Hausdorf, 2012). However, we feel that this stringency helps providing a robust and unequivocal taxonomic foundation, which can further be tested with more elaborate methods and/or by denser sampling.

This study demonstrated that species limits in *Parachloritis* could best be resolved by a combined evaluation of morphological and genetic evidence. In fact, mtDNA sequence data has been most useful in identifying monophyletic groups as a prerequisite to the evaluation of morphological features. We observed no discordance in the patterns of mitochondrial and morphological differentiation at the species level, which could have fuelled doubts into the applicability of some of these data for species delineation. Certainly, proper identification of *Parachloritis* species needs to rely on more than a few shell characters. While several species possess highly derived shells that permit species identification, most others exhibit plesiomorphic character states shared with other congeners. This is exemplified by the evolution of the general shell types (Fig. 3): Most species exhibit moderately sized shells of the general chloritid shape. Such species are found in three of four clades of the Timorese radiation (B-D). Clade (A) exclusively contains species with aberrant shells, such as *P. mundiperdidi* n. sp. (trochoid, large) as well as the dwarf species *P. pseudolandoria* n. sp. – *P. reidi* n. sp. *Parachloritis mendax* represented a second, phylogenetically distinct dwarf lineage within clade B. Because *P. mendax* nests amongst species with typical shells, the most parsimonious hypothesis is that small shells have evolved independently in clades A and B. Consequently, most other species have retained the 'typical' shell shape as a plesiomorphic trait; therefore being of little taxonomic utility. Amongst these species some have developed distinct colorations (*e.g.*, *P. newtoni*, *P. mariae*, *P. ramelau* n. sp.) or larger shells (*P. herculea* n. sp., *P. sylvatica* n. sp., *P. manuelmendesi* n. sp.) (Fig. 2). The remaining species are not always readily distinguishable by macroscopic shell characters (Tables 4-5). Instead, an assessment of their taxonomic status requires combination of molecular phylogenetic and additional morphological evidence.

However, even a distinct shell colour may be misleading. Three species (*P. newtoni*, *P. baucauensis* n. sp., *P. atauroensis* n. sp.) exhibited virtually identical shell banding. All these species occur along the northern shore of the mainland of Timor-Leste between Dili and

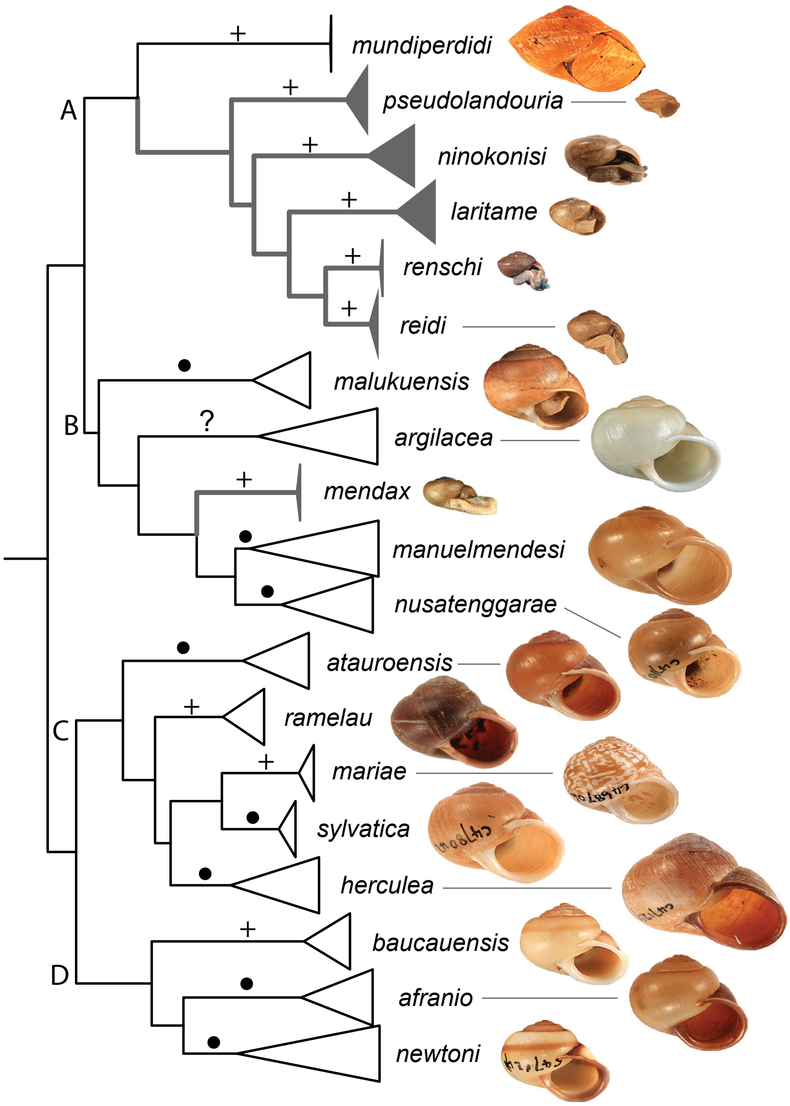

Fig. 3. Backbone of the phylogenetic tree shown in Fig. 1 with species clades shown as collapsed. Clades with dwarf species in thick, grey lines with filled boxes; +) indicating narrowly endemic species; •) indicating more widespread species; ?) indicating unknown size of species range.

Baucau. Interestingly, populations of *P. atauroensis* on Atauro Island consistently had unbanded shells. The geographically well-circumscribed occurrence of banded shells and the polymorphism in *P. atauroensis* n. sp. poses interesting questions against the background of widespread polymorphism known from other stylommatophoran pulmonates. It has been shown in several groups that shell colour patterns may be controlled by dominant/recessive Mendelian genetic inheritance plus selection by predation or climatic factors (*e.g.*, Murray and Clarke, 1976a, b; Jones *et al.*, 1977; Johnson, 1981, 2011; Ożgo, 2005). If such polymorphism existed also in *Parachloritis*, than altogether shell colour was of no or little taxonomic utility.

Within the Camaenidae, *Parachloritis* appears to be more closely related to north-western Australian than the Southeast Asian camaenid lineages amongst the outgroup taxa (Fig. 1). Recent systematic studies of north-western Australian camaenids have demonstrated that penial characters are frequently diagnostic at both species and genus level (*e.g.*, Solem, 1979, 1981a, b; Köhler, 2010, 2011b, c; Criscione *et al.*, 2012; Köhler, 2012). Correspondingly, most species of *Parachloritis* revealed typical features in penial anatomy, such as relative length of penis, epiphallus and flagellum and thickness and inner sculpture of penial and epiphallic wall. However, intraspecific variation was comparatively high and the development of certain features may

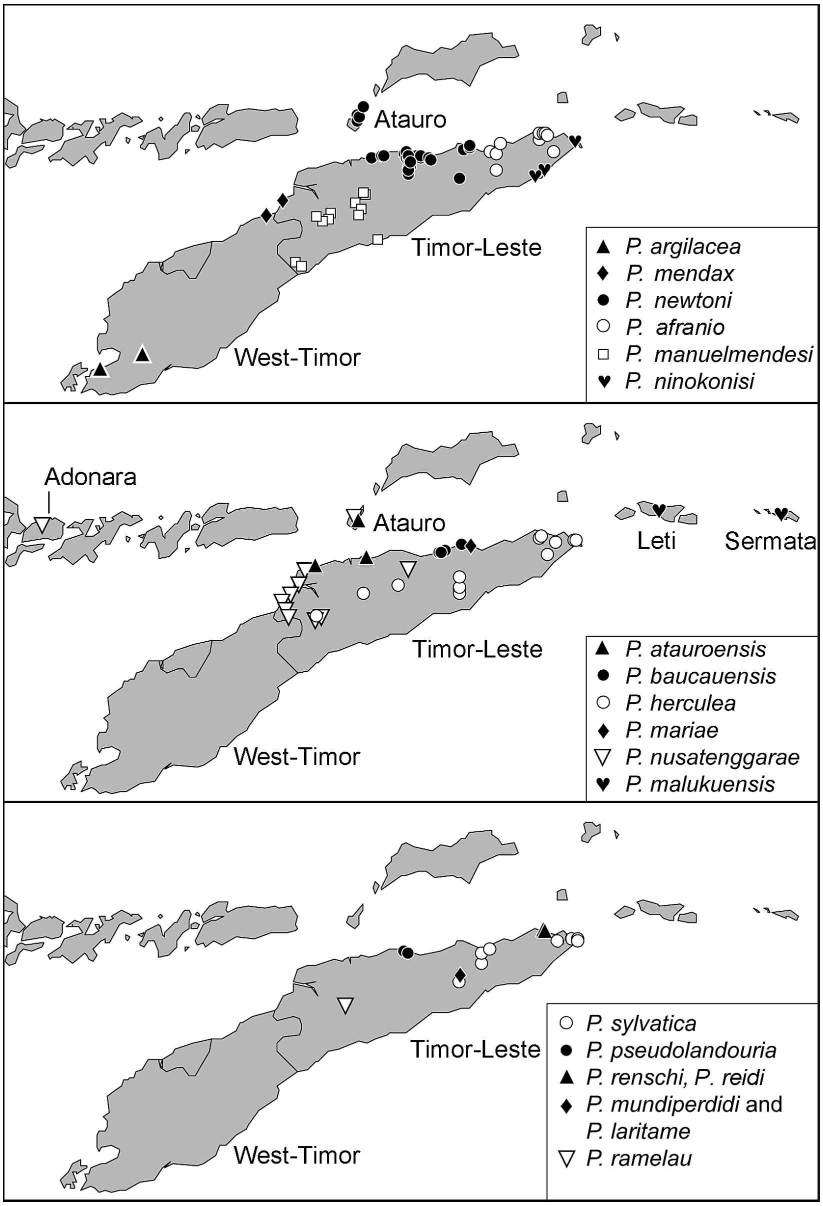

Fig. 4. Map showing known occurrence records of *Parachloritis* species treated herein.

also depend on age and reproductive status of the dissected animals. Similar to the shell, an unambiguous identification of species by means of penial characters alone may be difficult or impossible.

Species as delimited herein were found to display a relatively clear separation between intra- and interspecific genetic distances, with a narrow zone of overlap between about 7.3 – 8.4% in COI and 4.7 – 6.4% in 16S (MCL distances). Thus, analyses of mitochondrial differentiation might best be used as a first-pass approach in species identification. The amounts of intra- and interspecific mitochondrial variation are comparable to those found in several north-western Australian lineages, such as *Exiligada* Iredale, 1939 (intraspecific distances < 3%; Criscione *et al.*, 2012), *Rhagada* (intraspecific distances < 4%; Johnson *et al.*, 2012) or *Amplirhagada* Iredale, 1933 (intraspecific distances < 6%; Köhler and Johnson, 2012), *Nanotrachia* Köhler & Criscione, 2013 (intraspecific distances < 8%, Köhler and Criscione, 2013a), as well as several other stylommatophorans (average intraspecific distances < 4%; Davison *et al.*, 2009) in COI.

Diversity and distributions

The present study unravelled a diverse radiation previously unknown to exist. In addition to the four already described species, fifteen new species have been found in Timor-Leste alone. This discovery can mainly be explained by the almost complete neglect of the countries' land snail fauna in the past, which has never been studied apart from smaller works that were based on opportunistic samples (Nobre, 1917; Dharma, 1999; Severns, 2006). However, because many of the species identified herein are difficult to differentiate by shell characters, the conclusion can be drawn from this study that many shell-wise cryptic species may also exist on other Lesser Sunda Islands, including West-Timor. Targeted surveys that employ more 'advanced' methods of identification may well lead to the discovery of yet unrecognised chloritid species throughout the IAA.

The radiation of *Parachloritis* surely has more members from throughout the Lesser Sundas and Moluccas. However, its evolutionary origin remains uncertain for the restricted sampling of material from outside Timor-Leste. Also the patterns of distribution and endemism of its constituent members cannot be fully resolved. *Parachloritis nusatenggarae* appears to be the most widespread species as it has been found also on Atauro and Adonara islands. In addition, *P. malukuensis* (Sermata and Leti islands) and *P. atauroensis* (Atauro Island) have been recorded on other islands, too. However, from the little we know about the phylogenetic relationships of the Timorese species with north-western Australian and New Guinean lineages, *Parachloritis* may well have originated on the Australian plate (Fig. 1). Such an Australian origin has recently been revealed for *Rhagada*, another camaenid known from throughout the Lesser Sunda Islands. This genus was shown to have originated in north-western Australia spreading throughout the archipelago most likely during the Plio-Pleistocene (Köhler and Criscione, 2013b). However, in the case of *Parachloritis*, in terms of coverage of areas and taxa a more comprehensive study is needed to completely resolve biogeographic patterns.

While some *Parachloritis* species are widespread in Timor-Leste and beyond, others evidently have quite narrow distributions and are endemic to certain regions within Timor-Leste (Fig. 4). These species with narrow ranges are found in all main phylogenetic clades; but clade A exclusively contains narrow range endemics (Fig. 3). Two trends are apparent with respect to narrow-range endemism amongst *Parachloritis*: All dwarf species have constricted ranges, often being found at sampling localities within very close proximity of each other. Secondly, narrow-range endemism is common amongst species inhabiting mountain peaks (*R. ramelau* n. sp., *R. mundiperdidi* n. sp., *R. laritame* n. sp.). These mountain endemics are found at altitudes of about 1,200-1,500 m on Mt. Laritame in central Timor-Leste and at about 1,800-2,800 m on Mt. Ramelau in western Timor-Leste. The ranges of most widespread species overlap with each other or with those of narrow-range endemics. However, rarely have species been found in direct sympatry with each other (Fig. 4). Sympatric occurrences have most commonly been observed between dwarf species and 'typical' chloritids, indicating that both forms may utilize different ecological niches. Never have more than two species been found at the same collecting site indicating that *Parachloritis* species of each size cohort likely utilize similar ecological niches. Clearly, more refined analyses of fine-scale patterns of distribution are needed to test these postulates.

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References

Andersen A, Kohout R, Trainor C. 2013. Biogeography of Timor and surrounding Wallacean islands: Endemism in ants of the genus *Polyrhachis* Fr. Smith. *Diversity* 5: 139-148.

Benthem Jutting WSS van. 1928. Non-marine Mollusca of Sumba. *Treubia* 10: 153-162.

Chiba S. 1999. Accelerated evolution of land snails *Mandarina* in the oceanic Bonin Islands: Evidence from mitochondrial DNA sequences. *Evolution* 53: 460-471.

Criscione F, Köhler F. 2013. Conserved shell disguises diversity in *Mesodontrachia* land snails from the Australian Monsoon Tropics (Gastropoda: Camaenidae). *Zoologica Scripta* 42: 389-405.

Criscione F, Law ML, Köhler F. 2012. Land snail diversity in the monsoon tropics of Northern Australia: revision of the genus *Exiligada* Iredale, 1939 (Mollusca: Pulmonata: Camaenidae), with description of 13 new species. *Zoological Journal of the Linnean Society* 166: 689-722.

Davison A, Blackie RLE, Scothern GP. 2009. DNA barcoding of stylommatophoran land snails: a test of existing sequences. *Molecular Ecology Resources* 9: 1092-1101.

Dharma B. 1999. *Asperitas stuartiae* (Sowerby in Pfeiffer 1845) from Timor island, Indonesia with a description of two new subspecies (Gastropoda: Pulmonata: Ariophantidae). *Schriften zur Malakozoologie* 13: 19-24.

Ehrmann P. 1912. Die Landmollusken-Fauna der Tenimber-Inseln. *Sitzungsberichte der Naturforschenden Gesellschaft zu Leipzig* 38: 32-71.

Férussac AEJPJFA de 1821-1822. *Deuxième partie: Tableau particuliers des mollusques terrestres et fluviatiles, tableau de la famille des Limaçons et tableau de la famille des Auricules*. Paris: Didot.

Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294-299.

Funk DJ, Omland KE. 2003. Species-level paraphyly and polyphyly: Frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology Evolution and Systematics* 34: 397-423.

Haig DW, McCartain E. 2007. Carbonate pelagites in the post-Gondwana succession (Cretaceous - Neogene) of East Timor. *Australian Journal of Earth Sciences* 54: 875-897.

Hall R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* 20: 353-431.

Haniel CB. 1921. Variationsstudie an timoresischen Amphidromusarten. *Zeitschrift für induktive Abstammungs- und Vererbungslehre* 25: 1-88.

Hugall AF, Stanisic J. 2011. Beyond the prolegomenon: a molecular phylogeny of the Australian camaenid land snail radiation. *Zoological Journal of the Linnean Society* 161: 531-572.

ICZN 1999. *International Code of Zoological Nomenclature*. London: The International Trust for Zoological Nomenclature.

Johnson MS. 1981. Effects of migration and habitat choice on shell banding frequencies in *Theba pisana* at a habitat boundary. *Heredity* 47: 121-133.

Johnson MS. 2011. Thirty-four years of climatic selection in the land snail *Theba pisana*. *Heredity* 106: 741-748.

Johnson MS, Hamilton ZR, Teale RJ, Kendrick PG. 2012. Endemic evolutionary radiation of *Rhagada* land snails (Pulmonata: Camaenidae) in a continental archipelago in northern Western Australia. *Biological Journal of the Linnean Society* 106: 316-327.

Jones JS, Leith BH, Rawlings P. 1977. Polymorphism in *Cepaea*: A problem with too many solutions? *Annual Review of Ecology and Systematics* 8: 109-143.

Kaiser H, Carvalho VL, Ceballos J, Freed P, Heacox S, Lester B, Richards SJ, Trainor CR, Sanchez C, O'Shea M. 2011. The herpetofauna of Timor-Leste: a first report. *ZooKeys* 109: 19-86.

Katoh K, Misawa K, Kuma Ki, Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059-3066.

Köhler F. 2010. Uncovering local endemism in the Kimberley, Western Australia: Description of new species of the genus *Amplirhagada* Iredale, 1933 (Pulmonata, Camaenidae). *Records of the Australian Museum* 62: 217-284.

Köhler F. 2011a. The camaenid species of the Kimberley Islands, Western Australia (Stylommatophora: Helicoidea). *Malacologia* 54: 203-406.

Köhler F. 2011b. Descriptions of new species of the diverse and endemic land snail *Amplirhagada* Iredale, 1933 from rainforest patches across the Kimberley, Western Australia (Pulmonata, Camaenidae). *Records of the Australian Museum* 63: 167-202.

Köhler F. 2011c. *Australocosmica*, a new genus of land snails from the Kimberley, Western Australia (Eupulmonata, Camaenidae). *Malacologia* 53: 199-216.

Köhler F. 2012. Taxonomic revision of two endemic land snail genera from the Top End of Northern Australia with remarks on two problematic species named by de Férussac and Le Guillou (Eupulmonata, Camaenidae). *Zoosystematics and Evolution* 88: 53-62.

Köhler F, Johnson MS. 2012. Species limits in molecular phylogenies: A cautionary tale from Australian land snails (Camaenidae: *Amplirhagada*). *Zoological Journal of the Linnean Society* 165: 337-362.

Köhler F, Criscione F. 2013a. Small snails in a big place: A radiation in the semi-arid rangelands in northern Australia (Eupulmonata, Camaenidae, *Nanotrachia* n. gen.). *Zoological Journal of the Linnean Society* 169: 103-123.

Köhler F, Criscione F. 2013b. Plio-Pleistocene out-of-Australia dispersal in a camaenid land snail. *Journal of Biogeography* 40: 1971-1982.

Köhler F, Deein G. 2010. Hybridisation as potential source of incongruence in the morphological and mitochondrial diversity of a Thai freshwater gastropod (Pachychilidae, *Brotia* H. Adams, 1866). *Zoosystematics and Evolution* 86: 301-314.

Martens Ev. 1864. Diagnosen neuer Heliceen aus dem ostasiatischen Archipel. *Monatsberichte der Königlichen Akademie der Wissenschaften zu Berlin*: 523-529.

Martens Ev. 1867. *Die Preussische Expedition nach Ost-Asien. Nach amtlichen Quellen. Zoologische Abtheilung. Die Landschnecken mit XXII Illustrationen*. Berlin: Verlag der Königlich Geheimen Ober-Hofbuchdruckerei.

Martens Ev. 1892. Landschnecken des Indischen Archipels. Pp. 209-263 in: M Weber, ed., *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien*. Leiden: Brill.

Martens Ev. 1897. *Süß- und Brackwasser-Mollusken des Indischen Archipels*. Leiden: Brill.

Michaux B. 2010. Biogeology of Wallacea: geotectonic models, areas of endemism, and natural biogeographical units. *Biological Journal of the Linnean Society* 101: 193-212.

Moellendorff, Ov. 1892. Die Landschneckenfauna der Tenimber-Inseln (Timorlaut). *Nachrichtsblatt der Deutschen Malakozoologischen Gesellschaft* 24: 81-102.

Murray J, Clarke B. 1976a. Supergenes in polymorphic land snails. I. *Partula taeniata*. *Heredity* 37: 253-269.

Murray J, Clarke B. 1976b. Supergenes in polymorphic land snails. II. *Partula suturalis*. *Heredity* 37: 271-282.

Nguyen N, Duffy B, Shulmeister J, Quigley M. 2013. Rapid Pliocene uplift of Timor. *Geology* 41: 179-182.

Nobre A. 1907. Mollusques de l'expedition scientifique de Francisco Newton a Timor. *Bulletin de la Société Portugaise des Sciences Naturelles* 1: 205-233.

Nobre A. 1917. Duas espécies novas de *Chloritis* da Ilha de Timor. *Congreso de Sevilha, Asociacion Española para el Progreso de las Ciencias* pp. 9-10.

Nobre A. 1937. Moluscos novos e poueo conhecidos de fauna de Timor. *Anais da Faculdade de Ciencias do Porto* 22: 151-161.

Nylander JAA. 2002. MrModeltest v2.0b. Uppsala: Department of Systematic Zoology, Uppsala University.

Ożgo M. 2005. *Cepaea nemoralis* (L.) in southeastern Poland: Association of morph frequencies with habitat. *Journal of Molluscan Studies* 71: 93-103.

Pfeiffer L. 1848. *Monographia Heliceorum viventium*. Leipzig: Brockhaus.

Quigley MC, Duffy B, Woodhead J, Hellstrom J, Moody L, Horton T, Soares J, Fernandes L. 2012. U/Pb dating of a terminal Pliocene coral from the Indonesian Seaway. *Marine Geology* 311-314: 57-62.

Rensch B. 1931a. Zur Kenntnis der Molluskenfauna Timors. *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere* 60: 429-456.

Rensch B. 1931b. Die Molluskenfauna der Kleinen Sunda-Inseln Bali, Lombok, Sumbawa, Flores und Sumba. I. *Zoologische Jahrbücher Abteilung für Systematik Ökologie und Geographie der Tiere* 61: 361-396.

Rensch B. 1935. Zur Landschneckenfauna von Timor. *Sitzungsberichte der Gesellschaft naturforschender Freunde zu Berlin* 1984: 311-336.

Ronquist F, Huelsenbeck JP. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572-1574.

Sauer J, Hausdorf B. 2012. A comparison of DNA-based methods for delimiting species in a Cretan land snail radiation reveals shortcomings of exclusively molecular taxonomy. *Cladistics* 28: 300-316.

Schileyko AA. 2003. Treatise on recent terrestrial pulmonate molluscs. Part 11. Trigonochlamydidae, Papillodermidae, Vitrinidae, Limacidae, Bielziidae, Agriolimacidae, Boettgerillidae, Camaenidae. *Ruthenica* Suppl. 2: 1467-1626.

Severns M. 2006. A new species and a new subspecies of *Amphidromus* from Atauro Island, East Timor (Gastropoda, Pulmonata, Camaenidae). *Basteria* 70: 23-28.

Silvestro D, Michalak I. 2010. A userfriendly graphical front-end for phylogenetic analyses using RAxML (Stamatakis, 2006). *Organisms Diversity & Evolution* 12: 335-337.

Simões AR, Silva H, Silveira P. 2011. The Convolvulaceae of Timor with special reference to East Timor. *Blumea* 56: 49-72.

Sites JW, Marshall JC. 2004. Operational criteria for delimiting species. *Annual Review of Ecology Evolution and Systematics* 35: 199-227.

Solem A. 1979. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). I. Taxa with trans-Australian distribution. *Records of the Western Australian Museum* Suppl. 10: 5-142.

Solem A. 1981a. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). III. Taxa from the Ningbing Ranges and nearby areas. *Records of the Western Australian Museum* Suppl. 11: 321-425.

Solem A. 1981b. Camaenid land snails from Western and central Australia (Mollusca: Pulmonata: Camaenidae). II. Taxa from the Kimberley, *Amplirhagada* Iredale 1933. *Records of the Western Australian Museum* Suppl. 11: 147-320.

Sparkman W, Hall R. 2010. Surface deformation and slab-mantle interaction during Banda Arc subduction rollback. *Nature Geoscience* 3: 562-566.

Stankowski S. 2011. Extreme, continuous variation in an island snail: local diversification and association of shell form with the current environment. *Biological Journal of the Linnean Society* 104: 756-769.

Sutcharit C, Asami T, Panha S. 2007. Evolution of whole-body enantiomorphy in the tree snail genus *Amphidromus*. *Journal of Evolutionary Biology* 20: 661-672.

Tamura K, Nei M, Kumar S. 2004. Prospects for inferring very large phylogenies by using the neighbor-joining method. *Proceedings of the National Academy of Sciences of the United States of America* 101: 11030-11035.

Tamura K, Peterson D, Peterson N, Stecher G, Nei M, Kumar S. 2011. MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution* 28: 2731-2739.

Tavaré S. 1986. Some probabilistic and statistical problems in the analysis of DNA sequences. *Lectures on Mathematics in the Life Sciences* 17: 57-86.

Trainor CR, Andersen AN. 2010. The ant fauna of Timor and neighbouring islands: potential bridges between the disjunct faunas of South East Asia and Australia. *Australian Journal of Zoology* 58: 133-144.

Vermeulen JJ, Whitten AJ. 1998. *Fauna Malesiana. Guide to the land snails of Bali*. Leiden: Backhuys.

Wiegmann F. 1893. Beiträge zur Anatomie der Landschnecken des Indischen Archipels. Pp. 112-259 in: M Weber, ed., *Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien*. Leiden: Brill.

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Appendix

Taxonomic account and descriptions

Family Camaenidae Pilsbry, 1895
Genus *Parachloritis* Ehrmann, 1912

Type species: *Eulota* (*Plecteulota*) *telitecta* Moellendorff, 1892 [from Tanimbar (= Timorlaut), lectotype SMF 6143, paralectotypes SMF 6144, 162920, figured by Moellendorff (1892: pl. 1, fig. 6)], by original designation.

Diagnosis. Shell broadly subglobose to subglobose, protoconch with crowded, radially arranged pustulations, teleoconch with or without periostracal setae, umbilicus open. Penis without penial sheath, penial verge or vergic papilla; with well-developed epiphallus, long epiphallic flagellum and epiphallic lobe, short free oviduct, long, simple, tubular bursa copulatrix extending to anterior end of albumen gland.

Taxonomic remarks. In past taxonomic treatments, Asian and Australasian camaenids with similar shells of a subglobose ('chloritid') type were usually lumped together under the genus name *Chloritis* Beck, 1837. The few species previously described from Timor have also been placed within this genus in revisions and species lists (Rensch, 1931a, b, 1935; Solem, 1979). However, the type species of the genus, *Helix ungulina* Linneaus, 1758 from Seram, is very distinctive by its sunken shell spire. This feature is not found in the species from Timor treated herein, underpinning their distinctiveness from *Chloritis ungulina* (see Solem, 1979). Other generic names were subsequently introduced for species from the IAA and New Guinea, but their systematic affinities have remained dubious for the lack of anatomical (apart from macroscopic shell features) and molecular phylogenetic data. Here, the species from Timor are assigned to *Parachloritis*, which appears to be next available generic name for a

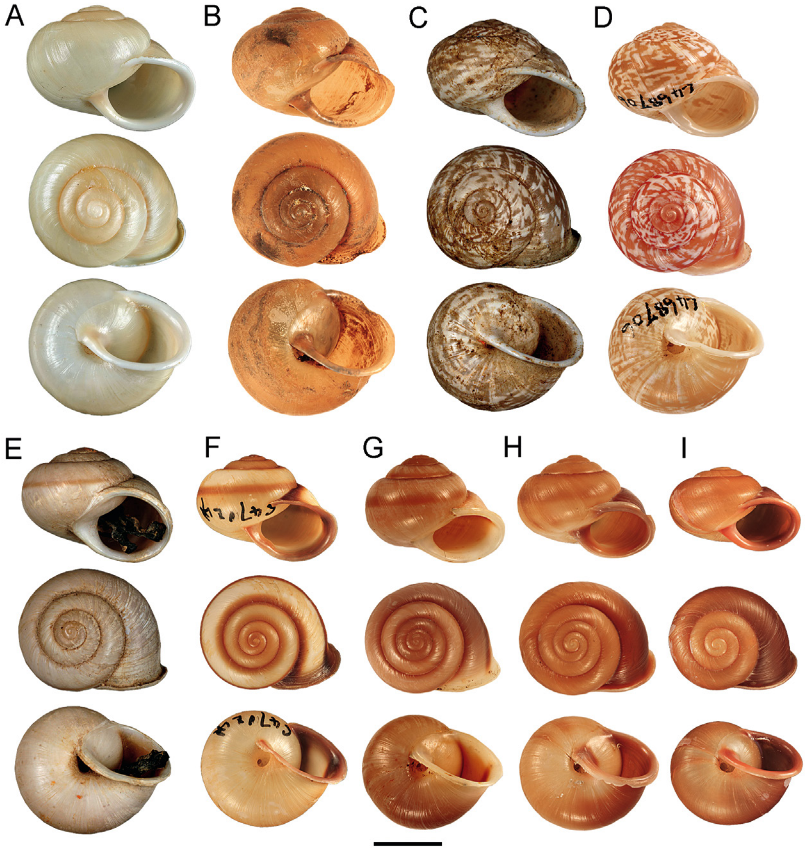

Fig. 5. Shells. A-B) *Parachloritis argilacea*. A) Syntype of *Helix argilacea* MNHN 1821, Kupang, courtesy P. Maestrati, Paris. B) Specimen AM C.471161, Kupang. C-D) *P. mariae*. C) Lectotype of *Chloritis mariae* ZMB Moll.75312, 'Dili', courtesy C. Zorn, Berlin. D) Specimen AM C.468706, Baucau. E-I) *P. newtoni*. E) Lectotype of *Chloritis newtoni* ZMB Moll.75314, 'Dili', courtesy C. Zorn, Berlin. F) Specimen AM C.471241, Metinaro. G) AM C.468762, Laleila. H) Specimen AM C.468718, Atauro Island. I) Specimen AM C.470202, Atauro Island. Scale bar = 10 mm.

'chloritid' from the IAA. Shell features observed in the species from Timor fit the generic diagnosis given by Ehrmann (1912) well, which was subsequently reiterated by Schileyko (2003). However, the genus-level taxonomy established here remains tentative and requires further scrutiny in a more comprehensive revisionary framework.

Comparative remarks. The shell variation of the species treated below is summarized in Tables 4-5. A key for the identification of species from Timor-Leste by means of shell and penial characters is given at the end of this chapter. Female external anatomy was found to vary little amongst the studied species and is therefore not depicted or described in further detail.

Parachloritis argilacea (Férussac, 1821)

Helix argilacea Férussac, 1821 [in Férussac, 1821-22]: 30, no. 38 ('Timor, voyage de Péron')
Helix argillacea [sic] – Pfeiffer, 1848: 320-321
Helix (*Hadra*) *argillacea* – Wiegmann, 1893: 171-189, pl. 13, figs. 1-9
Chloritis argillacea argillacea – Rensch, 1931a: 442-444, 1935: 335-336
Chloritis argillacea – Nobre, 1937: 155, pl. 1, fig. 8
Chloritis argilacea – Solem, 1979: 126: 126-127, pl. 11c-d, figs. 31a-b

Taxonomic remarks. The type material was collected by François Péron during the French expedition to Australia in 1800 to 1803 on board the ships 'Géographe' and 'Naturaliste'. This expedition called in Kupang as the only port in Timor; hence the type locality. Wiegmann (1893) and Solem (1979) described the anatomy based on material from Kupang, which we consider conspecific with the types. The genital anatomy of wet material studied here is consistent with these descriptions. Based on shells only, Rensch (1931a, b, 1935) assumed a wide distribution throughout Timor, Alor, Solor, Adonara, Flores and Sumba. However, most samples subsumed by him under this taxon name are probably not conspecific. A proper delimitation of the species range awaits comparative studies of molecular and anatomic differentiation of samples from throughout West-Timor (= Timor Barat, in Indonesian) and neighbouring islands. The species has not been found in Timor-Leste during extensive field work between 2008 and 2012 and is therefore very unlikely to occur in this country. The correct original spelling of the name is '*argilacea*'; the unjustified emendation '*argillacea*' by authors is erroneous and therefore invalid (ICZN, 1999: Art. 33.3).

Material examined
Syntype. MNHN 1821 (Indonesia, Nusa Tenggara Timur Prov., **Timor Barat**, Kupang; Fig. 5A).
Non-type material. Indonesia, **Timor Barat**, Kupang, 10° 11' S, 125° 35' E (AM C.471161; 3 wet, AM C.112947, 4 dry, AM C.292179, 1 dry); 5 miles E of Camplong, 10° 02' 18" S, 123° 55' 39" E (AM C.468971, 2 wet).

Diagnosis. Shell (Fig. 5A-B, Tables 4-5). Moderate to large in size (D = 20 – 23.5 mm), subglobose with moderately elevated spire; 3.9 to 4.3 whorls, separated by moderately deep suture, last whorl well rounded in diameter, teleoconch covered with short periostracal setae (or hairs or hair scars), with fine axial growth lines; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, rounded, with well expanded, well reflected lip, parietal wall inconspicuous; colour uniform hornish brown, outer whitish horn, transparent, rendering marbled mantle roof visible.

Genital anatomy. Penis straight, short, inner penial wall with smooth longitudinal pilasters; epiphallus two to three times longer than penis, epiphallic flagellum shorter than epiphallus, epiphallic lobe well developed, epiphallus communicating with penis through pore, epiphallic wall with several thick, corrugated longitudinal pilasters extending entire length of epiphallus, extending distally into flagellum (depicted by Wiegman (1893) and Solem (1979), confirmed by own dissection).

Comparative remarks. Shell unbanded, differs from most congeners by having well developed periostracal setae. Regular, smooth, well-developed longitudinal penial pilasters and strong, corrugated epiphallic pilasters are typical features of this species.

Parachloritis mariae (Nobre, 1917)

Chloritis mariae Nobre, 1917: 10, 1937: 154, pl. 1, fig. 5; Rensch, 1935: 313

Taxonomic remarks. The original description has not been accessible to me. Relevant taxonomic information has been extracted from a later publication of the same author, which included a diagnosis and figure (Nobre, 1937). Nobre (1937) gave 1907 as date of publication but the description has been published together with that of *P. newtoni* in 1917 in an abstract band of a conference held from 2 to 5 May 1917 in Sevilla. Thus, the correct publication date for this name is 1917. Nobre (1907) is a species list, which does not contain taxonomic descriptions. It is unclear on how many specimens the original description of Nobre (1917) was based, but measurements were provided for one specimen only.

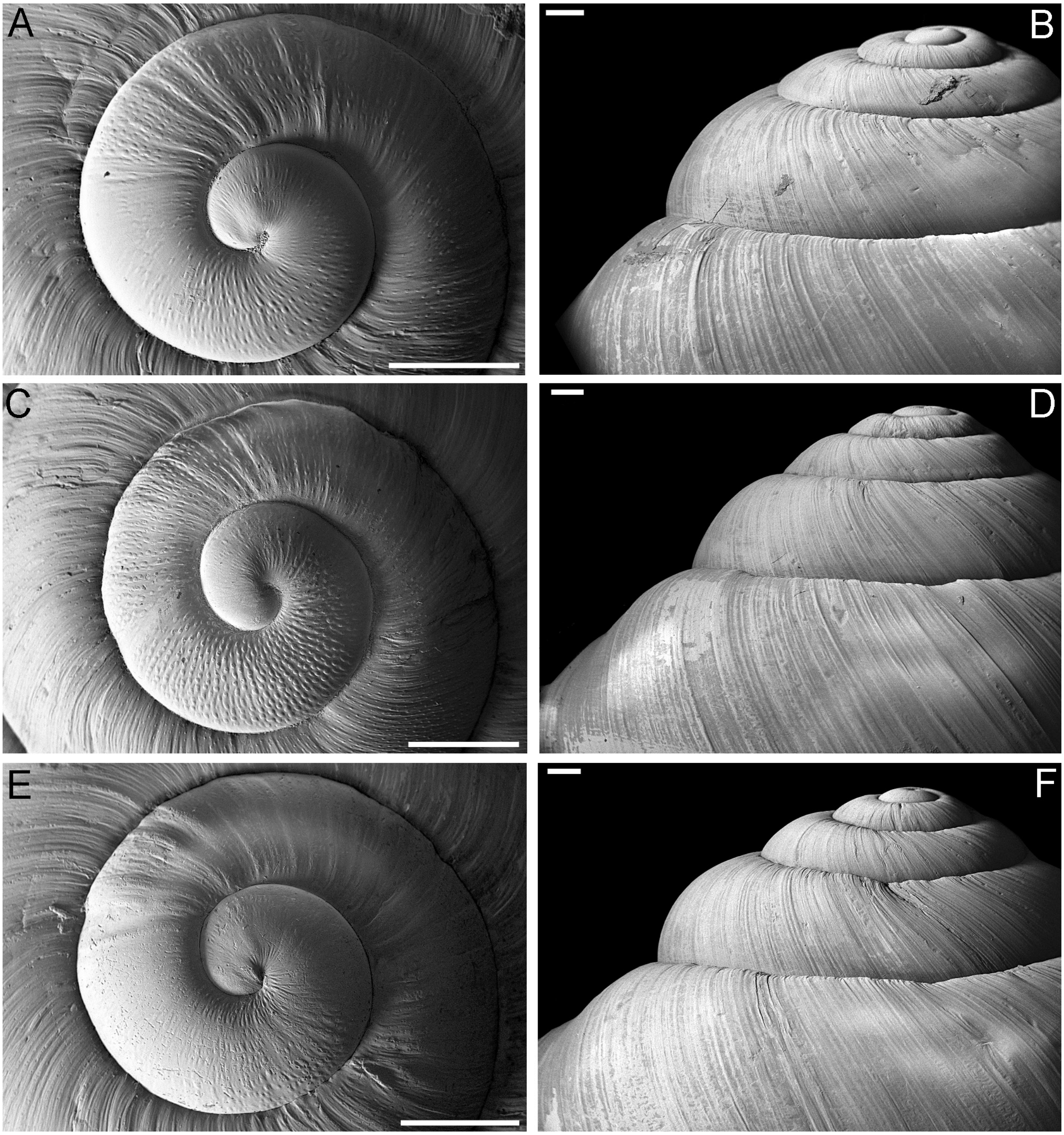

Fig. 6. Scanning electron micrographs of shell showing microsculpture. A-B) *Parachloritis mariae* AM C.468706, Baucau. A) Protoconch viewed from above. B) Front view of tip of shell. C-D) *P. newtoni* AM C.468762, Laleila. C) Protoconch viewed from above. D) Front view of tip of shell. E-F) *P. newtoni* AM C.468718, Atauro Island. E) Protoconch viewed from above. F) Front view of tip of shell. Scale bars = 1 mm.

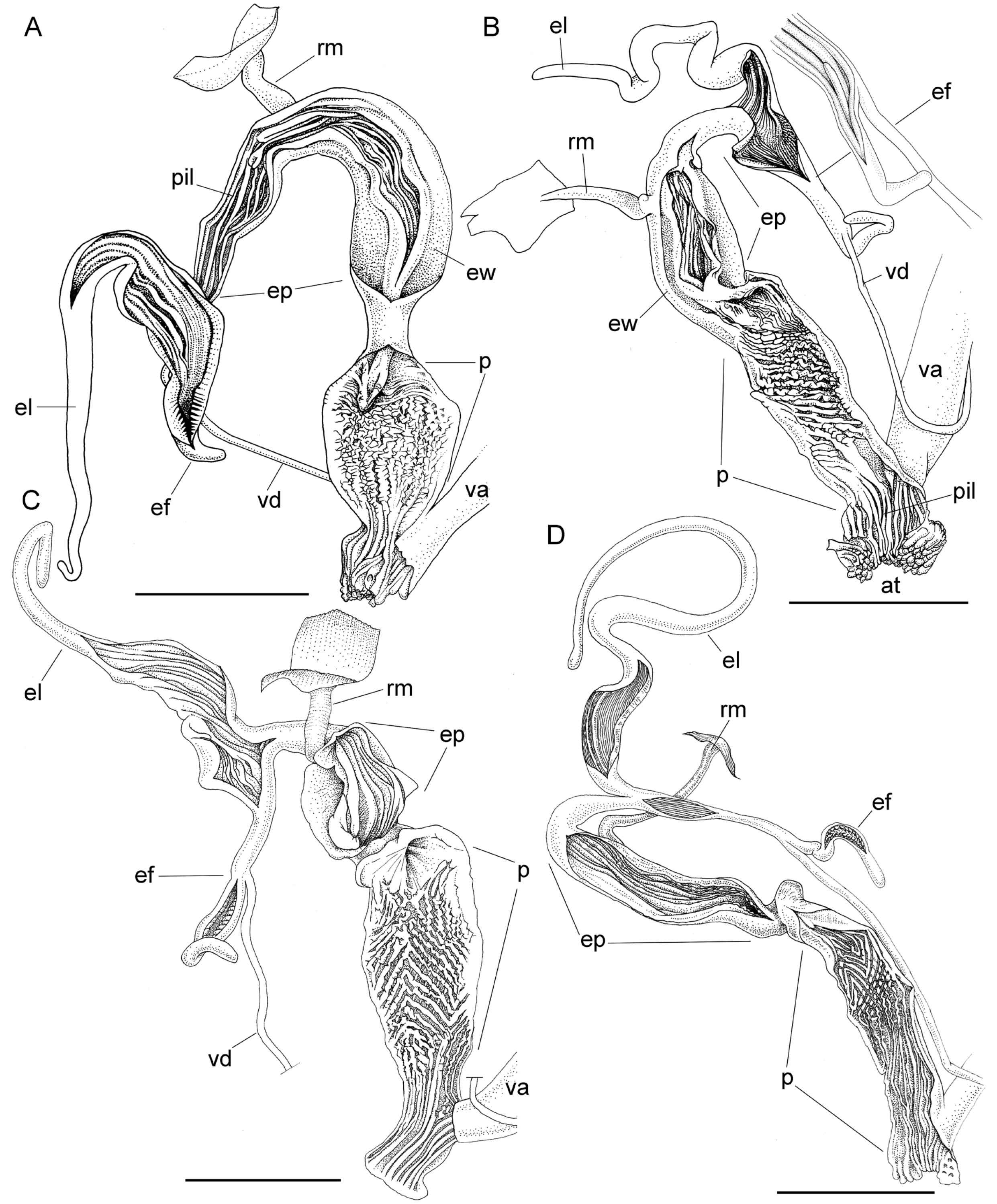

Fig. 7. Penial anatomy. A) *Parachloritis mariae* AM C.468706, Baucau. B) *P. newtoni* AM C.468762, Laleila. C) *P. baucauensis* n. sp. holotype AM C.477774, Vemasse. D) *P. afranio* n. sp. holotype AM C.477775, Sicara. Scale bars = 5 mm.

The type(s) were received in 1896 from Newton, deposited in the museum in Lisbon, and lost in 1978 in a fire that destroyed large parts of the museum (Luzia Sousa, MNHML, pers comm.). However, in 1931 a specimen from Lisbon was sent to Bernhard Rensch in Berlin, who at the time worked on non-marine molluscs of the Lesser Sunda Islands. This material must have been part of the original series collected by Newton. Since no original type designation has been made, this specimen is considered a syntype. Since the type material in Lisbon has been lost, it is herein designated as the lectotype of *Chloritis mariae* for the stabilization of the name (ICZN, 1999: Art. 74). The anatomy of this species is described for the first time. Based on our survey in Timor-Leste, *P. mariae* does not occur in Dili, as the original reference may imply, but is restricted to Baucau.

Material examined
Lectotype. ZMB Moll.75312 ('Timor, Dili' [Timor-Leste, Baucau, corrected herein], coll. Newton), present designation (Fig. 5C).
Non-type material. Timor-Leste, **Baucau District**, Baucau, Watabo Beach, 8° 26' 42" S, 126° 28' 07" E, alt. 57 m. On coconut palms and trees (AM C.478618, 7 dry, AM C.468706, 9 dry, 12 wet, AM C.473958, 6 wet, AM C.474092, 14 dry), 2.1 km ENE of historic centre, 8° 27' 28" S, 126° 28' 12" E (AM C.471029, 3 wet).

Diagnosis. Shell (Figs 5C-D, 6A-B, Tables 4-5). Moderate in size (D = 18.9 – 23 mm, n = 21), subglobose with moderately elevated spire; 4.2 to 4.5 whorls, separated by deep suture, last whorl well rounded in diameter, teleoconch smooth except for faint axial growth lines, no periostracal setae; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, rounded, with well expanded, well reflected lip, parietal wall inconspicuous; colouration of irregular, radial white patterns on reddish pink background, outer lip pinkish white.

Genital anatomy (Fig. 7A). Penis coiled, short, inner penial wall with crowded corrugated, only proximally smooth longitudinal pilasters; epiphallus about three times longer than penis, epiphallic flagellum long, about same length as epiphallus, epiphallic lobe short, length of lobe equivalent to about one third of length of flagellum, epiphallus opens into penis through pore, epiphallic wall extremely thick, distally tapering in thickness, inner epiphallic wall with numerous well-developed longitudinal pilasters extending proximally into penial lumen, comprising entire length of epiphallus, extending distally into flagellum.

Comparative remarks. This species is readily distinguished from all other species by its marbled, pinkish-white shell colouration, no periostracal setae or hair scars. Penial anatomy differs from *P. argilacea* by corrugated (instead of smooth) penial wall pilasters, fine and smooth instead of thick, partly corrugated epiphallic pilasters. Narrowly endemic distribution restricted to north coast in and close to Baucau.

Parachloritis newtoni (Nobre, 1917)

Chloritis newtoni Nobre, 1917: 9, 1937: 155, pl. 1, fig. 6; Rensch, 1935: 313-335

Taxonomic remarks. The original description has not been accessible to me. Relevant taxonomic information has been extracted from a later publication of the same author, which included a diagnosis and figure (Nobre, 1937). The description is clearly based on a series of specimens, hence syntypes ('numerosos exemplares colhidos por Francisco Newton', Nobre, 1937). As for *P. mariae* above, all but one of these specimens were lost in the 1978 fire, while one syntype was sent to the ZMB. Because no original or subsequent type designation has been made, the ZMB specimen is herein designated as the lectotype of *P. newtoni* for the stabilization of the name (ICZN, 1999: Art. 74). The anatomy of *P. newtoni* is described herein for the first time. Although the types were stated to originate from Dili, this information is not necessarily accurate as shown above for *P. mariae*. However, Dili is within the historic range of the species and therefore accepted as type locality although the species has not been found here during field work between 2008 and 2012.

Material examined
Lectotype. ZMB Moll.75314 ('Timor, Dili' [Timor-Leste, Dili], coll. Newton), present designation (Fig. 5E). *Non-type material*. Timor-Leste, **Atauro Island**, 2.5 km SSW of Beloi, 8° 14' 17" S, 125° 35' 56" E, alt. 210 m. Steep upper slopes, pockets of vine thicket, fig trees over large boulders, under rocks (AM C.468718, 3 dry, 6 wet), 1.5km N of Beloi, 8° 12' 22" S, 125° 36' 27" E, alt. 50 m. Logged rainforest on steep mid slopes in gully, under rocks, on trees (AM C.468716, 5 wet), plateau above Acrema, 8° 07' 59" S, 125° 38' 04" E, alt. 72 m. Vine thicket on karst limestone with large fig trees, under rocks (AM C.468717, 5 wet), 2.6 km NW of Beloi, 8° 12' 08" S, 125° 35' 32" E, alt. 386 m.

Abandoned fields near top of range, under limestone rocks (AM C.477787, 1 dry), 1.3 km NNW of Beloi Village, 8° 12' 30" S, 125° 36' 20" E, alt. 196 m. Open eucalyptus woodland on slopes on limestone outcrop, on trees (AM C.470202, 4 dry); **Dili District**, Metinaro, 2 km NE of army barracks, 8° 30' 34" S, 125° 47' 53" E, alt. 6 m. On acacias and tamarind trees (AM C.471027, 11 dry, 7 wet), 8° 30' 40" S, 125° 46' 40" E. Acacia, tamarind and *Eucalyptus alba* dominated coastal vegetation behind mangroves (AM C.471241, 4 dry, 12 wet), 4.5 km ENE of Hera, 8° 31' 54" S, 125° 42' 32" E, alt. 30 m. Open grassy *Eucalyptus* woodland (AM C.476573, 12 wet); **Manatuto District**, 5 km E of Manatuto, 8° 31' 16" S, 126° 03' 24" E, alt. 6 m. On acacias, on mudflats (AM C.478024, 20 dry, 10 wet), 7.5 km E of Manatuto, 8° 31' 55" S, 126° 04' 59" E, alt. 42 m. *Acacia*/deciduous vine thicket on alluvial soil, on trees (AM C.468724, 4 wet), 6.7 km ENE of Manatuto, 8° 31' 47" S, 126° 04' 39" E, alt. 10 m. *Acacia nilotica* shrub, edge of tidal flats (AM C.476999, 1 dry), 2 km W of Laleia, 8° 32' 10" S, 126° 08' 53" E. On bushes, dry, open slopes (AM C.478617, 7 dry), 8° 32' 10" S, 126° 08' 53" E. Limestone outcrop, vine thicket on steep slope, on trees (AM C.470261, 7 dry), 3 km W of Laleia, 8° 31' 24" S, 126° 05' 18" E. Decidual vine thicket, on trees (AM C.470415, 7 dry), 1.8 km S of Laleia, 8° 33' 15" S, 126° 09' 32" E, alt. 50 m. Secondary vegetation along river, on tamarind trees (AM C.473964, 12 wet, AM C.474094, 15 dry), Lima Kaduak, 5.2 km NW of Manatuto, 8° 29' 08" S, 125° 58' 41" E, alt. 15 m. Patches of vine thicket, limestone outcrops above beach, under rocks (AM C.468726, 5 dry, 15 wet), Laclo River bank near Condar, 4 km WSW of Manatuto, 8° 31' 32" S, 125° 58' 51" E, alt. 15 m. On palms (AM C.478025, 9 wet), 5.2 km SW of Manatuto, 8° 31' 44" S, 125° 58' 12" E, alt. 25 m. On tamarind trees (AM C.478026, 7 wet), spring, N-side Mt. Kuri, 3.8 km WNW of Manatuto, 8° 30' 30" S, 125° 58' 58" E, alt. 130 m. *Acacia nilotica* and grassland adjacent to creek (AM C.476591, 34 wet, AM C.476587, 1 wet), Desa Obrato, 3 km W of Manatuto, 8° 30' 58" S, 125° 59' 15" E. Limestone hills, small patches of vine thicket, secondary vegetation on steep slopes, in rock piles (AM C.468727, 6 wet), gully near Ilimanu, 8° 29' 38" S, 125° 57' 17" E, alt. 150 m. Dry rainforest with *Pandanus* understory (AM C.476936, 2 wet), 6.5 km N of Cribas, road to Laclubar, 8° 37' 02" S, 125° 59' 16" E, alt. 300 m. Closed canopy woodland on steep slopes, on trees and shrubs (AM C.478017, 5 wet), 9 km SSW of Manatuto, road to Laclubar, 8° 35' 25" S, 125° 59' 50" E, alt. 50 m. Low hills, savannah dominated by acacias and tamarinds, on trees (AM C.478016, 4 wet), 3 km N of Cribas, 8° 39' 47" S, 125° 59' 17" E, alt. 380 m. *Eucalyptus alba*/Teak plantation with Siam weed (AM C.476581, 8 wet), 5.6 km SSW of Manatuto, road to Laclubar, 8° 33' 36" S, 125° 59' 59" E. *Acacia nilotica* and tamarind-dominated road-side vegetation, on trees (AM C.478015, 4 dry, 10 wet), near Beskem, 5.7 km S of Manatuto, 8° 34' 09" S, 125° 59' 52" E, alt. 100 m. Vine thicket (AM C.476571, 20 wet, AM C.476594, 14 wet), 17 km S of Manatuto, 8° 37' 50" S, 125° 59' 22" E, alt. 230 m. Riverine vegetation (AM C.476584, 6 wet), gully 11 km S of Manatuto, Manatuto-Laclubar Road, 8° 36' 11" S, 125° 59' 24" E, alt. 260 m. *Acacia* / *Eucalyptus alba* grassland (AM C.476585, 25 wet); **Baucau District**, 1.5 km W of Laleia, 8° 32' 09" S, 126° 08' 56" E, alt. 130 m. Vine thicket and limestone outcrops on upper E-facing slope (AM C.468762, 7 wet), Baucau Plateau, 4.5 km W of Baucau, 8° 28' 21" S, 126° 24' 44" E. Aestivating on trees (AM C.473962, 5 wet, AM C.474126, 6 dry), Baucau, Watabo Beach, 8° 26' 42" S, 126° 28' 07" E, alt. 57 m. Coconut plantation, on palms and fig trees (AM C.475875, 2 dry, AM C.473057, 2 wet); **Viqueque District**, Mt. Laritame, 8° 41' 28" S, 126° 23' 19" E, alt. 1200 m. Primary rainforest on limestone (AM C.478009, 4 wet).

Diagnosis. Shell (Figs 5E-I, 6D-F, Tables 4-5). Moderate in size (D = 16.6 – 23.4 mm, n = 69), subglobose with moderately elevated spire; 3.7 to 4.6 whorls, separated by deep suture, last whorl well rounded in diameter, teleoconch smooth except for faint axial growth lines; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, rounded, with well expanded, well reflected lip, parietal wall inconspicuous; with diffuse to well-defined brown peripheral and subsutural bands on white, horn to yellowish brown background, outer lip white, inner lip often with brown suffusion, last whorl behind aperture occasionally with brown suffusion, outer lip horn to yellowish brown.

Genital anatomy (Fig. 7B). Penis usually coiled, rather long, proximal part of inner penial wall with multiple crowded, smooth longitudinal pilasters, distal two thirds with multiple crowded, undulating, obliquely arranged pilasters, varying in prominence; epiphallus about as long as penis, epiphallic flagellum rather short, epiphallic lobe well developed, much longer than flagellum, epiphallic wall extremely thick, inside supporting numerous well-developed longitudinal pilasters, comprising entire length of epiphallus, extending distally into flagellum, proximally into penial lumen.

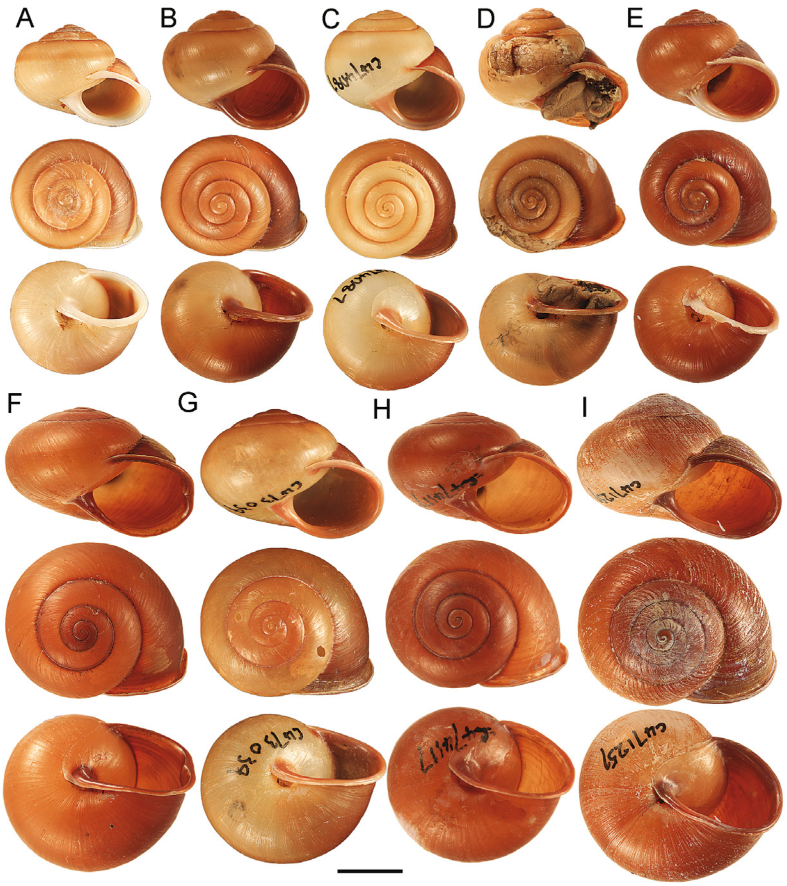

Fig. 8. Shells, continued. A) *Parachloritis baucauensis* n. sp. holotype AM C.477774, Vemasse. B-C) *P. afranio* n. sp. B) Holotype AM C.477775, Sicara. C) Paratype AM C.474087, Sicara. D-E) *P. atauroensis* n. sp. D) Holotype AM C.477776, Atauro Island. E) Paratype AM C.470203. F-I) *P. herculea* n. sp. F) Holotype AM C.468721, Loihuno. G) Specimen AM C.473039, Fuiloro Plateau. H) Paratype AM C.474117, Loihuno. I) Specimen AM C.471257, Mt. Laritame.

Comparative remarks. This species differ from most species by presence of shell banding. However, virtually identical shells are found in north shore populations of *P. baucauensis* n. sp. and *P. atauroensis* n. sp., which can be distinguished only by comparative study of genital and mitochondrial data. *P. baucauensis* differs by the fishbone-pattern of penial pilasters and corrugated pilasters within the epiphallic flagellum (smooth in *P. newtoni*); *P. atauroensis* differs by thinner penial and epiphallic wall, distinct shape of penial pilasters and corrugated pilasters within epiphallic flagellum. *Chloritis newtoni* is one of the most widely distributed species and has locally been found in sympatry with either *P. nusatenggarae*, *P. pseudolandouria*, *P. mariae* or *P. laritame* and *P. mundiperdidi*, but not with *P. atauroensis* and *P. baucauensis*. However, co-occurrence with the latter two species might have remained undetected for their identical shells. At Mt Laritame exclusively found in human settlements, considered introduced to this area.

Parachloritis baucauensis n. sp.

Material examined

Holotype. AM C.477774 (Timor-Leste, **Baucau District**, ca. 2 km E of Vemasse, 8° 29’ 07” S, 126° 16’ 01” E, alt. 6 m. Patches of vine thicket in swampy area behind beach, on palms and trees; coll. V. Kessner, 9 Dec 2010), dissected specimen (Fig. 8A).

Paratypes. Same as holotype (AM C.468725, 5 wet).

Non-type material. Timor-Leste, **Baucau District**, Baucau Plateau, 5 km NW of Baucau Historic Centre, 8° 26’ 31” S, 126° 24’ 28” E, alt. 440 m. Open low karst limestone plateau, small patches of trees and shrub, on trees (AM C.471028, 6 wet), E of Vemasse, 8° 30’ 22”

S, 126° 13' 56" E, alt. 7 m. On vegetation (AM C.471239, 7 wet), 1 km E of Vemasse, 8° 29' 51" S, 126° 14' 43" E. Vine thicket (AM C.478614, 7 dry).

Etymology. For the type locality, Baucau, adjective.

Description. Shell (Fig. 8A; Tables 4-5). Moderate in size (D = 14 – 19 mm, n = 14), subglobose with moderately elevated spire; 4.0 to 4.4 whorls, separated by deep suture, last whorl well rounded in diameter, teleoconch smooth except for faint axial growth lines; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, rounded, with well expanded, well reflected lip, parietal wall inconspicuous; with diffuse to well-defined brown peripheral and subsutural bands on white, horn to yellowish brown background, outer lip white, inner lip often with brown suffusion, last whorl behind aperture occasionally with brown suffusion, outer lip horn to yellowish brown.

Genital anatomy (Fig. 7C). Penis coiled, long, inner penial wall with oblique, regularly arranged, thin, corrugated, pilasters, proximally with smooth longitudinal pilasters, forming fishbone pattern; epiphallus slightly longer than penis, epiphallic flagellum same length as epiphallus, epiphallic lobe longer than flagellum, epiphallic wall thin, inner wall with numerous well-developed longitudinal pilasters comprising entire length of epiphallus, extending distally into flagellum and lobe; pilasters in flagellum regularly corrugated.

Comparative remarks. This species differs from most species by presence of shell banding. Virtually identical shells are found in *P. newtoni* and populations of *P. atauroensis* n. sp. from the mainland's north shore. These two species can only be distinguished by comparative study of genital and mitochondrial data. Present species differs from *P. newtoni* by weaker developed, in fishbone pattern arranged penial pilasters, and by corrugation of pilasters within epiphallic flagellum. From banded populations of *P. atauroensis* it differs by distinct corrugation and longitudinal orientation of penial pilasters. Narrowly endemic distribution in and around Baucau.

Parachloritis afranio n. sp.

Material examined

Holotype. AM C.477775 (Timor-Leste, **Lautem District**, Sicara, 3.7 km NW of Com, 8° 20' 37" S, 127° 01' 41" E, alt. 120m. Secondary forest on moderately steep lower slopes, limestone, under rocks; coll. V. Kessner, Z. Afranio, 24 May 2011), dissected specimen (Fig. 8B).
Paratypes. Same as holotype (AM C.473048, 19 wet, AM C.473049, 5 wet, AM C.474087, 15 dry).
Non-type material. Timor-Leste, **Baucau District**, hills nr Laga, 8° 29' 06" S, 126° 37' 10" E, alt. 200 m. Patches of dense *Acacia* on grassy slopes, on bushes and trees (AM C.472998, 3 wet), Larisula between Laga and Baguia, 8° 29' 31" S, 126° 40' 21" E, alt. 538 m. Gardens, on trees (AM C.478023, 1 wet), Lacamuto, Alawa Afagia, 2.4 km SE of Baguia, 8° 38' 02" S, 126° 40' 24" E, alt. 190 m. Secondary forest and teak plantation, in rock piles (AM C.478020, 4 wet), 11.8 km NE of Laga, 8° 25' 35" S, 126° 41' 42" E. Tamarind dominated coastal vine thicket, seasonal black soil swamp, on trees (AM C.471030, 2 wet); **Lautem District**, Fuiloro Plateau, Ira-Unu, 5.5 km N of Fuiloro, 8° 23' 33" S, 127° 00' 24" E, alt. 494 m. Remnant vine thicket patches on limestone (AM C.473043, 5 wet, AM C.474119, 4 dry), Wecacar near Ira Ara, 8° 20' 07" S, 127° 00' 38" E, alt. 71 m. Vine thicket patches, tamarind trees, belly bush on limestone, under bark (AM C.471100, 2 wet), Seipeli, near Com harbour, 8° 21' 52" S, 127° 03' 58" E, alt. 14 m. Lontar palms, secondary bush, under bark (AM C.473055, 2 wet), Com, ca. 0.5 km SE of harbour, 8° 21' 51" S, 127° 03' 58" E, alt. 15m. Secondary vine thicket, lantana, palms, under limestone rocks (AM C.468782, 3 wet), 2.4 km NW of Com, 8° 20' 43" S, 127° 02' 45" E, alt. 30 m. Tamarind dominated coastal vine thicket on limestone, under rocks (AM C.471249, 10 wet, 5 dry), Irinpala near Muapitine, 14.3 km ENE of Lospalos, 8° 29' 06" S, 127° 07' 21" E, alt. 343 m. Secondary forest, swampy area, under bark, on trees (AM C.473002, 2 wet).

Etymology. For Zito Afranio Soares, in recognition of his indispensable help with field work, noun in apposition.

Description. Shell (Figs 8B-C, 9A-B, Tables 4-5). Moderate in size (D = 19.5 – 22.5 mm), subglobose with moderately elevated spire; 3.7 to 4.4 whorls, last whorl well rounded in diameter to slightly angulated at periphery, separated by deep suture, last part of last whorl slightly compressed, teleoconch with very fine periostracal setae and fine, regular axial growth lines; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, rounded, with well expanded, well reflected lip, parietal wall inconspicuous; not banded, colour uniform hornish-light brown, frequently with very diffuse brown spiral band and dark brown suffusion behind aperture, outer lip horn, frequently with brown suffusion.

Genital anatomy (Fig. 7D). Penis coiled, very long, proximal part of inner penial wall with regularly arranged, thin, smooth longitudinal pilasters, distal part with oblique, more irregular pilasters; epiphallus longer than penis, epiphallic flagellum longer as long as epiphallus, epiphallic lobe extremely long, penial and epiphallic wall thin, inner epiphallic wall with numerous, very fine longitudinal pilasters comprising entire length of epiphallus, extending distally into lobe and flagellum, epiphallic flagellum with corrugated pilasters.

Comparative remarks. It differs from previous species by absence of shell banding, differs from most species by presence of periostracal setae; shell colour somewhat

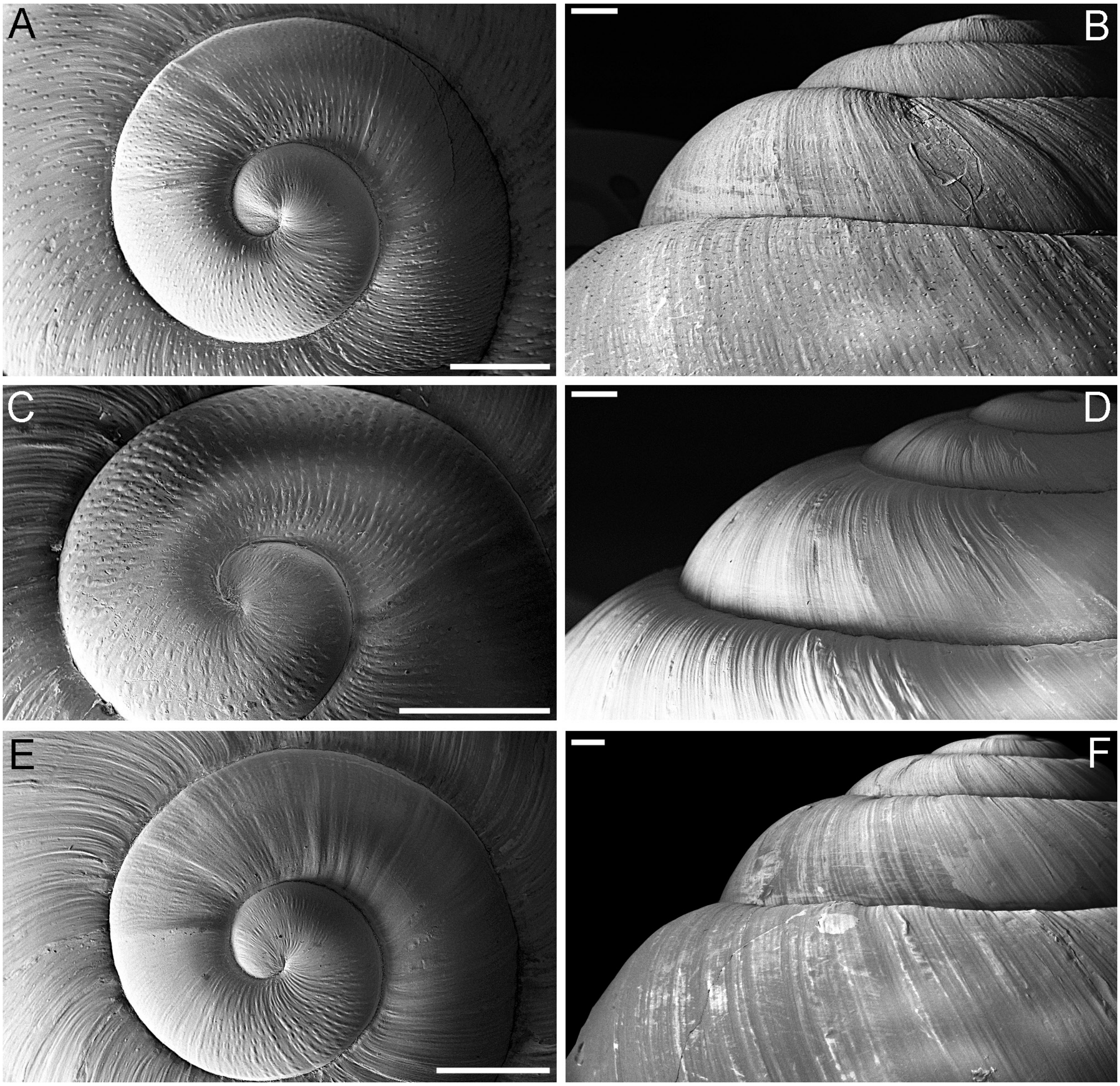

Fig. 9. Scanning electron micrographs of shell showing microsculpture. A-B) *Parachloritis afranio* n. sp. holotype AM C.477775, Sicara. A) Protoconch viewed from above. B) Front view of tip of shell. C-D) *P. herculea* n. sp. AM C.468761, near Com. C) Protoconch viewed from above. D) Front view of tip of shell. E-F) *P. sylvatica* n. sp. holotype AM C.477779, Valu Sere. E) Protoconch viewed from above. F) Front view of tip of shell. Scale bars = 1 mm.

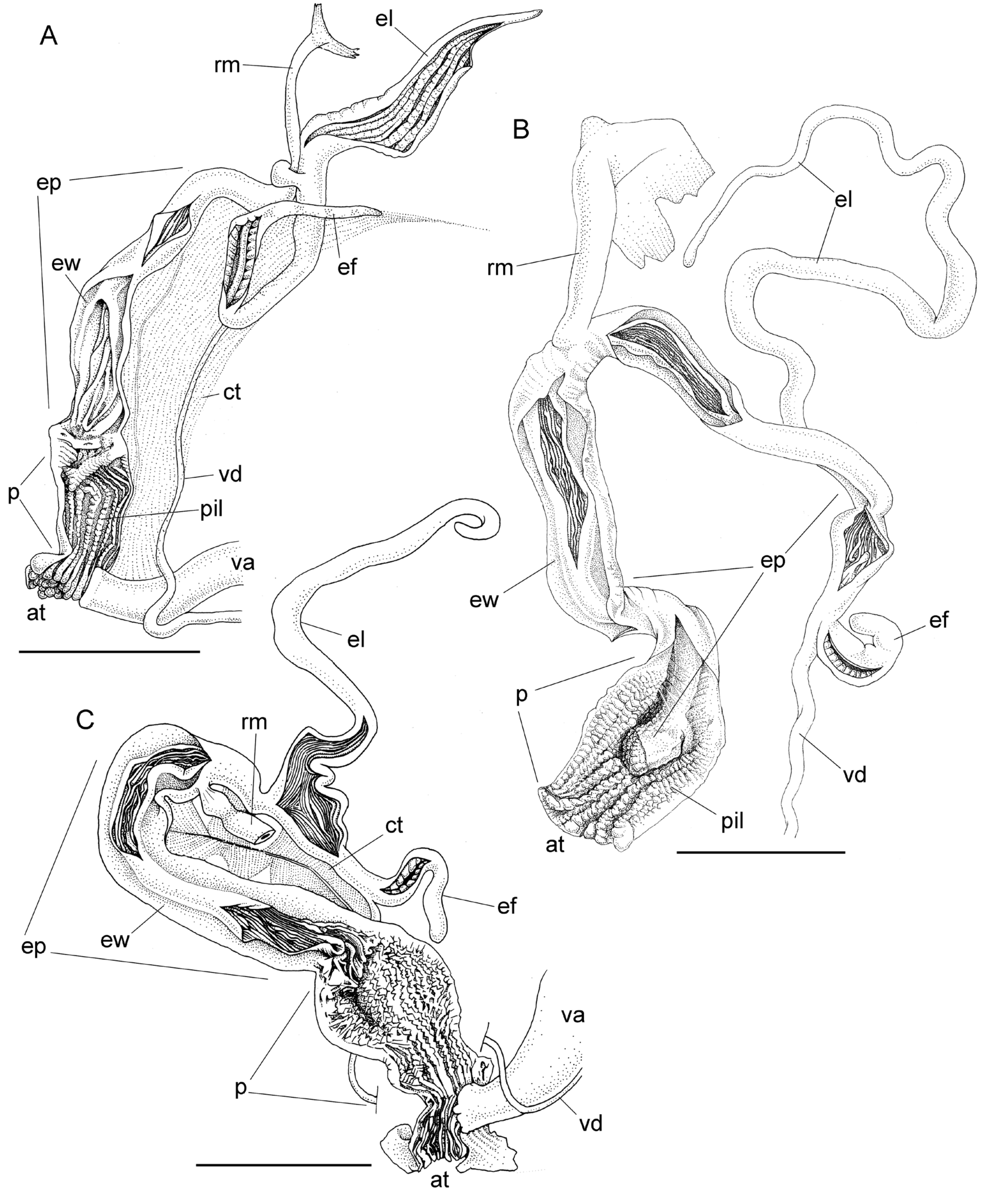

Fig. 10. Penial anatomy. A) *Parachloritis atauroensis* n. sp. paratype AM C.470465, Atauro Island. B) *P. herculea* n. sp. holotype AM C.468721, Loihuno. C) *P. sylvatica* n. sp. holotype AM C.477779, Valu Sere. Scale bars = 5 mm.

similar to *P. nusatenggarae* n. sp., *P. atauroensis* n. sp. from Atauro Island (but not from the mainland) and *P. sylvatica*, but contrast between light background and dark suffusion on last whorl stronger than in any other species. Shell differs from *P. herculea* n. sp. and *P. manuelmendesi* n. sp. by smaller size and more conical shape. Penial anatomy similar to *P. mariae*, *P. newtoni* and *P. baucauensis* n. sp., differs by having longer epiphallus and epiphallic lobe and flagellum, much finer penial and epiphallic pilasters.

Parachloritis atauroensis n. sp.

Material examined

Holotype. AM C.477776 (Timor-Leste, **Dili District**, Atauro Island, Villa, 1.8 km WSW of Tua Coin Eco Village, 8° 15’ 27” S, 125° 35’ 29” E, alt. 187 m. Degraded rainforest patch at base of steep slopes, volcanic substrate, under bark; coll. V. Kessner, 15 Aug 2010), sequenced specimen (Fig. 8D).

Paratypes. Same as holotype (AM C.470465, 4 wet), **Atauro Island**, 0.3 km W of Tua Coin Eco Village, 8° 15’ 11” S, 125° 36’ 17” E, alt. 20 m. Small limestone outcrop with a solitary tree, overgrown with weeds such as *Hyptus*, on trees under bark (AM C.470203, 4 dry, 6 wet, Fig. 8D), ca. 1.9 km N of Vila, 8° 15’ 02” S, 125° 36’ 22” E, alt. 15 m. Low, exposed limestone hill, secondary vegetation, under rocks (AM C.468715, 8 dry, 4 wet).

Non-type material. Timor-Leste, **Liquica District**, Lake Maubara, 5 km E of Maubara, 8° 36’ 23” S, 125° 15’ 16” E, alt. 9 m. Vine thicket and mangroves, lake shore, under bark (AM C.471033, 7 wet, coll. V. Kessner, Z. Afranio, 20 Nov 2011); **Dili District**, Fatukama Beach, ca. 4.7 km E of Cape Fatukama, 8° 31’ 35” S, 125° 38’ 58” E, alt. 2 m. Acacia and tamarind dominated beach vegetation, under bark on trees (AM C.471026, 13 wet, AM C.471237, 11 dry, AM C.471238, 10 wet).

Etymology. For Atauro Island, adjective.

Description. Shell (Figs 8D-E, Tables 4-5). Moderate in size (D = 8.3 – 25 mm), subglobose with moderately elevated spire; 3.8 to 4.4 whorls, separated by deep suture, last whorl well rounded in diameter to slightly compressed at periphery, teleoconch smooth except for axial growth lines; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, rounded, with well expanded, well reflected lip, parietal wall inconspicuous; on north shore of mainland shells with well-developed, brown peripheral and subsutural bands on hornish-crème background, on Atauro Island nearly uniform beige, frequently with very diffuse reddish brown spiral band and reddish brown subsutural and periapical suffusion, outer lip whitish, horn or beige.

Genital anatomy (Fig. 10A). Penis short, penial wall thin, inner penial wall with regularly arranged, regularly corrugated, only proximally smooth longitudinal pilasters; epiphallus extremely long, three times longer than penis, with thick wall, epiphallic flagellum moderate in length, epiphallic lobe very long, inner epiphallic wall with numerous, well-developed longitudinal pilasters comprising entire length of epiphallus, extending distally into flagellum and lobe, epiphallic lobe and flagellum with corrugated pilasters; penial complex embedded into relatively thick connective tissue.

Comparative remarks. Shell banded populations virtually identical with *P. newtoni* and *P. baucauensis* n. sp., shells from Atauro Island similar to *P. afranio* n. sp., *P. nusatenggarae* n. sp. and *P. sylvatica* n. sp.; but only *P. afranio* n. sp. has a diffuse spiral brown band and darker suffusion behind the aperture. Shell differs from *P. herculea* n. sp. and *P. manuelmendesi* n. sp. by smaller size and more conical shape. Most characteristic feature of penial anatomy: shape and arrangement of penial wall pilasters.

Parachloritis herculea n. sp.

Material examined

Holotype. AM C.468721 (Timor-Leste, **Viqueque District**, Loihuno, 8° 46’ 35” S, 126° 22’ 49” E, alt. 290 m. Primary and secondary forest on very steep slopes, base of limestone cliffs, in rock piles; coll. V. Kessner, 30 Nov 2010), dissected specimen (Fig. 8F).

Paratypes. Same as holotype (AM C.477777, 1 wet), 8° 46’ 50” S, 126° 22’ 51” E, alt. 330 m. Secondary vegetation, upper slopes, base of limestone cliffs, under rocks (AM C.472991, 3 wet, AM C.474117, 3 dry, coll. V. Kessner, Z. Afranio, 15 May 2011), 8° 46’ 30” S, 126° 22’ 46” E (AM C.478029, 1 wet, coll. V. Kessner, 30 May 2012), 8° 46’ 35” S, 126° 22’ 54” E, alt. 357, secondary forest (AM C.472966, 3 wet, coll. V. Kessner, Z. Afranio, 13 May 2011).

Non-type material. Timor-Leste, **Bobonaro District**, Mt. Loelako above Muntane village, 6 km NE of Maliana, 8° 59’ 06” S, 125° 16’ 33” E, alt. 1100 m. Primary rainforest on steep limestone slopes, at base of cliffs (AM C.471039, 1 wet, AM C.474124, 1 dry);

Manatuto District, Laclubar, 8° 44' 47" S, 125° 54' 54" E, alt. 1030 m. Secondary forest (AM C.476937, 3 wet); **Viqueque District**, lower slopes of Mt. Laritame, above Lari-Gutu, near Uaguia, 8° 41' 30" S, 126° 23' 17" E, alt. 1180 m. Primary forest on limestone, under rocks (AM C.472974, 1 wet, AM C.472975, 1 wet), Mt. Laritame, 8° 41' 28" S, 126° 23' 19" E, alt. 1200 m. Primary rainforest on limestone, on ground (AM C.471257, 4 dry, 5 wet), Mt. Laritame, 8° 41' 24" S, 126° 23' 23" E, alt. 1300 m. Primary rainforest on limestone, on ground (AM C.478011, 3 dry, 2 wet), 2.9 km S of Loihuno, 8° 48' 33" S, 126° 22' 52" E, alt. 165 m. Teak plantation, on trees (AM C.472958, 1 wet, AM C.474120, 5 dry); **Lautem District**, 1.5 km SW of Com, 8° 21' 54" S, 127° 03' 04" E, alt. 165 m. Secondary vine thicket on limestone, lantana, on trees and lantana (AM C.468722, 1 wet), 5 km SW of Com, near Kampung Pipileti, 8° 22' 32" S, 127° 00' 56" E, alt. 454 m. Secondary vine thicket on limestone, lantana, on ground (AM C.468761, 6 dry, 7 wet) , 6.2 km SW of Com, 8° 23' 19" S, 127° 00' 39" E, alt. 495 m. Secondary vine thicket on limestone, lantana (AM C.468722, 1 wet), Poros, Kakaru, 8° 24' 51" S, 127° 07' 37" E, alt. 400 m. Primary and secondary rainforest on limestone, in rock piles (AM C.476995, 2 dry), Maca-Kuru near Poros, ca. 7 km W of Mehara, 8° 24' 53" S, 127° 07' 37" E. Rainforest on lower, steep limestone slopes, under large rocks (AM C.473031, 2 wet, AM C.474113, 2 dry, AM C.474133, 2 dry), Fuiloro Plateau, ca. 800 m W of Ira-Unu, 5.7 km N of Fuiloro, 8° 23' 28" S, 127° 00' 12" E, alt. 552 m. Patches of primary vine thicket on limestone, in talus and crevices of large boulders (AM C.473039, 3 wet, AM C.474112, 9 dry).

Etymology. Derived from 'herculeus' (Latin = herculean), in reference to its large size, adjective.

Description. Shell (Figs 8F-I, 9C-D, Tables 4-5). Large (D = 27 – 36 mm), broadly subglobose with low spire; 4.0 to 4.8 whorls, last whorl slightly to moderately angulated at periphery, separated by shallow suture, teleoconch smooth except for axial growth lines, no periostracal setae or hair scars, glossy; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, ovate, with well expanded, well reflected lip, parietal wall inconspicuous; not banded, colour uniform hornish brown to dark brown, outer lip horn to brown.

Genital anatomy (Fig. 10B). Penis very short, penial wall thin, inner penial wall with regularly arranged, longitudinal rows of pustulations; epiphallus four to five times longer than penis, with very thick wall, proximally extending into penis as tube, epiphallic flagellum moderate in length, epiphallic lobe extremely long, inner epiphallic wall with numerous, fine longitudinal pilasters comprising entire length of epiphallus, extending distally into flagellum, flagellum with corrugated pilasters.

Comparative remarks. Shell not banded, larger and broader than most species, differs from *P. argilacea* by absence of periostracal setae; closely similar with *P. manuelmendesi* n. sp., which tends to be thicker and lighter in colour; *P. mundoperdidi* n. sp. is similarly large but differs conspicuously by strong angulation of last whorl. Shells of all remaining species are significantly smaller, with more tightly coiled whorls. Differs from other species by combination of very short penis, inner penial wall sculpture of regularly arranged postulation, extremely long epiphallus and epiphallic lobe.

Parachloritis sylvatica n. sp.

Material examined

Holotype. AM C.477779 (Timor-Leste, **Lautem District**, Valu Sere, 5 km ESE of Tutuala, 8° 24' 33" S, 127° 17' 54" E, alt. 24 m. Coastal vine thicket on limestone, under bark, on trees; coll. V. Kessner, 8 Dec 2010), dissected specimen (Fig. 11A).

Paratypes. Same as holotype (AM C.468723, 2 wet; AM C.473021, 8 wet, AM C.474118, 5 dry, coll. V. Kessner, Z. Afranio, 21 May 2011), Valu Sere, 8° 24' 34" S, 127° 17' 56" E, alt. 3 m. Tall rainforest / secondary vegetation on limestone, on trees (AM C.471252, 10 wet, coll. V. Kessner, 26 May 2012).

Non-type material. Timor-Leste, **Baucau District**, W of Matebian Mountains, Lawaliu near Desa Quelicai, 8° 35' 27" S, 126° 33' 11" E, alt. 698 m. Secondary vegetation, gardens, on steep slopes (AM C.478042, 7 dry, 6 wet), 3.9 km S of Mulia, road to Quelicai, 8° 31' 13" S, 126° 33' 39" E, alt. 220 m. Acacia and tamarind dominated savannah, on trees, under rocks (AM C.478027, 6 dry, 12 wet), Hills above Laga, 08° 29' 06" S, 126° 37' 10" E, alt. 200 m. Patches of dense *Acacia* on grassy slopes, on trees (AM C.477778, 2 wet); **Viqueque District**, Wai-eu-Lau near Usu Decima, 8° 44' 36" S, 126° 22' 50" E. On trees in gardens (AM C.472959, 3 wet); **Lautem District**, Poros, 8° 24' 58" S, 127° 08' 20" E, alt. 342 m. Large fig trees and secondary vegetation, limestone, under bark, on trees (AM C.471031, 16 wet), Himacaldi-ara, Tutuala, 8° 23' 57"

S, 127° 15’ 36” E, alt. 357 m. Secondary forest, abandoned gardens on steep slopes, below limestone cliffs, under rocks and logs (AM C.473018, 3 wet), Tutuala, near Telecom tower, 8° 23’ 56” S, 127° 17’ 02” E, alt. 340 m. Rainforest on limestone (AM C.471248, 1 wet), Ira-Cau, 1.3 km ESE of Tutuala, 8° 23’ 54” S, 127° 15’ 59” E. Secondary rainforest on steep slopes, under rocks (AM C.473025, 1 wet), Jako Island, 8° 24’ 58” S, 127° 18’ 40” E. Deciduous vine thicket on limestone (AM C.474116, 4 dry).

Etymology. From ‘sylvaticus’ (Latin = pertaining to woods or forests) for its preference for forests and woodland, adjective.

Description. Shell (Fig. 9E-F, 11A-B, Tables 4-5). Moderate to large in size (D = 20 – 28 mm), subconical to broadly subglobose with low to moderate spire; 4.0 to 4.4 whorls, last whorl well rounded in diameter to slightly compressed at periphery, separated by shallow suture, teleoconch smooth except for axial growth lines, no periostracal setae or hair scars, glossy; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, ovate, with well expanded, well reflected lip, parietal wall inconspicuous; not banded, colour uniform hornish brown to dark brown, outer lip white to horn.

Genital anatomy (Fig. 10C). Penis short, inner penial wall crowded, irregularly arranged, corrugated, oblique pilasters, varying in prominence; epiphallus twice as long as penis, with very thick wall, epiphallic lobe much than epiphallus and flagellum, inner epiphallic wall with numerous, fine longitudinal pilasters, comprising entire length of epiphallus, extending distally into flagellum and lobe, proximally into penial lumen, epiphallic flagellum with corrugated

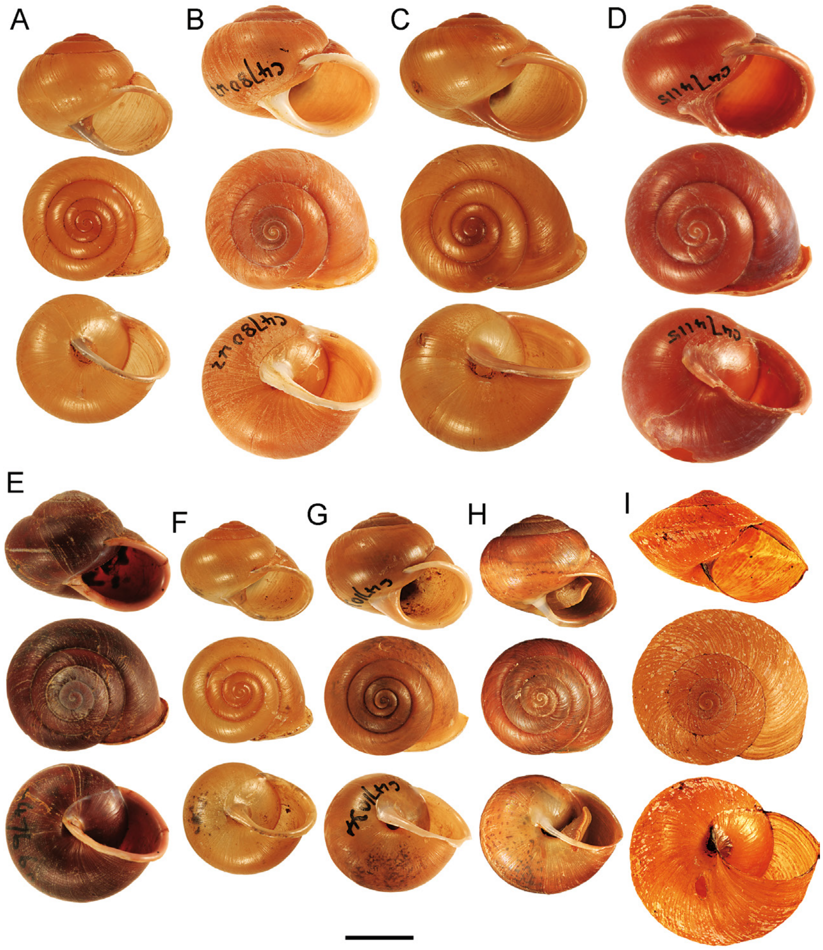

Fig. 11. Shells, continued. A-B) *Parachloritis sylvatica* n. sp. A) Holotype AM C.477779, Valu Sere. B) AM C.478042, Lawaliu. C-D) *P. manuelmendesi* n. sp. C) Holotype AM C.477780, Fatubessi. D) Specimen AM C.474115, Wecasa. E) *P. ramelau* n. sp. holotype AM C.476605, Mt. Ramelau. F-G) *P. nusatenggarae* n. sp. F) Holotype AM C.477781, Atauro Island. G) Specimen AM C.471034, Maubara. H) *P. malukuensis* n. sp. holotype AM C.477783, Leti Island, note foot protruding from aperture. I) *P. mundiperdidi* n. sp. holotype AM C.477782, Mt. Laritame. Scale bar = 10 mm.

pilasters; penial complex embedded into thick connective tissue.

Comparative remarks. Shell not banded, differs from *P. argilacea* by absence of periostracal setae; similar to *P. afranio* n. sp. and *P. atauroensis* n. sp. in size but broader, with less elevated spire, lower suture, glossy surface, lack of dark suffusion; similar in shape to *P. herculea* n. sp. and *P. manuelmendesi* n. sp. but smaller in size, outer lip brighter. Armature of inner penial wall differs from more regular arrangement in most other species, but similar to *P. mariae*, its sister species.

Parachloritis manuelmendesi n. sp.

Material examined

Holotype. AM C.477780 (Timor-Leste, **Ainaro District**, Fatubessi, 5.3 km NE of Maubisse, 8° 48' 13" S, 125° 37' 57" E, alt. 1490 m. Exposed karst limestone, small patches of vine thicket, in crevices; coll. V. Kessner, Z. Afranio, 30 Nov 2011), dissected specimen (Fig. 11C).

Paratypes. Same as holotype (AM C.471043, 4 dry, 1 wet).

Non-type material. Timor-Leste, **Bobonaro District**, near Odomau Foho, Maliana-Bobonaro road, 9° 00' 35" S, 125° 17' 05" E, alt. 870 m. Secondary forest at base of limestone cliff, in rock piles (AM C.471040, 1 wet), Bobonaro, 9° 01' 48" S, 125° 19' 29" E, alt. 835 m. Gardens, under rocks (AM C.471041, 3 dry, 3 wet), Bulobu, 6 km NE of Bobonaro, 9° 00' 14" S, 125° 22' 22" E, alt. 780 m. Gardens, (AM C.471236, 1 dry); **Manufahi District**, base of Mt Kablaki, Same-Dili Road, 9.6 km N of Holarua, 8° 56' 12" S, 125° 37' 12" E, alt. 1220 m. Vine thicket (AM C.476588, 2 wet), Hatoudo, 8° 58' 55" S, 125° 37' 27" E, alt. 735 m. Rainforest (AM C.476600, 1 wet), southern slopes of Kablaki Ranges, NW of Same, 8° 57' 44" S, 125° 36' 40" E, alt. 970 m. Abandoned gardens, coffee plantation (AM C.476941, 2 wet, AM C.476997, 1 dry); **Ainaro District**, 9 km from turnoff Dili-Same Road, Turiscai Road, Mt. Uraco, 8° 48' 41" S, 125° 38' 51" E, alt. 1550 m. Grazed woodland with *Eucalyptus urophylla*, billberries (AM C.476603, 4 wet); **Cova Lima District**, Haelisa, 0.8 km E of Tilomar, 9° 20' 41" S, 125° 07' 31" E, alt. 434 m. Patches of vine thicket/secondary vegetation on limestone, under rocks (AM C.473987, 9 wet, AM C.474122, 6 dry, coll. V. Kessner, Z. Afranio, 1 Jun 2011), Wecasa, 9° 22' 39" S, 125° 09' 16" E. Small patches of evergreen lowland rainforest and secondary vegetation/old teak plantation (AM C.473983, 2 wet, AM C.474115, 5 dry, coll. V. Kessner, Z. Afranio, 1 Jun 2011).

Etymology. For Manuel Mendes, Head of the Department for Protected Areas and National Parks, in recognition of his vital support of our work, adjective.

Description. Shell (Fig. 11C-D, 13A-B, Tables 4-5). Large (D = 24 – 30 mm), broadly subglobose with rather low spire; 4.0 to 4.4 whorls, last whorl well rounded in diameter, separated by shallow suture, teleoconch smooth except for axial growth lines, no periostracal setae or hair scars, glossy; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, ovate, with well expanded, well reflected lip, parietal wall inconspicuous; not banded, colour uniform hornish brown to dark or reddish brown, outer lip horn.

Genital anatomy (Fig. 12B). Penis straight, with very thick, glandular wall, extremely short, communicating with epiphallus through wide pore, inner penial wall with regularly arranged, strong, smooth longitudinal pilasters; epiphallus about three times longer than penis, epiphallic flagellum and lobe longer than epiphallus, inner epiphallic wall with well-developed longitudinal pilasters, comprising entire length of epiphallus, extending distally into flagellum and lobe, proximally into penial lumen, epiphallic lobe with delicate pilasters, flagellum with two strong, smooth pilasters; penial complex embedded into strong connective tissue.

Comparative remarks. Shell not banded, larger and broader than most species, differs from *P. argilacea* by absence of periostracal setae; closely similar to *P. herculea* n. sp., which usually has a thinner, darker shell; *P. mundoperdidi* n. sp. is similarly large but differs conspicuously by strong angulation of last whorl. Shells of remaining species significantly smaller, with more tightly coiled whorls. Genital anatomy differs from all other species by extremely short and thin penis, very thick penial and epiphallic wall with straight pilasters.

Parachloritis nusatenggarae n. sp.

Material examined

Holotype. AM C.477781 (Timor-Leste, Dili District, **Atauro Island**, near Makadade, 8° 12' 42" S, 125° 34' 55" E, alt. 548 m. Open grassy slopes and vine thicket on limestone, under rocks; coll. V. Kessner, 25 Nov 20100), dissected specimen (Fig. 11F).

Paratypes. Same as holotype (AM C.468719, 7 wet), Atauro Island, hills above Beloi, 8° 11' 55" S, 125° 35'

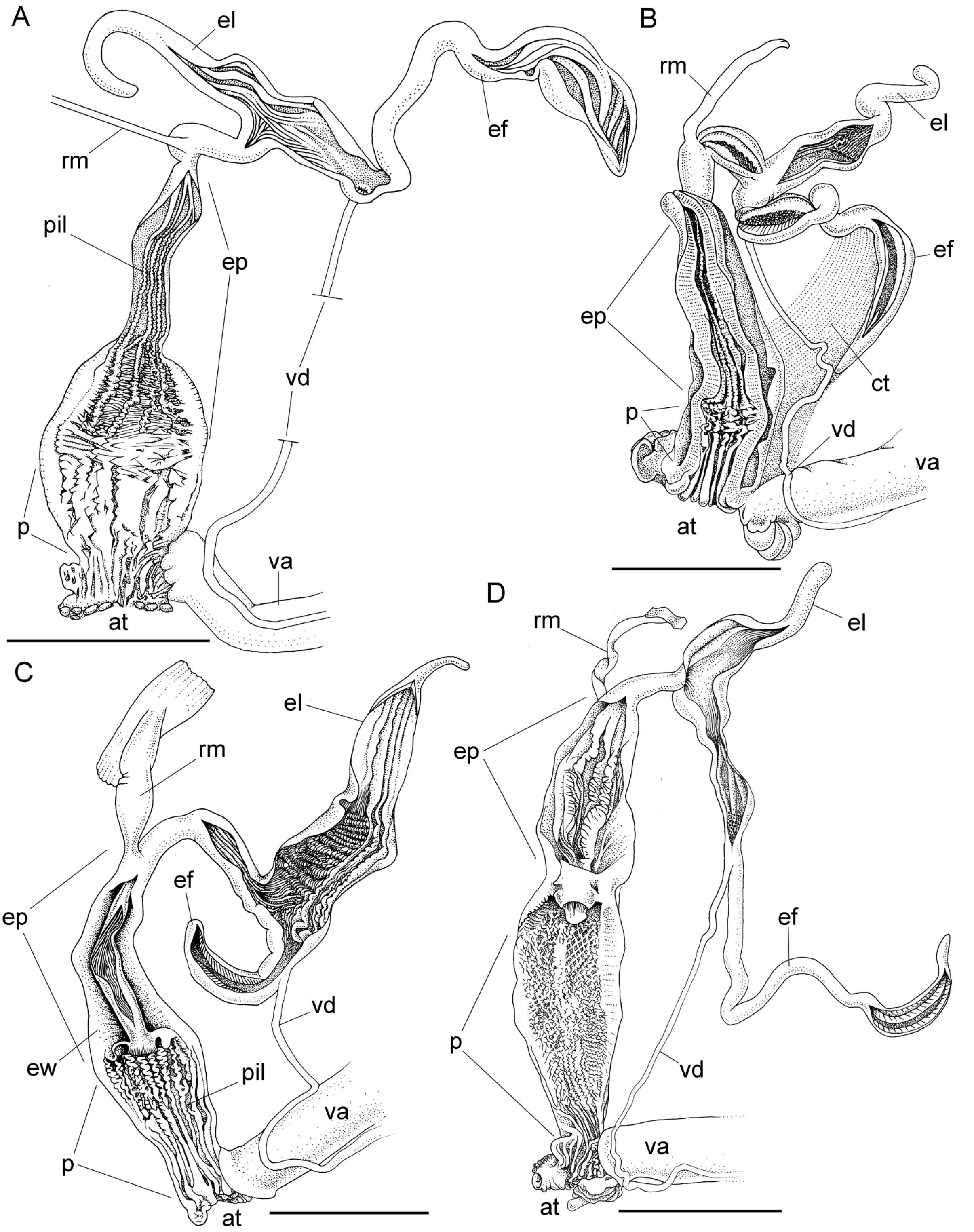

Fig. 12. Penial anatomy. A) *P. nusatenggarae* n. sp. holotype AM C.477781, Atauro Island. B) *Parachloritis manuelmendesi* n. sp. holotype AM C.477780, Fatubessi. C) *P. ramelau* n. sp. holotype AM C.46605, Mt. Ramelau. D) *P. malukuensis* n. sp. paratype AM C.471151, Leti Island. Scale bars = 5 mm.

41” E, alt. 310 m. Vine thicket on limestone, moderately steep slopes, in rock piles (AM C.468720, 5 wet, coll. V. Kessner, 26 Nov 2010), 2.8 km NNW of Beloi, 8° 11’ 49” S, 125° 35’ 46” E, alt. 314 m. Semi-deciduous vine thicket patch on top of limestone hill, under limestone rocks (AM C.470209, 3 dry, 2 wet, coll. V. Kessner, 16 Aug 2010), 2.6 km NW of Beloi, 8° 12’ 08” S, 125° 35’ 32” E, alt. 386 m. Abandoned fields, under limestone rocks (AM C.468872, 1 dry, coll. V. Kessner, 25 Nov 2010).

Non-type material. Indonesia, Nusa Tenggara Timur, **Adonara Island**, 8° 15’ S, 123° 09’ E (AM C.471159, 2 wet, 2 dry); Timor-Leste, **Bobonaro District**, Bemalai Lagoon near Palaca, 8° 52’ 51” S, 125° 00’ 27” E, alt.

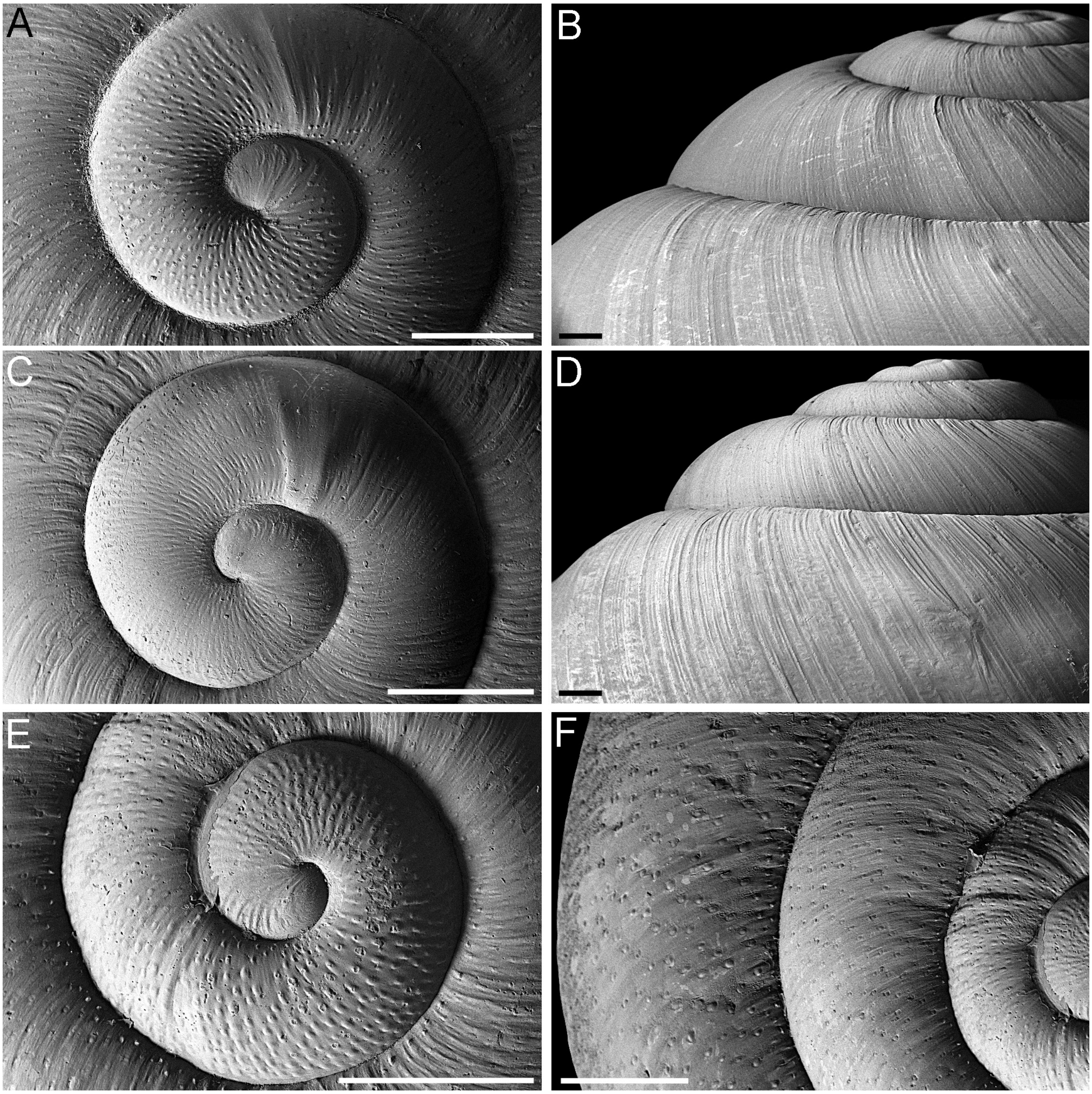

Fig. 13. Scanning electron micrographs of shell showing microsculpture. A-B) *Parachloritis manuelmendesi* n. sp. holotype AM C.477780, Fatubessi. A) Protoconch viewed from above. B) Front view of tip of shell. C-D) *P. nusatenggarae* n. sp. holotype AM C.477781, Atauro Island. C) Protoconch viewed from above. D) Front view of tip of shell. E-F) *P. mendax* AM C.477020, Bemalai Lagoon. E) Protoconch viewed from above. F) Entire shell viewed from above showing sculpture on upper part of whorls. Scale bars = 1 mm.

2 m. Coastal vine thicket above beach, on trees (AM C.471036, 13 wet, AM C.471243, 7 dry, 6 wet, AM C.477020, 20 wet), Moltao Cave, 1.8 km NW of Balibo, 8° 57' 23" S, 125° 02' 01" E. Limestone hill with closed canopy forest/vine thicket, under limestone rocks (AM C.471038, 3 dry, 3 wet), 1 km from Leohitu, 2.8 km SE of Balibo, 8° 59' 26" S, 125° 03' 33" E, alt. 474 m. Trees along seasonal stream, under limestone rocks (AM C.471037, 1 wet), 3 km SW of Atabae, 8° 48' 38" S, 125° 05' 11" E. Closed canopy forest, dry, under rocks and logs (AM C.471035, 5 wet); **Liquica District**, 8° 44' 36" S, 125° 07' 24" E, alt. 40 m. Secondary forest on steep slopes, under rocks and logs, volcanic/sedimentary substrate (AM C.471032, 7 wet), 3 km W of Maubara, 8° 37' 14" S, 125° 10' 45" E, alt. 60 m. Closed canopy forest, in rock piles (AM C.471034, 7 dry, 8 wet), Odomau Foho, Maliana-Bobonaro road, 9° 00' 28" S, 125° 16' 42" E, alt. 810 m. Hedges (AM C.471103, 1 wet), Marobo Hot Springs, 5 km N of Bobonaro, 8° 59' 14" S, 125° 18' 53" E, alt. 450 m. Secondary vegetation, in rock piles (AM C.471042, 8 wet); **Manatuto District**, River crossing, 17 km S of Manatuto, 8° 37' 50" S, 125° 59' 22" E, alt. 230 m. Riverine vegetation with buffalo wallows (AM C.477773, 8 wet).

Etymology. For 'Nusa Tenggara' (Bahasa Indonesia for Lesser Sunda), for its presumably wide distribution throughout this region; adjective.

Description. Shell (Fig. 11F-G, 13D-E, Tables 4-5). Large (D = 16.5 – 23 mm, n = 19), subglobose with moderately elevated spire; 3.8 to 4.4 whorls, last whorl slightly depressed to slightly angulated in diameter, separated by moderately deep suture, teleoconch smooth except for axial growth lines; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, ovate, with well expanded, well reflected lip, parietal wall inconspicuous; not banded, colour uniform hornish brown to brown, outer lip lighter than shell.

Genital anatomy (Fig. 12A). Penis straight, rather short, with thick wall, inner penial wall with irregular, broad, partly corrugated longitudinal pilasters; epiphallus about three times longer than penis, thin walled, epiphallic flagellum longer than epiphallus, epiphallic lobe well developed, inner epiphallic wall with well-developed, proximally corrugated, distally smooth longitudinal pilasters, comprising entire length of epiphallus, extending distally into flagellum and lobe, proximally into penial lumen, epiphallic flagellum and lobe with smooth pilasters.

Comparative remarks. Shell not banded, differs from *P. argilacea* by lack of periostracal setae, smaller and more tightly coiled than *P. herculea* n. sp. and *P. manuelmendesi* n. sp.; similar to other unbanded species of moderate size. Characteristic features of penial anatomy include, short penis length, thin epiphallic wall, broad shape of penial pilasters, smooth pilasters within epiphallic flagellum and lobe. This species is probably widely distributed between Adonara and Timor, possibly even further than that.

Parachloritis ramelau n. sp.

Material examined

Holotype. AM C.476605 (Timor-Leste, **Ainaro District**, near summit of Mt. Ramelau, 8° 54' 51" S, 125° 29' 31" E, alt. 2750 m. Grazed *Leucopogon*/*Eucalyptus urophylla* shrub land; coll. F. Köhler, Z. Afranio, C. Reid, 28 May 2012), dissected specimen (Fig. 11E).

Paratypes. Same as holotype (AM C.476606, 11 wet, 12 dry, AM C.476604, 12 wet).

Non-type material. Ainaro District, upper slopes of Mt. Ramelau, 8° 54' 51" S, 125° 29' 31" E, alt. 2750 m. Eucalyptus woodland, grassland, shrubs and rocky outcrops, volcanic (AM C.478013, 10 wet, AM C.478014, 3 wet), lower slopes of Mt Ramelau, 8° 54' 28" S, 125° 30' 10" E, alt. 2360m. *Eucalyptus urophylla* woodland with *Leucopogon* understory (AM C.476577, 1 wet), above Hatu Builico, 8° 54' 07" S, 125° 30' 59" E, alt. 1971 m. Open grazed *Eucalyptus urophylla* woodland (AM C.476602, 7 dry), Desa Liurai, Hatu-Builico road, 2.5 km W turnoff Dili-Same Road, 8° 52' 41" S, 125° 34' 36" E, alt. 1885 m. Open *Eucalyptus urophylla* woodland (AM C.476574, 1 wet).

Etymology. For Mt. Ramelau, noun in apposition.

Description. Shell (Fig. 11E, Tables 4-5). Moderate in size (D = 20 – 27 mm, n = 16), subglobose with moderately elevated spire; 4.3 to 4.6 whorls, separated by deep suture, last whorl slightly angulated to slightly compressed in diameter, teleoconch with fine axial growth lines, without periostracal setae; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, ovate, with well expanded, well reflected lip, parietal wall inconspicuous; not banded, colour uniform dark reddish brown, occasionally brown, outer lip white to horn.

Genital anatomy (Fig. 12C). Penis straight, moderate in length, thick walled, inner penial wall with regularly arranged, proximally smooth, distally corrugated longitudinal pilasters; epiphallus twice as long as penis, epiphallic lobe longer than epiphallus and flagellum, epiphallic wall very thick, inside with multiple, fine longitudinal pilasters, comprising entire length of epiphallus, extending distally into flagellum and lobe, epiphallic flagellum with corrugated pilasters.

Comparative remarks. Shell not banded, readily distinguished from all other species by its usually dark reddish brown colour, tight coiling. Thick epiphallic wall with multiple, extremely fine pilasters is characteristic for this species.

Parachloritis malukuensis n. sp.

Material examined

Holotype. AM C.477783 (Indonesia, Maluku Province, Leti islands, **Leti Island**, 8° 11' S, 127° 56' E; coll. J. Abbas, Apr 2012; Fig. 11H).

Paratypes. Same as holotype (AM C.471151, 4 dry, 2 wet).

Non-type material. Indonesia, Maluku Province, **Sermata Island**, NW side, near Elo Village, 8° 11' 33" S, 128° 52' 25" E, alt. 200 m. Gardens (AM C.468986, 1 wet, coll. C. Trainer, 2010).

Etymology. Derived from 'Maluku' (Bahasa Indonesia = 'Moluccas'), for occurring in this region, noun in apposition.

Description. Shell (Fig. 11H, Tables 4-5). Small to medium-sized (D = 12.5 – 20 mm, n = 3), subglobose with moderately elevated spire; 3.0 to 3.5 whorls, separated by shallow suture, last whorl slightly depressed in diameter, teleoconch with fine axial growth lines and periostracal setae or hair scars, particularly underneath suture, last whorl constricted behind apertural lip; umbilicus narrowly open, largely concealed by reflection of aperture; aperture simple, ovate, with well expanded, well reflected lip, parietal wall inconspicuous; not banded, colour uniform hornish brown to brown, outer lip thin, lighter than shell.

Genital anatomy (Fig. 12D). Penis straight, long, inner penial wall with irregular web of oblique, fine corrugations, proximal end with smooth, fine longitudinal pilasters; epiphallus about as long as penis, epiphallic flagellum extremely long, epiphallic lobe well developed, inner epiphallic wall with thick, partly corrugated longitudinal pilasters, epiphallic lobe with extremely fine pilasters, flagellum with stronger, corrugated pilasters.

Comparative remarks. Shell not banded, smaller than *P. argilacea*, much smaller and more tightly coiled than *P. herculea* n. sp. and *P. manuelmendesi* n. sp.; similar to other unbanded species of moderate size, but differing from many species by having periostracal setae and constriction behind apertural lip. Inner penial wall sculpture typical for only this species.

Parachloritis mundiperdidi n. sp.

Material examined

Holotype. AM C.477782 (Timor-Leste, **Viqueque District**, Mt. Laritame, 8° 41' 24" S, 126° 23' 23" E, alt. 1300 m. Primary rainforest on limestone; coll. V. Kessner, 31 May 2012), dissected specimen (Fig. 11I).

Paratypes. Same as holotype (AM C.478010, 4 wet), Mt. Laritame, alt. 1200 m (AM C.471256, 5 dry, 16 wet, coll. V. Kessner, 30 May 2012), lower slopes of Mt. Laritame, Lari-Gutu nr Uaguia, 8° 41' 30" S, 126° 23' 17" E, alt. 1180 m. Primary forest on limestone, under rocks (AM C.472970, 2 wet, 3 dry, AM C.472973, 1 wet, coll. V. Kessner, Z. Afranio, 14 May 2011).

Etymology. Derived from 'mundi perdidi' (= Latin for 'Lost World'), in reference to the 'Mundo Perdido Protected Area', where this species occurs; adjective.

Description

Shell (Fig. 11I, Tables 4-5). Large (D = 26 – 29 mm, n = 7), delicate, transparent, depressed conical with very low spire; 4.2 to 4.4 whorls, last whorl strongly angulated at periphery, flattened above periphery, separated by shallow suture, teleoconch with strong axial growth lines, extending onto base of shell, upper whorls with radial corrugations; umbilicus narrowly open, partly concealed by reflection of aperture; aperture simple, thin, not expanded, not reflected, parietal wall inconspicuous; not banded, colour uniform hornish brown.

Genital anatomy (Fig. 14A). Penis very long, epiphallus not well differentiated from penis; inner penial and epiphallic wall with irregular longitudinal corrugations extending entire length, epiphallus much shorter than penis, epiphallic flagellum well developed, with crowded, corrugated pilasters, epiphallic flagellum extremely long, with regularly segmented, thick longitudinal pilasters.

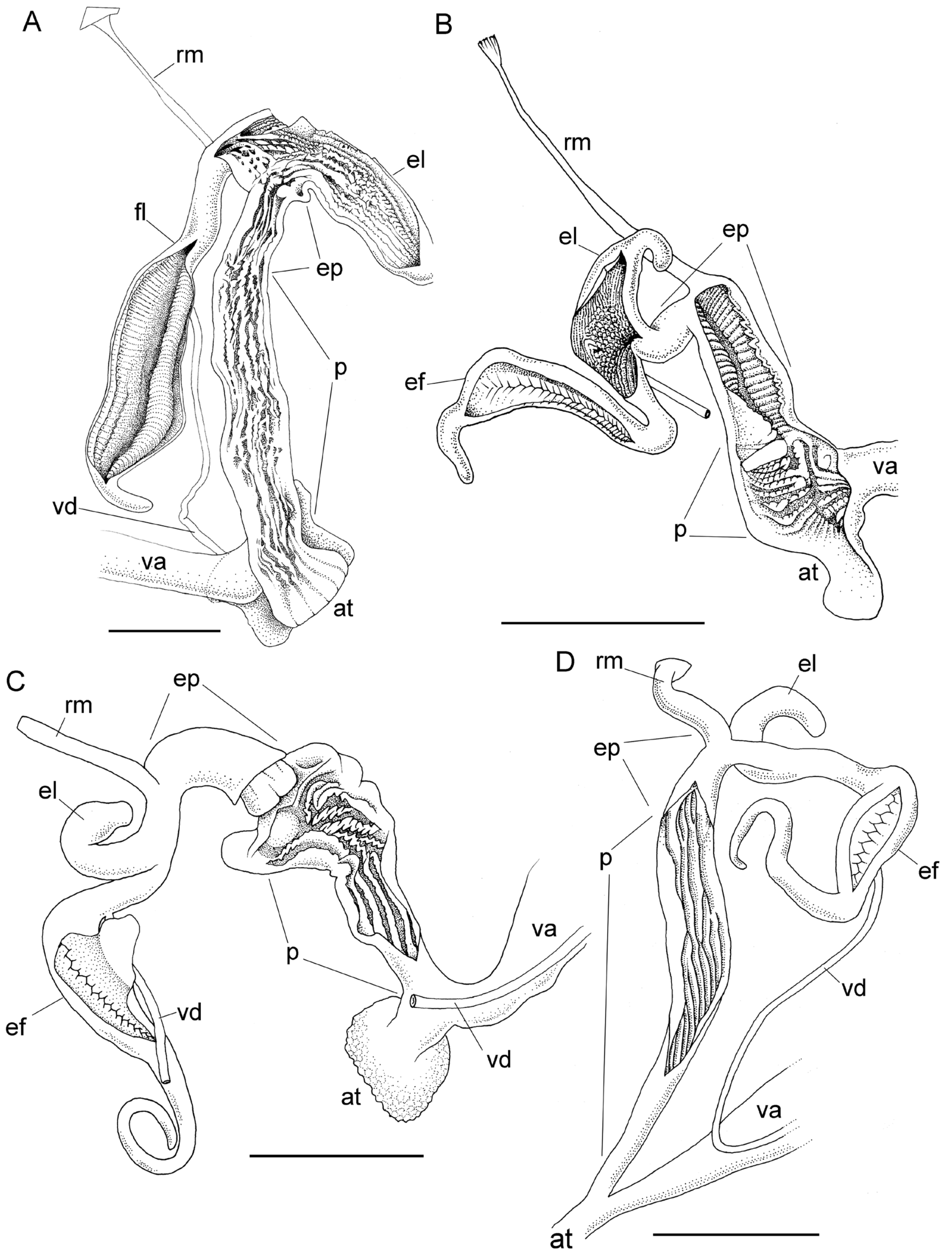

Fig. 14. Penial anatomy. A) *Parachloritis mundiperdidi* n. sp. holotype AM C.477782, Mt. Laritame. Scale bar = 5 mm. B) *P. mendax* AM C.471244, Bemalai Lagoon. C) *P. renschi* n. sp. paratype AM C.468747, near Com. D) *P. reidi* n. sp. holotype AM C.477025, Sicara. Scale bars B-D = 2 mm.

Comparative remarks. Shell larger than most other species, clearly distinct by its conical shape and strongly angulated last whorl. Not well differentiated epiphallus, sculpture of inner penial and epiphallic wall and segmentation of pilasters in flagellum characteristic for this species. Species is narrowly endemic to Mt. Laritame.

Parachloritis mendax (Martens, 1864)

Helix mendax Martens, 1864: 524, 1867: 272-273, pl. 13, fig. 14
Landouria mendax – Rensch, 1931a: 431, 1935: 313

Taxonomic remarks. No original or subsequent type designation is available. The original description provided measurements for one specimen (D = 11 mm). Subsequently, Martens (1867) provided an illustration and mentioned two syntypes, the larger one corresponding in size with the measurements given in the original description. However, the type lot contains four conspecific specimens. The largest specimen corresponds well in size with the measurements of Martens (1864, 1867). It is herein designated as the lectotype of *Helix mendax* Martens, 1864 for the stabilization of the name (ICZN, 1999: Art. 74). Material sequenced and dissected herein was collected not far from the type locality and closely resembles the type material. It is therefore considered conspecific. The anatomy of the species is described here for the first time.

Material examined
Lectotype. ZMB Moll.5496a (‘Timor, bei Atapupu’ [Indonesia, Nusa Tenggara Timur, **Timor Barat**, near Atapupu, 8° 59’ 34” S, 124° 52’ 14” E]; coll. von Martens, dry), present designation (Fig. 15A).
Paralectotypes. Same as lectotype (ZMB Moll.5496b, 3 dry).
Non-type material. Timor-Leste, **Bobonaro District**, Bemalai Lagoon near Palaca, 8° 52’ 51” S, 125° 00’ 27” E, alt. 2 m. Vine thicket above beach, on trees (AM C.471244, 9 wet, AM C.477020, 30 wet).

Diagnosis. Shell (Fig. 13E-F, 15A-B, Tables 4-5). Small (D = 8.5 – 11 mm, n = 10), broadly subglobose with very low spire; about 3.3 whorls, separated by deep suture, last whorl well rounded in diameter, teleoconch with well-developed microsculpture of obliquely axially arranged tubercules and wavy ridglets; umbilicus widely open, not concealed by reflection of aperture; aperture simple, rounded, with well expanded, well reflected lip; last whorl slightly constricted behind aperture; parietal wall inconspicuous; colour uniform hornish brown, transparent.

Genital anatomy (Fig. 14B). Penis very short, with longitudinal pilasters (perspective of drawing is longitudinally into penis), epiphallus longer than penis, inside with numerous, smooth, well-developed oblique pilasters, epiphallic lobe with numerous, fine, corrugated pilasters, flagellum with two well developed, corrugated pilasters.

Comparative remarks. Differs from most other species by its small size and nearly flat shell; for comparison with similarly small species see further below. Only known from type locality in West-Timor and Bemalai Lagoon in Timor-Leste, where it occurs in sympatry with *P. nusatenggarae* n. sp. *Chloritis mendax* can easily be mistaken for juveniles of *P. nusatenggarae* but adults of *P. mendax* differ by having completed apertural lip. In addition, *P. mendax* differs by its granulose shell sculpture and a conspicuously marbled mantle roof, visible through transparent shell.

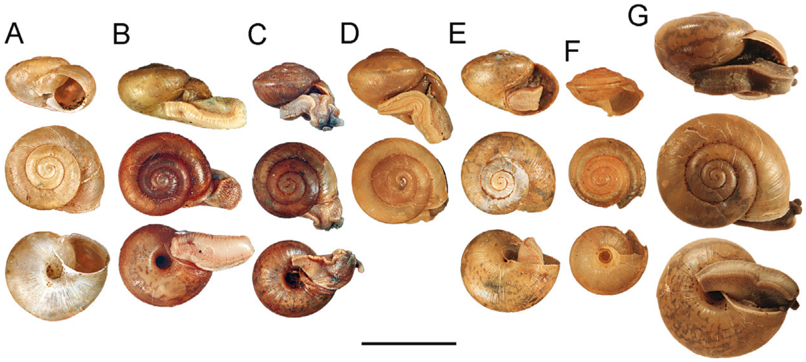

Fig. 15. Shells. A-B) *Parachloritis mendax*. A) Lectotype of *Helix mendax* ZMB Moll.5496a, Atapupu. B) Specimen AM C.477020, Bemalai Lagoon. C) *P. renschi* n. sp. holotype AM C.477785, near Com. D) *P. reidi* n. sp. paratype AM C.473047, Sicara. E) *P. laritame* n. sp. holotype AM C.472971, Mt. Laritame. F) *P. pseudolandouria* n. sp. paratype AM C.468775, Ilimanu. G) *P. ninokonisi* n. sp. holotype AM C.473024, Ira-cau. Scale bar = 10 mm.

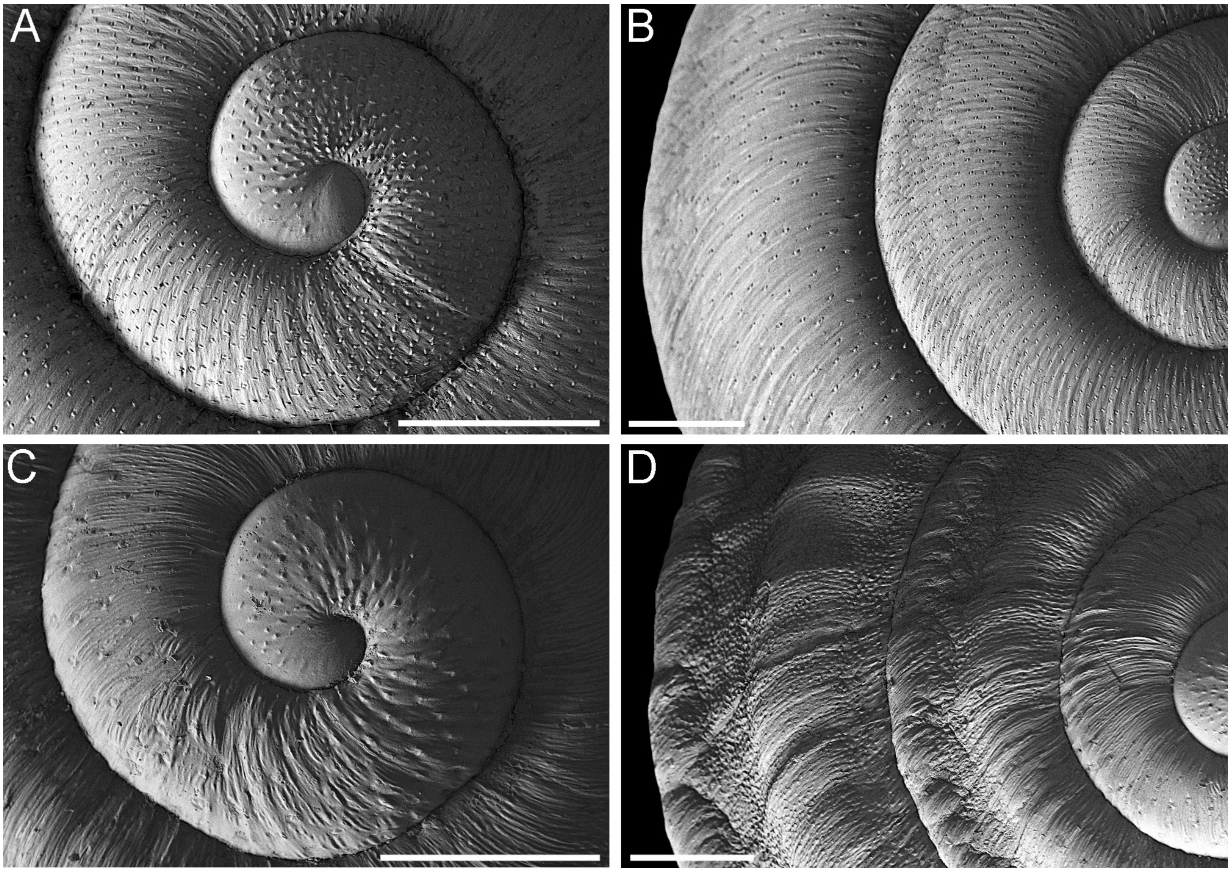

Fig. 16. Scanning electron micrographs of shell showing microsculpture. A-B. *Parachloritis reidi* n. sp. paratype AM C.474125, Sicara. A) Protoconch viewed from above. B) Entire shell viewed from above showing sculpture on upper part of whorls. C-D) *P. pseudolandouria* n. sp. paratype AM C.468775, Ilimanu. C) Protoconch viewed from above. D) Entire shell viewed from above showing sculpture on upper part of whorls. Scale bars = 1 mm.

Parachloritis renschi n. sp.

Material examined

Holotype. AM C.477785 (Timor-Leste, **Lautem District**, 3.3 km NW of Com, 8° 20' 36" S, 127° 01' 49" E, alt. 47 m. Vine thicket on limestone, under rocks; coll. V. Kessner, 4 Dec 2010; Fig. 15C).

Paratypes. Same as holotype (AM C.468747, 4 wet).

Etymology. For Bernhard Rensch, who pioneered studies of non-marine gastropods from the Lesser Sunda Islands, adjective.

Description. Shell (Fig. 15C, Tables 4-5). Small (D = 9.0 – 9.5 mm, n = 3), broadly subglobose with low spire; about 3.3 whorls, separated by shallow suture, last whorl angulated at periphery, teleoconch with axial growth lines; umbilicus widely open, not concealed by reflection of aperture; aperture simple, rounded, lip weakly expanded and reflected; parietal wall inconspicuous; colour uniform hornish brown, transparent.

Genital anatomy (Fig. 14C). Penis moderately long, with well developed, straight, smooth longitudinal pilasters, epiphallus about as long as penis, epiphallic lobe rather short, epiphallic flagellum with two well developed, with two tightly interlocked, corrugated pilasters.

Comparative remarks. Shell differs from most other species by its small size; differs from *P. mendax* most conspicuously by shallower suture, absence of granulose microsculpture, angulated periphery, no constriction behind non expanded apertural lip. Differs from sister species *P. reidi* n. sp. by smaller size, slightly more elevated shape, less prominent angulation of last whorl, bright body colour (dark in *P. reidi* n. sp.), less pronounced mantle colouration (visible through shell). Well-developed penial pilasters and interlocked corrugated pilasters in flagellum typical for this species. Narrowly endemic, only known from type locality.

Parachloritis reidi n. sp.

Material examined
Holotype. AM C.477786 (Timor-Leste, **Lautem District**, 2.4 km NW of Com, 8° 20' 43" S, 127° 02' 45" E, alt. 30 m. Tamarind dominated coastal vine thicket on limestone, under rocks; coll. V. Kessner, 26 May 2012), dissected specimen (Fig. 14D).
Paratypes. Same as holotype (AM C.477025, 3 wet); Sicara, 3.7 km NW of Com, 8° 20' 37" S, 127° 01' 41" E, alt. 120 m. Secondary forest on lower slopes, limestone, under rocks (AM C.473047, 28 wet, AM C.474125, 21 dry, coll. V. Kessner, Z. Afranio, 24 May 2011).

Etymology. For Christopher Athol McEwan Reid, in recognition of his significant contribution to the Timor-Leste Survey of the Australian Museum, adjective.

Description. Shell (Fig. 15D, 16A-B, Tables 4-5). Small (D = 9.5 – 11 mm, n = 13), broadly subglobose with low spire; about 3.4 whorls, separated by shallow suture, last whorl angulated at periphery; protoconch with well-developed, dense, radially arranged microscopic pustules; teleoconch with axial growth lines; umbilicus widely open, not concealed by reflection of aperture; aperture simple, rounded, lip weakly expanded and reflected; parietal wall inconspicuous; colour uniform hornish brown, transparent.

Genital anatomy (Fig. 14D). Penis very long, with well developed, straight, smooth longitudinal pilasters, epiphallus shorter than penis, epiphallic lobe rather short, epiphallic flagellum with two well developed, with two tightly interlocked, corrugated pilasters.

Comparative remarks. Shell differs from most other species by its small size; differs from *P. mendax* most conspicuously by shallower suture, absence of granulose microsculpture, angulated periphery, no constriction behind non expanded apertural lip. Most similar is its sister species *P. renschi* n. sp., found in a few hundred metres distance, but not in sympatry. The present species differs by its larger size, slightly less elevated shape, stronger angulation of last whorl, dark body colour (bright in *P. reidi* n. sp.), more pronounced mantle colouration (visible through shell). Penial anatomy similar to *P. renschi* n. sp., differing by longer penis. Narrowly endemic, known only from type locality, occurs in sympatry with *P. afranio* n. sp.

Parachloritis laritame n. sp.

Material examined
Holotype. AM C.472971 (Timor-Leste, **Viqueque District**, lower slopes of Mt Laritame, above Lari-Gutu, near Uaguia, 8° 41' 30" S, 126° 23' 17" E, alt. 1180 m. Primary forest on limestone, under rocks; coll. V. Kessner, Z. Afranio, 14 May 2011), dissected specimen (Fig. 15E).
Paratypes. Timor-Leste, **Viqueque District**, Mt. Laritame, 8° 41' 28" S, 126° 23' 19" E, alt. 1200 m. Primary rainforest on limestone (AM C.477034, 3 wet, AM C.477035, 5 wet, coll. V. Kessner, 30 May 2012).

Etymology. For Mt. Laritame, noun in apposition.

Description. Shell (Fig. 15E, Tables 4-5). Small (D = 9 – 10.5 mm, n = 3), very thin, broadly subglobose with low spire; about 3.1 whorls, separated by shallow suture, last whorl slightly angulated at periphery, teleoconch essentially smooth with weak axial growth lines, glossy; umbilicus widely open, not concealed by reflection of aperture; aperture simple, rounded, lip weakly expanded and reflected; parietal wall inconspicuous; colour uniform hornish brown, transparent.

Genital anatomy (Fig. 17A). Penial complex delicate, with long penis, long epiphallus, about as long as penis, well-developed epiphallic lobe, extremely long epiphallic flagellum. Inner wall structure simple throughout.

Comparative remarks. Shell differs from most other species by its small size; differs from *P. mendax* most conspicuously by shallower suture, absence of microsculpture, no constriction behind non expanded apertural lip. Differs from both *P. renschi* n. sp. and *P. reidi* n. sp. thinner shell, less angulated body whorl. Differs from *P. pseudolandouria* by lack of spiral angulation, spiral depression and microsculpture. Narrowly endemic, found only on Mt. Laritame, where it occurs in sympatry with *P. newtoni* and *P. mundiperdidi* n. sp.

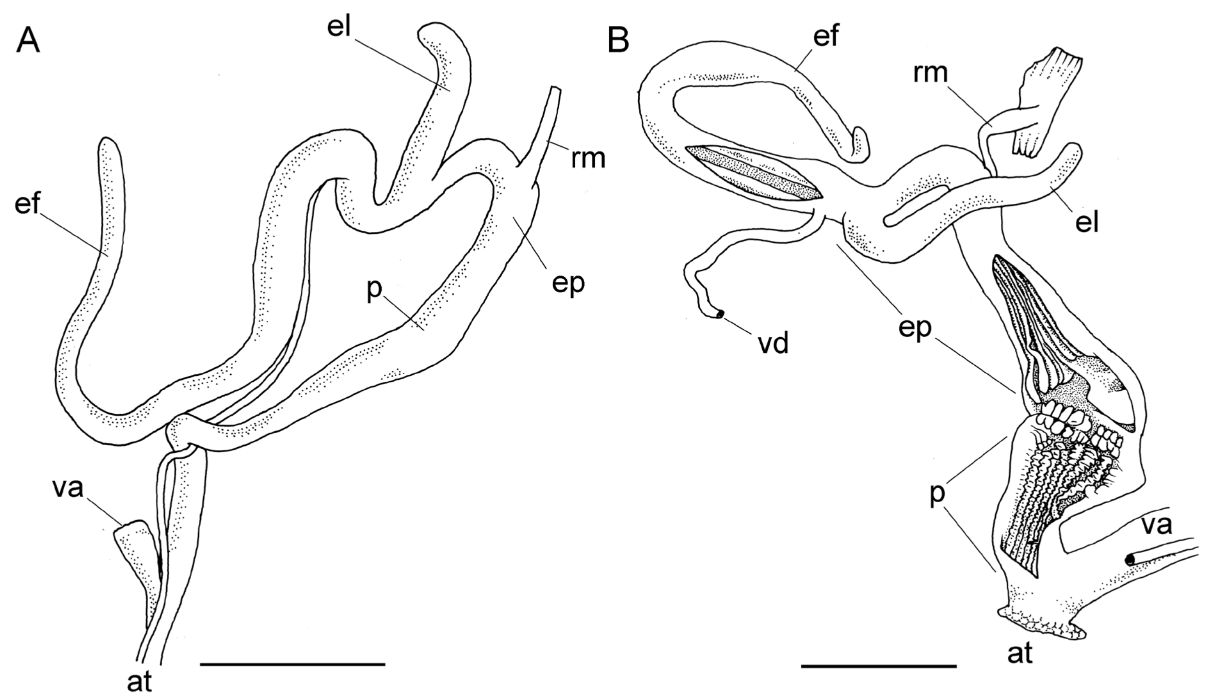

Fig. 17. Penial anatomy. A) *Parachloritis laritame* n. sp. holotype AM C.472971, Mt. Laritame. Scale bar = 1 mm. B) *P. pseudolandouria* n. sp. holotype AM C.477784, Ilimanu. Scale bar = 2 mm.

Parachloritis pseudolandouria n. sp.

Material examined

Holotype. AM C.477784 (Timor-Leste, **Manatuto District**, llimanu, 7.5 km NW of Manatuto, 8° 29' 38" S, 125° 57' 18" E, alt. 165 m. Rainforest patch in gully, in litter, coll. V. Kessner, 10 Dec 2010), dissected specimen (Fig. 17B).

Paratypes. Same as holotype (AM C.468775, 3 wet), Desa Obrato, 3 km W of Manatuto, 8° 30' 58" S, 125° 59' 15" E. Limestone hills, small patches of vine thicket, secondary vegetation, steep slopes, in talus (AM C.468776, 6 wet, coll. V. Kessner, 10 Dec 2010).

Etymology. Combination of the word 'pseudo-' (Greek = false) and the genus name '*Landouria*', for the close resemblance of this species with species of this genus, noun in apposition.

Description. Shell (Figs 15F, 16C-D, Tables 4-5). Small (D = 7.6 – 11 mm, n = 6), broadly subglobose with low spire; about 3.4 whorls, separated by shallow suture, last whorl angulated to slightly keeled at periphery and spiral supra-peripheral depression; protoconch with coarse, sparse, radially arranged microscopic pustules; teleoconch with microsculpture of dense pustulation and well-developed, irregularly spaced axial ribs; umbilicus widely open, not concealed by reflection of aperture; aperture simple, rounded, lip weakly expanded and reflected; parietal wall inconspicuous; colour uniform hornish brown, transparent.

Genital anatomy (Fig. 17B). Penis rather short, inner penial wall with well-developed, straight, regularly corrugated penial pilasters; epiphallus longer than penis, inner wall with regular, straight, smooth longitudinal pilasters, epiphallic lobe log, epiphallic flagellum long, inside with two smooth, strong pilasters.

Comparative remarks. Shell differs from most other species by its small size. Differs from *P. mendax* most conspicuously by shallower suture, angulated periphery, spiral supra-peripheral depression, no constriction behind non expanded apertural lip. Differs from both *P. renschi* n. sp. and *P. reidi* n. sp. by pustulose microsculpture and spiral supra-peripheral depression. Narrowly endemic.

Parachloritis ninokonisi n. sp.

Material examined

Holotype. AM C.473024 (Timor-Leste, **Lautem District**, Ira-Cau, 1.3 km ESE of Tutuala, 8° 23' 54" S, 127° 15' 59" E. Secondary rainforest on steep slopes, under rocks; coll. V. Kessner, Z. Afranio, 21 May 2011; Fig. 15G).
Paratypes. Timor-Leste, Lautem District, Ira Kava, 3.8 km NE of Lore 1, 8° 38' 35" S, 127° 03' 01" E, alt. 2 m. *Pandanus* patch behind beach, near tidal stream (AM C.473007, 1 wet, coll. V. Kessner, Z. Afranio, 18 May 2011), 2.5 km SW of Lore 1, 8° 41' 00" S, 127° 00' 30" E, alt. 2 m. Beach vegetation, secondary vine thicket on sandy soil (AM C.473004, 1 wet, coll. V. Kessner, Z. Afranio, 18 May 2011).

Etymology. For freedom fighter Nino Konis Santana, name patron of Nino Konis Santana National Park, adjective.

Description. Shell (Fig. 15G; Table 5). Small (D = 13 – 15 mm, n = 2), broadly subglobose with low spire; about 4 whorls, separated by shallow suture, last whorl angulated at periphery, teleoconch with axial growth lines, periostracal setae underneath suture; umbilicus widely open, not concealed by reflection of aperture; aperture simple, rounded, lip weakly expanded and reflected; parietal wall inconspicuous; colour uniform hornish brown, transparent.

Comparative remarks. Shell differs from most other species by its small size, but larger than *P. mendax*, *P. pseudolandouria* n. sp., *P. renschi* n. sp., *P. reidi* n. sp. and *P. laritame* n. sp. Differs from all these species by presence of periostracal setae. Genital anatomy unknown. Narrowly endemic, found in sympatry with *P. sylvatica* n. sp.

Identification key to the species from Timor-Leste

The following key assists with the identification of the species currently known to occur in Timor-Leste by means of shell and, if required, anatomical characters. It does not cover species only found elsewhere. Because of the variability in shell characters, identifications should be confirmed by using additional information given in taxonomic descriptions below as well as in Tables 4-5.

1.	Shell diameter >12 mm, umbilicus narrow, partly concealed by apertural lip	2
-	Shell diameter <12 mm, umbilicus saucer-shaped, not or almost not concealed	14
2.	Shell with red-white marbled coloration	*P. mariae*
-	Shell coloration different	3
3.	Shell banding present in significant proportion of population, can be subtle	4
-	Shell never banded	6
4.	Penis coiled, longer than or as long as epiphallus; penial and epiphallic wall thick, penial pilasters in oblique fishbone-pattern	5
-	Penis rather straight, shorter than epiphallus; penial and epiphallic wall rather thin, penial pilasters longitudinally, corrugated	*P. atauroensis*
5.	Inner wall of epiphallus, flagellum with fine pilasters, epiphallic pilasters smooth	*P. newtoni*
-	Inner wall of epiphallus, flagellum with coarse pilasters, epiphallic pilasters corrugated	*P. baucauensis*
6.	From Atauro Island, some shells with very indistinct peripheral band, inner penial wall with corrugated longitudinal pilasters	*P. atauroensis*
-	Not from Atauro Island, or penial wall pilasters not corrugated	7
7.	Shell large, trochoid with keeled periphery	*P. mundiperdidi*
-	Shell subglobose without keel	8
8.	Shell dark reddish brown, from Mt Ramelau	*P. ramelau*
-	Shell not reddish	9
9.	Shell light crème in colour, with marked, dark brown suffusion on body whorl, particular directly behind aperture and below the upper suture; glossy; shell almost globose, thin translucent	*P. afranio*
-	Shell without marked dark suffusion on body whorl	10
10.	Shell smaller (H < 18 mm, D < 27 mm), subglobose	11
-	Shell large, broadly subglobose (much wider than tall, H > 18 mm, D > 27 mm)	12
11.	Shell rather small (D < 15), depressed with microscopic periostracal projections	*P. ninokinosi*
-	Shell medium to large, subglobose, without microscopic periostracal projections	12
12.	Penial complex very short, penis thick, thick walled, epiphallus very short	*P. manuelmendesi*
-	Penial complex and epiphallus longer	13
13.	Inner penial wall with irregular, crowded corrugations, epiphallus thick-walled with many fine, smooth longitudinal pilasters	*P. sylvatica*
-	Inner penial wall with irregular, broad, rather indistinct longitudinal pilasters, epiphallus thin-walled, with few, corrugated pilasters	*P. nusatenggarae*
14.	Shell with well-rounded periphery, open umbilicus	*P. mendax*
-	Shell periphery angulated or keeled	15
15.	Shell periphery angulated, with sparse periostracal projections	16
-	Shell periphery keeled, with dense periostracal projections	*P. pseudolandouria*
16.	From high altitudes, Mt. Laritame	*P. laritame*
-	From lowlands, Lautem District	17
17.	Shell larger (H > 6 mm, D > 9.5 mm), weak penial pilasters	*P. reidi*
-	Shell smaller (H < 6 mm, D < 9.5 mm), strong penial pilasters	*P. renschi*