Introduction
The 50 described species, in eight genera, of chlorodielline crabs (Xanthidae) are widely distributed throughout the tropical and subtropical Indian and Pacific oceans, with one western Atlantic representative (Ng et al. 2008; Mendoza & Manuel-Santos 2012; Lasley et al. 2013). Members of the subfamily are abundant on rocky seashores, within live coral, and, most notably, in coral rubble. They often dominate coral reef cryptofauna in terms of biomass (pers. obs.; Peyrot-Clausade 1977, 1979) and are especially common in microhabitats that have been recently targeted in large-scale biodiversity surveys, for example dead *Pocillopora* heads, and ARMS (autonomous reef monitoring structures) (Plaisance et al. 2011). Furthermore, chlorodielline crabs likely play a major ecological role in reef food webs, as a recent study carried out on five species of reef-associated fishes in French Polynesia indicated that 37% of the crustaceans found in gut contents were chlorodielline crabs (extrapolated from Leray et al. 2012).

Delimiting Chlorodiellinae Ng & Holthuis 2007 is difficult due to tenuous interfamilial relationships. The taxonomy of most of the 16 subfamilies of Xanthidae is in serious need of revision based on morphology and molecular phylogenetics, including the Chlorodiellinae (Ng et al. 2008; Lai et al. 2011; Mendoza & Guinot 2011; Mendoza & Manuel-Santos 2012; Mendoza et al. 2012). This subfamily is characterized by spoon-tipped chelae; a non-projecting front; a broad, transversely ovate carapace; and a dactylopropod locking mechanism on the walking legs (*sensu* Serène 1984). Many of these characters, however, are present in genera of other subfamilies (e.g. *Cymo*, *Cymoinae*; *Leptodius*, *Xanthinae*; *Etisus*, *Etisinae*; *Kraussia*, *Kraussiinae*; and *Garthiella*, *Garthiellinae*) (Ng et al. 2008; Mendoza & Manuel-Santos 2012). Furthermore, the closest relatives of...
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Chlorodiellinae, namely Eitisinae, are polyphyletic and defined by morphological characters of doubtful homology, making generic assignment based on common ancestry difficult (Ng et al. 2008; Felder & Thoma 2010; Lai et al. 2011).

Dana (1851) described the subfamily ‘Chlorodinae’ in four sentences and included genera from several xanthid subfamilies, as well as Daiva (Dairidae). Subsequent authors split and reorganized the subfamily with varying results. Most notably, Serène (1984) gave a concise historical review of ‘Chlorodinae’ and limited the taxon to five genera: Chlorodiella Rathbun, 1897; Cyclopidius Dana, 1851; Pilodius Dana, 1851; Lioarcipodes Klunzinger, 1913; and Tweedieia Ward, 1934. Three monotypic genera were subsequently assigned to this group: Sukodiobius Clark & Ng, 1999; Vellodius Ng & Yang, 1998; and Carthiella Titgen, 1986. The latter genus was eventually elevated to a monotypic subfamily (Mendoza & Manuel-Santos 2012). The monotypic genera Sukodiobius and Vellodius were compared to Cyclopidius, Pilodius and Chlorodiella in their original descriptions (Ng & Yang 1998; Clark & Ng 1999). However, only cursory attention was given to Lioarcipodes and Tweedieia historically; both only mentioned briefly and without supporting figures. The focus on Cyclopidius, Pilodius and Chlorodiella may suggest a notion of the authors that these three genera are monophyletic to the exclusion of Lioarcipodes and Tweedieia. This has recently been supported in part by recent molecular phylogenetic studies (Lai et al. 2011; Lasley et al. 2013).

Provided here is the first comprehensive molecular phylogeny of the Chlorodiellinae. Chlorodiellinae taxa are analyzed within a framework of previously published xanthid sequences to emphasize the polyphyletic state of the subfamily. The Chlorodiellinae is restricted to a well-supported, monophyletic clade and redefined based on a suite of morphological characters, and two new genera are described. Any chlorodielline genera outside of this clade are regarded as incertae sedis for the time being.

Materials and methods

Taxon sampling

Two hundred and two specimens representing 189 nominal species, 89 genera and 14 xanthid subfamilies were selected for the molecular analyses. All eight chlorodielline genera were represented, and 37 of 48 chlorodielline species were included. The sequences generated for this study are recorded in Table S1. Specimens for morphological and molecular analyses are deposited at the following institutions: the Florida Museum of Natural History, Gainesville, Florida, USA (UF); the Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore (ZRC); the Queensland Museum, Brisbane, Australia (QM); and the Senckenberg Museum, Frankfurt am Main, Germany (SMF). Seven additional etisine species were added, as the taxon is morphologically similar and, in previous molecular phylogenetic studies, tends to group with the Chlorodiellinae, albeit with low support (Ng & Yang 1998; Clark & Ng 1999; Ng et al. 2008; Lai et al. 2011; Lasley et al. 2013). Menippe runmbi (Menippidae), Benthebaxon bemiingi (Por-tunidae), Trapezia cymodece and Quadrella corona (Trapeziiidae) were selected as outgroups following Lai et al. (2011). The following abbreviated subfamilial and familial names are used for clades recovered in our analyses that are congruent with clades recovered in Lai et al. (2011): Eux (= Euxanthinae), Lio (= Liomerinae), Xan (= Xanthinae), Act (= Actaeinae), Zos (= Zosiminae), Pol (= Poly-dectinae), Cym (= Cymoinae), Pse (= Pseudorhombilidae), Pan (= Panopeidae) and Chl (= Chlorodiellinae).

Phylogenetic analysis

Single-gene trees were constructed to examine congruence between loci (not shown), in addition to trees based on the concatenated data set (Fig. 1). A total of 753 mitochondrial (12S rDNA gene = 199, 16S rDNA gene = 200, COX1 = 170) and nuclear (H3 = 184) sequences were used for the analyses, of which 151 were generated for this study (Table 1); the remaining sequences, most of which are non-chlorodielline taxa, were previously published and obtained from GenBank (Lai et al. 2011; Lasley et al. 2013). New sequences were amplified following Thoma et al. (2009) (12S and 16S rRNA genes), Buhay et al. (2007) (12S rRNA gene), Lai et al. (2009) (16S rRNA gene) Colgan et al. (1998) (H3), Thoma et al. (2013) (COX1) and Geller et al. (2013) (COX1). As these publications comprise several primer and PCR profile combinations, we provide our optimized combinations using Promega PCR Master Mix. The most successful primers used were as follows: 12sf and 12slr (12S) (Buhay et al. 2007); crust16sf1 and crust16sr2 (16S) (Lai et al. 2009); jgHCO2198 and jgLCO1490 (COX1) (Geller et al. 2013); and H3sf and H3ar (H3) (Colgan et al. 1998). Reactions were carried out using the following cycling parameters: initial denaturation at 95°C for 5 min; four cycles at 94°C for 30 s, 57°C (12S), 52°C (16S), 50°C (COX1), 50°C (H3) for 45 s, 72°C for 1 min; then 34 cycles at 94°C for 30 s, 52°C (12S), 47°C (16S), 45°C (COX1), 47°C (H3) for 45 s; and a final extension at 72°C for 8 min. All new sequences were submitted to GenBank (Table 1). COX1 and H3 sequences were checked for stop codons.

Alignments were generated with MUSCLE (multiple sequence comparison by log expectation) (Edgar 2004) using the default settings in Geneious version 7.1.4 (Biomatters Ltd., Auckland, New Zealand). The length of the aligned and concatenated data set was 1843 bp (12S rRNA = 443 bp, 16S rRNA = 490, COX1 = 582 and H3 = 328) and was partitioned according to locus.
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Fig. 1 Bayesian consensus tree inferred from combined 12S and 16S rRNA genes, COX1 and histone H3 sequences. Catalogue numbers are included. Numbers above, below left and below right indicate Bayesian inference posterior probability (pP), maximum-likelihood bootstrap support (ML BS) and maximum parsimony bootstrap (MP BS) support, respectively. The latter two support values are separated by ‘-’. Values below 95 (pP) and 70 (ML BS and MP BS) are represented by ‘-/-’. Missing bootstrap values indicate clades not recovered in ML or MP analyses. Red indicates chlorodielline s. s. taxa. Brown indicates Eitsus taxa. Other coloured taxa are Chlorodiellinae s. str. Three-letter abbreviations correspond with clades of the same name and sequences in Lai et al. (2011).
Phylogenetic trees were inferred from the concatenated data set using maximum-likelihood (ML), maximum parsimony (MP) and Bayesian inference (BI) methods. Likelihood trees were generated using Randomized Accelerated Maximum Likelihood (RAxML) version 7.7.7 (Stamatakis 2014). COXI and H3 were partitioned by codon. The general time-reversible model with a gamma distribution of rate heterogeneity was selected as substitution model. Confidence was assessed using 1000 nonparametric bootstrap replicates. Deeper splits within the resulting ML tree were not well supported (see Results section), and therefore, the monophyly of Chlorodiellinae s. lat. could not be rejected. Consequently, Chlorodiellinae s. lat. was constrained to monophyly in RAxML. The constrained and unconstrained (Chlorodiellinae s. lat. polyphyletic) best trees were analysed with the log-likelihood test (SH test) as implemented in RAxML.

The BI analyses were carried out using MrBayes 3.2.2 (Ronquist & Huelsenbeck 2003) on the computer cluster of CIPRES (CyberInfrastructure for phylogenetic RESearch project) (Miller et al. 2010). Prior to the analyses, substitution models for each partition were selected using the Akaike information criterion implemented in JMODELTEST version 2.1.4 (Posada 2008). Two parallel runs were used with three hot chains and one cold chain per run. The temperature was set to 0.2. Trees were sampled every 1000 generations for 50 million generations. The first 2000 trees were discarded as burn-in. Clade support was assessed with posterior probabilities (pP). Convergence of the two runs was confirmed using TRACER version 1.5 (Rambaut & Drummond 2009). The average standard deviation of split frequencies in the Bayesian analyses reached 0.009121 after 50 million generations.

The MP analyses were conducted using POY 5.0.0 BETA (Varon et al. 2010). POY was run using the simple search option. The prealigned option was selected so that all runs (BI, ML and MP) would be comparable. Node support was assessed using 1000 bootstrap replicates.

Scanning Electron Microscopy
Mucus and debris were removed from G1s, following Felgenhauer (1987). Samples were dehydrated through a graded ethanol series, followed by two changes in HMDS (hexamethyldisilazane). The specimens were subsequently mounted on stubs using Elmer’s glue and then coated with 25 nm 60:40 gold:palladium using a Cressington Sputter Coater 108auto. Images were produced using a Leica Stereoscan 440.

Results
Models selected for COXI, 12S and 16S rRNA genes and histone H3 were TrN+I+G, HKY+G, HKY+I+G and K80+G, respectively. The separate gene trees did not provide support—that is, >0.95 pP or 70 BS—for phylogenetic relationships for most nodes above sister species pairs. The deeper nodes with high support were generally in agreement with the concatenated data set. There were three notable exceptions: (i) a clade recovered in the COXI-only BI analysis comprising Pilodius areolatus (H. Milne Edwards, 1834), P. moranti Clark & Galil, 1933, Soliella flava, comb. n. (Rathbun, 1894), and S. melanospinis, comb. n. (Rathbun, 1911) (pP = 0.96) (vs. P. areolatus and P. moranti with the other Pilodius species in the combined data set); (ii) a clade recovered in the COXI-only BI analysis comprising Pilodius and Cycloides, but excluding Cycloides obscurus (pP = 1.00) (vs. C. obscurus included in the combined data set); and (iii) a clade recovered in the H3-only ML and BI analyses comprising Chlorodiella cytherea, C. davaoensis and C. spinimera (pP = 1.00, BS = 92) (vs. C. spinimera sister to C. nigra and C. xixbaensis in the combined data set) (Fig. 1; Figs S6–S8). These clades were not supported in any other single-gene analysis. All analyses (BI, ML and MP) produced similar trees with differences in nodes with low support (Fig. 1). Most of the non-chlorodielline taxa from Lai et al. (2011) were recovered in clades congruent with their study (i.e. Act 1, 2, 3; Chl 2; Cym; Eux 1, 3; Lio 1, 2; Pol; Xan 1, 3, 4, 10; Pan+Pse+Spe+Xan 6+Xan?+Xan 8; and Zos 1, 2). The log-likelihood test showed that the constrained topology (Chlorodiellinae s. lat. monophyletic) is not significantly worse on a 1% significance level than the best topology found by the ML analysis (Fig. 1); thus, monophyly of the Chlorodiellinae s. lat. cannot be rejected.

The three most species-rich chlorodielline genera (Chlorodiella, Pilodius and Cycloides) were recovered in a well-supported, monophyletic clade (pP = 1.00, ML BS = 87, but MP BS < 50). The remaining chlorodielline genera (Ratha, Licarpilodes, Tweedia, Sulcodius and Vellodius) were recovered outside of this clade, in various positions with other subfamilies. Sulcodius was sister to Etisus laevimans Randall, 1840 (Etisus 1), but only in the BI analysis and with low support (pP = 0.93). Rathua longimana (H. Milne Edwards, 1834) grouped with ‘Xan 5’ species although not supported (pP = 0.78, ML BS < 50) in the BI and ML analyses. Similarly, Vellodius etiosideus (Takeda & Miyake, 1968a) was recovered sister to Etisus sakaii Takeda & Miyake, 1968b; E. frontal(is (Dana, 1852) and E. electra (Herbst, 1801) with low support (pP = 0.79, not recovered in the ML and MP analyses). However, its sister clade (Etisus 2) is well supported (pP = 1.00, ML BS = 89, MP BS = 72).

Furthermore, the analyses indicate that Licarpilodes is polyphyletic. Licarpilodes integerrimus (Dana, 1852) is included in a clade with moderate support (pP = 0.97, ML BS = 54, not recovered in MP), sister to several etisines [Etisus bifrontalis (Edmondson, 1935), E. odhneri Takeda,
diagnostic features has been called into question recently (Ng et al. 2008; Lai et al. 2011). Our analyses indicate that these characters are indeed paraphyletic and have evolved independently in different lineages. Chlorodiellinae is redefined and delimited based on a new suite of characters (see Taxonomic Accounts).

Lioarripodes is polyphyletic, with members segregating into three clades that possess strikingly different morphological features used in xanthid taxonomy to define genera (e.g. characteristics of the male abdomen, sternum and G1; spination of the chelipeds; tip of the ambulatory dactylus; and anterolateral margin of the carapace). Based on our phylogeny, L. integerrimus is allied with Etisus bifrontalis, E. odhneri, E. demani and E. albus with moderate support (pP = 0.97, ML BS = 54, not recovered in MP). Lioarripodes armiger and L. pacificus are well-supported (pP = 1.00, ML BS = 100, MP BS = 100) sister species, but their relationship with other xanthid genera is not supported. The same is true for L. harmsi. The only Lioarripodes species not included was L. biunguis. Given the almost indistinguishable G1s, and similar sternum and abdomen, L. biunguis is likely allied with L. harmsi. Further commentary is beyond the scope of this study, except to say that Lioarripodes likely comprises three genera and is in need of taxonomic revision.

Etisinae, as currently defined (Ng et al. 2008), comprises only two genera: Etisus and the monotypic Pareatisus Ward, 1933. However, the topology of our phylogeny indicates that Etisus comprises at least three independent lineages (see Results; Lai et al. 2011: 434), each defined by suites of uniting morphological characters (Fig. 1). The Etisinae, as presently defined, likely comprises several genera and requires revision.

Based on the present data, the Chlorodiellinae is confined to only three currently recognized genera (i.e. Pilodius, Cylocladius and Chlorodiellia), excluding Rattha, Vellocladius, Sukodius, Lioarripodes and Tuwedcieia. The excluded genera are regarded as incertae sedis, pending a systematic study of xanthid subfamilial relationships (see Chlorodiellinae Remarks). The type species of Lioarripodes, L. integerrimus, was recovered with Etisus 4 (pP = 0.97, ML BS < 70), so the genus may be assigned to the Etisinae, pending necessary revisions of Lioarripodes and Etisinae. Vellocladius and Sukodius grouped with Etisus 2 and Etisus 1, respectively, in the combined BI analysis, albeit with low support. Based on these data and the similar transversely hexagonal carapaces in these taxa, spoonlike tips of the cheliped dactylus and dactylo-propodal locking mechanisms on the ambulatory legs, these genera are probably close to Etisus s. lat. Greater taxon sampling of Etisinae for morphological comparisons (e.g. investigating male sternal and male gonopod characters) and molecular phylogenetics will

Discussion
Phylogenetic relationships
The topology of the present tree indicates a monophyletic Chlorodiellinae, including Pilodius, Cylocladius, Chlorodiellia, Soliella, gen. n., and Luniella, gen. n., but excluding Lioarripodes, Rattha, Sukodius, Tuwedcieia and Vellocladius (Fig. 1).

Two characters, spoonlike tips of the cheliped dactylus and a dactylo-propodal locking mechanism on the walking legs, have historically been used to unite members of Chlorodiellinae and Etisinae. However, the utility of these supposedly
undoubtedly be necessary and insightful. The same applies to *Tweedieia* (see Phylogenetic Relationships). *Ratha* is also interesting as although it is excluded from the Chlorodiellinae, its position in the Xanthidae is less clear. Lai et al. (2011) and Thoma et al. (2013) showed that many eastern American xanthid genera now classified in the Euxanthininae, Actaeinae and Zosiminae actually form natural groups and likewise for *Ratha*. This ‘east American clade’ will also require revision. Two new genera of Chlorodiellinae *s. str.* are described to accommodate the several atypical members previously classified in *Pilodius* and *Cyclodius*.

**Taxonomy**

Subfamily Chlorodiellinae Ng & Holthuis 2007

**Diagnosis**

Carapace transversely hexagonal (Fig. S1). Front arched or sinusoid; not produced; submedian lobes separated by V- or U-shaped notch, lateral lobes confluent with or distinct from submedian lobes. Anterolateral margin relatively straight. Chelipeds subequal, propodus and dactylus gaping, tips spoonlike; merus with anterior margin smooth, granular, or with short spines or teeth; dorsal surface without deep longitudinal sulcus. Ambulatory legs moderately long; dactylo-propodal locking mechanism well developed; chitinous, distal spine of dactylus roughly equal to or longer than calcareous subdistal spines. Male thoracic sternum broad (Fig. S2). Anterior margin of male telson reaching beyond imaginary line between posterior margin of first ambulatory leg sternal condyles, not reaching more than halfway between sutures of sternites 2–3 and 4–5. Episternites 6, 7 not delimited by sulcus. Abdominal somite 3 not locking with thoracic episternite 7. G1 tip spatulate, tubular, recurved or flat; often with stout, proximally directed subdistal setae, sometimes with long subdistal setae (Figs S3, S4).

**Genera included**

*Chlorodiella* Rathbun, 1897; *Pilodius* Dana, 1851; *Cyclodius* Dana, 1851; *Soliella* gen. n.; *Luniella* gen. n.

**Remarks**

The present definition of the Chlorodiellinae excludes *Ratha, Vellodius, Sulcodius, Liocarpilodes* and *Tweedieia*. As defined here, chlorodiellines have a distinct transversely hexagonal carapace without conjoined, transverse granules on anterior regions; a broad thoracic sternum; a telson reaching beyond the imaginary line between the posterior margin of the first ambulatory leg condyles; relatively short chelipeds without a longitudinal sulcus or row of large teeth of roughly equal size on the merus; and dactyli of the ambulatory legs with a chitinous distal tip that is equal to or longer than accessory, calcareous, subdistal spine(s) (Figs S1, S2). *Vellodius, Sulcodius* and *Ratha* are most similar to Chlorodiellinae in having a similarly shaped transversely hexagonal carapace, a non-projecting front, chelar propodus and dactylus with spoonlike tips and well-developed dactylo-propodal locking mechanisms of the ambulatory legs (Ng & Yang 1998: Figs 1–3, 7; Clark & Ng 1999: Figs 1, 2, 7; Lasley et al. 2013: Figs 2–4). However, *Vellodius* differs from Chlorodiellinae in having a relatively long, narrow sternum; a male telson with an anterior margin not reaching beyond the imaginary line between the posterior margin of first ambulatory leg sternal condyles; transverse striae of the anterior and posterior regions of the carapace; and a bifid tip of ambulatory leg dactylus with a subdistal calcareous tip that is longer than the terminal, chitinous tip (Takeda & Miyake 1968a: 186; Fig. 2, pl. 8c,d; Ng & Yang 1998: Figs 1, 2A, B, 3B, 7D) [vs. broad sternum; male abdomen with telson reaching beyond line; no anterior transverse striae of the carapace; and a chitinous tip longer or equal to the calcareous tip in Chlorodiellinae] (Figs S1, S2). *Vellodius* also has a distinct G1 morphology (truncate and bearing two long, distal setae) not seen in Chlorodiellinae (Figs S3, S4) (Ng & Yang 1998: Fig. 4A–D).

*Sulcodius* differs from the Chlorodiellinae by its long, relatively narrow chelipeds with a deep, longitudinally grooved merus and vestigial chitinous tip of the ambulatory leg dactylus (Clark & Ng 1999: Figs 1, 3B, 7) [vs. shorter, stouter chelipeds (although large specimens of *C. nigra* are close in length) without a deep longitudinal groove on the merus and bifid tip of ambulatory leg dactylus with a subdistal calcareous tip that is longer than, or equal to, the terminal chitinous tip in Chlorodiellinae] (Fig. S1).

*Ratha* is distinct with respect to its relatively narrow orbits; long chelipeds with three large, roughly equal, acute teeth on the anterior margin; and western Atlantic distribution (Lasley et al. 2013: Fig. 2A–C) [vs. relatively wide orbits; short chelipeds (although similarly long in large specimens of *C. nigra*) with a merus that is smooth, granular or adorned with short spines; and Indo-West Pacific distribution in Chlorodiellinae *s. str.* (Fig. S1)].

The similarity of chlorodiellines to *Tweedieia* and *Liocarpilodes* is primarily in possessing well-developed dactylo-propodal locking mechanisms on the ambulatory legs and spoon-tipped chelae. However, *Tweedieia* and *Liocarpilodes* differ markedly in having a transversely ovate carapace (Serène 1984: pl. 37) [vs. generally transversely hexagonal in Chlorodiellinae (Fig. S1)]. *Tweedieia* differs further in possessing a male telson that almost reaches the imaginary line between the posterior margin of the first ambulatory leg sternal condyles and short, stout movable fingers of the
Chlorodiella Rathbun, 1897

Subfamilies. A systematic study of Etisinae and reassessment of xanthid family Tweedieia. Consequently, the Etisinae is polyphyletic as currently defined and not morphologically cohesive (see Phylogenetic Relationships).

Subfamilial placement of Vellodius, Sulcodius, Liocarpilodes, Tweedieia and Ratba is complicated, but given the morphological and molecular data, these genera do not belong to Chlorodiellinae. Etisinae is the most obvious choice for these taxa based on superficial external morphology, although the available data strongly suggest that the Etisinae is also polyphyletic (Fig. 1; Ng et al. 2008; Lai et al. 2011). However, the log-likelihood test indicates that the constrained topology—all chlorodiellines s. lat. monophyletic—is not significantly worse than the topology recovered in our ML tree. This result is presumably due to unresolved deep nodes. Despite similarity to the Etisinae, there is morphological evidence and high clad support for excluding these taxa from the Chlorodiellinae. Consequently, Vellodius, Sulcodius, Liocarpilodes, Tweedieia and Ratba will remain incertae sedis, pending a systematic study of Etisinae and reassessment of xanthid subfamilies.

Chlorodiella Rathbun, 1897

Type species
Cancer nigra Forskål, 1775

Diagnosis
Carapace transversely hexagonal (Fig. S1A). Surface appearing smooth, glabrous without magnification, sometimes with minute granules or punctuations. Regions undefined medially and usually laterally, sometimes raised laterally with indistinct furrows. Front arched; submedian lobes separated by shallow notch, arched or slightly sinus, anterior margin smooth, serrated or lined with minute granules; lateral lobes indistinct or confluent with submedian lobes. Anterolateral margin with 0–4 teeth, excluding exorbital tooth; without denticles between teeth, margins smooth or granular. Basal antennal article without elongated anterolateral extension blocking orbital hiatus; flagellum generally free to enter orbit (Fig. S5A). Surface of chelae glabrous, smooth, free of granules or spines; tips of fingers spoonlike, deeply hollowed. Ambulatory legs long, narrow. Tip of ambulatory leg dactylus bifid; subdistal spine approximately equal in length to distal pigmented spine. G1 tip spatulate, hooked, curled or truncate, usually with stout proximally directed setae (Fig. S4A).

Species included
Chlorodiella barbata (Borradaile, 1900); C. coralliosa Miyake & Takeda, 1968; C. crispipleopa Dai, Yang, Song & Chen, 1986; C. cythera (Dana 1852); C. davaoensis Ward 1941; C. laevisima (Dana 1852); C. nigra (Forskål 1775); C. ohshimai Miyake & Takeda 1967; C. quadrilobata Dai, Cai, & Yang, 1996; C. spinimera Dai, Cai, & Yang, 1996; and C. xishaensis Chen & Lan, 1978.

Remarks
The most conspicuous characteristic of Chlorodiella is its smooth, glabrous carapace with undefined or poorly defined regions (Fig. S1A). Large specimens of C. xishaensis and, most notably, C. nigra sometimes have raised regions of the carapace, but these are not defined by distinct furrows, as in other chlorodiellines (Serène 1984: pl. 36 B, 43 E). The raised regions of these two species are usually restricted to the lateral areas of the carapace, with a smooth or slightly defined mesial area. All of the other Chlorodiella species have a more or less smooth carapace (Serène 1984: pl. 36).

The monotypic Ratba is the only genus previously classified as a chlorodielline with a similarly smooth carapace (Lasley et al. 2013: Fig. 2A). However, like C. nigra and C. xishaensis, the lateral regions of Ratba are sometimes raised. Ratba differs from Chlorodiella in having single-tipped dactyli of the ambulatory legs, long cheliped meri with several separated teeth and relatively narrow orbits (Lasley et al. 2013: Figs 2A, B, 3B, 4A) [vs. bifid dactyli, no or few small teeth on the merus of the chelipeds and wider orbits in Chlorodiella (Figs S1A, S5A)]. Furthermore, Ratba is only known from the western Atlantic, whereas all Chlorodiella are from the Indo-West Pacific.

Pilodius Dana, 1851

Type species
Chlorodiella pilumnoides White, 1848

Diagnosis
Carapace transversely hexagonal (Fig. S1F). Surface granular, adorned, especially laterally, with pearlfom granules or short, conical spines. Carapace with dark, long, simple setae; long, plumose setae; or short pubescence. Regions defined by deep furrows. Front sinus; submedian lobes divided by relatively deep notch, margin granular or spinose; lateral lobes narrow, distinct. Anterolateral margin with four lobes, each tipped with emergent anteriorly directed spine (short conical granule in P. areolatus) and smaller accessory spines or granules. Basal antennal article with elongated disto-lateral extension completely blocking or extending more than halfway...
into orbital hiatus, excluding flagellum (Fig. S5C). Superior margin of chelae granular or spinose; propodus and dactylus gaping. Ambulatory legs moderately stout with numerous setae; tip of dactylus with long, distal chitinous spine; subdistal calcareous spines almost equal in length to minute. G1 tip spatulate, truncate, tubular, curved or hooked (Fig. S4B).

**Species included**

*Pilodius arvelatus* (H. Milne Edwards, 1834); *P. cephalalgicus* Clark & Galil, 1993; *P. concors* Clark & Galil, 1993; *P. granulatus* Stimpson, 1858; *P. maotieni* Serène, 1971; *P. miersi* (Ward, 1936); *P. moranti* Clark & Galil, 1993; *P. nigrocrinitus* Stimpson, 1858; *P. philippinensis* (Ward, 1941); and *P. pilumnoides* (White, 1848).

**Remarks**

In their revision of the genus, Clark & Galil (1993) provided a thorough account of the taxonomic history of *Pilodius* and indicated that *P. pilumnoides* is the type species. Ng et al. (2008) subsequently reversed their decision stating, ‘Serène (1984: 233) was apparently the first to nominate […] that *Pilodius pubescens* is the type species, and his action therefore has precedence’. They further stated that the composition of the genus would not change depending on which species is the type. However, Forest & Guinot (1961: 90) had earlier selected *Chlorodius pilumnoides* White, 1848, as type species for *Pilodius*. Thus, *P. pilumnoides* remains the type species of *Pilodius*.

Clark & Galil (1993: 1124) remarked that the sole character distinguishing *Pilodius* from other chlorodielline genera is the presence of a disto-lateral extension of the basal antennal article which blocks the orbital hiatus. They also pointed out that Crosnier had stated, in a footnote in Serène (1984: 233), that this character varies with age and that some species only possess a feeble prolongation of the disto-lateral extension. *Pilodius paumotensis* was the only species mentioned that does not have a fully prolonged basal antennal extension (Fig. S5D).

Given the currently included species in *Pilodius*, the utility of the basal antennal article for generic delimitation is problematic. *Pilodius flavius* (= *Soliella flava*, comb. n.) and *P. melanospinis* (= *S. melanospinis*, comb. n.) have basal antennal articles with a disto-lateral extension that reaches less than halfway the length of the orbital hiatus (Fig. S5F). Furthermore, the disto-lateral extensions of *P. arvelatus* and *P. miersi* do not fully block the orbital hiatus. Interestingly, molecular evidence suggests that *P. flavius* and *P. melanospinis* form a monophyletic clade sister to the remaining *Pilodius* species, with the exception of *P. paumotensis* which falls in *Cyclodius* (see Phylogenetic Relationships; Fig. 1). Based on these and further morphological data, the inclusion of *P. flavius* and *P. melanospinis* in a new genus, *Soliella* gen. n., and the placement of *P. paumotensis* in *Cyclodius*, is sensible. In summary, *Pilodius*, as defined here, possesses a disto-lateral extension of the basal antennal article that extends more than halfway into the orbital hiatus, usually completely blocking it. In comparison, *Chlorodius*, *Soliella* and *Cyclodius* either lack this extension or possess one that reaches less than halfway into the orbital hiatus (Fig. S5). However, *Luniella* gen. n. shares this feature in common with *Pilodius*. These genera are differentiated by other features (see *Luniella* Remarks).

The setation of the carapace, even in preserved specimens, is another important character worth discussion, despite the fact that the setae can sometimes be worn down, damaged or lost with age. Based on the topology of *Pilodius*, setation within the genus is phylogenetically informative. Most species in the genus (*P. cephalalgicus*, *P. concors*, *P. maotieni*, *P. nigrocrinitus* and *P. pilumnoides*) are covered with stout black setae on the dorsal surface of the carapace. *Pilodius arvelatus*, on the other hand, has diagnostic dense, plumose setae surrounding prominent peariform granules. *Pilodius moranti* is unique, covered with short, dark setae and long, plumose, light-coloured setae. *Pilodius granulatus*, *P. philippinensis* and *P. miersi* usually bear short, plumose, white or yellow pubescence, although specimens are commonly encountered with some or all of the setae removed. None of the species, however, have a carapace densely covered with long and short, yellow, simple setae like that of *Soliella pubescens*, *S. spinipes* (more scattered), *Luniella* and *Cyclodius paumotensis*.

Thus, *Pilodius* is differentiated from other chlorodielline genera based on the following characters: carapace adorned with dark, long, simple setae; long, plumose setae; or short pubescence (vs. glabrous or covered in short and long, yellow setae in other chlorodiellines); and disto-lateral extension of basal antennal article completely filling or reaching more than halfway into orbital hiatus (vs. extension absent or reaching less than halfway in all genera except *Luniella*, gen. n.) (Fig. S5). Furthermore, it is distinguished from *Soliella* gen. n. and *Luniella* gen. n. in having a G1 with a spatulate, truncate, tubular, curved or hooked tip (vs. tip conserved tubular or spatulate in *Soliella* gen. n., or conserved sickle-shaped in *Luniella* gen. n.) (Figs S3C, D, S4B–D).

**Cyclodius Dana, 1851**

**Type species**

*Cyclodius ornatus* Dana, 1852 [= *Cyclodius obscurus* (Hombron & Jacquinot, 1846)]

**Diagnosis**

Carapace transversely hexagonal (Fig. S1B, C). Surface generally glabrous or with few tufts of plumose setae, smooth.
or granular, usually appearing smooth to naked eye, with regions well defined by distinct furrows (with numerous simple, blond setae only in *C. paumotensis*). Front relatively straight or sinuose; submedian lobes separated by deep or shallow notch, margins smooth, granular or spinose; lateral lobes distinct, narrow. Anterolateral margin with four teeth, generally without apical or accessory spines (*C. paumotensis* with accessory spines). Basal antennal article with disto-lateral extension absent or blocking less than half length of orbital hiatus (Fig. S5B, D). Cheliped surface smooth, spinose or granular. Ambulatory legs long or stout; tip of dactylus with long distal chitinose spine; calcareous spine almost equal in length to minute. G1 tip ovate, spatulate, tubular, hooked or adorned with numerous subdistal, straight setae or two emergent setae (e.g. Fig. S3A).

**Species included**

*Cyclodius drachi* Guinot, 1964; *C. granulatus* (Targioni Tozzetti, 1877); *C. granulosus* de Man, 1888; *C. obscurus* (Hombron & Jacquinot, 1846); *C. nitidus* (Dana, 1852); *C. paumotensis* (Rathbun, 1907); *C. perlatus* Nobili, 1905; and *C. ungulatus* (H. Milne Edwards, 1834).

**Remarks**

Despite Dana (1851: 126) having described *Cyclodius* 12 years before the description of *Phymodius* by A. Milne-Edwards (1863), Gordon (1934: 32) stated in a footnote that *Cyclodius* probably ought to be included in *Phymodius*, not the other way around. Forest & Guinot (1961: 104) confirmed the suggestion of Gordon (1934), and *Phymodius* was in use until Davie (2002: 520) resurrected the name *Cyclodius*. Ng et al. (2008) also used *Cyclodius*, citing the submission of 99 generic names by Rathbun (see ICZN 1922, 1956–1957) to the International Commission for Zoological Nomenclature (Opinion 73, Direction 37). Hence, by virtue of the principle of priority, *Cyclodius* is used instead of *Phymodius*.

*Cyclodius* had been the subject of several revisionary works. Alcock (1898: 396) gave a diagnosis of the genus (as *Phymodius*, see above) and, most notably, stated that members possess carapace regions that are ‘well delimited and broken up into numerous convex areolae which have a smooth bare surface’. This feature is the most conspicuous character for most *Cyclodius* species. However, as Gordon (1934: 32) pointed out, *C. granulosus* and small specimens of several species have carapace granulation to varying degrees.

Recently, Ng & Yang (1998) and Clark & Ng (1999) differentiated between *Cyclodius* and other chlorodielline genera by features of the basal antennal article, tip of the ambulatory leg dactylus and male thoracic sternum. The last character is difficult to use for the genera as now defined. The authors stated that *Cyclodius* has a relatively narrow sternal plastron compared to other chlorodielline genera (Ng & Yang 1998: Fig. 6; Clark & Ng 1999: Fig. 8). Although, this feature is not evident from their figures or from current examination of *Cyclodius* specimens. However, the long thoracic sternite 4 of *Sulcodius* is useful for distinguishing it from *Cyclodius* and other chlorodielline genera. Furthermore, the arrangement and length of dactylar spines on the ambulatory legs may not work. Ng & Yang (1998: 1687) characterized *Cyclodius* as having ‘two subdistal spines positioned side by side on the ambulatory dactylus’. They also stated that the chitinous ‘spine is much larger than the [calcareous] spine and is distal in position’. The problem with this character is that it varies between species, and the strength of the subdistal spines often wears with age. *Cyclodius ungulatus* and *C. nitidus* possess ambulatory leg dactyli like that described and figured by Ng & Yang (1998: Fig. 7B) and Clark & Ng (1999: Fig. 7C). However, *Cyclodius obscurus* and *C. granulosus* are more similar to *Pilodius* or *Chlorodiella*, according to their figures and descriptions (Ng & Yang 1998: Fig. 7A, C; Clark & Ng 1999: Fig. 7B, D). *Cyclodius granulatus* and *C. drachi* are intermediate.

The decision to place *C. paumotensis* in *Cyclodius* was made with some hesitation. It is the only *Cyclodius* species without the typical glabrous, well-defined regions of the carapace (Fig. S1C). However, unlike *Pilodius* species, it has an open orbital hiatus with only a slight disto-lateral extension (Fig. S5D) (see Remarks for *Pilodius*). Furthermore, despite being most superficially similar to species of *Soliella*, *C. paumotensis* was recovered in the *Cylodius* clade with high support in our molecular analyses. Beyond strong molecular evidence, the decision to move *C. paumotensis* to *Cyclodius* was based on G1 morphology and the absence of lateral spiniform granules of the carapace, which are present in *Soliella*. The G1 of *Soliella* is conserved—that is, narrow with a tubular spatulate or ladlelike tip and numerous stout, subdistal, proximally directed setae [vs. broad with a wide, ovate tip and less numerous, narrow subdistal setae, of which the most distal are not proximally directed in *C. paumotensis* (Fig. S3B)]. The form of the G1 is considered to be a stronger character in classifying species, as has already been demonstrated in other studies (e.g. Lai et al. 2011; Thoma et al. 2013). *Cyclodius paumotensis* is also a much smaller species than *S. flavus* or *S. melanopiniss*.

*Soliella* gen. n.

**Type species**

*Pilodius flavus* Rathbun, 1894, by present designation.

**Diagnosis**

Carapace transversely hexagonal (Fig. S1D). Surface granular, covered with short, long, yellow setae; regions well
defined. Front sinuous; submedian lobes arched, separated by narrow U-shaped notch, margins granular or spinose; lateral lobes distinct, narrow. Antero-lateral margin with four lobes tipped with emergent, anteriorly directed spine, smaller accessory spines. Basal antennal article with disto-lateral extension reaching approximately halfway into orbital hiatus (Fig. S5F). Exterior, superior surface of chelipeds spinose, granular, with numerous long, simple, yellow setae. Ambulatory legs relatively stout; tip of dactylus with long, pigmented spine; non-pigmented, subdistal spines minute. G1 narrow, relatively straight; tip tubular or spatulate with numerous subdistal stout, proximally directed setae (Fig. S3C, D).

Species included
Soliella flava (Rathbun, 1894); S. melanospinis (Rathbun, 1911).

Remarks
Clark & Galil (1993: 1132) synonymized P. melanospinis (= Soliella melanospinis, comb. n.) with P. flavus (= Soliella flava, comb. n.), stating that the characters used to distinguish between the two species—that is, areolation of the carapace, pigmentation of the chelae and spinulation of the orbits—amount to ‘just variation’. They also stated that the G1s are identical. While the external characters do vary and are difficult to use for delimitation, there are two distinct gonopod morphologies for the two species (Fig. S3C, D). This difference is supported by our molecular phylogeny (Fig. 1). Therefore, both are recognized as distinct species in this study.

Soliella gen. n. is closest in morphology to Luniella pubescens, L. scabricula and Cyclodius paumotensis in general shape of the carapace and, especially, the presence of long and short, light-coloured setae (see Cyclodius Remarks for comparison with C. paumotensis). However, Soliella differs from Luniella in having a conserved G1 with a spatulate or tubular tip and a basal antennal article with a disto-lateral extension that reaches less than halfway into the orbital hiatus (vs. a G1 with a flattened, sickle-shaped tip and disto-lateral extension of the basal antennal article completely blocking the orbital hiatus in Luniella) (Fig. S3C, D, S4C, S5E, F).

Etymology. Soliella is derived from a combination of the Latin word for sun, ‘sol’, and the last five letters of the subfamilies’ type genus, Chlorodiella. ‘Sol’ alludes to the blond or golden setae on the surface of the carapace of these crabs.

Luniella gen. n.

Type species
Pilodius pugil Dana, 1852, by present designation.

Diagnosis
Carapace transversely hexagonal (Fig. S1E). Surface granular, glabrous or with numerous short yellow setae and scattered long setae. Front broad; submedian lobes arched, separated by shallow or deep median notch, margins smooth, granulate or spinose; lateral lobes distinct, narrow. Antero-lateral margin with four spinose teeth, few or no accessory teeth. Basal antennal article with disto-lateral extension generally completely blocking orbital hiatus, excluding flagellum (Fig. S5E). External, superior surfaces of chelipeds granular and/or spinose; with or without setae. Ambulatory legs granular or smooth, with numerous setae sometimes restricted to extensor margin; tip of dactylus with long, pigmented spine; non-pigmented subdistal spines minute. G1 tip longitudinally flattened, sicklelike or twisted (Fig. S4C, D).

Species included
Pilodius pubescens Dana, 1852; Pilodius pugil Dana, 1852; Pilodius scabricula Dana, 1852; Pilodius spinipes Heller, 1861.

Remarks
Luniella gen. n. is most readily distinguished from other chlorodielline s. str. species by its unique sickle-shaped G1 tip. This feature is conserved even when it is longitudinally twisted like in L. scabricula (Fig. S4C). Luniella also varies in another important character: the disto-lateral extension of the basal antennal article. Like most Pilodius species, the other Luniella species have an orbital hiatus that is completely blocked by the extension. However, most large specimens of L. scabricula possess a basal antennal article that extends more than halfway into the orbital hiatus, but not completely blocking it. Despite these variations, L. scabricula was recovered in the well-supported Luniella clade (Fig. 1). The genus is therefore defined as having a disto-lateral extension of the basal antennal article that extends more than halfway into the orbital hiatus and a sickle-shaped tip of the G1. See Remarks for Luniella, Cyclodius and Pilodius for further comparisons.

Etymology. Luniella gen. n. name is derived from a combination of the Latin word for moon, ‘luna’, and the last five letters of the subfamilies’ type genus, Chlorodiella. ‘Luna’ alludes to the sickle moon-shaped tip of the G1 of these crabs.

Conclusions
The decision to restrict Chlorodiellinae to Chlorodiella, Cyclodius, Pilodius, Luniella gen. n. and Soliella gen. n., while excluding and provisionally considering the other genera as incertae sedis, was made with some hesitation. Given the high support for the Chlorodiellinae s. str. clade and cohesive morphology of this group, it was clear that these genera had to be withdrawn. The problem, then, was the...
unresolved state of many xanthid subfamilial diagnoses, obvious in this molecular analysis with Etisinae and several other subfamilies divided and scattered throughout the xanthid phylogeny. There were two options: treat Tweedicia, Ratbha, Sukodius, Vellodius and Liocarapidus as incertae sedis, or place them tentatively in other subfamilies. The former was chosen as a compromise solution and in concordance with the constrained topology test. This present study advances a more stable framework for chlorodielline classification while advocating future systematic work on this most diverse family of crabs.

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Additional Supporting Information may be found in the online version of this article:

Table S1. List of sequences generated for this study with catalogue and GenBank accession numbers.

Fig. S1. Dorsal habitus of representative chlorodielline s. str. genera: A – Chlorodiella laevissima (Dana, 1852) 6.5 x 3.9 (UF 13733); B – Cyclodius nitidus (Dana, 1852), 23.8 x 14.3 (USNM 154905); C – Cyclodius paumotensis (Rathbun, 1907), holotype, 8.0 x 5.3 (USNM 32852); D – Soliella flava (Rathbun, 1894), 10.2 x 6.9 (USNM 1181377); E – Luniella spinipes (Dana, 1852), 11.4 x 7.4 (USNM 33412); F – Pilobius concors Clark & Galil, 1993, holotype, 62.25 x 42.00 (ZRC 1965.11.11.147).

Fig. S2. Male thoracic sterna and abdomens of representative chlorodielline s. lat. and related genera: A – Luniella spinipes (Dana, 1852), 11.2 x 7.3 mm (SMF 7161); B – Soliella flava (Rathbun, 1894), 10.2 x 6.9 mm (USNM 1181377); C – Velobius etioides (Takeda & Miyake, 1968a), 15.4 x 9.9 mm (ZRC 1998.50); D – Tweedicia odnneri (Gordon, 1934), 11.3 x 7.9 mm (USNM 41260); E – Etius sakaii Takeda & Miyake, 1968b; 10.3 x 8.2 mm (UF 16901); F – Etius anagyptus H. Milne Edwards, 1834, 34.1 x 23.0 mm (USNM 1014269).

Fig. S3. G1s of representative chlorodielline s. str. genera. For each species, arrangement is left to right: internal detail, external detail, and external full. Scale bar measurements presented left to right: A – Cyclodius ungulatus (H. Milne Edwards, 1834) left G1, 200 µm, 200 µm, 1 mm (UF 25663); B – Cyclodius paumotensis (Rathbun, 1907) left G1, 200 µm, 200 µm, 200 µm (UF 15600); C – Soliella flava (Rathbun, 1894) left G1, 200 µm, 200 µm, 1 mm (UF 12254); D – Soliella melanospinis (Rathbun, 1911) left G1, 200 µm, 200 µm, 1 mm (ZRC 2013.1647).

Fig. S4. G1s of representative chlorodielline s. str. genera. For each species, arrangement is left to right: internal detail, external detail, and external full (D is internal detail, lateral left detail, and external full). Scale bar measurements presented left to right: A – Chlorodiella laevissima (Dana, 1852) left G1, 200 µm, 100 µm, 200 µm (UF 13803); B – Pilobius nigrocrinitus (Stimpson, 1858) right G1 (reflected), 200 µm, 200 µm, 1 mm (UF 17075); C – Luniella scabricula (Dana, 1852), right G1 (reflected), 200 µm, 200 µm, 1 mm (UF 1614); D – Luniella spinipes (Heller, 1861), left G1, 200 µm, 200 µm, 1 mm (UF 14361).

Fig. S5. Basal antennal articles of representative chlorodielline s. lat. genera. Scalebar = 1 mm. A–C after Ng & Yang (1998): Fig. A–C: A – Chlorodiella nigra (Forskal, 1775) (ZRC 1998.48); B – Cyclodius ungulatus (H. Milne Edwards, 1834) (ZRC 1965.11.11.16); C – Pilobius granulatus (Stimpson, 1859) (ZRC 1998.49); D – Cyclodius paumotensis (Rathbun, 1907) (ZRC 1999.1221); E – Luniella spinipes (Heller, 1861) (UF 14361); F – Soliella flava (Rathbun, 1894) (UF 12254).

Fig. S6. Bayesian consensus tree inferred from COXI. Catalog numbers and, in some cases, localities are included.

Fig. S7. Bayesian consensus tree inferred from H3. Catalog numbers and, in some cases, localities are included.

Fig. S8. Maximum likelihood tree inferred from H3. Catalog numbers and, in some cases, localities are included.