Molecular phylogeny of porcelain crabs (Porcellanidae: *Petrolisthes* and allies) from the south eastern Pacific: the genera *Allopetrolisthes* and *Liopetrolisthes* are not natural entities (#8341)

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J. Antonio J. Baeza

Porcelain crabs from the closely related genera *Petrolisthes*, *Liopetrolisthes*, and *Allopetrolisthes* are known for their diversity of lifestyles, habitats, and coloration. The evolutionary relationships among the species belonging to these three genera is not fully resolved. A molecular phylogeny of the group may help to resolve the long-standing taxonomic question about the validity of the genera *Allopetrolisthes* and *Liopetrolisthes*. Using both 'total evidence' and single-marker analyses based on a 362-bp alignment of the 16S rRNA mitochondrial DNA and a 328-bp alignment of the Histone 3 nuclear DNA, the phylogenetic relationships among 11 species from *Petrolisthes* (6 species), *Liopetrolisthes* (2 species), and *Allopetrolisthes* (3 species), all native to the south eastern Pacific, were examined. The analyses supported three pairs of sister species: *L. mitra* + *L. paragonicus*, *P. tuberculatus* + *P. tuberculosus*, and *A. angulosus* + *A. punctatus*. No complete segregation of species, according to genera, was evident from tree topologies. Bayesian-factor analyses revealed strong support for the unconstrained tree instead of an alternative tree in which monophyly of the three genera was forced. Thus, the present molecular phylogeny does not support the separation of the species within this complex into the genera *Petrolisthes*, *Liopetrolisthes*, and *Allopetrolisthes*. Taking into account the above and other recent molecular phylogenetic analyses focused on other representatives from the family Porcellanidae, it is tentatively proposed to eliminate the genera *Liopetrolisthes* and *Allopetrolisthes*, and to transfer their members to the genus *Petrolisthes*.

Running title: Molecular phylogeny of *Petrolisthes* and allies

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ABSTRACT

Porcelain crabs from the closely related genera *Petrolisthes*, *Liopetrolisthes*, and *Allopetrolisthes* are known for their diversity of lifestyles, habitats, and coloration. The evolutionary relationships among the species belonging to these three genera is not fully resolved. A molecular phylogeny of the group may help to resolve the long-standing taxonomic question about the validity of the genera *Allopetrolisthes* and *Liopetrolisthes*. Using both 'total evidence' and single-marker analyses based on a 362-bp alignment of the 16S rRNA mitochondrial DNA and a 328-bp alignment of the Histone 3 nuclear DNA, the phylogenetic relationships among 11 species from *Petrolisthes* (6 species), *Liopetrolisthes* (2 species), and *Allopetrolisthes* (3 species), all native to the south eastern Pacific, were examined. The analyses supported three pairs of sister species: *L. mitra* + *L. paragonicus*, *P. tuberculatus* + *P. tuberculosus*, and *A. angulosus* + *A. punctatus*. No complete segregation of species, according to genera, was evident from tree topologies. Bayesian-factor analyses revealed strong support for the unconstrained tree instead of an alternative tree in which monophyly of the three genera was forced. Thus, the present molecular phylogeny does not support the separation of the species within this complex into the genera *Petrolisthes*, *Liopetrolisthes*, and *Allopetrolisthes*. Taking into account the above and other recent molecular phylogenetic analyses focused on other representatives from the family Porcellanidae, it is tentatively proposed to eliminate the genera *Liopetrolisthes* and *Allopetrolisthes*, and to transfer their members to the genus *Petrolisthes*.

Keywords: *Petrolisthes*, *Allopetrolisthes*, *Liopetrolisthes*, phylogeny, half-crab, Chile

INTRODUCTION

Among the Decapoda, crabs from the infraorder Anomura MacLeay, 1838 are renowned for their astounding anatomical, ecological, and behavioral diversity (McLaughlin et al., 2010; Osawa & McLaughlin 2010; Tudge et al., 2012). During the last decade, various phylogenetic studies have supported monophyly of the Anomura, have begun to reveal internal relationships, and they have clarified the position of this clade relative to other major, decapod lineages (Porter et al., 2005; Ahyong et al., 2009; Bracken-Grissom et al., 2013). Recent studies also have uncovered an evolutionary history much more complex than originally recognized (Schnabel et al., 2011; Bracken-Grissom et al., 2013). Furthermore, some systematic studies, combined with behavioral and ecological observations, have exposed the evolutionary basis for most peculiar behaviors and the conditions favoring them (territoriality and vicious agonistic behaviors in *Allopetrolisthes spinifrons*, living in symbiosis with sea anemones - Baeza et al., 2001, 2002; colonization of hydrothermal vents and unique feeding behavior and associated body parts such as bacterophorian setae in the 'yeti crab' *Kiwa hirsuta* - Macpherson et al., 2006; Goffredi et al., 2008; multiple transitions to crab-like forms from hermit crab ancestors - Tsang et al., 2011). Our knowledge of the evolutionary history of anomuran crabs has increased substantially, nevertheless, the internal relationships between many genera and families still remain unknown.

Among anomuran crabs of the superfamily Galatheoidea Samouelle, 1819, one of the most species-rich clades of anomurans, the family Porcellanidae Haworth, 1825 is of particular interest. Crabs from the family demonstrate a considerable diversity of lifestyles, body sizes, habitats, and coloration. More than 280 recognized species (Osawa & McLaughlin, 2010; Osawa & Uyeno, 2013; Werding & Hiller, 2015) inhabit intertidal or shallow subtidal, cold-, warm-temperate, subtropical, and tropical rocky and coral reefs. Some species live in large aggregations, whereas, others remain solitarily within shelters (Antezana et al., 1965; Viviani, 1969; Baeza et al., 1995). Species with cryptic coloration usually dwell under rocks or in crevices, but other, more-colorful species inhabit sea anemones in shallow temperate or tropical reefs (Antezana et al., 1965; Baeza et al., 2001). Some colorful species are traded in the marine aquarium industry (e.g., *Porcellana sayana* - Baeza et al., 2013). The ecological disparity of crabs from this family has already attracted the attention of systematists (Werding et al., 2001; Hiller et al., 2006; Rodriguez et al., 2006; Miranda et al., 2014), evolutionary ecologists (Baeza & Thiel 2003; Baeza & Asorey, 2012), and ecophysiologists (Gebauer et al., 2010; Stillman & Hurt 2015 and references therein). The same diversity suggests that these crabs are ideal model systems to explore the role of environmental conditions in explaining evolutionary innovations in the marine environment. Phylogenetic studies in the family Porcellanidae are warranted because of the implications for evolutionary ecology, conservation biology, and biodiversity.

In the family Porcellanidae, the genus *Petrolisthes* Stimpson, 1858, was originally established to contain various species of porcelain crabs characterized, among other traits, by a rounded or subquadrate carapace, (usually about as broad as long), a triangular or trilobate front often prominent and produced beyond the eyes, a basal segment of the antenna not produced forward to meet the anterior margin of the carapace, either not produced inward, or with a distinct in-ward projection forming a partial suborbital margin, ambulatory legs (pereopods) of moderate length with the propodus bearing movable spinules on the posterior margin and with the dactylus ending in a simple spine, and a telson almost invariably composed of seven plates (Stimpson, 1858; Haig, 1955). The morphology and taxonomic terminology for the group is shown in Suppl. Fig. 1.

Later, Haig (1960) established three new genera, *Allopetrolisthes*, *Liopetrolisthes*, and *Clastotoechus* for a few of the 'most aberrant' species within the genus *Petrolisthes*. The combination of characters setting the genus *Liopetrolisthes*, including the type species *L. mitra*, apart from the closely related *Petrolisthes, Allopetrolisthes*, and *Clastotoechus*, includes a carapace subovate and slightly longer than broad, a front trilobated and strongly produced beyond the eyes, a basal antennal segment lacking a strong anterior projection in contact with the carapace margin, chelipeds small and flattened in relation to the carapace and with the carpus armed with prominent teeth on the anterior margin, and a telson composed of five plates (also, see Weber, 1991). In turn, *Allopetrolisthes* differs from species belonging to the remaining closely related genera in exhibiting a combination of the following traits: a carapace rounded and approximately as broad as long, a trilobate front sometimes with two supplementary smaller lobes, a weak anterior projection of the basal antennal segment, which slightly excludes the movable segments from the orbit, a dactylus of the ambulatory legs very short and with posterior movable spinules absent or greatly reduced in size, and a telson composed of five plates (Haig, 1960).

Haig’s (1960) suggestion was followed by scientists throughout the 20th century, and her view has been supported by recent taxonomical studies and the list of porcellanid species from the world (cf. Osawa & McLaughlin, 2010). On the other hand, based on molecular characters (i.e., a fragment of the 16S mitochondrial rRNA gene), both Stillman & Reeb (2001) and Rodriguez et al. (2006) have shown that the genus *Petrolisthes*, as currently recognized, is paraphyletic on the basis of the nested positions of members from the genera *Allopetrolisthes* and *Liopetrolisthes*, among a few others (i.e., *Clastotoechus*, *Megalobrachium*, and *Parapetrolisthes*). Similarly, the study of larval characters also suggest that the genus

Petrolisthes is paraphyletic and can be subdivided in various natural entities (Osawa, 1995; Wehrtmann et al. 1996; Hernández, 1999; Fujita et al., 2002; Hernández & Magán, 2012) Certainly, additional taxonomic studies are needed to resolve outstanding systematic problems within the family Porcellanidae (Hiller et al., 2006).

This study represents a contribution to the phylogeny of crabs from the genus *Petrolisthes* and two of its closely allied genera (i.e., *Allopetrolisthes, Liopetrolisthes*) restricted to the temperate south eastern Pacific (Fig. 1). I have focused specifically on addressing the hypothesis of monophyly of the three genera above. It was predicted that, a molecular phylogeny of the species included within the three genera should segregate the species into three well-supported monophyletic clades. Based upon the large-subunit, 16S mitochondrial rRNA and the Histone 3 [H3] nuclear DNA, a molecular phylogeny of the species native to the temperate south eastern Pacific is presented in order to approach the goal above.

MATERIAL AND METHODS

TAXON SAMPLING, INGROUPS, AND OUTGROUP TERMINALS

A total of 11 species in the genus *Petrolisthes* (6 species) and the related two genera *Allopetrolisthes* (3 species) and *Liopetrolisthes* (2 species), all of them native to the south eastern Pacific, were included as ingroup terminals in the molecular analyses (Fig 1). Four other species, *Polyonyx gibbesii*, *Megalobrachium soriatum*, *Pachycheles monilifer*, and *Neopisosoma angustifrons*, were also included in the analyses and used as outgroup terminals. Most crab species were collected by the present author off the coast of Chile. Immediately after collection, specimens were preserved in 95–99% ethanol. The different species were identified using Haig (1955; 1960), Viviani (1969), and Weber (1991). For further details of voucher specimens and

GenBank accession information, see Table 1. Altogether, the set of species above was used to reveal the relationship among the genera *Petrolisthes*, *Allopetrolisthes*, and *Liopetrolisthes*.

I also tested for the main hypotheses of monophyly of the genera *Petrolisthes*, *Allopetrolisthes*, and *Liopetrolisthes* (see section HYPOTHESES TESTING OF MONOPHYLETIC CLADES). In total, 22 sequences were generated and 8 other sequences were retrieved from Genebank (Table 1).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total genomic DNA was extracted from pleopods or abdominal muscle tissue using the QIAGEN® DNeasy® Blood and Tissue Kit following the manufacturer's protocol. The polymerase chain reaction (PCR) was used to amplify target regions of one mitochondrial gene (16S [~550 bp] – Schubart et al., 2000) and one nuclear gene (H3 [328 bp] – Colgan et al., 1998). For amplification of the 16S and H3 gene segments, I used the primers 16L2 (5'-TGCCTGTTTATCAAAAACAT -3') and 161472 (5'- AGATAGAAACCAACCTGG -3') (Schubart *et al*., 2000) for the 16S gene fragment, and H3AF (5'- ATG GCT CGT ACC AAG CAG ACV GC-3') and H3AR (5'- ATA TCC TTR GGC ATR ATR GTG AC - 3') for the H3 gene fragment (Colgan et al., 1998), respectively.

Standard PCR 25-µl reactions (17.5 µl of GoTaq® Green Master Mix [Promega®], 2.5 µl each of the two primers [10 mM], and 2.5 µl DNA template) were performed on a Peltier Thermal Cycler (DYAD®) and C1000 Touch™ Thermal Cycler (BIORAD®) under the following conditions: initial denaturation at 95°C for 5 minutes followed by 40 cycles of 95°C for 1 minute, 52-57°C (depending on the species) for 1 minute, and 72°C for 1 min, followed by chain extension at 72°C for 10 min. PCR products were purified with ExoSapIT (a mixture of exonuclease and shrimp alkali phosphatase, Amersham Pharmacia) and then sent for sequencing with the ABI Big Dye Terminator Mix (Applied Biosystems) to the Laboratory of Analytical Biology of the National Museum of Natural History, Smithsonian Institution (LAB – NMNH, Maryland) and to the Clemson University Genomics Institute (CUGI – Clemson University, Clemson. South Carolina), which are equipped with an ABI Prism 3730xl Genetic Analyzer (Applied Biosystems automated sequencer). All sequences were confirmed by sequencing both strands and a consensus sequence for the two strands was obtained using the software Sequencer 5.4.1 (Gene Codes Corp.).

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSES

Alignment of each set of sequences was conducted using Multiple Sequence Comparison by Log-Expectation in MUSCLE (Edgard, 2004) as implemented in MEGA6 (Tamura et al., 2013). The alignment of the H3 gene fragment had no indels and was unambiguous. In contrast, the aligned sequences of the 16S gene fragment did contain several indel 'islands'. Therefore, positions that were highly divergent and poorly aligned in the 16S gene segment were identified using the default settings in the software GBlocks v0.91b (Castresana, 2000), and omitted from the analyses. After highly divergent positions were pruned, the 16S dataset consisted of 362 bp.

The two datasets were first analyzed with the software jModelTest 2 (Darriba et al., 2012), which compares different models of DNA substitution in a hierarchical hypothesis–testing framework to select a base substitution model that best fits the data. For the two gene fragments, the optimal models found by jModelTest 2 (selected with the corrected Akaike Information Criterion [AIC_c]) are shown in Table 2. These models were implemented in MrBayes (Huelsenbeck and Ronquist, 2001) for Bayesian Inference (BI) analysis and GARLI version 2.1

(available at http://www.molecularevolution.org/software/phylogenetics/garli - Bazinet et al., 2014) for maximum likelihood (ML) analysis.

A 'total evidence' analysis (Grant & Kluge, 2003) was conducted and thus the two different alignments were concatenated into a single dataset consisting of 15 sequences and 690 bp. However, the dataset was partitioned into two different segments, each with a different model of evolution. Missing data were designated as a ‘?’ in the alignment. All the parameters used for the ML analysis were those of the default option in GARLI. For BI, unique random starting trees were used in the Metropolis–coupled Markov Monte Carlo Chain (MCMC) (see Huelsenbeck & Ronquist, 2001; Ronquist et al., 2012). The analysis was performed for 6 000 000 generations. Visual analysis of log-likelihood scores against generation time indicated that the log-likelihood values reached a stable equilibrium before the 100 000th generation. Thus, a burn-in of 1000 samples was conducted, every 100th tree was sampled from the MCMC analysis obtaining a total of 60 000 trees and a consensus tree with the 50% majority rule was calculated for the last 59 900 sampled trees. The robustness of the ML tree topology was assessed by bootstrap reiterations of the observed data 2000 times. Support for nodes in the BI tree topology was obtained by posterior probability.

Total evidence analyses enhances the detection of real phylogenetic groups if there is no or minimal heterogeneity among different (e.g., H3 and 16S) datasets (de Queiroz et al., 1995). Therefore, we also conducted separate ML and BI phylogenetic analyses for each gene fragment to reveal any possible discordance in the relationships among the studied species. These phylogenetic analyses using only one gene fragment at a time demonstrated minimal heterogeneity (see results). Thus, the 'total evidence' analysis has the ability to more accurately reflect phylogenetic relationships in this study (see de Queiroz et al., 1995). Total evidence analyses have been used before to infer the phylogeny of many other clades of marine and terrestrial vertebrates and invertebrates, including marine decapods, e.g., in other shrimps (Duffy et al., 2000; Anker & Baeza, 2012; Baeza 2013) and spider crabs (Hultgren & Stachowicz, 2009), among others.

HYPOTHESES TESTING OF MONOPHYLETIC CLADES

I tested if the different species of the genera *Petrolisthes*, *Liopetrolisthes* and *Allopetrolisthes* segregated and formed different genus-specific monophyletic clades. For this purpose, a constrained tree (in which the monophyly of all three genera was enforced) was obtained in MrBayes with the command *constraint*. MCMC searches were run and the harmonic mean of the tree-likelihood value was obtained by sampling the post burn-in, posterior distribution as above. Next, Bayes factors were used to evaluate whether or not there was evidence against monophyly (constrained versus unconstrained trees) according to the criteria of Kass & Raftery (1995). Bayes factors compare the total harmonic mean of the marginal likelihood of unconstrained vs. monophyly-constrained models. A higher value of the Bayes factor statistic implies stronger support against the monophyly of a particular group (Kass & Raftery, 1995). Specifically, a value for the test statistic $2 \log_e(B_{10})$ between 0 and 2 indicates no evidence against H_0; values from 2 to 6 indicate positive evidence against H_0; values from 6 to 10 indicate strong evidence against H_0; and values >10 indicate very strong evidence against H_0 (Kass & Raftery, 1995; Nylander et al., 2004).

RESULTS

The final molecular data matrix was comprised of a total of 690 characters, of which 133 of them are parsimony informative, for a total of 11 ingroup species from the south eastern Pacific pertaining to the genera *Petrolisthes*, *Allopetrolisthes*, and *Liopetrolisthes* and 4 outgroup terminals. Both 'total evidence' molecular phylogenetic trees obtained with different inference methods (ML and BI) resulted in the same general topology (Fig. 2).

In the two 'total evidence' phylogenetic analyses, with the exception of *P. desmarestii*, species from the genera *Petrolisthes, Allopetrolisthes*, and *Liopetrolisthes* clustered together into a single monophyletic clade strongly supported by a high posterior probability obtained from the BI analysis and was well supported by the bootstrap support values from the ML analysis. Within this clade, *P. granulosus* was revealed as sister to all other species of *Petrolisthes* (excluding *P. desmarestii*), *Allopetrolisthes* and *Liopetrolisthes* from the south eastern Pacific. The status of *A. punctatus* and *A. angulosus* as a pair of sister species is well supported by the BI and ML analyses. The tree topology recovered *P. laevigatus* as sister to *A. punctatus* and *A. angulosus*. Nonetheless, the sister relationship above was poorly supported by a low posterior probability obtained from the BI analysis and bootstrap support values from the ML analysis, respectively. Interestingly, *Allopetrolisthes spinifrons* did not cluster together with the two other congeneric species and its position was not well resolved in the two phylogenetic trees.

In the two phylogenetic analyses, two species from the genus *Liopetrolisthes, L. mitra* and *L. patagonicus,* were recovered as well supported sister species. *Petrolisthes violaceus* was recovered as sister to the genus *Liopetrolisthes* with moderate to high support. Lastly, *P. tuberculatus* and *P. tuberculosus* were recovered as sister species with strong support from both ML and BI analyses.

Unexpectedly, *P. desmarestii* did not cluster together with other congeneric species. Indeeed, *P. desmarestii* was recovered as sister to a clade including all the remaining species of *Petrolisthes, Allopetrolisthes*, and *Liopetrolisthes*, and also containing *Polyonyx gibbesi* and *Megalobrachium soriatum*.

Overall, the 'total evidence' phylogenetic analyses demonstrated that species from the genera *Petrolisthes, Allopetrolisthes*, and *Liopetrolisthes* altogether did not segregate according to genera and did not form well-supported, monophyletic clades, as should be expected according to adult morphology. Similarly, the Bayes factor analysis revealed no support for the separation of the studied species into three different genera (*Petrolisthes, Allopetrolisthes*, and *Liopetrolisthes*). Comparisons of the unconstrained tree (harmonic mean = -3496.7) *versus* the tree wherein *Petrolisthes, Allopetrolisthes*, and *Liopetrolisthes* were imposed as monophyletic clades (harmonic mean = -3402.17), indicated strong support for the unconstrained tree ($2\ln(B_{10}) = 9.09$).

Phylogenetic trees obtained with ML and BI using only a single, either mitochondrial (16S) or nuclear (H3), marker resulted in similar general topologies (Fig. 3, 4). As expected, these single-marker phylogenetic trees were less resolved than those produced by the 'total evidence' ML and BI phylogenetic analyses. Nonetheless, the single-gene analyses retrieved various monophyletic clades observed in the 'total evidence' analyses described above. For instance, in both the ML and BI trees based on the 16S and H3 gene fragments, both *L. mitra* and *L. patagonicus*, and *A. angulosus* and *A. punctatus*, were well supported as sister species. Also, *P. desmarestii* was recovered as sister to a clade including all the remaining species of *Petrolisthes, Allopetrolisthes*, and *Liopetrolisthes*, but also containing *Polyonyx gibbesi* and *Megalobrachium soriatum* (Fig. 3, 4).

DISCUSSION

This study presents a two-locus molecular phylogeny of crabs from the genera *Petrolisthes, Liopetrolisthes,* and *Allopetrolisthes*. This pool of species represents the totality of the members from the genus *Petrolisthes* and allies (*Allopetrolisthes* and *Liopetrolisthes*) native to the south eastern Pacific (Haig, 1960; Viviani, 1969; Weber, 1991). The analyses with two different phylogenetic reconstruction methods recognized only one monophyletic group consisting of two species of *Liopetrolisthes* (*L. mitra* and *L. patagonicus*) and also supported two members from the genus *Allopetrolisthes* as sister species (*A. angulosus* and *A. punctatus*). The positions of *A. spinifrons*, the remaining congeneric species, was not well resolved. In disagreement with hypotheses based solely upon adult morphology (e.g., Haig, 1960), a well-resolved grouping of all of the species belonging to a particular genus and segregation of species from different genera was not revealed by our analyses. Also, Bayesian factors analyses strongly supported unconstrained trees over trees in which monophyly of *Petrolisthes, Liopetrolisthes,* and *Allopetrolisthes* was imposed. Overall, the present results do not support the separation of these species into three different genera as proposed by Haig (1960) that was based upon adult morphology alone. Instead, the present study agrees with previous larval and molecular phylogenetic studies indicating that the division of *Petrolisthes, Liopetrolisthes,* and *Allopetrolisthes*, within the Porcellanidae is not natural (Osawa, 1995; Wehrtmann et al. 1996; Hernández, 1999; Fujita et al., 2002; Stillman & Reeb, 2001; Rodriguez et al., 2006; Hernández & Magán, 2012). This study argues in favor of future phylogenetic studies using various types of evidence (molecular, adult morphology, larval anatomy) to improve our knowledge of the natural relationships within these species/genera complex and their position in the Porcellanidae.

The set of species considered in the present study allows a few relevant systematic questions for the group to be addressed. For instance, the two species from the genus *Liopetrolisthes*, *L. mitra* and *L. patagonicus*, clustered together and formed a well supported monophyletic group. *Liopetrolisthes mitra* inhabits the body surface of the black sea urchin *Tetrapygus niger* from Ancon, Peru (~11.8º S latitude) to Bahia San Vicente, Chile (~36º S latitude) while *L. patagonicus* dwells among the spines of the red sea urchin *Loxechinus albus* from Ancon, Peru (~11.8º S latitude) to the strait of Magellan, Chile (~54º S latitude) (Weber, 1991). This suggests that the genus *Liopetrolisthes* likely diversified in the south eastern Pacific via sympatric or micro-allopatric speciation. It remains to be addressed whether or not speciation in the genus *Liopetrolisthes* was host-driven. Importantly, although the genus *Liopetrolisthes* represents a natural clade in the present phylogenetic analyses, its generic status, different from *Petrolisthes*, is not supported as they clustered within a clade including other members from the genus *Petrolisthes* (also, see below).

The present study also retrieved *P. tuberculosus* and *P. tuberculatus* as a single well supported monophyletic clade. The close relationship between the two species was recognized early on by Ortmann (1897) who named them as belonging to the 'Gruppe des *Petrolisthes tuberculatus*', a view supported by Haig (1960). The two species are characterized by a strongly trilobate front, two narrow lobes that project strongly from the anterior margin of the basal segment of the antennule, and a row of uneven, serrate teeth on the anterior margin of the cheliped carpus (Haig, 1960; Viviani, 1969). Given the particular distinctiveness of the two species, Haig (1960) suggested that they should form a separate genus or subgenus. However, at present, it seems inadvisable to split *P. tuberculosus* and *P. tuberculatus* from the remaining species in the genus until *Petrolisthes* can be studied on a worldwide basis.

Lastly, unexpectedly, *P. desmarestii*, the largest known species of porcelain crab (Haig, 1960; Antezana et al., 1965), did not cluster together with the other congeneric representatives included in this study. *Petrolisthes desmarestii* was recovered as sister to a clade that included *Petrolisthes, Allopetrolisthes*, *Liopetrolisthes* as well as *Polyonyx gibbesi* and *Megalobrachium soriatum*. The clustering of *P. desmarestii* with members from the genera *Polyonyx* and *Megalobrachium* likely results from incomplete taxon sampling in Porcellanidae. Nonetheless, *Petrolisthes desmarestii* is unique among other congeneric representatives from the south eastern Pacific because of the carapace, covered with fine plications, the presence of a single epibranchial spine on the carapace, a triangular front, a carpus of the cheliped with four or five broad, serrate-edged teeth on the anterior margin, and a manus covered with small flattened tubercles (Haig, 1960). The traits above, in particular, the presence of an epibranchial spine on the carapace, teeth on the anterior margin of the cheliped carpus, and the postero-distal spines on the merus of the first ambulatory pereopod, suggest that *P. desmarestii* belongs to either the 'Gruppe des *Petrolisthes galathinus*' or 'Gruppe des *Petrolisthes lamarcki*' recognized by Ortmann (1897), both containing more than twenty species in the eastern Pacific and western Atlantic (Haig, 1960; Hiller et al., 2006). A preliminary molecular phylogenetic analysis based on the 16S mtDNA ribosomal gene (Bayesian inference, 95 terminals, GTR+G model, not shown here) provides support for the close relationship between *P. desmarestii* and members from the *P. galathinus* species complex. The above suggests more than a single colonization event in the south eastern Pacific during the evolutionary history of porcelain crabs.

In general, this study has shown that the separation of *Petrolisthes* + *Allopetrolisthes* + *Liopetrolisthes* into three taxonomic entities is not natural based on molecular characters of the studied species set. Crabs from these three genera demonstrate a considerable diversity of lifestyles, body sizes, microhabitats, and coloration (Haig, 1960; Antezana et al., 1965; Baeza & Thiel, 2003; 2007). Studies describing the life history and ecology of *Petrolisthes, Allopetrolisthes,* and *Liopetrolisthes* within a phylogenetic framework are underway (e.g., Baeza & Thiel 2003; Baeza & Asorey, 2012; Gebauer et al., 2010; Stillman & Hurt 2015). This approach is expected to prove most useful in understanding the role of environmental conditions in driving the evolution of morphological, ecological, and behavioral traits in the marine environment (e.g., Baeza & Thiel, 2003; Baeza & Asorey, 2012). The present study included only porcellanid species from the south eastern Pacific; nevertheless, the amphi-American nature of *Petrolisthes* and allies (see Haig, 1960) suggests that this group might also be a model to study speciation mechanisms, as in other transisthmian clades of fish (Bermingham et al., 1997), sea urchins (Lessios, 2008), caridean shrimps (Williams et al., 2001), and brachyuran crabs (Windsor and Felder 2014).

PROPOSAL OF A PHYLOGENETIC REARRANGEMENT

Taking into account the discussion above and recent molecular phylogenetic analyses focused on other representatives from the family Porcellanidae (i.e., Weber, 1991; Rodriguez et al., 2006; Stillman & Reeb, 2006; Hiller et al., 2006), the following taxonomic rearrangement is tentatively proposed for the south eastern Pacific species hitherto belonging to the genera *Allopetrolisthes* and *Liopetrolisthes*.

Family Porcellanidae Haworth, 1825
Petrolisthes Stimpson 1858
Petrolisthes angulosus (Guérin, 1835)

Petrolisthes punctatus (Guérin, 1835)

Petrolisthes spinifrons (H. Milne Edwards, 1837)

Petrolisthes mitra (Dana 1852)

Petrolisthes patagonicus (Cunningham, 1871)

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FIGURES

Fig. 1. Species in the genera *Petrolisthes* (6 species) and the related genera *Allopetrolisthes* (3 species) and *Liopetrolisthes* (2 species), all of them native to the south eastern Pacific. a. *Allopetrolisthes spinifrons*, b. *Petrolisthes tuberculosus*, c. *Allopetrolisthes angulosus*, d. *Liopetrolisthes mitra*, e. *Liopetrolisthes patagonicus*, f. *Petrolisthes granulosus*, g. *Petrolisthes desmarestii*, h. *Petrolisthes tuberculatus*, i. *Petrolisthes laevigatus*, j. *Petrolisthes violaceus*, k. *Allopetrolisthes punctatus*.

Fig. 2. 'Total evidence' phylogenetic tree obtained from BI analysis of the partial mitochondrial 16S rRNA and nuclear Histone 3 genes for crabs from the *Petrolisthes* - *Allopetrolisthes* - *Liopetrolisthes* species complex, and other selected taxa from the family Porcellanidae. Numbers above and/or below the branches represent the posterior probabilities from the BI analysis in MrBayes and bootstrap values obtained from ML in GARLI (ML/BI). The general topology of the trees obtained from MP and ML analyses was the same. The inset shows a juvenile of *Liopetrolisthes mitra* after Meredith (1939).

Fig. 3. Phylogenetic tree obtained from ML analysis of the partial nuclear Histone 3 gene for crabs from the *Petrolisthes* - *Allopetrolisthes* -*Liopetrolisthes* species complex, and other selected taxa from the family Porcellanidae. Numbers above and/or below the branches represent the posterior probabilities from the BI analysis in MrBayes and bootstrap values obtained from

ML in GARLI (ML/BI). The general topology of the trees obtained from MP and ML analyses was the same.

Fig. 4. Phylogenetic tree obtained from ML analysis of the partial mitochondrial 16S rRNA and nuclear Histone 3 genes for crabs from the *Petrolisthes* - *Allopetrolisthes* -*Liopetrolisthes* species complex, and other selected taxa from the family Porcellanidae. Numbers above and/or below the branches represent the posterior probabilities from the BI analysis in MrBayes and bootstrap values obtained from ML in GARLI (ML/BI). The general topology of the trees obtained from MP and ML analyses was the same.

SUPPLEMENTARY FIGURES

Suppl. Fig. 1. Morphology and taxonomic terminology in porcelain crabs from the genus *Petrolisthes* and allies. A. Crab habitus in dorsal view. B. Ambulatory leg (pereopod). C. Antenna. D. Cheliped. Modified from Osawa & Chan (2010).

Table 1. *Mithrax - Mithraculus* species and other porcelain crabs used for the phylogeny reconstruction. The museum catalogue number and the Genbank accession numbers (GenBank) are shown for each species (NA = not available).

Species	CN	16S Genbank N	H3 GenBank N
Allopetrolisthes angulosus	CU.CC.2016-01-01	AF260609	KU641128
Allopetrolisthes punctatus	CU.CC.2016-01-06	AF260615	KU641133
Allopetrolisthes spinifrons	CU.CC.2016-01-07	AF260617	KU641134
Liopetrolisthes mitra	CU.CC.2016-01-04	KU641139	KU641131
Liopetrolisthes patagonicus	CU.CC.2016-01-05	KU641140	KU641132
Petrolisthes desmarestii	CU.CC.2016-01-11	KU641141	KU641138
Petrolisthes granulosus	CU.CC.2016-01-02	AF260613	KU641129
Petrolisthes laevigatus	CU.CC.2016-01-03	AF260606	KU641130
Petrolisthes tuberculatus	CU.CC.2016-01-08	AF260607	KU641135
Petrolisthes tuberculosus	CU.CC.2016-01-09	AF260618	KU641136
Petrolisthes violaceus	CU.CC.2016-01-10	HM352469	KU641137
Megalobrachium soriatum	ULLZ 5262	DQ865325	JF900738
Neopisosoma angustifrons	ULLZ 5373	DQ865336	JF900752
Pachycheles monilifer	ULLZ 5348	DQ865331	JF900750
Polyonyx gibbesi	NA	DQ865341	JF900736

Table 2. Molecular markers including informative sites and maximum likelihood (ML) models selected through AICc criterion as implemented in jModelTest2. Base frequencies, rate matrix, and gamma shape parameters resulting from jModelTest2 are shown.

	Gene Fragment	
	H3	16S
Total sites	328	362
Informative sites	50	83
Model	GTR+G	TVM+G
Base frequency		
%A	0.2234	0.3507
%C	0.3116	0.1255
%G	0.2684	0.1903
%T	0.1966	0.3336
Rate matrix		
[A-C]	1.3411	0.5967
[A-G]	4.4940	8.6307
[A-T]	4.1603	3.0555
[C-G]	0.6098	0.0001
[C-T]	10.6755	8.6307
[G-T]	1.0000	1.000
Shape parameter	0.1780	0.2770

Figure 1(on next page)

Species in the genera *Petrolisthes* (6 species) and the related genera *Allopetrolisthes* (3 species) and *Liopetrolisthes* (2 species), all of them native to the south eastern Pacific.

a. *Allopetrolisthes spinifrons*, b. *Petrolisthes tuberculosus*, c. *Allopetrolisthes angulosus*, d. *Liopetrolisthes mitra*, e. *Liopetrolisthes patagonicus*, f. *Petrolisthes granulosus*, g. *Petrolisthes desmarestii*, h. *Petrolisthes tuberculatus*, i. *Petrolisthes laevigatus*, j. *Petrolisthes violaceus*, k. *Allopetrolisthes punctatus*.

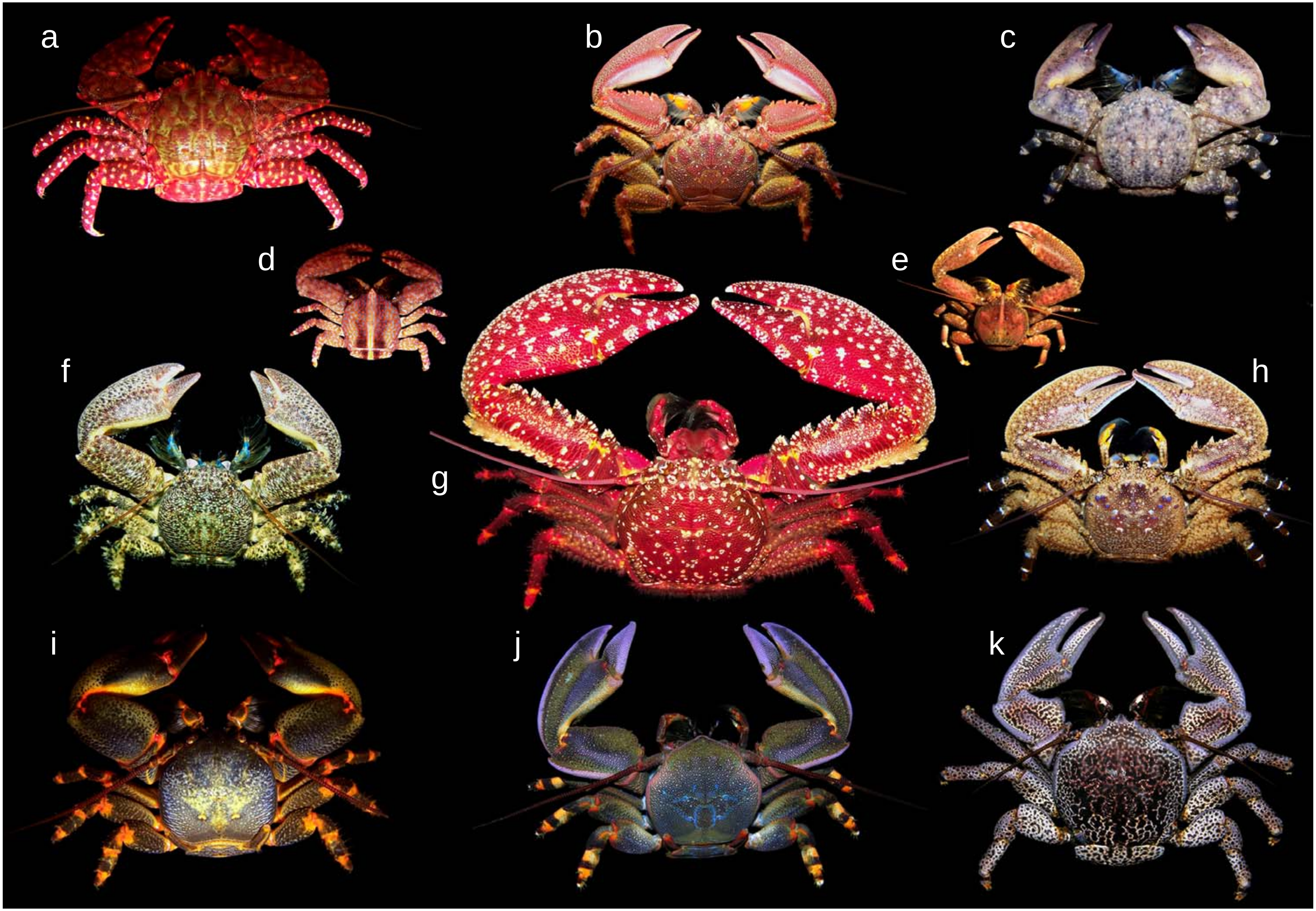
a
b
c
d
e
f
g
h
i
j
k

Figure 2(on next page)

Fig. 2. 'Total evidence' phylogenetic tree obtained from BI analysis of the partial mitochondrial 16S rRNA and nuclear Histone 3 genes for crabs from the *Petrolisthes* and allies.

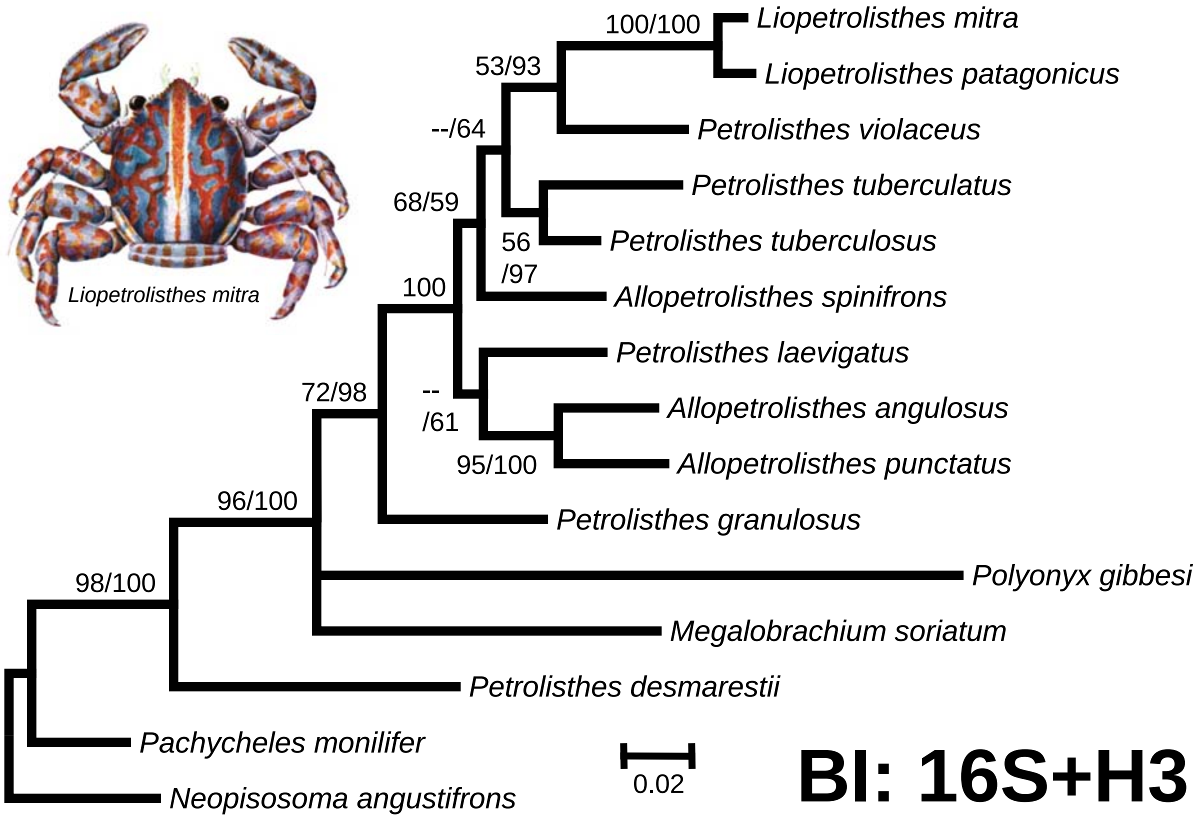
Liopetrolisthes mitra
100/100
Liopetrolisthes mitra
Liopetrolisthes patagonicus
53/93
Petrolisthes violaceus
--/64
Petrolisthes tuberculatus
68/59
56
/97
Petrolisthes tuberculosus
100
Allopetrolisthes spinifrons
Petrolisthes laevigatus
72/98
--
/61
Allopetrolisthes angulosus
95/100
Allopetrolisthes punctatus
96/100
Petrolisthes granulosus
98/100
Polyonyx gibbesi
Megalobrachium soriatum
Petrolisthes desmarestii
Pachycheles monilifer
0.02
Neopisosoma angustifrons
BI: 16S+H3

Figure 3(on next page)

Phylogenetic tree obtained from ML analysis of the partial nuclear Histone 3 gene for crabs from the *Petrolisthes* species complex, and other selected taxa from the family Porcellanidae.

Numbers above and/or below the branches represent the posterior probabilities from the BI analysis in MrBayes and bootstrap values obtained from ML in GARLI (ML/BI). The general topology of the trees obtained from MP and ML analyses was the same.

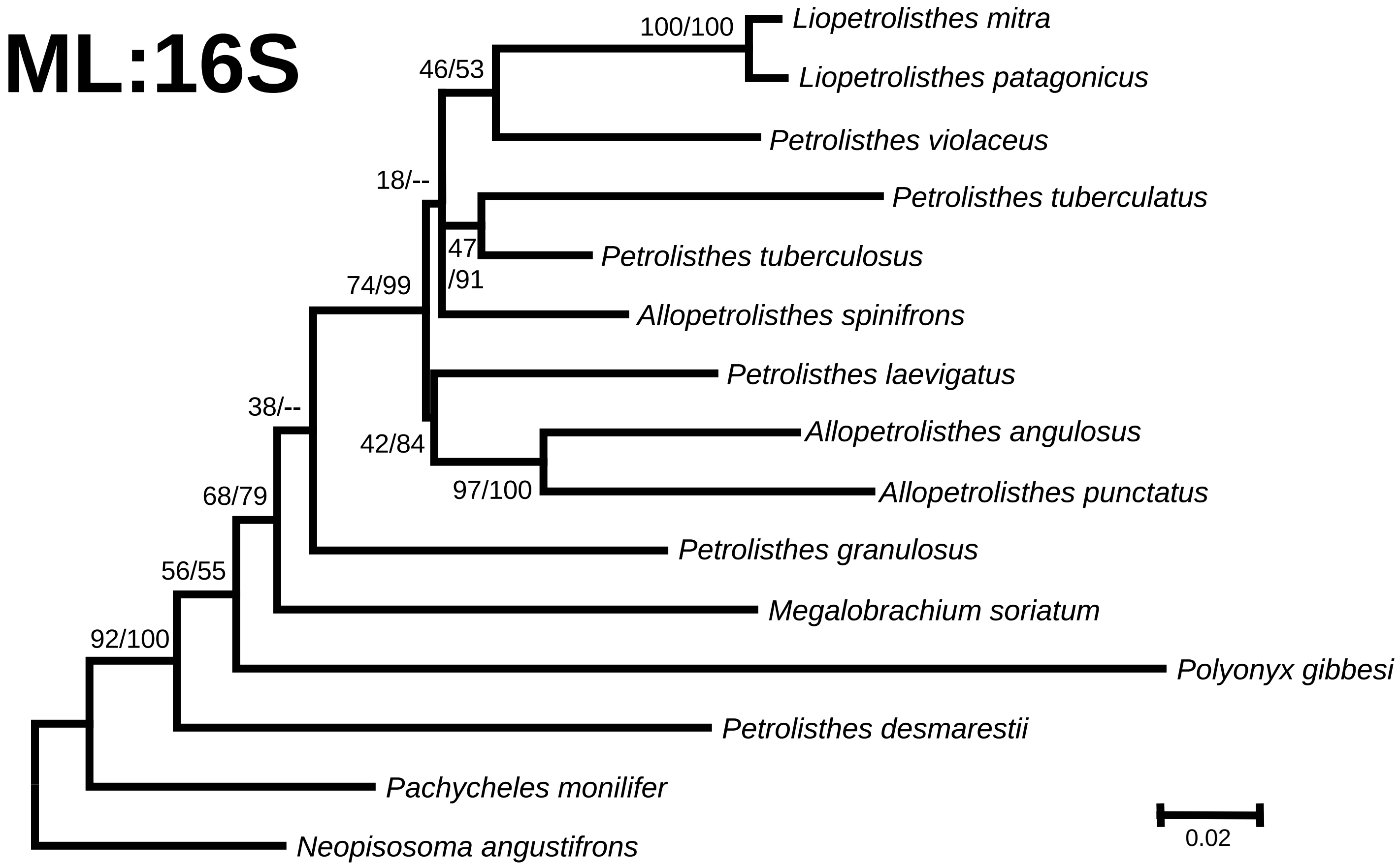
ML:16S
100/100
Liopetrolisthes mitra
Liopetrolisthes patagonicus
46/53
Petrolisthes violaceus
18/--
Petrolisthes tuberculatus
47
/91
Petrolisthes tuberculosus
74/99
Allopetrolisthes spinifrons
Petrolisthes laevigatus
38/--
Allopetrolisthes angulosus
42/84
97/100
Allopetrolisthes punctatus
68/79
Petrolisthes granulosus
56/55
Megalobrachium soriatum
92/100
Polyonyx gibbesi
Petrolisthes desmarestii
Pachycheles monilifer
Neopisosoma angustifrons
0.02

Figure 4(on next page)

Phylogenetic tree obtained from ML analysis of the mitochondrial 16S rRNA and nuclear Histone 3 genes for crabs from the *Petrolisthes* and other selected taxa from the family Porcellanidae

Numbers above and/or below the branches represent the posterior probabilities from the BI analysis in MrBayes and bootstrap values obtained from ML in GARLI (ML/BI). The general topology of the trees obtained from MP and ML analyses was the same.

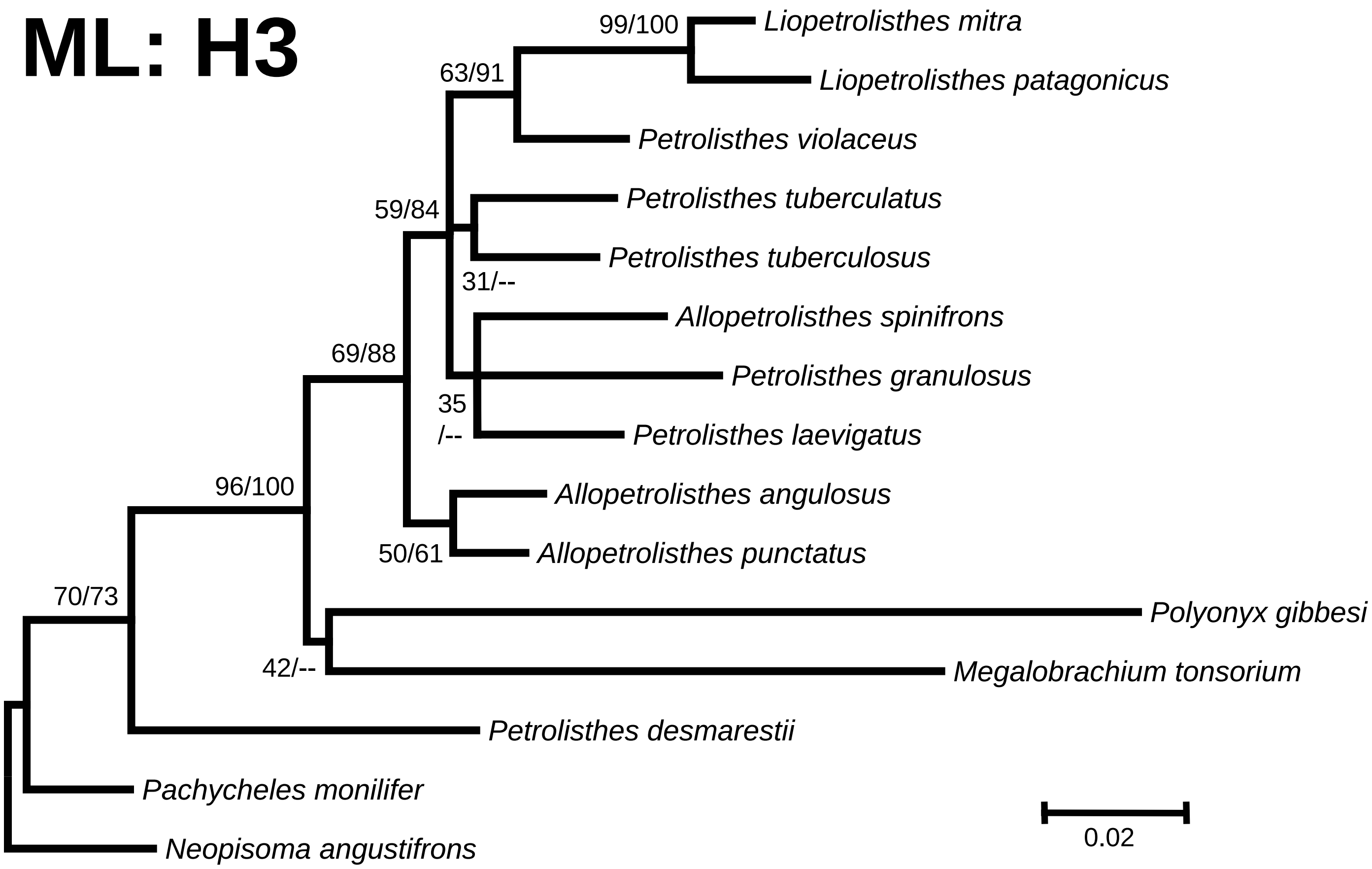
ML: H3
99/100
Liopetrolisthes mitra
Liopetrolisthes patagonicus
63/91
Petrolisthes violaceus
59/84
Petrolisthes tuberculatus
Petrolisthes tuberculosus
31/--
Allopetrolisthes spinifrons
69/88
Petrolisthes granulosus
35
/--
Petrolisthes laevigatus
96/100
Allopetrolisthes angulosus
50/61
Allopetrolisthes punctatus
70/73
Polyonyx gibbesi
42/--
Megalobrachium tonsorium
Petrolisthes desmarestii
Pachycheles monilifer
Neopisoma angustifrons
0.02

Table 1(on next page)

Table 1. Mithrax - Mithraculus species and other porcelain crabs used for the phylogeny reconstruction.

The museum catalogue number and the Genbank accession numbers (GenBank) are shown for each species (NA = not available).

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Species	CN	16S Genbank N	H3 GenBank N
Allopetrolisthes angulosus	CU.CC.2016-01-01	AF260609	KU641128
Allopetrolisthes punctatus	CU.CC.2016-01-06	AF260615	KU641133
Allopetrolisthes spinifrons	CU.CC.2016-01-07	AF260617	KU641134
Liopetrolisthes mitra	CU.CC.2016-01-04	KU641139	KU641131
Liopetrolisthes patagonicus	CU.CC.2016-01-05	KU641140	KU641132
Petrolisthes desmarestii	CU.CC.2016-01-11	KU641141	KU641138
Petrolisthes granulosus	CU.CC.2016-01-02	AF260613	KU641129
Petrolisthes laevigatus	CU.CC.2016-01-03	AF260606	KU641130
Petrolisthes tuberculatus	CU.CC.2016-01-08	AF260607	KU641135
Petrolisthes tuberculosus	CU.CC.2016-01-09	AF260618	KU641136
Petrolisthes violaceus	CU.CC.2016-01-10	HM352469	KU641137
Megalobrachium soriatum	ULLZ 5262	DQ865325	JF900738
Neopisosoma angustifrons	ULLZ 5373	DQ865336	JF900752
Pachycheles monilifer	ULLZ 5348	DQ865331	JF900750
Polyonyx gibbesi	NA	DQ865341	JF900736

Table 2(on next page)

Table 2. Molecular markers including informative sites and maximum likelihood (ML) models selected through AICc criterion as implemented in jModelTest2.

Base frequencies, rate matrix, and gamma shape parameters resulting from jModelTest2 are shown.

Table 2. Molecular markers including informative sites and maximum likelihood (ML) models selected through AICc criterion as implemented in jModelTest2. Base frequencies, rate matrix, and gamma shape parameters resulting from jModelTest2 are shown.

	Gene Fragment	
	H3	16S
Total sites	328	362
Informative sites	50	83
Model	GTR+G	TVM+G
Base frequency		
%A	0.2234	0.3507
%C	0.3116	0.1255
%G	0.2684	0.1903
%T	0.1966	0.3336
Rate matrix		
[A-C]	1.3411	0.5967
[A-G]	4.4940	8.6307
[A-T]	4.1603	3.0555
[C-G]	0.6098	0.0001
[C-T]	10.6755	8.6307
[G-T]	1.0000	1.000
Shape parameter	0.1780	0.2770