## ARTICLE IN PRESS

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# Characterisation of the complete mitochondrial genome of *Helice wuana* (Grapsoidea: Varunidae) and comparison with other Brachyuran crabs

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#### ABSTRACT

The mitochondrial genome (mitogenome) provides important information for phylogenetic analysis and understanding evolutionary origins. Herein, we sequenced, annotated, and characterised the mitogenome of the crab *Helice wuana* to better understand its molecular evolution and phylogeny. The 16,359 bp mitogenome includes 13 protein-coding genes (PCGs), 22 transfer RNA (tRNA) genes, two ribosomal RNA (rRNA) genes and one control region. The genome composition is highly A + T biased 68.42%, and exhibits a negative AT–skew (-0.036) and GC–skew (-0.269) among Brachyura crabs. Gene rearrangements were detected, as was tandem duplication followed by random loss, which explains the translocation of mitochondrial genes. Phylogenetic analysis showed that *H. wuana* and *H. tientsinensis* clustered on one branch with high nodal support values. These results confirm that the placement of *H. wuana* within the Varunidae family of Thoracotrematan crabs. This study will provided a better understanding for gene rearrangements and crab evolution in the further.

#### 1. Introduction

Decapoda is an economically important order of crustaceans comprising 18,000 living and extinct species [1], such as freshwater crayfish, lobsters, hermit crabs, shrimps, and 'true' crab [2]. Decapoda is the most species-rich, abundant, visible, popular, and economically important order of crustaceans, supporting seafood and marine industries worth billions of dollars each year to the world economy. Traditionally, Decapoda are divided into Dendrobranchiata and Pleocyemata sub-orders, and the Brachyura infra-order, belonging to Pleocyemata, is among the most diverse group, with over 7000 described species in 98 families inhabiting marine, freshwater, and terrestrial habitats [3-6]. Brachyura, the true crabs, is the largest clade Decapod Crustacea [7,8]. Due to the extreme morphological and ecological diversity, phylogenetic relationships within Brachyura are complicated [9]. The Grapsoidea crab, belonging to the higher taxa in the classification system, appeared late in the evolution of crustaceans, multiplied in the Tertiary period of the Cenozoic era, and gradually became dominant. Helice wuana is a mudflat crab inhabiting Chinese coastal regions including Guangdong, Fujian, Jiangsu, and Shandong peninsulas, and the Gulf of Bohai and Liaotung [2,10]. It is also common in North Korea and Japan. H. wuana burrows in intertidal mudflats, swamps, salt marshes and

estuaries, especially in the high intertidal and supralittoral zones [10,11]. It is semi-terrestrial, returning to sea to spawn [12]. *H. wuana* also has a salinity requirement which lies between those of two other estuarine crabs in Japan, *Helicana japonica* and *Chiromantes dehaani* [13]. *H. wuana* is one of the most economically important crustacean species in aquaculture in China.

In metazoans, the mitochondrial genome (mitogenome) is usually small (~14-16 kb) and contains 13 protein-coding genes (PCGs), 22 transfer RNA genes (tRNAs), two ribosomal RNA genes (rrnS and rrnL) and a control region [14]. In animals, the mitochondrial control region is the only non-coding sequence in the mitogenome, and it is called Dloop region in vertebrates and the A + T-rich region in invertebrate [15,16]. The control region contains initiation sites for transcription and replication. With the development of sequencing technologies, complete mitogenomes can now be rapidly sequenced to investigate phylogenetic matters. Besides being used for reconstruction of phylogenetic relationships, complete mitogenomes can also provide information on gene rearrangements and nucleotide bias [17]. Mitogenome sequences are now widely used in population genetics, comparative and evolutionary genomics, reconstruction of phylogenetic relationships, and molecular evolutionary research [18-21]. Numerous analyses of Decapoda have been published based on molecular from the

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Details of the primers used to amplify the mitogenome of H. wuana.

Primer	Sequence (5'-3')	Annealing temperature	Location	Length (bp)
F1	GGTCAACAAATCATAAAGATATTGG	55 °C	cox1	698
R1	TAAACTTCAGGGTGACCAAAAAATCA		cox1	
F2	TAGTWATHAANGGHCTACGVTGRGG	50 °C	cox3	388
R2	AAGTCCRTGRAAYCCDGTDGCHAC		cox3	
F3	GTGCCAGCCGCCGCGGTTA	52 °C	rrnS	568
R3	ATGCACTTTCCAGTACATCTA		rrnS	
F4	CCHTGAGGHCAAATRTCHTTYTGAGG	49 °C	cob	477
R4	GCDATWACTCCTCCTARTTTRTTRGG		cob	
F5	AGTAGAAAGAGGAGTAGGCACA	57 °C	cox1 - cox3	3421
R5	CTGAATCGGCAATAGTAAAA		cox1 - cox3	
F6	TTACTATTGCCGATTCAGTT	56 °C	cox3 - rrnS	3788
R6	GAATCTTACTTGCCTTTGTA		cox3 - rrnS	
F7	TACAAAGGCAAGTAAGATTC	60 °C	rrnS - cob	7012
R7	AAAGTAAAGTAAGGGTGGAA		rrnS - cob	
F8	CCCATTTATCGGGACTGACTTG	58 °C	cob - cox1	2632
R8	GTAGTAAGAGGATGGCGGTAAT		cob - cox1	

Table 2

List of 49 Brachyura species analyzed in this paper with their GenBank accession numbers.

Helics institutionsGrapoides/Varnuklae16,212KN33555Urblics institutions is dramsGrapoides/Varnuklae16,300UN24273Drichchr japonica is dramsGrapoides/Varnuklae16,335EV516998Drichchr japonica is dramsGrapoides/Varnuklae16,335EV516998Drichchr japonica is dramsGrapoides/Searnuklae16,335EV516998Drichchr japonica is dramsGrapoides/Searnuklae15,305KN15994Parsacamar tripectmisGrapoides/Searnuklae15,612KN15994Parsacamar tripectmisGrapoides/Searnuklae15,612KN15994Parsacamar tripectmisGrapoides/Searnuklae15,656KN118277Chrocoedom sinnsisGrapoides/Searnuklae15,658KN15994Parsacamar tripectmisGrapoides/Grapidae15,568KN159941Chrocoedom sinnsisGrapoides/Grapidae15,551MY56127Grapoides/Grapidae15,551MY56127MY56127Grapoides/Grapidae15,551MY56127MY56127Androgues trausingNatholides/Krongrapidae15,588KX599943Lapdatis anguineusNatholides/Dortunidae15,628KX599943Lapdatis anguineusNatholides/Dortunidae15,628KX5991943Lapdatis anguineusPortunoides/Dortunidae15,628KX5991943Lapdatis anguineusNatholides/Dortunidae15,628KX59924Partans grapisNatholides/Dortunidae15,628KX59924Partans grapisPortunoides/Dortunidae15,628KX5	Species	Taxonomic position	Size (bp)	GenBank No.
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Nenograpsic sextufnatusXenograpside15,798EU72703Pseudocarcinus gigasXanthoides,Eriphilae15,515AY562127Myomenippe fornasiniXanthoides,Kenippidae15,658Li230143Leptodius sanguineusNanthoides,Xenthidae15,620AY363392Callinectes sighidusPortunoidea,Portunidae16,026AB093006Portunus triuberculatusPortunoidea,Portunidae16,024KT385674Callinectes sighidusPortunoidea,Portunidae15,738EP460517Scylla paranamosainPortunoidea,Portunidae15,723FJ4257150Scylla paranamosainPortunoidea,Portunidae15,723FJ827759Scylla tranqueboricaPortunoidea,Portunidae15,757FJ827758Scylla tranqueboricaPortunoidea,Portunidae15,767KJ827759Scylla tranqueboricaPortunoidea,Portunidae15,767KJ827758Charpohis firataPortunoidea,Portunidae15,775KJ827758Charpohis firataPortunoidea,Portunidae15,767KM97882Chacon granulatusPortunoidea,Portunidae15,126KM97883Chaccon granulatusPortunoidea,Portunidae15,126KM97883Chaccon granulatusPortunoidea,Portunidae15,126KM95084Romino des,Raninidae15,126KM95084KA05084Romino des,Raninidae15,126KM95084Romino des,Raninidae15,631L005058Chacon granulatusBythograeoidea,Bythograeidae15,641L0035566Austinograe alor	Grapsus tenuicrustatus	Grapsoidea;Grapsidae	15,858	KT878721
Perdocarcinus gigasXanthoides,Eriphidae15,515AY562127Myomenippe fornasinitXanthoides,Eriphidae15,658LK301943Leptodius sanguineusXanthoides,Xanthidae15,480KT896744Callinectes sapidusPortunoidea,Portunidae16,263AY363392Portunus is unguinolenusPortunoidea,Portunidae16,024KT438509Charydas iponicaPortunoidea,Portunidae15,738KT438509Charydas iponicaPortunoidea,Portunidae15,733KT435509Scylla paronanosainPortunoidea,Portunidae15,733KT435750Scylla serataPortunoidea,Portunidae15,633FJ827759Scylla serataPortunoidea,Portunidae15,660KT386147Thalamita crenataPortunoidea,Portunidae15,767KS9187758Charydas ipriataPortunoidea,Portunidae15,787KS91833Chacon granulatusPortunoidea,Portunidae16,157KM977882Chacon granulatusPortunoidea,Portunidae16,126KM978833Chacon granulatusPortunoidea,Raninidae16,563KM85684Lanio arcinatasRaninoidea,Raninidae15,563KM85684Lanio arcinatasBythograeoidea,Bythograeidea15,561J005566Oxpode cordinamasOxpodoidea,Oxpodidae15,561LM96333Chacon granulatusBythograeoidea,Bythograeidea15,561LM963566Lanio arcinatasBythograeoidea,Bythograeidea15,561LM963566Oxpode cordinamasOxpodoidea,Oxpodidae15,604 <td>Xenograpsus testudinatus</td> <td>Xenograpsoidea;Xenograpsidae</td> <td>15,798</td> <td>EU727203</td>	Xenograpsus testudinatus	Xenograpsoidea;Xenograpsidae	15,798	EU727203
Myonerippe formasinitXanthoidea;Menippidae15,658LK391943Leptodius sanguineusXanthoidea;Xanthidae15,640KT996744Callinectes sapidusPortunoidea;Portunidae16,026Ab093006Portunus triubercultatusPortunoidea;Portunidae16,024KT39509Charybdis iponicaPortunoidea;Portunidae15,738FJ40517Scylla pramosoinPortunoidea;Portunidae15,738FJ40517Scylla pramosoinPortunoidea;Portunidae15,738FJ40517Scylla tranquebaricaPortunoidea;Portunidae15,733FJ827759Scylla tranquebaricaPortunoidea;Portunidae15,775FJ827759Scylla tranquebaricaPortunoidea;Portunidae15,775KJ827789Charybdis feriataPortunoidea;Portunidae15,787KK991945Portunoidea;Portunidae15,787KK991945Portunoidea;Geryonidae16,157KM977882Chacon granulatusPortunoidea;Geryonidae16,126KV95798Lyreidus brevifronsRaninoidea;Raninidae15,661KM35084Raninoidea;Raninidae15,663KM198917Gandalfus puiaRaninoidea;Raninidae15,664KM35084Raninoidea;Raninidae15,654KU199738Lyreidus brevifronsBythograeoidea;Bythograeidae15,654KU199738Chacon granulatusCycpodoidea;Oxypodidae15,654KM35084Raninoidea;Raninidae15,604KT395084Raninoidea;Raninidae15,610J0035686Ocypodoidea;Oxypodidae<	Pseudocarcinus gigas	Xanthoidea;Eriphiidae	15,515	AY562127
I-products anguineasXanthidae15,480RT896744Callinectes saguitusPortunoidea;Portunidae16,263AY363392Portunus tituberculatusPortunoidea;Portunidae16,026AB093006Portunus sanguinolentusPortunoidea;Portunidae16,024KT438509Charydki sponicaPortunoidea;Portunidae15,738FJ460517Scylla paramanosainPortunoidea;Portunidae15,834JX457150Scylla paramanosainPortunoidea;Portunidae15,833FJ327759Scylla serataPortunoidea;Portunidae15,660KF386147Thalamita crenataPortunoidea;Portunidae15,660KF386147Thalamita crenataPortunoidea;Portunidae16,157KJ91945Portunu pelagitasPortunoidea;Portunidae16,157KM977822Chaceon sgranulatusPortunoidea;Geryonidae16,126KU507298Urnatia orientalisRaninoidea;Raninidae15,563KM189817Urnatia orientalisRaninoidea;Raninidae15,563KM189817Gondalfus yunohanaBythograeidea15,564KM02727Austingerae andriguezensisBythograeidea15,564KM02727Austingerae andriguezensisBythograeidea15,564KM02727Sopola cordinanusOcypodoidea;Dythograeidae15,611JQ035658Ocypodoidea;Dythograeidae15,611JQ035658Ocypodoidea;Dythograeidae15,611JQ035658Ocypodoidea;Dythograeidae15,611JQ035658Ocypodoidea;Dythograeidae15,611<	Myomenippe fornasinii	Xanthoidea;Menippidae	15,658	LK391943
Callinectes sapidusPortunoidea;Portunidae16,263AX80392Portunus trituberculatusPortunoidea;Portunidae16,026AB093006Portuns orgunolentusPortunoidea;Portunidae16,024KT438509Charybdis japonicaPortunoidea;Portunidae15,738FJ460517Scylla paramansainPortunoidea;Portunidae15,723FJ827750Scylla tranquebaricaPortunoidea;Portunidae15,723FJ827759Scylla tranquebaricaPortunoidea;Portunidae15,757FJ827758Charybdis feriataPortunoidea;Portunidae15,767H3827759Charybdis feriataPortunoidea;Portunidae15,767K39145Thalamita crenataPortunoidea;Portunidae16,157KM977822Charcon granulatusPortunoidea;Portunidae16,157KM977822Charcon granulatusPortunoidea;Portunidae16,156KK99383Lyreidus brevifronsRaninoidea;Raninidae15,563KM98394Lyreidus brevifronsRaninoidea;Raninidae15,563KM189817Gondalfus yunohanaBythograeoidea;Bythograeidae15,564LM05084Ocypodo cardaphingarea15,564LM0350564Austinograea alaysaeOcypodo cardaphinalinge15,504LM61722GM3632Ocypodo cardaphinalingaBythograeoidea;Bythograeidae15,564LM6169Macrophindamus gaponicusOcypodoidea;Ocypodidae15,504LM61782Ocypodoidea;Ocypodidae15,504LM6169SM62767Austinograea alaysaeBythograeoidea;Bythog	Leptodius sanguineus	Xanthoidea;Xanthidae	15,480	KT896744
Portunus triuberculatusPortunoides;Portunidae16,026AB093006Portunus sanguinolenusPortunoides;Portunidae16,024KT438509Charybdis japonicaPortunoides;Portunidae15,738FJ460517Scylla olracaPortunoides;Portunidae15,824JX457150Scylla olracacaPortunoides;Portunidae15,723FJ827759Scylla serrataPortunoides;Portunidae15,723FJ827759Scylla serrataPortunoides;Portunidae15,650KF386147Thalamita crenataPortunoides;Portunidae15,757KS9187759Charybdis feriataPortunoides;Portunidae15,757KS9187758Chaccon granulatusPortunoides;Portunidae16,157KM977882Chaccon granulatusPortunoides;Geryonidae16,125AB769383Chaccon sp.Portunoides;Geryonidae16,126KU507298Urnalia orientalisRaninoidea;Raninidae15,660KM365084Ranina craninaRaninoidea;Raninidae15,661KM355084Ranina araninaSythograeoidea;Bythograeidae15,563KM189817Gandaliys yunohanaBythograeoidea;Bythograeidae15,611JQ035650Austinograe adopseaBythograeoidea;Bythograeidae15,604KT896743Ocypode cordinanusOcypodoidea;Ocypotidae15,614KT896743Ocypode cordinanusOcypodoidea;Ocypotidae15,614K1896743Ocypode cordinanusOcypodoidea;Ocypotidae15,614K1896743Ocypodoidea;Ocypotidae15,614K1896743 <td>Callinectes sapidus</td> <td>Portunoidea;Portunidae</td> <td>16,263</td> <td>AY363392</td>	Callinectes sapidus	Portunoidea;Portunidae	16,263	AY363392
Portunsi songuinolentusPortunoidea;Portunidae16,024KT438509Charybdis japonicaPortunoidea;Portunidae15,738FJ40517Scylla oranamosainPortunoidea;Portunidae15,824JX457150Scylla olivaceaPortunoidea;Portunidae15,733FJ827759Scylla ranquebaricaPortunoidea;Portunidae15,753FJ827759Scylla ranquebaricaPortunoidea;Portunidae15,757FJ827759Charybdis feriataPortunoidea;Portunidae15,767KJ821748Charybdis feriataPortunoidea;Portunidae15,767KJ891945Portunoidea;Portunidae16,157KM977882Chaccon granulatusPortunoidea;Geryonidae16,135AB769383Chaccon granulatusPortunoidea;Geryonidae16,12KM98394Umalia orientalisRaninoidea;Raninidae15,563KIM89817Gandalfus yunohanaBythograeidea;Bythograeidae15,563KIM98194Gandalfus puidBythograeidea;Bythograeidae15,564KM02727Austinograea aloyseaBythograeidea;Bythograeidae15,564KI04221Oxopode ceratophthalmus iponicusOcypodidea;Ocypodidae15,564LN811669Macrophthalmus iponicusOcypodidea;Otypodidae15,564LN81751Oxopode ceratophthalmus iponicusOcypodidea;Ocypodidae15,564LN8165984Ocypodidea;Ocypodidae15,564LN8165984Ocypodidea;Ocypodidae15,564LN81750Macrophthalmus iponicusOcypodidea;Ocypodidae15,564LN81570 <t< td=""><td>Portunus trituberculatus</td><td>Portunoidea;Portunidae</td><td>16,026</td><td>AB093006</td></t<>	Portunus trituberculatus	Portunoidea;Portunidae	16,026	AB093006
Charybdis japonicaPortunoidea;Portunidae15,738F/460117Scylla paramanosainPortunoidea;Portunidae15,824JX457150Scylla olixocaPortunoidea;Portunidae15,733FJ827759Scylla airxaaPortunoidea;Portunidae15,733FJ827758Scylla serraaPortunoidea;Portunidae15,775FJ827758Charybdis feriataPortunoidea;Portunidae15,767LX391945Portunoidea;Portunidae15,787LX391945Portunoidea;Portunidae16,157KM977882Chaceon granulatusPortunoidea;Ceryonidae16,126KU507298Lyreidus brevifronsRaninoidea;Raninidae16,112KM983394Unatia orientalisRaninoidea;Raninidae15,563KM189817Gandafus puiaBythograeidea;Bythograeidae15,563KM189817Gandafus puiaBythograeidea;Bythograeidae15,563KM189817Ocypode cardineussiBythograeidea;Bythograeidae15,564K002727Austinograea radviguezensisBythograeidea;Bythograeidae15,664K1896743Ocypode cardineussiOcypodidea;Ocypodidae15,564LN011669Macrophthalmus japonicusOcypodidea;Ocypodidae15,564LN01169Sinograea novicusOcypodidea;Ocypodidae15,564LN01169Macrophthalmus japonicusOcypodidea;Ocypodidae15,564LN01169Sinograea radviguezensisPotamoidea;Potamidae15,517KM343211Ocopode cardinphtalmus japonicusOcypodidea;Ocypodidae15,514LN01169<	Portunus sanguinolentus	Portunoidea;Portunidae	16,024	KT438509
Scylla par.amamosainPortunoidea;Portunidae15,824JX457150Scylla carvatebaricaPortunoidea;Portunidae15,733FJ827759Scylla serrataPortunoidea;Portunidae15,755FJ827759Scylla serrataPortunoidea;Portunidae15,775FJ827758Charybdis feritatPortunoidea;Portunidae15,660KF386147Thalamita crenataPortunoidea;Portunidae15,787LK391945Portunoidea;Portunidae16,157KM977882Chaceon granulatusPortunoidea;Geryonidae16,135AB769383Chaceon sp.Portunoidea;Raninidae16,126KU507298Lyreidus brevifronsRaninoidea;Raninidae15,563KM1898174Gandalfus yunohanaBythograeoidea;Bythograeidae15,563KM1898174Gandalfus puiaBythograeoidea;Bythograeidae15,664KK002727Austinograea aloyseaBythograeoidae;Bythograeidae15,664KK1986743Ocypode cordinanusOcypodoidea;Ocypodidae15,664KT896743Ocypode cordinanusOcypodoidea;Ocypodidae15,664KT896743Ocypode cordinanusOcypodoidea;Ocypodidae15,664KU305058Ocypode cordinanusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus ignonicusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus ignonicusOcypodoidea;Ocypodidae15,564LN61169Macrophthalmus ignonicusPotamoidea;Potamidae15,304KX03924Sinopatanon xiushuiensePotamoidea;Potamidae <t< td=""><td>Charybdis japonica</td><td>Portunoidea;Portunidae</td><td>15,738</td><td>FJ460517</td></t<>	Charybdis japonica	Portunoidea;Portunidae	15,738	FJ460517
Scylla olivaceaPortunoidea;Portunidae15,723FJ827760Scylla ranquebaricaPortunoidea;Portunidae15,833FJ827759Scylla serrataPortunoidea;Portunidae15,660KF386147Charybdis feriataPortunoidea;Portunidae15,660KF386147Thalamita crenataPortunoidea;Portunidae15,787LK391945Portunoidea;Portunidae16,157KM977882Chaceon granulatusPortunoidea;Geryonidae16,157KM977882Chaceon granulatusPortunoidea;Raninidae16,112KM98394Umalia orientalisRaninoidea;Raninidae15,166KU507298Umalia orientalisRaninoidea;Raninidae15,567EU647222Gandalfus yunhanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus yunhanaBythograeoidea;Bythograeidae15,611JQ035668Ocypodoidea;Ocypodidae15,611JQ035668Ocypodoidea;Ocypodidae15,614LN611669MacrophthalmusOcypodoidea;Ocypodidae15,604K1896743Ocypodoidea;Ocypodidae15,567KU042041Huanapotamon lichuamensePotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Ocypodidae15,564KU042041Gondalfus yunhanaOcypodoidea;Ocypodidae15,564KU630844Ocypodoidea;Ocypodidae15,564KN6365743Sinopotamon xiushuienseOcypodoidea;Ocypodidae15,580KK038244Ocypodoidea;Ocypodidae15,580KK038244Omoidea;Pot	Scylla paramamosain	Portunoidea;Portunidae	15,824	JX457150
Scylla tranquebaricaPortunoidea;Portunidae15,833FJ827759Scylla serrataPortunoidea;Portunidae15,775FJ827758Charybdis feriataPortunoidea;Portunidae15,660KF386147Thalamita crenataPortunoidea;Portunidae15,787LK391945Portunoidea;Portunidae16,157KM977882Portunoidea;Geryonidae16,126KU507298Lyreidas brevifronsPortunoidea;Raninidae16,126KU507298Lyreidas brevifronsRaninoidea;Raninidae15,563KM1983394Umalia orientalisRaninoidea;Raninidae15,563KM198171Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus yunohanaBythograeoidea;Bythograeidae15,564KR002727Austinograea alayseaBythograeoidea;Bythograeidae15,604KT896743Ocypode cordimanusOcypodoidea;Ocypodiae15,564LK054743Ocypode cordimanusOcypodoidea;Qcypodiae15,564LK034211Gondalfus puiaPotamoidea;Potamidae18,197AB187570MacrophthalmusOcypodoidea;Ocypodiae15,564LK01692Macrophthalmus japonicusOcypodoidea;Qcypodiae15,380KX639824Shopatamon xishuiensePotamoidea;Potamidae15,341AB187570Shopatamon xishuiensePotamoidea;Potamidae15,341AB735678Hunanpotamon lichuanensePotamoidea;Potamidae15,341AB735678Homoidea;PotamidaeSa17KM405156Chionocetes papficusMajoidea	Scylla olivacea	Portunoidea;Portunidae	15,723	FJ827760
Scylla serrataPortunoidea;Portunidae15,775FJ827758Charybdis feriataPortunoidea;Portunidae15,660KF336147Thalamita cernataPortunoidea;Portunidae15,787KJ31945Portunus pelagicusPortunoidea;Portunidae16,157KM977882Chaceon granulatusPortunoidea;Geryonidae16,125KJ57298Lyreidus brevifronsPortunoidea;Geryonidae16,112KM98394Umalia orientalisRaninoidea;Raninidae15,466KM365084Ranino araninaRaninoidea;Raninidae15,563KH19817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus yunohanaBythograeoidea;Bythograeidae15,611J0035660Austinograea alayseaeBythograeoidea;Bythograeidae15,611J0035658Ocypodo cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypodo cordimanusOcypodoidea;Ocypodidae16,170KU343211Gondalptus uinsuiensePotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KC39824Somanniathelphusa boyangensisPotamoidea;Potamidae15,031KU042042Damithrax spinosismusMajoidea;Mithracidae15,331AB7575678Homologense pilourons dei,Foramidae15,793KL182070Mohoha majoraHomoloidea;Homolidae15,793KL182070Domindea;Potamidae15,793KL182070Sinopotamon riushuienseFotamoidea;Homolidae15,793KL182070<	Scylla tranquebarica	Portunoidea;Portunidae	15,833	FJ827759
Charybdis feriataPortunoidea;Portunidae15,660KF386147Thalmita crenataPortunoidea;Portunidae15,787LK391945Portunus pelagicusPortunoidea;Portunidae16,157KM977882Chaceon granulatusPortunoidea;Geryonidae16,126KU507298Lyreidus brevifronsRaninoidea;Raninidae16,112KM983394Umalia orientalisRaninoidea;Raninidae15,563KM189817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus puiaBythograeoidea;Bythograeidae15,660JQ035660Austinograea alayseaeBythograeoidea;Bythograeidae15,611JQ035658Ocypode ceratophthalmusOcypodoidea;Ocypodidae15,564KT386743Ocypode ceratophthalmusOcypodoidea;Ocypodidae15,564KU04221Muanapotamon tikuluraseOcypodoidea;Ocypodidae15,564KU042041Huanapotamon tikuluraseOcypodoidea;Ocypodidae15,564KU042041MacophtahanisOcypodoidea;Ocypodidae15,564KU042041MacophtahanisOcypodoidea;Ocypodidae15,564KU042041MacophtahanisOcypodoidea;Ocypodidae15,380KK038516OrdinousOcypodoidea;Potamidae15,380KK039824MacophtahaniPotamoidea;Potamidae15,380KK039824Monoidea;Potamidae15,381KU042042KU042042Huanapotamon tikulurasePotamoidea;Patantlephusidae15,381AB735678Ordinous spinosisimusMajoidea;Hamoildae15	Scylla serrata	Portunoidea;Portunidae	15,775	FJ827758
Thalamita crenataPortunoidea;Portunidae15,787LK391945Portunoidea;CorunidaePortunoidea;Ceryonidae16,157KM977882Chaceon graulatusPortunoidea;Geryonidae16,135AB769383Chaceon sp.Portunoidea;Geryonidae16,126KU507298Lyreidus brevifronsRaninoidea;Raninidae16,112KM983394Umalia orientalisRaninoidea;Raninidae15,466KM365084Gandalfus yunohanaBythograeoidea;Bythograeidae15,563KH189817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus yunohanaBythograeoidea;Bythograeidae15,620JQ035660Austinograea alayseaeBythograeoidea;Bythograeidae15,611JQ035658Ocypode cordimanusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus japonicusOcypodoidea;Ocypodidae16,170KU343211Geothelphusa dehaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Potamidae15,381KM042041Hunanpotamon lichuanensePotamoidea;Potamidae15,311AB735678Damiltrark spinosisimusMajoidea;Matroptanidae15,381KM042042Chionoecetes japonicus pacificusMajoidea;Matroptanidae15,593KX639824Domiltrark spinosisimusMajoidea;Matroptanidae15,593KX639824Damiltrark spinosisimusMajoidea;Matricidae15,793KJ612407 <td>Charybdis feriata</td> <td>Portunoidea;Portunidae</td> <td>15,660</td> <td>KF386147</td>	Charybdis feriata	Portunoidea;Portunidae	15,660	KF386147
Portunus pelagicusPortunoidea;Portunidae16,157KM977882Chaceon granulatusPortunoidea;Geryonidae16,135AB769383Chaceon sp.Portunoidea;Geryonidae16,12KU507298Lyreidus brevifronsRaninoidea;Raninidae16,112KM983394Umalia orientalisRaninoidea;Raninidae15,466KM365084Ranina raninaRaninoidea;Raninidae15,567EU47222Gandaflus yunohanaBythograeoidea;Bythograeidae15,567EU47222Gandaflus puiaBythograeoidea;Bythograeidae15,564KR002727Austinograea alayseaeBythograeoidea;Bythograeidae15,604KT896743Ocypode cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypode cordimanusOcypodoidea;Ocypodidae15,564LN611669MacrophthalmusOcypodoidea;Ocypodidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB17570Sinopatamon xiushuiensePotamoidea;Potamidae15,380KX639824Hunaanpotamon lichuanensePotamoidea;Potamidae15,381KW042041Hunaanpotamon siushuienseMajoidea;Macrophtusiade15,381KW05516Onioecets japonicus pacificusMajoidea;Hithracidae15,393KX639824Somanniathelphusa boyangensisMajoidea;Hithracidae15,393KX639824Damilhara spinosismusMajoidea;Hithracidae15,393KU042041Homologenus malayensisHomoloidea;Homolidae15,903KU12407Homolodea;Homolidae	Thalamita crenata	Portunoidea;Portunidae	15,787	LK391945
Chaceon granulatusPortunoidea;Geryonidae16,135AB769383Chaceon sp.Portunoidea;Geryonidae16,126KU507298Lyreidus brevifronsRaninoidea;Raninidae16,112KM98394Umalia orientalisRaninoidea;Raninidae15,466KM365084Ranina raninaRaninoidea;Raninidae15,563KM189817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus yunohanaBythograeoidea;Bythograeidae15,563KM025084Austinograea alayseaeBythograeoidea;Bythograeidae15,620JQ035660Austinograea rodriguezensisBythograeoidea;Bythograeidae15,611JQ035658Ocypode cordinanusOcypodoidae;Ocypodidae15,564LN611669Ocypode cordinanusOcypodoidae;Ocypodidae15,564LN61169Macrophthalmus japonicusOcypodoidae;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KX639824Somanniathelphusa bayangensisPotamoidea;Potamidae15,381KM0402041Hunanpotamon lichuanensePotamoidea;Potamidae15,3817KM405516Chioneecets japonicus pacificusMajoidea;Mithracidae15,793KJ12407Moloha majoraHomoloidea;Homolidae15,793KJ12407Pormiodres;Dormenidae15,903KJ12407KJ12407Pormiodees;Dormenidae15,793KJ12407KustopaceIsonoidea;Homolidae15,793KJ12407Poromiodes;DormenidaeIsonoidea;Homolidae15,903	Portunus pelagicus	Portunoidea;Portunidae	16,157	KM977882
Chaceon sp.Portunoidea;Geryonidae16,126KU507298Lyreidus brevifronsRaninoidea;Raninidae16,112KM983394Umalia orientalisRaninoidea;Raninidae15,466KM365084Ranina raninaRaninoidea;Raninidae15,563KU189817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus puiaBythograeoidea;Bythograeidae15,620JQ035660Austinograea adayseaeBythograeoidea;Bythograeidae15,611JQ035673Ocypode cordinguezensisOcypodoidea;Ocypodidae15,604KT896743Ocypode ceratophthalmusOcypodoidea;Ocypodidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopatamon xiushuiensePotamoidea;Potamidae15,380KK0393844Somanniathelphusa boyangensisPotamoidea;Potamidae15,311AB735678Huananpotamon lichuanenseMajoidea;Mithracidae15,341AB735678Homologenus malayensisMajoidea;Mithracidae15,341AB735678Homolodea;Potamidae15,341AB735678Homoloidea;Homolidae15,033KT182069Dynomene pilumnoidesDoranioidea;Potamidae15,033KT182069KT182070	Chaceon granulatus	Portunoidea;Geryonidae	16,135	AB769383
Lyreidus brevifronsRaninoidea;Raninidae16,112KM983394Umalia orientalisRaninoidea;Raninidae15,466KM365084Ranina raninaRaninoidea;Raninidae15,563KU189817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus puiaBythograeoidea;Bythograeidae15,548KR002727Austinograea alayseaeBythograeoidea;Bythograeidae15,611JQ035660Austinograea rodriguezensisBythograeoidea;Bythograeidae15,604LK7896743Ocypode ceratophthalmusOcypodoidea;Ocypodidae15,564LK611669Macrophthalmus japonicusOcypodoidea;Ocypodidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Potamidae15,311AP35678Hunonogenus malayensisMajoidea;Mitracidae15,311AP35678Homologenus malayensisMajoidea;Mitracidae15,393KI402042Damithrax spinosissimusMajoidea;Mitracidae15,793KJ402516Homologenus malayensisHomoloidea;Homolidae15,793KJ122069Joho majoraHomoloidea;Homolidae15,903KT182069Dynomen pilumnoidesDromioidea;Dynomenidae15,903KT182069	Chaceon sp.	Portunoidea;Geryonidae	16,126	KU507298
Umalia orientalisRaninoidea;Raninidae15,466KM365084Ranina raninaRaninoidea;Raninidae15,563KM189817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus puiaBythograeoidea;Bythograeidae15,548KR002777Gandalfus puiaBythograeoidea;Bythograeidae15,620JQ035668Austinograea alayseaeBythograeoidea;Bythograeidae15,611JQ035658Ocypode cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypode ceratophthalmusOcypodoidea;Ocypodidae16,170KU343211Gentelphusa dehaaniOcypodoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KK639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae15,341AB735678Homologenus malayensisMajoidea;Mithracidae15,341AB735678Homologenus malayensisHomoloidea;Homolidae15,093KT182067Dynomene pilumnoidesDromioidea;Homolidae15,903KT182070	Lyreidus brevifrons	Raninoidea;Raninidae	16,112	KM983394
Ranina raninaRaninoidea;Raninidae15,563KM189817Gandalfus yunohanaBythograeoidea;Bythograeidae15,567EU647222Gandalfus puiaBythograeoidea;Bythograeidae15,548KR002767Austinograea alayseaeBythograeoidea;Bythograeidae15,620JQ035658Austinograea rodriguezensisBythograeoidea;Bythograeidae15,604KT896743Ocypode cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypode ceratophthalmus japonicusOcypodoidea;Ocypodidae15,611JQ035658Macrophthalmus japonicusOcypodoidea;Ocypodidae15,64LN611669Macrophthalmus japonicusOcypodoidea;Potamidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,580KX639824Damithrax spinosissimusMajoidea;Mithracidae15,341AB735678Homologenus malayensisMajoidea;Homolidae15,793KJ012407Moloha majoraHomoloidea;Homolidae15,903KJ182069Dynomene pilumnoidesDromioidea;Dynomenidae15,903KJ182070	Umalia orientalis	Raninoidea;Raninidae	15,466	KM365084
Gandalfus yunohanaBythograeoidea;Bythograeoidae15,567EU647222Gandalfus puiaBythograeoidea;Bythograeoidae15,548KR002727Austinograea alayseaeBythograeoidea;Bythograeoidae15,620JQ035660Austinograea rodriguezensisBythograeoidea;Bythograeidae15,611JQ035658Ocypode cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypode cordimanusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus japonicusOcypodoidea;Ocypodidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae15,341AB73678Chionoecetes japonicus pacificusMajoidea;Mitracidae15,341AB73678Homologenus malayensisHomoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,793KJ612407Moloha majoraDormioidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae15,903KT182070	Ranina ranina	Raninoidea;Raninidae	15,563	KM189817
Gandalfus puiaBythograeoidea;Bythograeoidea15,548KR002727Austinograea alayseaeBythograeoidea;Bythograeoidea;Bythograeidae15,620JQ035660Austinograea rodriguezensisBythograeoidea;Bythograeoidea;Bythograeidae15,611JQ035658Ocypode cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypode cordimanusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus japonicusOcypodoidea;Ocypodidae16,170KU343211Geothelphusa dehaariPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae15,341AB1875678Chinoecetes japonicus pacificusMajoidea;Mitrracidae15,341AB736788Homologenus malayensisHomoloidea;Monolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae15,903KT182070	Gandalfus yunohana	Bythograeoidea;Bythograeidae	15,567	EU647222
Austinograea alayseaeBythograeoidea;Bythograeoidea15,620JQ035660Austinograea rodriguezensisBythograeoidea;Bythograeoidea15,611JQ035658Ocypode cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypode ceratophthalmusOcypodoidea;Ocypodidae15,564LN611669MacrophthalmusOcypodoidea;Ocypodidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae18,460KU042041Huananpotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae15,381KM405516Chinoecetes japonicus pacificusMajoidea;Mithracidae15,341AB736788Homologenus malayensisHomoloidea;Homolidae15,793KJ12407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Gandalfus puia	Bythograeoidea;Bythograeidae	15,548	KR002727
Austinograea rodriguezensisBythograeoidea;Bythograeoidea15,611JQ035658Ocypode cordimanusOcypodoidea;Ocypodidae15,604KT896743Ocypode ceratophthalmusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus japonicusOcypodoidea;Macrophthalmidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae15,380KU042041Huananpotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae17,032KU042042Damithrax spinosissimusMajoidea;Maridae15,341AB735678Homologenus malayensisHomoloidea;Homolidae15,793KJ12407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Austinograea alayseae	Bythograeoidea;Bythograeidae	15,620	JQ035660
Ocypode cordinanusOcypodoidea;Ocypodidae15,604KT896743Ocypode ceratophthalmusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus japonicusOcypodoidea;Macrophthalmidae16,170KU343211Geothelphusa dehaaniOcypodoidea;Macrophthalmidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae18,460KU042041Huanapotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Potamidae17,032KU042042Damithrax spinosissimusMajoidea;Mithracidae15,817KM405516Chionoecetes japonicus pacificusMajoidea;Homolidae15,793KJ12407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilunnoidesDromioidea;Dynomenidae16,475KT182070	Austinograea rodriguezensis	Bythograeoidea;Bythograeidae	15,611	JQ035658
Ocypode ceratophthalmusOcypodoidea;Ocypodidae15,564LN611669Macrophthalmus japonicusOcypodoidea;Macrophthalmidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae18,460KU042041Huananpotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae17,032KU042042Damithrax spinosissinusMajoidea;Maijdae15,341AB735678Chionoecetes japonicus pacificusHomoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Ocypode cordimanus	Ocypodoidea;Ocypodidae	15,604	KT896743
Macrophthalmus japonicusOcypodoidea;Macrophthalmidae16,170KU343211Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae18,460KU042041Huananpotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Potamidae17,032KU042042Damithrax spinosissimusMajoidea;Maithracidae15,817KM405516Chionoecetes japonicus pacificusMajoidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Ocypode ceratophthalmus	Ocypodoidea;Ocypodidae	15,564	LN611669
Geothelphusa dehaaniPotamoidea;Potamidae18,197AB187570Sinopotamon xiushuiensePotamoidea;Potamidae18,460KU042041Huananpotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae17,032KU042042Damithrax spinosissimusMajoidea;Mithracidae15,817KM05516Chionoecetes japonicus pacificusMajoidea;Majidae15,341AB73678Homoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Macrophthalmus japonicus	Ocypodoidea;Macrophthalmidae	16,170	KU343211
Sinoportamon xiushuiensePotamoidea;Potamidae18,460KU042041Huananpotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae17,032KU042042Damithrax spinosissimusMajoidea;Mithracidae15,817KU0420516Chionoecetes japonicus pacificusMajoidea;Majidae15,341AB73678Homologenus malayensisHomoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Geothelphusa dehaani	Potamoidea;Potamidae	18,197	AB187570
Huananpotamon lichuanensePotamoidea;Potamidae15,380KX639824Somanniathelphusa boyangensisPotamoidea;Parathelphusidae17,032KU042042Damithrax spinosissimusMajoidea;Mithracidae15,817KM405516Chionoecetes japonicus pacificusMajoidea;Majidae15,341AB735678Homologenus malayensisHomoloidea;Homolidae15,793KI612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Sinopotamon xiushuiense	Potamoidea;Potamidae	18,460	KU042041
Somanniathelphusa boyangensisPotamoidea;Parathelphusidae17,032KU042042Damithrax spinosissimusMajoidea;Mithracidae15,817KM405516Chionoecetes japonicus pacificusMajoidea;Migidae15,341AB735678Homologenus malayensisHomoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Huananpotamon lichuanense	Potamoidea;Potamidae	15,380	KX639824
Damithrax spinosissimusMajoidea;Mithracidae15,817KM405516Chionoecetes japonicus pacificusMajoidea;Majidae15,341AB735678Homologenus malayensisHomoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Somanniathelphusa boyangensis	Potamoidea;Parathelphusidae	17,032	KU042042
Chionoecetes japonicus pacificusMajoidea;Majidae15,341AB735678Homologenus malayensisHomoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Damithrax spinosissimus	Majoidea;Mithracidae	15,817	KM405516
Homologenus malayensisHomoloidea;Homolidae15,793KJ612407Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Chionoecetes japonicus pacificus	Majoidea;Majidae	15,341	AB735678
Moloha majoraHomoloidea;Homolidae15,903KT182069Dynomene pilumnoidesDromioidea;Dynomenidae16,475KT182070	Homologenus malayensis	Homoloidea;Homolidae	15,793	KJ612407
Dynomene pilumnoides Dromioidea;Dynomenidae 16,475 KT182070	Moloha majora	Homoloidea;Homolidae	15,903	KT182069
	Dynomene pilumnoides	Dromioidea;Dynomenidae	16,475	KT182070

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