Restoration of old genus name *Penaeus* based on molecular phylogenetic affiliations using complete mitochondrial genome

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Genus *Penaeus sensu lato* has been focus of intense scientific research for several decades owing to the high market demand of this group. Twenty eight species of shrimps, were grouped in this genus until Perez Farfante and Kensely raising the former six subgenera in this genus to generic status. Being a most valuable group, this decision made considerable concern among the end users. Recently research group from ICAR-Central Institute of Brackishwater Aquaculture made a comprehensive phylogenetic analysis and confirmed the monophyletic origin of genus *Penaeus*. In the present article we provide a summary of the revisionary work, and currently accepted binomial to encourage practitioners to use the modern up-to-date classification.

Keywords: Genus *Penaeus*, molecular phylogenetic affiliations, mitochondrial genome, scientific name.

BINOMIAL nomenclature (scientific names of species), which was originally formulated by Carl Linnaeus (1707–78), can be changed for several reasons; for example, improved understanding about physiology and ecology of the species, and clarification of phylogenetic relationship based on the generation of molecular data. This knowledge is extremely important to researchers working in different fields of life sciences. To Linnaeus, taxonomy was not more than simply to name a species, just like an individual is named in a family[1]. Taxonomy has progressed since the time of Linnaeus from simple naming to a multidisciplinary science that encompasses several biological disciplines. Taxonomy and trees of relationship are fundamental to the biologists working in basic as well as in applied sciences. The importance of taxonomy has been well acknowledged in aquaculture and fisheries[2]. In general, name changes or taxonomic revisions have rarely emerged from the boundaries of specialized academic disciplines. A taxonomic revision made in the recent past for the marine shrimp genus *Penaeus* has caused controversy, and sparked outrage and protests among scientific and industrial communities. According to Flegel[3], 'The controversy regarding the genus *Penaeus* may be the first of its particular nature to have arisen in the field of Zoology.'

The genus *Penaeus* was formed in 1798, named after the river God of Greek mythology, currently it has 34 species. Nearly all species are commercially important, and together make up one of the largest fisheries in the world; almost 90% of farmed shrimps belong to this genus (Table 1). Therefore, it is not surprising that change in the nomenclature raised concerns among end-users and stakeholders of this genus. This communication summarizes the taxonomic history of genus *Penaeus*, the background of revision of the genus, earlier molecular analyses on the phylogeny of this genus and finally, a summary of the present phylogenetic confirmation for the reversal of six-genus concept.

Since 1798, 34 species have been included in this genus, of which 17 were described before the 20th century. Burkenroad[4] divided the members of *Penaeus* into two distinct groups: grooved and non-grooved shrimps. Later, between 1969 and 1971, 6 subgenera were formed. The grooved shrimps were divided into three subgenera, namely *Melicertus*, *Marsuspenaeus* and *Farfantepenaeus* (American grooved). The non-grooved shrimps were divided into two groups: shrimps with hepatic carina (*Litopenaeus* and *Penaeus*) and those without hepatic carina (*Fenneropenaeus*) (Figure 1). Even this subgeneric level of classification was questioned: 'In a genus containing only 27 species it is difficult

Figure 1. Representative species of subgenus of *Penaeus*, viz. *Fenneropenaeus*, *Penaeus*, *Marsupenaeus* and *Melicertus* distributed in Indian waters. *Litopenaeus* was introduced for aquaculture purpose in 2010.

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Table 1. Traditional species names under different subgenera of old genus *Penaeus*

Genus	Subgenus	Species	Distribution	Remarks
Penaeus	*Fennneropenaeus*	*indicus*	South and East African coast, India, Sri Lanka, Gulf of Oman, Madagascar, Red Sea, China, Philippines and Australia	Total farmed global *P. indicus* production was 3368 mt in 2019. Less intensive farming is found in India, Mozambique, Oman, Saudi Arabia, South Africa, UAE, Vietnam and Yemen
		merguiensis	Indo-West Pacific: India, Sri Lanka, China, Philippines, Indonesia, Thailand, Vietnam and Australia	Farmed global production of *P. merguiensis* was 18,819 mt in 2019. Farmed in Indonesia, Malaysia, Philippines, Singapore, Thailand and Vietnam
		penicillatus	Pakistan, Taiwan and Indonesia	Fisheries in Pakistan, India, Bangladesh and Malaysia. Traditional farms in West Bengal, India
		chinensis	China, Korea and Hong Kong	Total farmed production of *P. chinensis* was 38,584 mt in 2019. Widely farmed in China
		silasi	Western Central Pacific: Singapore, Malaysia and Indonesia	No fisheries exist exclusively for this species
		konkani	Entire Maharashtra coast, India	No fisheries exist exclusively for this species
	Penaeus	*monodon*	Indo-West Pacific: Arabian Sea, Southeast Asia, Taiwan, China, Japan and Australia; also reported in the Atlantic Ocean	Widely cultured in Thailand, India, Malaysia, Indonesia, Bangladesh, Sri Lanka, Philippines and Australia. Total aquaculture production of tiger shrimp was 774,484 mt in 2019
		semisulcatus	From Southeast Africa to Japan, Red Sea, Malay Archipelago; colonized in eastern Atlantic and eastern Mediterranean Sea	Minor to moderate fisheries in Madagascar and Africa; farmed at experimental scale in India, Thailand and Taiwan
		esculentus	Across northern Australia down to central NSW	Experimental culture in Australia; of commercial importance in Western Australia
		simplex	Endemic to Indonesian waters; western coast of Aceh Province, Sumatra, Indonesia, from Lamno (Aceh Besar) to the coast of southern Aceh at depths of 10 to 40 m	Farmed in Aceh; there is reasonable demand for this species in the market
	Litopenaeus	*vannamei*	Eastern Pacific coast from Sonora (Mexico) to Tumbes (Peru)	Single-most valuable aquaculture species. Farmed in 18 countries, including India. Total farmed production was 5.5 million mt
		stylirostris	West coast of Mexico to Peru	It is fished both onshore and offshore in Mexico, Guatemala, El Salvador and Honduras. Total global farmed production of *stylirostris* was 2114 mt in 2019
		occidentalis	West coast of Mexico to Peru	Commercial fisheries exist in Panama, Columbia and Ecuador
		schmitti	Western Atlantic: from Honduras to southern Brazil	Minor species for aquaculture
		setiferus	Western Atlantic: from New Jersey, USA to Yucatan, Mexico	Minor species for aquaculture
	Marsupenaeus	*japonicus*	Native to Indian Ocean and southwest Pacific: east coast of South Africa, Korea, Japan, Taiwan, Malaysia, Philippines, Indonesia, New Guinea, Fiji and Australia. Invaded to Mediterranean: Egypt, Syria, southern Turkey, Israel, Cyprus, Lebanon, Greece and Rhode	The most valuable shrimp. In India, small fisheries exist. Total farmed production of *japonicus* was 52,458 mt
		Pulchricaudatus (P. japonicus Form 11)	Australia, west Indian Ocean, South China and Red Sea	Farmed in Australia and Taiwan. Minor fishery exists throughout its range
	Melicertus	*canaliculatu*s	Southeast Africa to Taiwan, Pakistan, India and Malay Archipelago	Found in commercial shrimp catches in Pakistan, India and Fiji
		kerathurus	Mediterranean Sea, England to Angola	Widely fished along the Mediterranean coasts; experimental culture only

(*Contd*)

Table 1. (*Contd*)

Genus	Subgenus	Species	Distribution	Remarks
		latisulcatus	Southeast Africa to Japan through Korea, Australia and Malay Archipelago	Minor fishery in Australia, experimental culture only
		longistylus	South China Sea, Malaysia and Australia	Commercial fishery exists in the Gulf of Carpentaria, North Queensland
		marginatus	East African coast, Madagascar to Singapore, Indonesia, Japan and Hawaii, USA	Minor fishery in Hawaii
		plebjus	Distributed along the east coast of Australia	Supports commercial trawling fishery in Australia
		hathor	Red Sea to Myanmar and the Mediterranean Sea	Minor commercial fisheries
		similis	Arabian Sea	No fisheries exist
	Farfantepenaeus	*aztecus*	East coast of USA (Massachusetts to Texas); east coast of Mexico (Tamaulipasto to Campeche)	Supports a valuable fishery off North Carolina, USA and the Gulf of Mexico
		brasiliensis	North Carolina, USA to Brazil, Bermuda and the West Indies	A small percentage of the total fish catch was found in the northern part of its range
		brevirostris	West coast of Mexico to Peru, Galapagos Islands	Supports a minor fishery in Mexico
		californiensis	California, USA to Peru	Important fishery in Mexico; almost 75% of Mexican Pacific shrimp catch
		duorarum	East coast of USA from Maryland to Texas; east coast of Mexico from Tamaulipas to Quintana Roo	Supports an important commercial fishery in the Gulf of Mexico; northwest Florida and Western Texas in USA
		notialis	West African coast from Mauritania to Angola; from Cuba to the Virgin Islands, Atlantic coast of Mexico to Brazil	Supports important fisheries in the Atlantic coast of central America, Venezuela and Brazil
		paulensis	Western Atlantic coast of Brazil to Argentina	Supports fisheries in Brazil and Argentina
		subtilis	From Atlantic coast of Honduras to Brazil and the West Indies	The species is fished throughout its range, often forming part of catches of other shrimps
		isabelae	Off Colombia, Trinidad, Venezuela, French Guiana, Paramaribo, Suriname and Brazil	No fisheries exist exclusively for this species

to see the justification for creating six subgenera'[5,6]. Subsequently, Farfante and Kensely[7] made an extensive revision, and all the six subgenera were raised to the generic status without discussion or supplying further evidences[6]. This unilateral decision created havoc among practitioners from different fields of academia and industry. Some taxonomic experts supported the work of Farfante and Kensely[7]. For example, Schram and Ng[8] reported: 'Their analysis of penaeid classification remains the most complete and detailed morphological analysis yet conducted and their resulting hypothesis is not only academically sound but also highly testable.' On the contrary, Flegel[9] reported that discarding the original single genus concept, *Penaeus*, would be the most disruptive option to general stakeholders. For the researchers who are unfamiliar with penaeid taxonomy, this revision had created confusion, and they had erroneously followed the new nomenclature. For example, Auttarat *et al.*[10] erroneously used *Litopenaeuos merguiensis* instead of *Fenneropenaeous merguiensis*. Several experts from academia and industry have argued against this unilateral decision of splitting a widely used genus without sufficient academic and scientific reasons[11].

The initial splitting of genus *Penaeus* into divisions or later subgenera, based on morphological characteristics, was for the sake of convenience[4]. Further, he has not considered phylogenetic evidences for their classification. Prior to Farfante and Kensley[7], only a few have published on the molecular phylogeny of this genus. Subsequent to this publication[7], many articles addressing the molecular phylogeny of *Penaeus* have been published[12–16]. Most researchers considered that the elevation of subgenera to generic status was premature. Lavery *et al.*[6] suggested that none of the proposed genera or even subgenera is strictly natural. A relatively recent publication by Ma *et al.*[17] using both mitochondrial and nuclear markers was not in agreement with the six generic or even subgeneric scheme, but strongly supported the old *Penaeus* genus concept.

Certainly, the DNA barcoding system has revolutionized the science of taxonomy. However, there are still concerns on using partial sequence of one or two genes. It is often insufficient to resolve the relationships among taxa[18]. In order to enhance the resolution of phylogenetic analysis, the sequence data should be increased[19,20]. It is, therefore, suggested that the complete mitochondrial

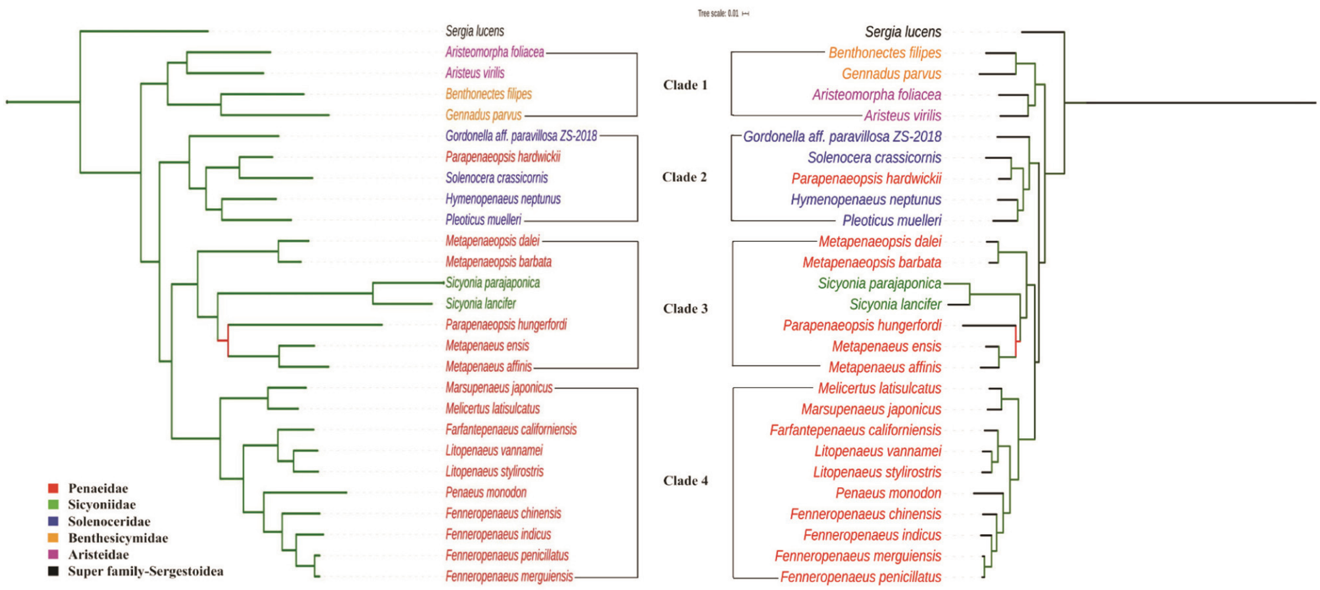

Figure 2. Phylogenetic trees: protein-coding genes derived by Bayesian method (left) and maximum likelihood (ML) method (right). The colour of the branches is based on the posterior probability values (≥0.9 – green, ≥0.7 and <0.9 – black, <0.7 – red) for Bayes tree and bootstrap values (≥90 – green, ≥70 and <90 – black, <70 – red) for ML tree.

genome could be used as an ideal marker for phylogenetic analysis[21]. In this context, Katneni *et al.*[22] studied the phylogenetic affiliations of all the representatives of the six subgenera of old *Penaeus* genus (*Fenneropenaeus*, *Litopenaeus*, *Penaeus*, *Melicertus*, *Marsupenaeus* and *Farfantepenaeus*) using complete mitochondrial genomes. Briefly, the best-fit model and partitioning schemes were obtained in Partition Finder v2.1.1, and then data on protein coding genes were analysed in RAxML version 8.2.9 (refs 23–26).

The phylogenetic analyses on robust maximum likelihood and Bayesian principles revealed that the *Penaeus* genus is monophyletic. In addition, the study also explored the utility of average amino acid identity (AAI) estimates as additional evidence to address the controversial taxonomic nomenclature. The genetic distance data followed the trend of between-species rather than between-genus for species of *Penaeus sensu lato*.

The major argument that supports the splitting of genus *Penaeus* is the shape of external genitalia of females (thelycum open versus closed)[27]. Owing to the difference in the reproductive morphology and the resulting reproductive behaviour of the open thelycum group, the level of divergence is considered to be greater than those among infra orders of other taxa; for example, carideans. Differences in the reproductive morphology of open thelycum taxa facilitate the prezygotic barriers, and this strongly prevents the hybridization of congeneric species. Ma *et al.*[17] suggested that this change in the external morphology may not reflect the phylogenetic relationship. Here, the open thelycum vannamei and closed thelycum indicus clearly fall under the same group in the phylogenetic tree constructed from the mitogenome. In conclusion, the phylogenetic analysis using complete mitochondrial genome clearly demonstrated the monophyletic status, where a group of organisms or species descended from a common ancestor (Figure 2). When we examined the evolutionary or phylogenetic diagram (Figure 2), all the six genera formed by Farfante and Kensely[7] arose from a single common ancestor. The study, therefore, confirms the appropriateness of single-genus nomenclature for shrimp species in the genus *Penaeus*.

In order to facilitate the identification of species of genus *Penaeus* reported in Indian waters, a modified key is presented in Box 1.

Taxonomy is a dynamic science; nevertheless, researchers should use the current nomenclature. A name that has been used for a long time may disappear or reappear, and this may be a nuisance for biologists[28]. However, this is how science works. Hypotheses are constantly changing in the light of new evidences. The current data based on the complete mitochondrial genome unambiguously demonstrate the monophyly and credibility of old genus *Penaeus*, and help restore the old genus name. In order to avoid confusion without compromising the rules of zoological nomenclature, the subgenus names proposed in 1969–71 can be provided within brackets between the traditional genus name *Penaeus* and name of the related species at first mention; for example, *Penaeus* (*Fenneropenaeus*) *indicus*. Subgeneric names are generally not used outside the academic discipline. As suggested by Flegel[9], it could also be stated in the introduction: 'In the present article the nomenclature followed is according to Katneni *et al.*[22].'

Box 1. Key to the species of genus *Penaeus* found in the Indian waters

1		Adrostral sulcus and carina extending beyond epigastric tooth, usually extends up to posterior margin of carapace	8
		Adrostral sulcus and carina short, or only extends to the level of epigastric tooth	2
2	(1)	Hepatic carina absent, or if present not well defined	3
		Hepatic carina well defined	7
3	(2)	Gastro-orbital carina reaching the posterior two-third distance between the hepatic spine and orbital angle; rostral crust is not triangular	4
		Gastro-orbital carina absent or not clear and if present reaching middle one-third distance between hepatic spine and orbital angle	5
4	(3)	The propodus of third maxilliped of adult male without bunch of setae or if present it is rudimentary, rostrum straight in adults	*Penaeus silasi* Muthu and Moto
		The propodus of third maxilliped of adult male with bunch of setae equal in length to the dactyl, rostrum sigmoid in adults	*Penaeus indicus* H. Milne Edwards
5	(3)	Third maxilliped reaching the tip of antennular peduncle, rostral formation 6 – 9 + 1; usually adrostral carina not reaching epigastric tooth; distal segment of third maxilliped short; one-third of penultimate segment; rostral crest triangular	*Penaeus merguinesis* De Man
		Third maxilliped reaching only up to the second segment of antennular peduncle, rostral formula 3 + 1 or 4 + 1; adrostral carina may or may not reach beyond epigastric tooth	6
6	(5)	Adrostral carina reaching just beyond epigastric tooth, rostral crest markedly elevated, distal segment of third maxilliped of adult male two and a half times longer than penultimate segment; rostral formula 3 + 1; first pereopod without ischial spine	*Penaeus penicillatus* Alcock
		Adrostral carina does not reach up to epigastric tooth, ends at the level of highest elevated point of rostrum, rostral formula 4 + 1; first pereopod with ischial spine	*Penaeus konkani* Chanda and Bhattacharya
7	(2)	Hepatic carina horizontally straight; fifth pereopod without exopodite	*Penaeus monodon* Fabricius
		Hepatic carina oblique, fifth pereopod with small exopodite. Antennal flagella uniformly reddish-brown, not banded	*Penaeus semisulcatus* De Haan
8	(1)	Telson unarmed	9
		Telson armed usually with three pairs of movable spines	10
9	(8)	First pereopod with a short ischial spine, thelycum possesses chisel-shaped antennal plate, wide gap between lateral plates	*Penaeus similis* Chanda and Bhatacharya
		First pereopod without ishial spine; thelycum without anterior plate; lateral plates placed closed to each other with no spines between median margin	*Penaeus canaliculatus* Oliveir
10	(8)	Post-rostral carina sulcate; not more than one ventral rostral teeth	11
		Post-rostal carina non sulcate, usually with two ventral rostral tooth	*Penaeus marginatus* Randall
11	(10)	Body with prominent reddish-brown bands on the carapace and abdominal segment. Thelycum with single plate forming pouch opening anteriorly	*Penaeus japonicu*s Bate
		Body without vertical band, thelycum closed by two flaps	12
12	(11)	Anterior process of thelycum flattened and broadly triangular; curvature of vertical coasta of petasma more pronounced; uropod peacock blue with a small patch of brown at the tip	*Penaeus latisulcatus* Kishionouye
		Anterior process of thelycum ending into two flattened horn like process; no spot on the uropod	*Penaeus hather* Burkenroad

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Transformation of arsenic by indigenous soil microbes as affected by phosphorus and arsenic

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Highly arsenic-polluted soil (16.5 mg kg^{-1}) of West Bengal, India, was used for isolation, screening and identification of indigenous soil microbes. *Citrobacter koseri* significantly removed (7.6) and bioaccumulated (4.95) highest arsenic in $P_{15}As_{15}$ treatment, while loss (2.9) was higher in $P_{10}As_{15}$. Similarly, *Pseudomonas putida* significantly removed (7.4) and bioaccumulate (4.8) highest As in $P_{15}As_{15}$ and while loss (2.8) was higher in $P_{10}As_{15}$. Percentage removal of As was 47–59, bioaccumulation was 29–38 and loss 17–23 with *Citrobacter* sp., while it was 47–58% (removal), 29–39% (bioaccumulation) and 17–21% (loss) with *Pseudomonas putida*. Maximum removal and bioaccumulation of phosphorus was 37.8% and 32.1% respectively, for $P_{10}As_{15}$ in *Citrobacter* sp. In *P. putida* it was 33.1% and 27.2% respectively, for $P_{10}As_{15}$. At the same level of arsenic, increase in phosphorus significantly increased its removal and bioaccumulation, but the opposite was true during calculation in terms of percentage removal and percentage bioaccumulation.

Keywords: Arsenic, bioaccumulation, *Citrobacter*, phosphorus, *Pseudomonas.*

ARSENIC (As) pollution in the environment has been detected on a large scale in many districts of West Bengal,

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