



Diversity of Indian Barnacles in Marine Provinces and Ecoregions of the Indian Ocean

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The present study is the first completed and taxonomically validated literature review of the biodiversity of barnacles (Cirripedia) in India. A total of 144 species in 75 genera and 19 families have been recorded in India. The highest number of species has been recorded from the Bay of Bengal province, located on the eastern side of the Indian Peninsula, comprising the Eastern India ecoregion (76 species) and Northern Bay of Bengal ecoregion (34 species). The West and South India Shelf province has fewer species (Western India ecoregion: 29 species; South India and Sri Lanka ecoregion: 40 species; and Maldives ecoregion: 10 species) compared to the Bay of Bengal province. The Andaman province is composed of the Andaman and Nicobar Islands, and contains 65 species. Most of the coral-associated barnacles (family Pyrgomatidae) have been recorded in the corals reefs of the Andaman and Nicobar Islands (7 species), Eastern India (6 species), and Northern Bay of Bengal ecoregions (5 species). Sponge-associated barnacles (mostly in the subfamily Acastinae) were recorded in the Eastern India ecoregion, Southern India and Sri Lanka, and Andaman and Nicobar Islands ecoregions. Deepwater species were recorded the most extensively in the Andaman and Nicobar Islands ecoregion (21 species), followed by the South India and Sri Lanka ecoregion (9 species) and Eastern India ecoregion (7 species). Six Atlantic/boreal cold water species previously reported in India were removed due to incorrect identification, and some incorrectly identified species were validated and corrected.

Keywords: India, checklist, cirripedia, barnacles, biodiversity

INTRODUCTION

India is one of the 12 mega-biodiversity countries and has 25 biodiversity hotspots, containing a considerable number of endangered species (Myers et al., 2000; Venkataraman and Wafar, 2005; Venkataraman and Raghunathan, 2015). India supports a rich diversity of marine habitats and invertebrate fauna (Aneesh et al., 2018; Trivedi et al., 2018; Kottarathil et al., 2019; Shih et al., 2019; Aneesh and Kappalli, 2020). India contains 7516.6 km of coastline—5422.6 km in the Indian Peninsula and 2094 km in islands (Andaman and Nicobar Islands: 1962 km; Lakshadweep Islands: 132 km) (Ahmad, 1972; Kumar et al., 2006; Trivedi et al., 2018).

More than 1400 species of barnacle were recorded from different oceanic regions across the world (Innocenti, 2006; Chan et al., 2009). Barnacles occur in almost all marine environments, from intertidal zones to the deepest parts of the oceans (Chan and Høeg, 2015). The greatest diversity of barnacles is observed in the tropical Indo-Pacific region (Newman and Abbott, 1980). Taxonomic studies of barnacles date back to the 16th century, when barnacles were identified as eggs of barnacle geese (Anderson, 1994). Burmeister (1834) was the first naturalist to classify barnacles into cirripedes which later attracted the attention of numerous taxonomists (Anderson, 1994). Darwin (1851, 1854) monographs on barnacles, written shortly after Burmeister's publication, became one of the major contributions to barnacle taxonomy.

Taxonomic studies on Indian barnacle fauna came out of the systemic work from one of these Darwin (1854) monographs, which included several species of barnacles from the Indian waters. Thomas Nelson Annandale, the first Director of the Zoological Survey of India, published a series of taxonomy papers (Annandale, 1905, 1906a,b, 1907, 1909, 1910a,b, 1911, 1913, 1914, 1916, 1924) based on the barnacle specimens deposited into the Indian Museum. Annandale (1906a) examined stalked barnacles collected from the R.I.M.S. (Royal India Marine Survey Ship) "Investigator" and described 11 new species. Later, Annandale (1909); (Annandale, 1910a,b) described eight new species and one new family (Poecilasmataidae; Annandale, 1909) of barnacles from Indian waters. Annandale (1924) published a list of cirripedia associated with Indian corals and described two new species. Sundararaj (1927) recorded five species of barnacles from the Krusadai Islands (Tamil Nadu). Nilsson-Cantell (1938) carried out a taxonomic study on barnacles of the Bay of Bengal, Arabian Sea and Indian Ocean, and listed a total of 139 species, 36 of which had a wide distribution beyond these three regions. Augustine Daniel of the Zoological Survey of India studied barnacle diversity of the Tamil Nadu state and recorded 42 species (Daniel, 1956). Daniel (1981) listed 15 species of barnacles collected from estuaries in both the east and south-west coasts of India. Fernando (2006) later published a monograph on Indian barnacles that contained more extensive records and listed 70 species.

Scientists at institutes and universities across Indian have contributed to our understanding of the taxonomy, diversity and biology of barnacles occurring in Indian waters (Gray, 1831; Gruvel, 1907; Hoek, 1913; Kemp, 1915; Pillai, 1958; Bhatt and Bal, 1960; Karande and Palekar, 1963, 1966; Daniel and Chakrabarathi, 1967; Prem-Kumar and Daniel, 1968; Balakrishnan, 1969; Wagh and Bal, 1969, 1974; Devaraj and Bennet, 1974; Karande, 1974; Desai and Senthilkumar, 1975; Fernando, 1978; Venkateswaran and Fernando, 1982; Wagh and Sawant, 1982; Newman and Killingley, 1984; Sudakaran and Fernando, 1987; Rao and Balaji, 1988; Frazier, 1989; Nandakumar, 1990; Rajaguru and Shantha, 1992; Ramakrishna and Talukdar, 2003; Karuppiah et al., 2004; Singh et al., 2004; Mitra and Misra, 2006; Sanjeeva Raj, 2006; Krishnamoorthy, 2007; Kumaravel et al., 2009; Pati et al., 2009; Mitra et al., 2010; Swami et al., 2011; Namboothri and Fernando, 2012; Patro, 2012; Ramamoorthy et al., 2012; Trivedi et al., 2015;

Sahadevan, 2016; Roy and Rath, 2017; Desai et al., 2018; Parmar et al., 2018; Mondal et al., 2019). In addition to diversity research, there are a considerable number of studies focusing on the larval biology and settlement ecology of the common Indian intertidal barnacle *Amphibalanus amphitrite* (Gaonkar and Anil, 2010, 2012, 2013a,b; Gaonkar et al., 2012). In Goa and Kochi, on the west coast of India, settlement of cypris larvae have been investigated for their responses to diatom exopolymers (Patil and Anil, 2005), conspecific cues (Khandeparker and Anil, 2011), specific bacteria associating with the barnacle shells (De Gregoris et al., 2012), and sponge extracts (Mol et al., 2010). The reproductive cycle and population dynamics of *A. amphitrite* in Goa, India is affected by the interactions among monsoons, temperature and chlorophyll *a* concentration in seawater (Desai and Anil, 2005; Desai et al., 2006). The breeding and settlement patterns of *A. amphitrite* in Tamil Nadu, southeast coast of India are affected by tidal patterns, temperature and phytoplankton abundance (Karuppaiyan and Raja, 2007; Sathesh and Wesley, 2009). To date, there has not been a complete literature review on those extensive records of barnacle diversity in India or their accuracy. The objective of the present study is to provide the most taxonomically updated, validated and complete diversity records on barnacles in India. Species identities were validated based on morphological identifications using relevant taxonomic references, and supported by recent results of molecular taxonomic studies of barnacles in the Indo-Pacific waters.

MATERIALS AND METHODS

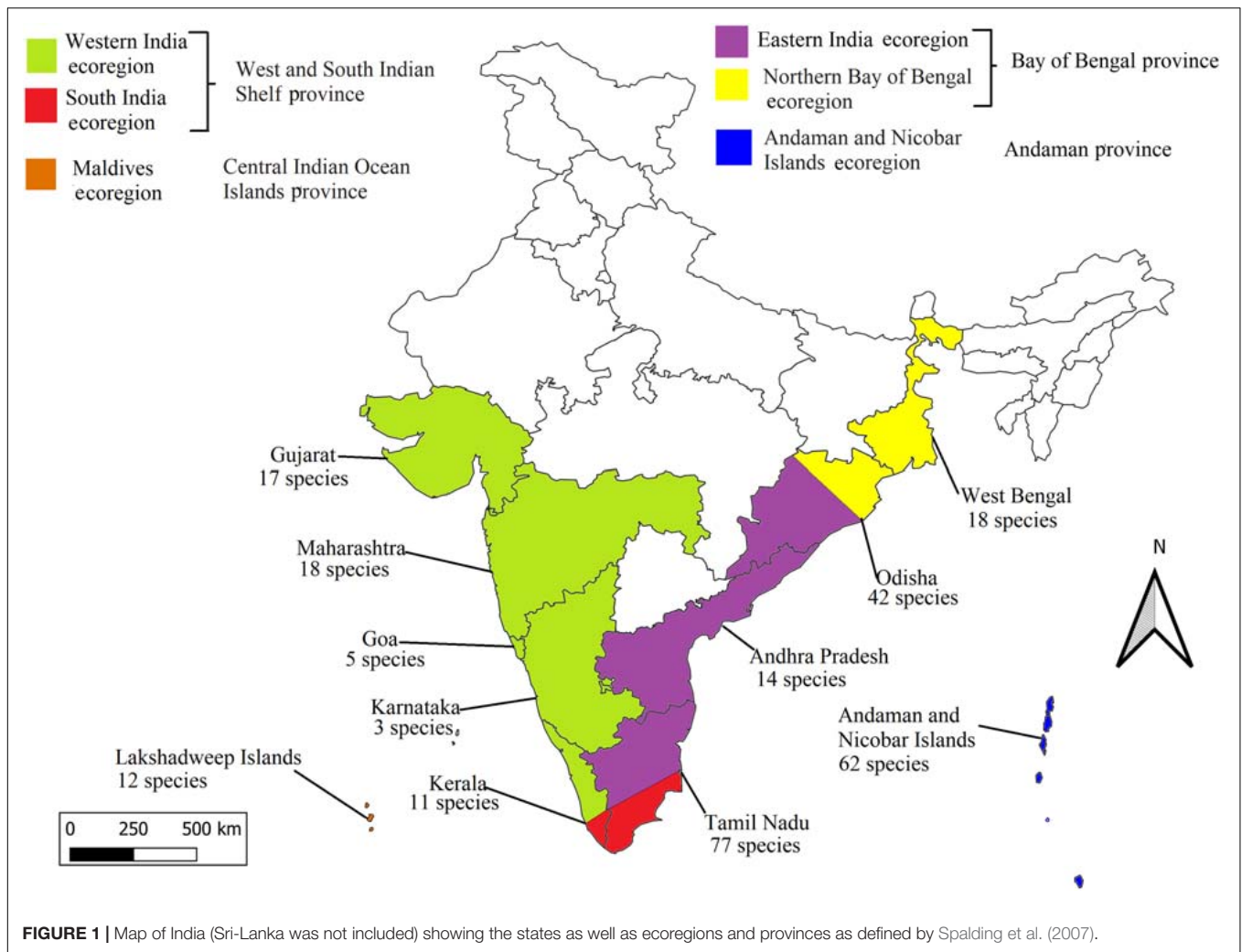
Provinces and Ecoregions in India

According to the definitions in Spalding et al. (2007), the coastline of India is comprised of four marine biogeographical provinces and six ecoregions (Figure 1). The West and South Indian Shelf province comprises the Western India ecoregion (from Kachchh district of Gujarat state to Ashtamudi Lake of Kerala state) and the South India ecoregion (Ashtamudi Lake of Kerala state to Karaikal, Puducherry of Tamil Nadu state) (Figure 1). The Central Indian Ocean Islands province includes the Maldives ecoregion, comprising Lakshadweep Islands and Minicoy. The Bay of Bengal province in India covers the Eastern India ecoregion (from Karaikal, Pondicherry of Tamil Nadu state to Konark of Odisha state) and the Northern Bay of Bengal ecoregion (Konark of Odisha state to Bidyadhari River Delta of West Bengal state). The Andaman province in India includes Andaman and Nicobar Islands ecoregion, which covers the Andaman and Nicobar Islands (Figure 1; Spalding et al., 2007).

Literature Review

The data on the barnacle fauna of India in the present study are based on peer-reviewed published literature and/or deposited material in marine collections. Only species present in Indian waters were recorded in the present study.

The collection site of each species is classified based on the Indian state and relevant marine provinces and ecoregions from Spalding et al. (2007). Species reported from adjacent



countries that formed a part of the former British Indian empire (Sri Lanka, Pakistan, Bangladesh, Maldives, and Myanmar) were excluded. A few old records without clearly stated collection sites were omitted. The synonyms, nomenclatural changes and classification of different species were validated based on Southward and Newman (2003), Chan et al. (2009), Jones and Hosie (2016).

Multivariate Analysis of Species Assemblages

Based on what is present and absent in the list of all recorded barnacle species, multivariate analysis (using species as variables) was performed using the PRIMER package (v6, Plymouth Routine in Multivariate Analysis, PRIMER-E Ltd; Clarke and Gorley, 2006) to examine variations in species assemblages among the ecoregions in India. Similarities among the ecoregions based on species data were calculated using the Sorensen similarity index. Non-metric Multidimensional Scaling (nMDS; Clarke, 1993) was conducted to generate two-dimensional plots on the species composition in all the ecoregions.

RESULTS

Diversity Patterns

A total of 155 barnacle species belonging to 75 genera and 19 families were reported from India (**Supplementary Appendix Table 1**). Of these, 40 species were described from Indian waters, of which 35 are valid species (**Table 1**) and five were synonymized: *Platylepas multidecorata* Daniel, 1962—described from Little Andaman, Andaman and Nicobar Islands—is now treated as a synonym of *Platylepas decorata* (Darwin, 1854). *Balanus longirostrum* var. *krusadaiensis* Daniel (1956), described from Tamil Nadu, is now treated as a synonym of *Membranobalanus longirostrum* (Hoek, 1913). *Balanus (Membranobalanus) roonwali* Prem-Kumar and Daniel (1968)—described from Chennai, Tamil Nadu—is now treated as a synonym of *M. longirostrum*. *Balanus amphitrite* var. *cochinensis* Nilsson-Cantell (1938)—described from Ernakulam, Cochin, Kerala—is now treated as a synonym of *Amphibalanus amphitrite* (Darwin, 1854). *Pollicipes polymerus madrasensis* Daniel, 1953—described from Royapuram, Chennai, Tamil Nadu—is now treated as a synonym of *Pollicipes polymerus* Sowerby (1833).

TABLE 1 | Barnacle species described from India.

Taxon name	Current identity	Type locality	World distribution
<i>Lepas anatifera indica</i> Annandale, 1909	<i>Lepas indica</i> Annandale, 1909	Off Ganjam coast, Orissa	India; Indian Ocean; Madagascar; South China Sea; East China Sea; China Jones and Hosie, 2016
<i>Lepas bengalensis</i> Daniel, 1952	<i>Hyalolepas bengalensis</i> Daniel, 1952	Madras (Chennai), Tamil Nadu	India Fernando, 2006
<i>Conchoderma indicum</i> Daniel, 1953	<i>Conchoderma indicum</i> Daniel, 1953	Krusadi Islands, Tamil Nadu	India Fernando, 2006
<i>Lepas guanamuthui</i> Daniel, 1971	<i>Dosima guanamuthui</i> Daniel, 1971	Great Nicobar, Andaman and Nicobar Islands	India; Northern Indian Ocean González et al., 2014
<i>Oxynaspis celata indica</i> Annandale, 1910	<i>Oxynaspis indica</i> Annandale, 1910	Odisha	India; Indo-Pacific; off Mauritius; Philippines to southwest Pacific; off New Zealand Rosell, 1991
<i>Dichelaspis grayii</i> var. <i>pernuda</i> Annandale, 1909	<i>Octolasmis grayii</i> var. <i>pernuda</i> Annandale, 1909	Chennai, Tamil Nadu	India Fernando, 2006
<i>Platylepas indicus</i> Daniel, 1958	<i>Platylepas indicus</i> Daniel, 1958	Chennai, Tamil Nadu	India Fernando, 2006
<i>Tetraclitella karandei</i> Ross, 1971	<i>Tetraclitella karandei</i> Ross, 1971	Madh Islands, Maharashtra	India; Taiwan; Philippines Chan et al., 2009
<i>Acasta sulcata</i> var. <i>spinosa</i> Daniel, 1956	<i>Acasta sulcata akanthosa</i> Daniel, 1956	Royapuram, Chennai, Tamil Nadu	India Fernando, 2006
<i>Balanus (Semibalanus) madrasensis</i> Daniel, 1958	<i>Semibalanus madrasensis</i> Daniel, 1958	Chennai, Tamil Nadu	India Daniel, 1972
<i>Balanus (Semibalanus) sinnurensis</i> Daniel, 1962	<i>Semibalanus sinnurensis</i> Daniel, 1962	Chennai, Tamil Nadu	India Fernando, 2006
<i>Dichelaspis rhinoceros</i> Annandale, 1909	<i>Octolasmis rhinoceros</i> Annandale, 1909	Bay of Bengal	India Nilsson-Cantell, 1938
<i>Dichelaspis stella</i> Annandale, 1909	<i>Octolasmis stella</i> Annandale, 1909	Bay of Bengal	Indian Ocean Zevina, 1982
<i>Heteralepas (Heteralepas) nicobarica</i> Annandale, 1909	<i>Heteralepas nicobarica</i> Annandale, 1909	Nicobar Island, Andaman and Nicobar Islands	India Buhl-Mortensen and Newman, 2004
<i>Scalpellum lambda</i> Annandale, 1910	<i>Annandaleum lambda</i> Annandale, 1910	Bay of Bengal near Andaman and Nicobar Islands (13°54'15"N 94°02'15"E)	India; Indo-west Pacific; Indian Ocean; Zanzibar; Sumbawa; Indonesia; Malay Archipelago; South-West of Calatagan Pt; Philippines; South Japan; South-West Pacific Jones and Hosie, 2016
<i>Scalpellum bengalens</i> Annandale, 1906	<i>Scalpellum (Smilium) bengalens</i> Annandale, 1906	Ganjam coast, Odisha	India Annandale, 1906b
<i>Scalpellum Alcockianum</i> Annandale, 1906	<i>Alcockianum alcockianum</i> Annandale, 1906	Gulf of Manaar, Tamil Nadu	India; Indian Ocean; Mozambique Channel; Indonesia; Malay Archipelago; Australia; New Zealand; South-West Pacific and mid-Pacific guyots Jones and Hosie, 2016
<i>Scalpellum laccadivicum</i> Annandale, 1906	<i>Annandaleum laccadivicum</i> Annandale, 1906	Laccadive sea	India; Gulf of Oman; Sri Lanka; Indonesia; Japan; Taiwan Chan et al., 2009
<i>Scalpellum subflavum</i> Annandale, 1905	<i>Annandaleum laccadivicum laccadivicum</i> Annandale, 1906	Cochin, Kerala and Gulf of Manaar, Tamil Nadu	India; Indian Ocean; Sumbawa; Indonesia; Malay Archipelago; South-West of Calatagan Pt; Taiwan; Philippines; South Japan (South of Honda Island); South-West Pacific Jones and Hosie, 2016
<i>Alepas xenophorae</i> Annandale, 1906	<i>Paralepas xenophorae</i> Annandale, 1906	Kerala	India; Japan Utinomi, 1958
<i>Megalasma striatum minus</i> Annandale, 1906	<i>Megalasma minus</i> Annandale, 1906	Andaman Sea	Cosmopolitan: India; Atlantic Ocean; Indo-west Pacific; East coast of Africa (Zanzibar); Indian Ocean; Indonesia; Malay Archipelago; Philippines; Taiwan; S Japan; Pacific Ocean Jones and Hosie, 2016
<i>Scalpellum gruvellii</i> Annandale, 1906	<i>Annandaleum gruvellii</i> Annandale, 1906	Gulf of Mannar, Tamil Nadu and between Lakshadweep and mainland	India; Atlantic Ocean; Indo-west Pacific: Indian Ocean; South China Sea; Pacific Ocean Jones and Hosie, 2016
<i>Annandaleum gruvellii</i> var. <i>quadratum</i> Annandale, 1906	<i>Annandaleum gruvellii quadratum</i> Annandale, 1906	Gulf of Mannar, Tamil Nadu	India Annandale, 1906b
<i>Creusia spinulosa</i> forma <i>transversalis</i> Nilsson-Cantell, 1938	<i>Cantellius transversalis</i> Nilsson-Cantell, 1938	North Bay, Port Blair, Andaman and Nicobar Islands	Indo-west Pacific: India; Indian Ocean; Malay Archipelago; Taiwan; Philippines Jones and Hosie, 2016
<i>Balanus cymbiformis</i> Darwin, 1854	<i>Conopea cymbiformis</i> Darwin, 1854	Tuticorin, near Chennai, Tamil Nadu	India; Indian Ocean; Gulf of Aden; Indonesia; North Australia; Malay Archipelago; China; Philippines; South Japan; Fiji Island Jones and Hosie, 2016
<i>Pyrgopsis annandalei</i> Gruvel, 1907	<i>Pyrgopsella annandalei</i> Gruvel, 1906	Andaman Islands, Andaman and Nicobar Islands	India; Israel Achituv and Simon-Blecher, 2006, 2014

(Continued)

TABLE 1 | Continued

Taxon name	Current identity	Type locality	World distribution
<i>Verruca plana</i> Gruvel, 1907	<i>Altiverruca plana</i> Gruvel, 1907	Andaman and Nicobar Islands	Andaman and Nicobar Islands Gruvel, 1907
<i>Verruca cristallina</i> Gruvel, 1907	<i>Cristallinaverruca cristallina</i> Gruvel, 1907	Andaman and Nicobar Islands	India; Indian Ocean; Indonesia; Malay Archipelago; China; Philippines; New Caledonia; Loyalty Islands; Chesterfield Islands; Vanuatu; Wallis & Futuna Islands Jones and Hosie, 2016
<i>Verruca multicosata</i> Gruvel, 1907	<i>Newmaniverruca multicosata</i> Gruvel, 1907	Andaman and Nicobar Islands	India; Indian Ocean; Malay Archipelago Jones and Hosie, 2016
<i>Pyrgoma indicum</i> Annandale, 1924	<i>Galkinius indica</i> Annandale, 1924	Bay of Bengal	India; Indian Ocean; Mergui Archipelago; Kei Islands; Singapore; Malay Archipelago; Vietnam; China; Taiwan; Philippines; Japan; Palau Islands Jones and Hosie, 2016
<i>Creusia spinulosa</i> forma <i>transversalis</i> Nilsson-Cantell, 1938	<i>Cantellius transversalis</i> Nilsson-Cantell, 1938	Andaman and Nicobar Islands	India; Indian Ocean; Malay Archipelago; Taiwan; Philippines Jones and Hosie, 2016
<i>Acasta funicularum</i> Annandale, 1906	<i>Eoatria funicularum</i> Annandale, 1906	Tamil Nadu	Gulf of Mannar Van Syoc and Newman, 2010
<i>Balanus (Megabalanus) squillae</i> Daniel and Ghosh, 1963	<i>Notomegabalanus squillae</i> Daniel and Ghosh, 1963	Tamil Nadu	Tamil Nadu, India Daniel and Ghosh, 1963
<i>Lithotrya nicobarica</i> Reinhardt, 1850	<i>Lithotrya nicobarica</i> Reinhardt, 1850	Andaman and Nicobar Islands	India; Indian Ocean; Australia; Timor; Malay Archipelago; Ream and Dama Islands (Cambodia); Gulf of Thailand; Vietnam; Condor Islands; South China Sea; Philippines; Taiwan; South Japan; Tuamotu, Caroline Islands; Fiji; Paumotu Islands; Pacific Ocean Jones and Hosie, 2016
<i>Balanus patelliformis</i> Bruguère, 1792	<i>Fistulobalanus patelliformis</i> Bruguère, 1792	South coast of India Henry and McLaughlin, 1975	India; Malacca; Java Sea, Malay Archipelago; Philippine Archipelago Jones and Hosie, 2016
<i>Platylepasmultidecorata</i> Daniel, 1962	<i>Platylepas decorata</i> Darwin, 1854	Little Andaman, Andaman and Nicobar Islands	India; West Australia; South China Sea; China; Pacific Ocean, Galapagos Islands Jones and Hosie, 2016
<i>Balanus longirostrum</i> var. <i>krusadaiensis</i> Daniel, 1956	<i>Membranobalanus longirostrum</i> Hoek, 1913	Tamil Nadu	India; Indian Ocean; Singapore; Malay Archipelago; Fu Kuoh Islands, Cambodia; Gulf of Siam; Vietnam; Condor Island; Lien Chien, Tourane; Bay of Along; China Jones and Hosie, 2016
<i>Balanus (Membranobalanus) roonwali</i> Prem-Kumar and Daniel, 1968	<i>Membranobalanus longirostrum</i> Hoek, 1913	Chennai, Tamil Nadu	India; Indian Ocean; Singapore; Malay Archipelago; Fu Kuoh Islands, Cambodia; Gulf of Siam; Vietnam; Condor Island; Lien Chien, Tourane; Bay of Along; China Jones and Hosie, 2016
<i>Pollicipes polymerus madrasensis</i> Daniel, 1953	<i>Pollicipespolymerus</i> Sowerby, 1833	Royapuram, Chennai, Tamil Nadu	India; Mexico, Baja California; North American coast; North Pacific; Aleutian Islands; Russia Van Syoc et al., 2010
<i>Balanus amphitrite</i> var. <i>cochinensis</i> Nilsson-Cantell, 1938	<i>Amphibalanus amphitrite</i> Darwin, 1854	Ernakulam, Cochin, Kerala	Cosmopolitan in tropical and subtropical waters: India; Bermuda and southeast United States to Brazil; England and W Europe to S coast of Africa Red, Black and Mediterranean Seas; Suez Canal; southeast Africa; Indian Ocean; Australia; Indonesia; Singapore; Malaysia; Réam (Cambodia); Gulf of Siam; Vietnam; Condor Islands; Tang Trien (South Annam); Cauda Nhatrang; Hongay, Tonkin; South China Sea; Hong Kong; China; Bohai Sea; Taiwan; Philippines; Japan; South Honsyu, Kyusyu and Ryukyu Islands; Vladivostok; Hawaii; central California to southeast Mexico Jones and Hosie, 2016

At the family level, the highest number of species were reported from the family Poecilasmatidae Annandale (1909) (mostly epibiotic on crustaceans; 27 species, 8 genera), followed by Archaeobalanidae Newman and Ross (1976) (epibiotic in various organisms; 25 species, 12 genera); Balanidae Leach (1817) (mostly intertidal and subtidal, 21 species, 6 genera); Pyrgomatidae Gray (1825) (coral-associated, 15 species, 12 genera); Scalpellidae Pilsbry (1907) (deepwater; 15 species, 7 genera); Lepadidae Darwin (1852) (pelagic; 8 species, 4 genera); Tetraclitidae Gruvel (1903) (8 species, 4 genera); Verrucidae Darwin (1854) (deepwater; 6 species, 4 genera); Chthamalidae Darwin (1854) (intertidal; 6 species, 3 genera); Calantidae Zevina (1978) (deepwater; 5 species, 3 genera); Heteralepadidae Nilsson-Cantell (1921) (deepwater; 5

species, 3 genera); Platylepadidae Newman and Ross (1976) (epibiotic on turtles; 5 species, 2 genera); Chelonibiidae Pilsbry (1916) (epibiotic on turtles; 2 species, 1 genus); and Oxynaspididae Pilsbry (1907) (epibiotic on corals; 2 species, 1 genus). The following families each contain only one species in one genus: Coronulidae Leach (1817) (on cetaceans); Iblidae Leach (1825) (intertidal); Lithotryidae Gruvel (1905) (intertidal); Pollicipedidae Leach (1817) (intertidal); and Sacculinidae Lilljeborg (1861) (parasitic).

State-wide data revealed that the highest number of species were reported from Tamil Nadu (77 species, 39 genera, 15 families) followed by Andaman and Nicobar Islands (62 species, 40 genera, 15 families), Odisha (42 species, 26 genera, 12 families), Maharashtra (18 species, 12 genera, 8 families), West

Bengal (18 species, 11 genera, 6 families), Gujarat (17 species, 11 genera, 7 families), Andhra Pradesh (14 species, 8 genera, 5 families), Lakshadweep Islands (12 species, 8 genera, 7 families), Kerala (11 species, 9 genera, 7 families), Goa (5 species, 4 genera, 3 families), and Karnataka (3 species, 3 genera, 2 families) (**Figure 1** and **Supplementary Appendix Table 2**).

The Eastern India ecoregion has the highest number of species (76 species), followed by Andaman and Nicobar Islands ecoregion (65), South India and Sri Lanka ecoregion (40), Northern Bay of Bengal ecoregion (34), Western India ecoregion (29), and Maldives ecoregion (11) (**Figure 2A** and

Supplementary Appendix Table 1). The low number of species recorded in the Maldives ecoregion is probably due to the low number of studies conducted there.

Most of the coral-associated barnacles (family Pyrgomatidae) were recorded in the Andaman and Nicobar Islands ecoregion (7 species), Eastern India ecoregion (6 species) and Northern Bay of Bengal ecoregion (5 species), which contain a great diversity of coral reefs (Venkataraman and Wafar, 2005; Venkataraman and Raghunathan, 2015; **Figure 2A**). The Maldives ecoregion covers the Lakshadweep Islands, which have extensive coral reefs; however, due to a lack of studies conducted in this ecoregion, only two coral barnacle species were recorded here. No coral-associated barnacles were recorded in the Western India ecoregion, the coastlines of which are characterized by mangroves and soft-bottomed shores and rocky shores in the urbanized Mumbai. There are, however, coral reefs in the Gulf of Kachchh of Gujarat state, but no detailed coral barnacle studies have been conducted there so far. Sponge-associated barnacles (mostly in the subfamily Acastinae) were recorded in the Eastern India, Southern India and Sri Lanka, and Andaman and Nicobar Islands ecoregions. Sponge diversity appears to be high in these three regions, supporting such diversity in barnacles (Ubare and Mohan, 2018; **Figure 2A**).

The deepwater scalpellid, calanticid and verrucid species were relatively extensively recorded in the Andaman and Nicobar Islands ecoregion (**Figure 2A** and **Supplementary Appendix Table 1**), followed by the Eastern India ecoregion (21 species) and the South India and Sri Lanka ecoregion (9 species). These three ecoregions contain deep-sea ecosystems and are often reported to contain deepwater crustaceans (Macpherson et al., 2020; Padate et al., 2020).

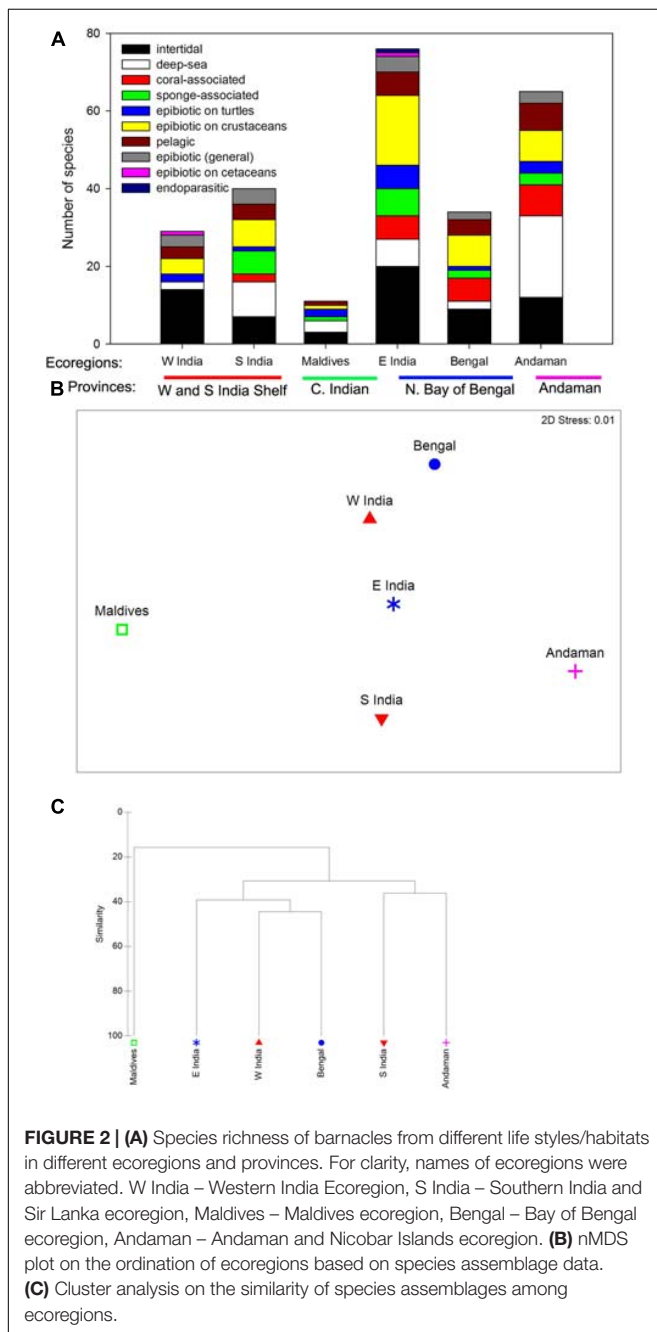
Multivariate Analysis of Species Assemblages

Based on the multivariate analysis, the distribution of the ecoregion clusters does not reflect clear separations among the provinces (**Figure 2B**). The Eastern India, Western India, and Northern Bay of Bengal ecoregions were located in the same cluster with 40% similarity (**Figure 2C**). The Andaman ecoregion is closer to the South India ecoregion. The Maldives ecoregion is separate from the other ecoregions (**Figures 2B,C**).

DISCUSSION

Diagnostic Species in Ecoregions

Some species are specific to certain ecoregions. *Chthamalus barnesi*, *Tetraclita ehsani* are Arabian species and are only recorded in the Western India ecoregion. The stalked barnacle *Lithotrya nicobarica*, which lives in the burrows of calcareous rocks, is only recorded in the Andaman and Nicobar Islands ecoregion, where the intertidal rocks are mostly coral formations and calcareous (Bandopadhyay and Carter, 2017). *Tetraclita squamosa*, which has green shells, is only recorded in the mid intertidal shore of the Eastern India ecoregion and Andaman and Nicobar Islands ecoregion; it is absent from the Western India ecoregion, the mid intertidal shore of which instead



harbors *Tetraclita ehasani* and *Tetraclitella karandei*. These two species were only reported in the Gujarat state in the Western India ecoregion (Trivedi et al., 2021). Differences in diagnostic species between the South India Shelf province (Western India ecoregion) and the Northern Bay of Bengal provinces may be a result of differences in major oceanographic currents between these two provinces. The Bay of Bengal is affected by monsoon gyres. Large anti-cyclonical gyres are generated in the Bay of Bengal during the winter months and weaken in summer (Potemra et al., 1991). On the other hand, the western coast of India faces the Arabian Sea, where the hydrography is affected by the counter flows of the northeast Monsoon Current and the Indian Monsoon Current during different seasons. This resulted in Northern Bay of Bengal province is different from South India Shelf province from the cluster analysis (Figures 2B,C).

Validating Incorrect Species Identification

There are several records of Atlantic cold-water species reported in India that are apparently misidentifications or have taxonomic ambiguities. Daniel (1956) and Krishnamoorthy (2007) recorded *Semibalanus balanoides* (Linnaeus, 1767) in Tamil Nadu. This species is a boreal intertidal barnacle in the Atlantic and Arctic waters (Southward, 2008), and therefore cannot live in the tropical Indian waters. Subsequently, Daniel (1958, 1962) described two new species from Tamil Nadu, namely *Semibalanus madrasensis* (Daniel, 1958) and *S. sinnurensis* (Daniel, 1962), and it is suggested that *S. balanoides* might be either one of these species. Ramamoorthy et al. (2012) identified *Balanus balanus* (Linnaeus, 1758), a boreal-arctic subtidal barnacle in the northern Atlantic (Southward, 2008), from a coral reef invertebrate survey on Pirotan Island, Gujarat, western India. This record, too, may be a misidentification, and hence was not considered as a valid record.

Daniel (1956) identified *Perforatus perforatus* (Bruguière, 1792), another Atlantic species, in Tamil Nadu, but its presence in the Indian waters has not been confirmed. A recent survey in Korea reported this to be an invader in southern Korean waters, probably through ballast water, that has established itself as an ecologically important species (Choi et al., 2013; Kim et al., 2020a,b). Another doubtful record is that of *Balanus glandula* Darwin (1854) from shrimp ponds in Odisha (Nayak and Berkes, 2014; Nayak, 2017); the species is an inhabitant of the temperate northeast and North West Pacific, so we considered the record to be invalid in the present study.

The high shore barnacle *Chthamalus challengerii* Hoek (1883)—a cold-water inhabitant of the West Pacific, including Japan and far-east Russia—was reported by Bhatt and Bal (1960) and Daniel (1972) from Maharashtra. However, a recent review of the genus *Chthamalus* Ranzani (1817) by Southward and Newman (2003) refutes the above record. Only *C. malayensis* was recorded from Tranquebar and Mumbai by Southward and Newman (2003). The presence of *C. malayensis* Pilsbry (1916) along the eastern and western coasts of India was further confirmed from molecular evidence (Tsang et al., 2012; Figures 3A,B). Based on the above, the record of *C. challengerii*

in Maharashtra is believed to actually be *C. malayensis*. In Mumbai, another chthamalid barnacle, *Microeuraphia withersi* (Figures 3E,F), was also recorded. *Microeuraphia* have three teeth on their mandible, whereas *Chthamalus* have four teeth on their mandible. It is therefore not possible that Daniel (1972) identified *Microeuraphia withersi* to *C. challengerii* due to such big morphological differences in mandibles between the two species.

Another chthamalid barnacle, *Chthamalus stellatus* (Poli, 1791), was recorded from Gujarat, North West India by Parmar et al. (2018) and is an intertidal species in the Atlantic Ocean and Mediterranean Sea (Pannacciulli et al., 1997). The record of *C. stellatus* in Gujarat appears to be erroneous. A recent examination of *Chthamalus* from Diu, Gujarat revealed that only *C. barnesi* Achituv and Safriel, 1980 is present on the rocky intertidal zone in this region (Trivedi et al., 2021). Geographical distribution of *C. barnesi* range from North Western India to the Persian Gulf (Shahdadi and Sari, 2011). The record of *C. stellatus* from Gujarat should be *C. barnesi* (Supplementary Appendix Table 1). Similarly, records of *Chthamalus malayensis* in Maharashtra, Gujarat (Karande and Palekar, 1963; Daniel, 1972; Wagh and Bal, 1974) should also be *C. barnesi* (Supplementary Appendix Table 1).

The stalked barnacle *Pollicipes polymerus* Sowerby (1833) is common in the intertidal regions of the northeast Pacific coast (Newman and Abbott, 1980). However, Daniel (1953b) recorded eight specimens of this temperate species attached to floating wood in Tamil Nadu as *Pollicipes polymerus madrasensis*. Newman and Abbott (1980) tried to investigate why such a temperate species is present in India by analyzing variations in the oxygen-18 stable isotope at different positions on its shell plates relative to the basal margin of the type specimen of *P. polymerus madrasensis*. Oxygen-18 stable isotope on shells can reflect the growth pattern of barnacle shells from different climatic environments. Results of the isotope analysis found that the type specimens of *Pollicipes polymerus madrasensis* found in India grew up in cold temperate waters, meaning that this species is not native to India. The present study did not consider this record to be an Indian record.

Tetraclita Schumacher (1817) is a common acorn barnacle on mid-intertidal shores of tropical and subtropical regions (Chan et al., 2007a). In India, several species of *Tetraclita* have been recorded, but a few of these records need clarification. In the Eastern India ecoregion, the green *Tetraclita squamosa* (Bruguière, 1792) was identified by Bruguière (1792) from Tranquebar, east coast of India (Figures 3C,D), which was a Danish colony in the 17th century. The illustration of *T. squamosa* in Bruguière (1792) shows an empty external shell without opercular plates. Bruguière (1792) probably collected an empty shell of *Tetraclita* that had washed onshore. The identification of *Tetraclita* could not be confirmed based on the external shell as identification requires the shapes of the scutum and tergum, and cirral morphology (Chan et al., 2007a). The third author (BKCC) visited several seashores in Tamil Nadu, including Pondicherry and Tranquebar, in 2007 (Figures 3A–D) and attempted to collect specimens of *Tetraclita squamosa* from its type locality for comparative studies, but he did not find any. Fernando (2006, 77) commented that *T. squamosa* “occurs



FIGURE 3 | Indian coastlines and barnacles. **(A)** Mamaharipuram, eastern coast of India. Most of the hard substrates are large boulders. **(B)** *Chthamalus malayensis* is the dominant intertidal species on eastern coast of India. **(C)** Tranquebar, the remnants of Danish fort on coastline. **(D)** Coastline of Tranquebar is composed of large brick walls deteriorated from the Danish fort and large boulders. **(E)** Mumbai, large extent of rocky shores just below the urbanized city. **(F)** *Microeuraphia withersi* on the Mumbai coastline. **(G)** Diu, Gujarat showing the sandstone rocky shores. **(H)** *Tetracilita ehsani* in northwest India. **(I)** *Tetracilitella karandei* at Diu, Gujarat.

not so commonly in Tranquebar and it takes about an hour to locate a single specimen,” thereby suggesting that it occurs in very low abundance and is not common on the Eastern coast of India. The above on-field observations and published reports suggest that the species identity of *T. squamosa* in eastern India is still uncertain.

In the Western Indian ecoregion, the pink *T. rufotincta* Pilsbry (1916) was recorded in Gujarat (Wagh and Bal, 1969;

Daniel, 1972; Fernando, 2006; Parmar et al., 2018). However, a detailed revision of *Tetracilita* in the West Indian Ocean using a molecular approach revealed that *T. rufotincta* is distributed in the Red Sea and the Persian Gulf; *Tetracilita ehsani* Chan et al., 2011 is common in the Gulf of Oman and Arabian Sea (Shahdadi et al., 2011; Tsang et al., 2012). In India, *T. ehsani* and *T. karandei* are only present in Gujarat, and absent south of Gujarat (Trivedi et al., 2021; **Figures 3G–I**).

In the Andaman and Nicobar Islands ecoregion, the pink *Tetraclita japonica formosana* (Hiro, 1939) was recorded in the Andaman and Nicobar Islands (Malakar et al., 2015). *Tetraclita japonica formosana* is only common along the east coast of Taiwan and the Pacific coast of Japan (Chan et al., 2007b; Tsang et al., 2007). The records from Andaman and Nicobar Islands need further investigation and clarification.

Suggestions for Further Studies

The present study revealed that most of the species reported from India are intertidal and epibiotic species of crustaceans and common fishery catches in India. More specialized species, including coral-associated barnacles, remain understudied. Previous coral barnacle records in India were mainly from old publications dating back as much as from 48 to 96 years ago (Annandale, 1924; Nilsson-Cantell, 1938; Daniel, 1972). No coral-associated barnacles were collected from the extensive corals in the Lakshadweep Islands and Minicoy or the Gulf of Kachchh of Gujarat state. The diversity of coral-associated barnacles in Indian waters is clearly a knowledge gap that requires more attention. There are presently no records of barnacles in the superorder Acrothoracica, and only one in the parasitic superorder Rhizocephala (**Supplementary Appendix Table 1**). More research is needed to understand the species diversity of these two superorders.

The Indian Exclusive Economic Zone (EEZ) is characterized by deepwater basins, including the Bay of Bengal to the east and the Arabian Basin to the west. The deepwater barnacle fauna of the Indian EEZ and the Indian Ocean are less studied than their Pacific counterparts. Recent deep-sea sampling in the Indian Ocean revealed the first deep-sea hydrothermal vent barnacles

from the region (Watanabe et al., 2018; Chan et al., 2020). Long-term dedicated exploration of the deepwater basins in the Indian EEZ waters would certainly offer a richer perspective on the species composition of deep-sea barnacles in the region.

AUTHOR CONTRIBUTIONS

JT, KP, BKKC, and VP wrote the manuscript. All authors involved in collection of barnacle specimens and literature review.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2021.657651/full#supplementary-material>

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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