ON THE GEOGRAPHICAL DISTRIBUTION OF INTERSTITIAL FAUNA OF MARINE BEACH SAND

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The earlier workers thought that the interstitial animals of marine beach sand have a limited range of distribution due to their restricted habitat, feeble powers of locomotion, thigmotactic activity and lack of pelagic larval stages in development. But, the taxonomic researches conducted recently in widely separated parts of the world, have shown a remarkable degree of identity of the species reported from different continents. It is interesting to note that the same species could occur in different geographical regions well isolated by the oceans. It is probable that the presentday interstitial fauna is actually a relic of the by-gone ages, before the continents have separated. In the present article, the geographical distribution of certain widely distributed interstitial species is discussed by the author in the light of the above concept.

The interstitial fauna of marine beach sand, discovered and studied in recent years, has made remarkable contribution to systematic zoology during the present century. This fascinating faunal realm, constituting several invertebrate groups of microfauna, is exclusively psammophilous and occupy niches between sand particles. A large number of genera and species have been described as typical inhabitants of the intertidal sands. In the two taxonomic categories, the present paper deals with the zoogeography of the species, which appear more or less cosmopolitan in their distribution. No previous attempt has been made to study the zoogeography of interstitial fauna in detail and the present account shows that such an investigation would be of considerable interest in elucidating problems of zoogeography, in general.

In order to understand the ecological significance of the problem on the geographical distribution of the fauna, it is relevant to ponder certain aspects of their biology in brief. The structure of interstitial environment has a paramount influence on the morphology and bionomics of the populations inhabiting it. Consequently, convergent evolution is seen in different groups of the interstitial community to suit the needs of the environment. Different structural modifications, such as small size, flattened and vermiform body, loss of eyes and pigment, development of special sensory and adhesive organs. etc. have taken place. The fauna is negatively phototactic and this response keeps the animals always at a depth from the surface. The animals exhibit thigmotactic activity during different stages of the life-cycle from the egg to the adult, to withstand wave-action and getting washed into the sea. Investigations have shown that 98 per cent of the species lack pelagic larval stages in development (Remane 1952). There is also a tendency for the suppression of a larval stage, the development tending to be more and more direct. As the binomics of the fauna indicate, the various adaptations ensure propagation of the species in the same habitat and the wave-action on shore is believed to play an important role in their dispersal in a shoreward direction.

The earlier workers thought that the interstitial animals of the marine beach sand have a limited range of distribution due to their restricted habitat, feeble powers of locomotion, thigmotactic activity and lack of pelagic larval stages in development. Accordingly, the oceans are expected to act as barriers for the distribution of the interstitial fauna to distant continents. But, contrary to the earlier thought, the taxonomic researches conducted recently in widely separated parts of the world have shown a remarkable degree of identity of the species reported from different continents. It is interesting to note, how the same species could occur in different geographical regions well isolated by the oceans.

Our knowledge of the geographical distribution of interstitial fauna is still incomplete due to lack of sufficient data from many parts of the world. Most of the work carried out to date is on the European coasts. The greatest gaps in our knowledge concern South America, Africa, Australia, Far East and the islands of the Indo-Pacific region. The taxonomic studies of the interstitial fauna, carried out recently by the present author on the Waltair coast, have revealed the occurrence of several European species on the Indian coast, throwing considerable light on the geographical distribution of the fauna (Chandrasekhara Rao and Ganapati 1968). Of the 420 interstitial species recorded on the Waltair coast, more than 80 species appear to have a cosmopolitan distribution (Figs. 1–4 and Table I). It is possible that many more species would be discovered cosmopolitan, when intensive faunistic surveys are carried out in different parts of the world. Some minor variations of non-specific or even sub-specific importance have, however, been recorded in some interstitial species, which may be considered only as local members of different populations or demes.

Although, in general, the tropics are known to support a rich variety of life compared to the temperate regions, the present zoogeographical knowledge of interstitial fauna is insufficient to formalize anything about their qualitative and quantitative distribution at the various latitudes of the globe. However, as the available data indicate, the bulk of interstitial fauna in temperate and tropical zones is more or less the same, the major groups comprising of Nematoda, Crustacea, Turbellaria, Annelida and Gastrotricha, in the order of their abundance (Chandrasekhara Rao 1969). The density of interstitial populations per unit volume of sand, also does not appear to vary much in temperate and tropical beaches (McIntyre 1968, 1969).

Discussion

The similarity of the faunal element on different continents which are widely separated by vast stretches of the oceans, obviously demands an explanation. In other animal communities, several species are known cosmopolitan where the oceanic currents play an important role in their dispersal, transporting their eggs, larvae or adults to distant regions. But, the interstitial fauna is best developed only in the intertidal zone and there is no evidence of the dispersal of fauna to distant continents through abyssal bottom or by the surface oceanic currents. In this context, Wegener's (1929) important hypothesis of continental drift, which is gaining more positive evidence in recent years, may offer an explanation for the distribution of interstitial fauna. It is probable that the coasts of the present-day continents might

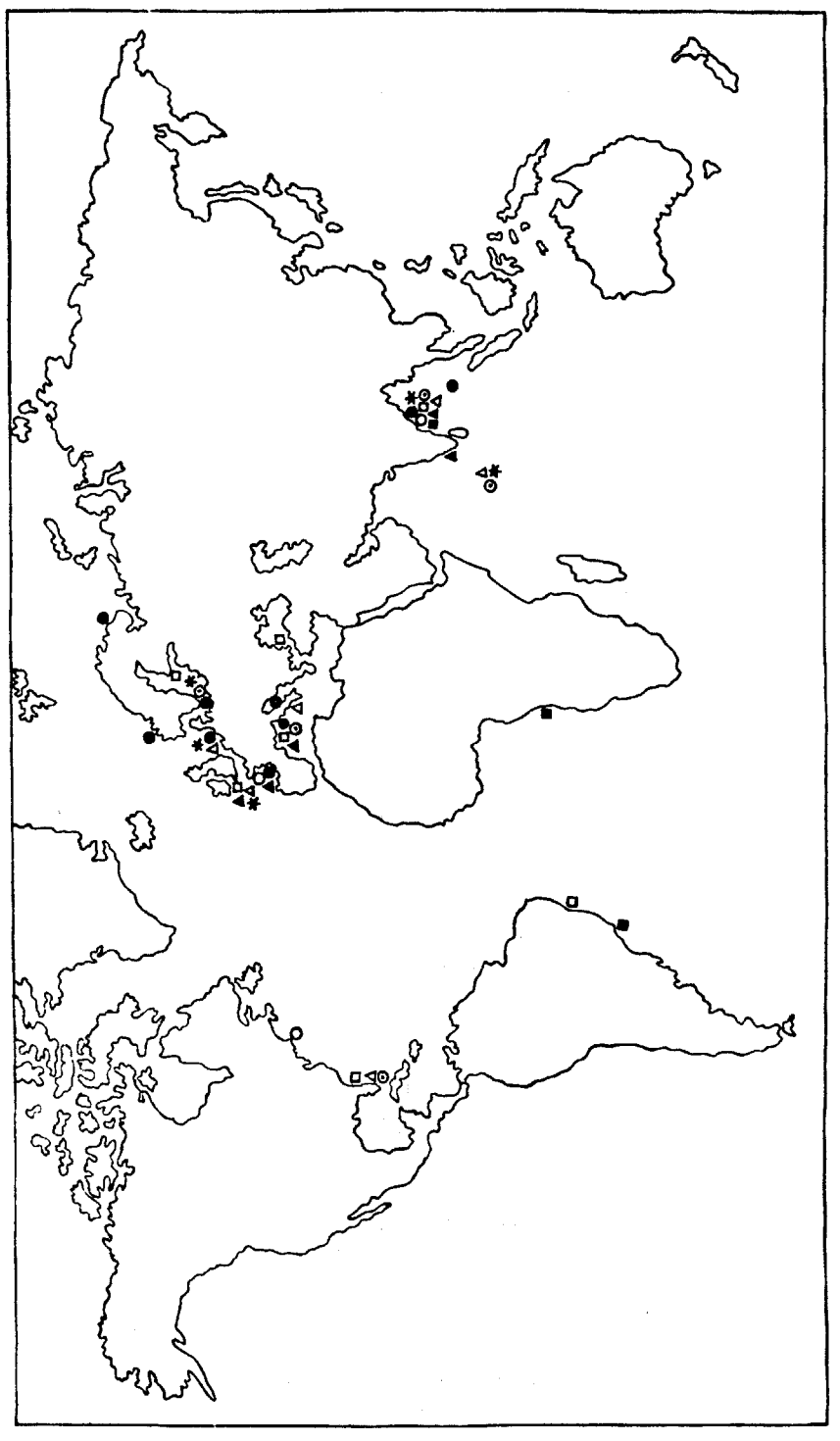

FIG. 1. Map showing the known distribution of some interstitial species. ○—ciliate *Epiclintes ambiguus* ; ●—hydrozoan *Halammohydra octopodides* ; □—turbellarian *Gyratrix hermaphroditus* ; ■—kinorhynch *Cateria styx* ; △—gastrotrich *Acanthodasys aculeatus* ; ▲—gastrotrich *Macrodasys caudatus* ; ⊙—gastotrich *Urodasys viviparus* ; ★—gastrotrich *Thaumastoderma heideri*.

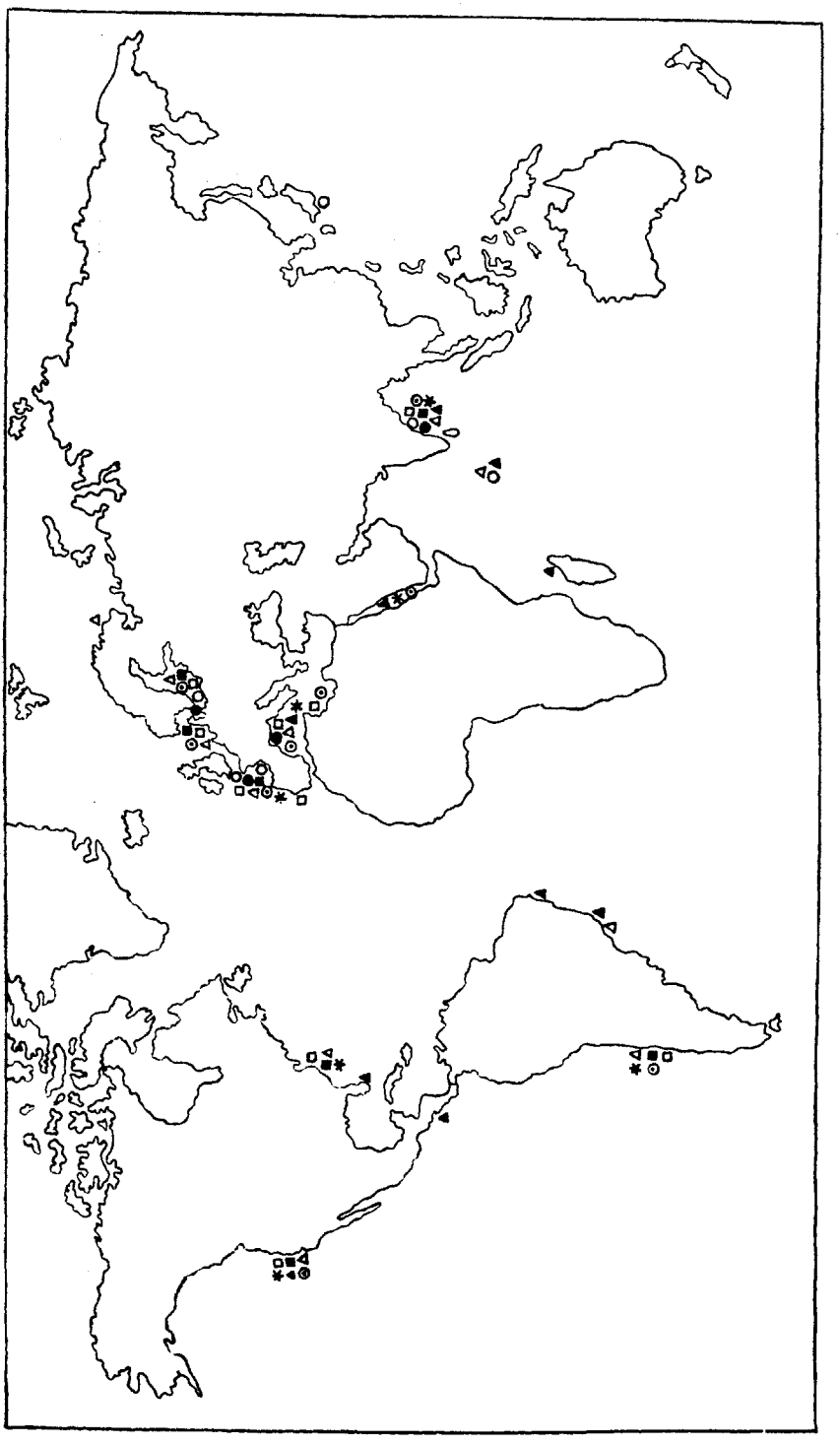

FIG. 2. Map showing the known distribution of some interstitial species. ○—gastrotrich *Aspidiophorus marinus* ; ●—gastrotrich *Xenotrichula velox* ; □—nematode *Dolicholaimus benepapillosus* ; ■—nematode *Oncholaimus brachycercus* ; △—nematode *Monoposthia costata* ; ▲—nematode *Synonchium obtusum* ; ⊙—nematode *Spilophorella paradoxa* ; ★—nematode *Monohystera parva*.

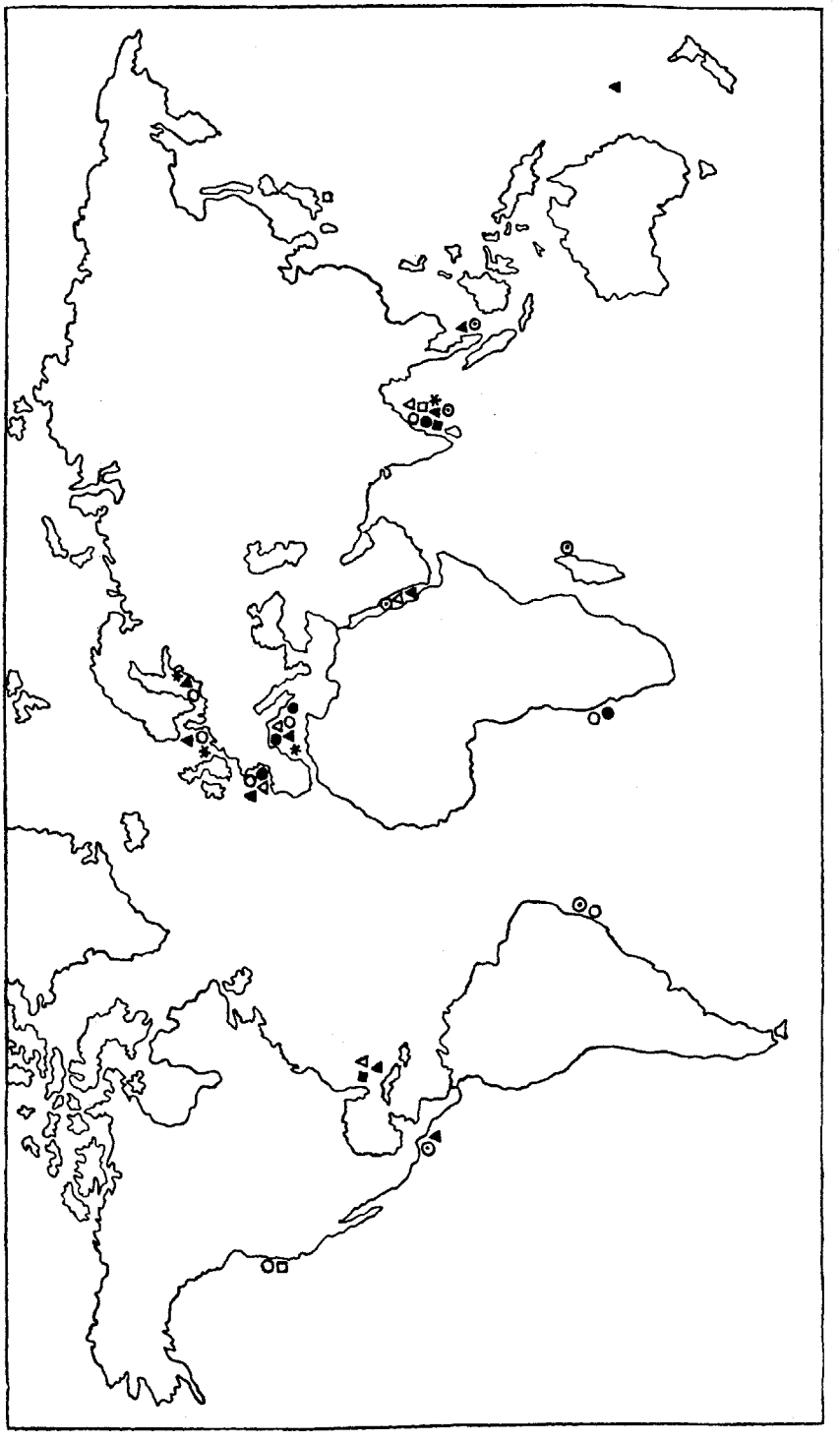

FIG. 3. Map showing the known distribution of some interstitial species. ○—archinnelid *Nerilla antennata* ; ●—archiannelid *Nerillidium mediterraneum* ; □—archiannelid *Trilobodrilus nipponicus* ; ■—polychaete *Eusyllis homocirrata* ; △—polychaete *Petitia amphophthalma* ; ▲—polychaete *Hesionides arenaria* ; ⊙—polychaete *Pisionidens indica* ; ★—oligochaete *Michaelsena subterranea*.

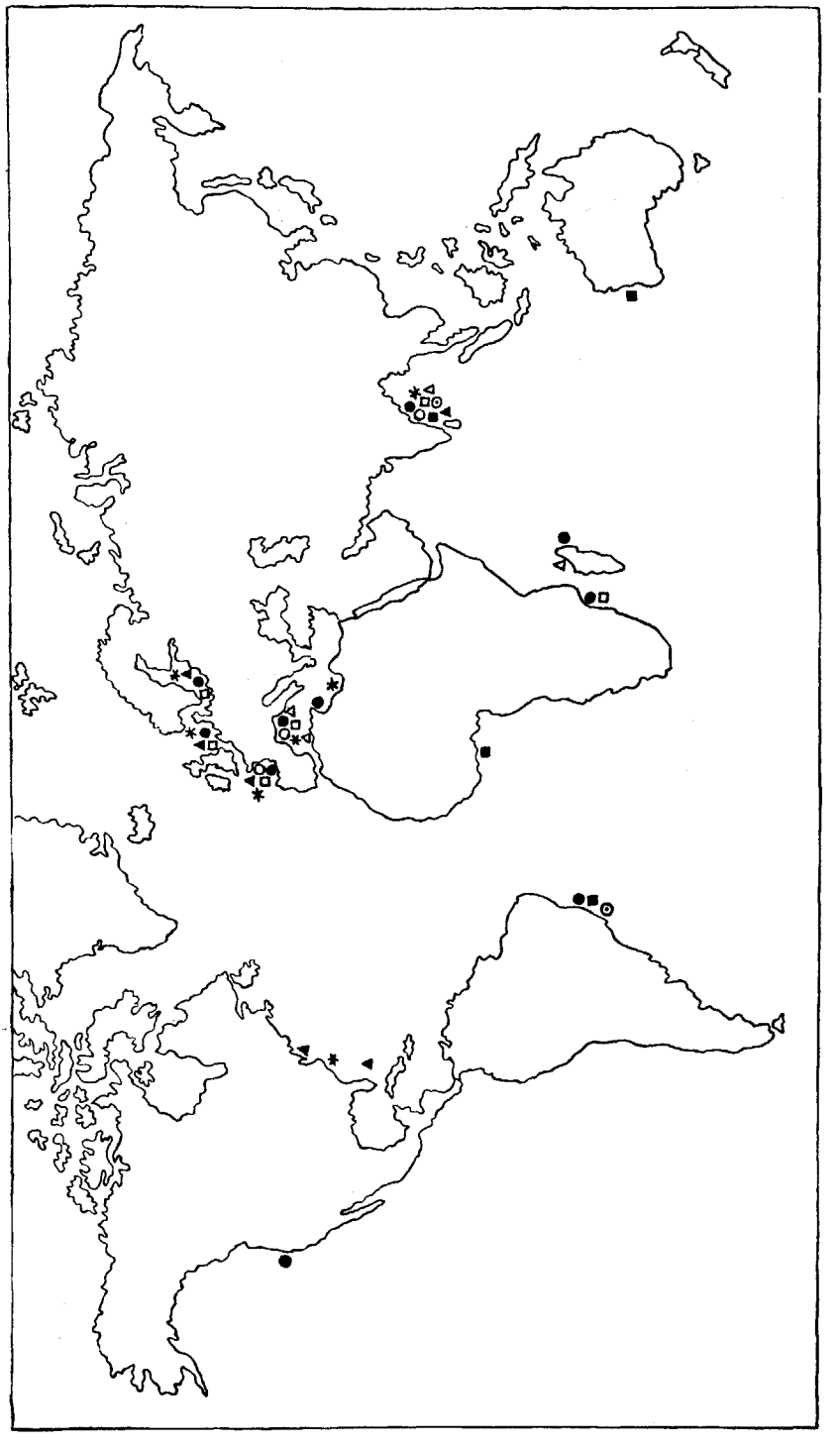

FIG. 4. Map showing the known distribution of some interstitial species. ○—ostracod *Microcythere subterranea* ; ●—copepod *Arenosetella germanica* ; □—copepod *Arenopontia subterranea* ; ■—copepod *Psammopsyllus operculatus* ; △—isopod *Angeliera phreaticola* ; ▲—tardigrade *Stygarctus bradypus* ; ★—acrine *Halacarus anomalus* ; ⊙—nudibranch *Pseudovermis salamandrops*.

TABLE I

Zoogeography of some marine interstitial species, which are most probably cosmopolitan, with records of their occurrence on different continents

Species	North America	South America	Europe	Africa	Asia	Australia
PROTOZOA						
Amphidinium scissum Kofoid and Swezy	California	–	Atlantic	–	Bay of Bengal	–
Coleps tesselatus Kahl	Cape Cod	–	Baltic, Atlantic	–	–do–	–
Geleia fossata Kahl	–do–	–	Baltic, North Sea, Roscoff	–	–do–	–
Tracheloraphis phoenicopterus (Cohn)	–do–	–	Baltic, Roscoff, Banyuls	–	–do–	–
Condylostoma patens (O. F. Muller)	Woods Hole	–	–do–	–	–do–	–
Epiclintes ambiguus (O. F. Muller)	Cape Cod	–	Baltic, Roscoff	–	–do–	–
Lacrymaria olar (O. F. Muller)	Florida	–	Baltic, North Sea, Atlantic, Mediterranean	–	–do–	–
Pleuronema coronatum Kent	–do–	–	Baltic, Roscoff, Banyuls	–	–do–	–
COELENTERATA						
Halammohydra octopodides Remane	–	–	Baltic, North Sea, Atlantic, Mediterranean	–	–do–	–
TURBELLARIA						
Monocelis lineata (O. F. Muller)	Florida	–	Baltic, North Sea, Atlantic, Mediterranean, Black Sea	–	–do–	–
Baltoplana magna Karling	–	–	Baltic, North Sea, Atlantic, Mediterranean	–	–do–	–
Cheliplana vestibularis Beauchamp	–	–	Atlantic, Mediterranean	–	–do–	–
Gyratrix hermaphroditus Ehrenberg	Florida	Brazil	Baltic, North Sea, Atlantic, Mediterranean, Black Sea	–	–do–	–

Vejdovskya pellucida (M. Schultze)	–	–	Baltic, Atlantic, Mediterranean, Black Sea	–	–do–	–
NEMATODA						
Anticoma arctica Steiner	Pacific	Chile, Brazil	North Sea, Atlantic	Red Sea	Arabian Sea, Bay of Bengal	Pacific
A. acuminata (Eberth)	–do–	–do–	Baltic, North Sea, Atlantic, Mediterranean	–do–	–do–	–do
Dolicholaimus benepapillosus (Schulz)	–do–	Chile	Baltic, North Sea, Atlantic, Mediterranean	–	–do–	–
Eurystomina ornatum var. *indicum* Micol and Kreis	–do–	Pacific	Atlantic, Mediterranean, Black Sea	Red Sea	–do–	Pacific
Halalaimus longicollis Allgen	–	Atlantic	North Sea, Atlantic	–do–	Indian Ocean, Bay of Bengal	–
H. supercirrhatus Gerlach	Pacific	–do–	–	–	Indian Ocean, Bay of Bengal	–
Oncholaimus brachycercus de Man	–do–	Pacific	Baltic, North Sea, Atlantic	–	Arabian Sea, Bay of Bengal	–
Oxystomina alpatovi (Filipjev) de Man	–	Atlantic	Atlantic	Red Sea	Indian Ocean Bay of Bengal	–
Syringolaimus striaticauda de Man	Pacific & Atlantic	Pacific & Atlantic	–do–	–do–	Arabian Sea, Bay of Bengal	–
Chromadorina germanica (Butschli)	Pacific	Pacific	Baltic, North Sea, Atlantic, Mediterranean	–do–	–do–	–
Eubostrichus exilis (Cobb)	Atlantic	–	Atlantic	–do–	Indian Ocean, Bay of Bengal	
Halichoanolaimus robustus (Bastian)	Atlantic & Pacific	–	Baltic, North Sea, Atlantic, Mediterranean, Black Sea	–	Bay of Bengal	–
Monoposthia costata (Bastian)	Pacific	Pacific	Baltic, North Sea, Atlantic, Mediterranean	–	Indian Ocean, Bay of Bengal	–
Latronema orcinum (Gerlach)	–	Atlantic	Atlantic	Red Sea	Indian Ocean	–
Sabatiera abyssalis (Filipjev)	–	–	Atlantic, Mediterranean, Black Sea	–	Bay of Bengal	–

TABLE 1—*contd.*

Species	North America	South America	Europe	Africa	Asia	Australia
S. hilarula de Man	–	–	North Sea, Atlantic, Mediterranean	–	–do–	–
Spilophorella paradoxa (de Man)	Pacific	Pacific & Atlantic	Atlantic, Mediterranean	Red Sea	Bay of Bengal	Pacific
Synonchium obtusum Cobb	Pacific & Atlantic	Atlantic	Mediterranean	–do–	Indian Ocean, Bay of Bengal	–
Camacolaimus prytherchi Chitwood	–do–	Atlantic & pacific	–	–	Indian Ocean, Bay of Bengal,	– –
Cytolaimium exile Cobb	Atlantic	–	–	–	Indian Ocean, Bayof Bengal	–
Monhystera disjuncta Bastian	Pacific	Pacific	Baltic, North Sea, Atlantic, Mediterranean	–	–do–	–
M. parva (Bastian)	Atlantic & Pacific	–do–	–do–	–do–	–do–	–
Rhynchonema cinctum Cobb	–	–do–	–	–do–	Arabian Sea, Bay of Bengal	–
Steineria pilosa (Cobb)	–	–do–	Baltic	–	–do	–
Theristus acer Bastian	Atlantic & Pacific	–do–	Barents Sea, Atlantic, Mediterranean	–	–do–	–
GASTROTRICHA						
Acanthodasys aculeatus Remane	Florida	–	Baltic, North Sea, Atlantic, Mediterranean	–	Maldives, Bay of Bengal	–
Paradasys hexadactylus Karling	–do–	–	Baltic, North Sea, Atlantic	–	–	–
Macrodasys caudatus Remane	–	–	Atlantic, Mediterranean	Red Sea	Arabian Sea, Bay of Bengal	–
Urodasys viviparus Wilke	Florida	–	Mediterranean	–	Maldives, Bay of Bengal	–

Turbanella cornuta Remane	Pacific	–	Baltic, Atlantic, Mediterranean	–	–	–
Paraturbanella dohrni Remane	Florida	–	–do–	–	–	–
Thaumastoderma heideri Remane	–	–	Baltic, North Sea, Atlantic	–	Maldives, Bay of Bengal	–
Tetranchyroderma megastoma (Remane)	–	–	Atlantic, Mediterranean	–	–do–	–
T. apus Remane	Florida	–	North Sea, Atlantic, Mediterranean	–	–	–
Dactylopodalia baltica (Remane)	–do–	–	Baltic, Atlantic	–	–	–
Aspidiophorus marinus Remane	–	–	–do–	–	Maldives, Bay of Bengal, Pacific (Japan)	–
A. tentaculatus Wilke	Florida	–	Mediterranean	–	–	–
Xenotrichula velox Remane	–	–	Baltic, Atlantic, Mediterranean	–	Bay of Bengal	–
KINORHYNCHA						
Cateria styx Gerlach	–	Brazil	–	Angola	–do–	–
ARCHIANNELIDA						
Diurodrilus benazzii Gerlach	–	–	Mediterranean,	–	–do–	–
Nerilla antennata Schmidt	Pacific	Atlantic	Baltic, North Sea, Atlantic, Mediterranean	Atlantic	–do	–
Nerillidium mediterraneum Remane	–	–	Atlantic, Mediterranean	–do–	–do–	–
Trilobodrilus nipponicus Uchida and Okuda	Pacific	–	–	–	Bay of Bengal, Pacific (Japan)	–
POLYCHAETA						
Eteonides elongata (Southern)	Atlantic	–	–	–	Bay of Bengal	–
Eusyllis homocirrata Hartmann-Schroder	–do–	–	–	–	Bay of Bengal	–
Hesionides arenaria Friedrich	Atlantic, Pacific	Pacific	Baltic, North Sea, Atlantic, Mediterranean	Red Sea	Arabian Sea, Bay of Bengal	New Caledonia

TABLE I—*contd.*

Species	North America	South America	Europe	Africa	Asia	Australia
H. gohari Hartmann-Schroder	–	–	Mediterranean	Red Sea	Bay of Bengal	–
Petitia amphophthalma Siewing	Atlantic	–	Atlantic, Mediterranean	–do–	–do–	–
Pisionidens indica Aiyar and Alikunhi	Pacific	Atlantic	–	–do– Madagascar	Indian Ocean, Bay of Bengal	–
Plakosysyllis brevipes Hartmann-Schroder	–	–	Atlantic, Mediterranean	Red Sea	–do–	New Caledonia
OLIGOCHAETA						
Enchytraeus albidus Henle	–	–	Baltic, North Sea, Atlantic, Mediterranean	–	Bay of Bengal	–
Fridericia bulbosa (Rosa)	–	–	–do–	–	–do–	–
Michaelsena subterranea Knollner	–	–	–do–	–	–do–	–
OSTRACODA						
Polycope levis Hartmann	–	Brazil	–	–	–do–	–
Cytheridea papillosa Bosquet	Pacific, Atlantic	Atlantic	Baltic, North Sea, Atlantic	–	–do–	–
Microcythere subterranea Hartmann	–	–	Atlantic, Mediterranean	–	Arabian Sea, Bay of Bengal	–
Microloxoconcha compressa Hartmann	–	–	Mediterranean	–	–do	–
COPEPODA						
Arenopontia subterranea Kunz	–	–	Baltic, North Sea, Atlantic, Mediterranean	Mozambique	Bay of Bengal	–
A. spinicaudata (Nicholls)	Pacific	–	–	–	–	Indian Ocean
Arenosetella germanica Kunz	–do–	Brazil	Baltic, North Sea, Atlantic, Mediterranean	Madagascar	Arabian Sea, Bay of Bengal	–

Kleionychocamptoides remanei Noodt	–	–	–	Teneriffa	–do–	–
Nitocra affinis rijekana Petkovski	–	–	Adriatic Sea	–do–	–do–	–
Paramesochra constricta orotavae Noodt	–	–	–	–do–	–do–	–
Psammopsyllus operculatus Nicholls	–	Brazil	–	Ghana, Senegal	–do–	Indian Ocean
Ameira parvula (Claus)	Atlantic	Atlantic	Baltic, North Sea, Atlantic, Mediterranean, Black Sea	Mozambique	Arabian Sea, Bay of Bengal	Pacific
Noodtiella arenosetelloides (Noodt)	–	–	–	Teneriffa	–do–	–
ISOPODA						
Angeliera phereaticola Chappuis and Delamare	–	–	Mediterranean	Madagascar	Bay of Bengal	–
MYSIDACEA						
Gastrosaccus sanctus (van Beneden)	Atlantic	–	Baltic, North Sea, Atlantic, Mediterranean, Black Sea	Indian Ocean	Arabian Sea, Bay of Bengal	–
AMPHIPODA						
Harpinia crenulata Boeck	–	–	North Sea, Atlantic, Mediterrenean	–do–	–do–	–
TARDIGRADA						
Batillipes carnonensis Fize	–	–	Mediterranean	–	–do–	–
B. mirus Richters	Atlantic	Atlantic	Baltic, North Sea, Atlantic, Mediterranean, Black Sea	–	Malaysia	–
B. pennaki Marcus	–do –	–do–	Arcachon	–	Bay of Bengal	–
Orzeliscus belopus B. R. Marcus	–	Brazil	Arcachon	–	–	New Caledonia

TABLE I—*Contd.*

Species	North America	South America	Europe	Africa	Asia	Australia
Halechiniscus perfectus Schulz	–	–	North Sea, Mediterranean	–	–	New Caledonia
Stygarctus bradypus Schulz	Atlantic	–	Baltic, North Sea, Atlantic	–	Bay of Bengal	–
Parastygarctus higginsi Renaud-Debyser	–	–	–	Madagas-car	Andamans, Malaysia	–
ACARINA						
Agauopsis brevipalpus (Trouessart)	Atlantic	Brazil	Atlantic, Mediterranean	Mediter-ranean	Bay of Bengal	Pacific
Copidognathus fabriciusi Lohmann	–do–	–	Baltic, Atlantic, Mediterranean	–	–do–	–
Halacarus anomalus Trouessart	–do–	–	–do–	Mediter-ranean	Arabian Sea, Bay of Bengal	–
MOLLUSCA						
Pseudovermis salamandrops B. R. Marcus	–	Brazil	–	–	Bay of Bengal	–
Unela odhneri (Delamare) Marcus	–	–	Mediterranean	–	–do–	–

have once been continuous and at least a part of the present-day interstitial fauna is actually a relic of the by-gone ages before the continents have separated. Since then, several species might have remained practically static, undergoing a retarded evolution, due to scanty variation in the interstitial habitat. Such a "retarded evolution" due to scanty variation in the microclimate, not affected by changes in the macroclimate, has been observed in certain other animal communities like Mallophaga (Insecta). Parallel evolution is a rare phenomenon in nature and is excluded in the interstitial environment due to the absence of identical conditions in beaches all over the world. The sandy beach is a very dynamic habitat and the influence of a similar environment could have led only to convergent development of the diverse animal groups showing various adaptations to suit life in the lacunar system, as briefed earlier. In general, the occurrence of a variety of species on different coasts may suggest that divergent development was more probable than parallel development.

The presence of endemic species and the absence of identical interstitial species in intertidal sands all over the world may possibly be explained due to the following factors : (i) Lack of intensive surveys of the fauna in different parts of the world. The zoogeographical ranges of the fauna will continue to change as more and more areas are investigated. Thus several species now considered endemic may also exist in other regions, revealing their wide geographical distribution, (ii) The present discontinuity of some species may be a secondary condition, which is derived from a primary continuity. Recessions and extinctions also might have taken place leaving behind some of the present species as relics. It is possible that after the continental drift, the climate has now become so different in the shore waters of the various continents that the former common fauna might have partly died out, while a few other new ones have evolved. Thus the endemic fauna might be also of a recent origin, and (iii) Species tolerant to wide fluctuations in the environment might have spread to different parts of the globe, while others are restricted to certain regions due to their susceptibility to such changes. Thus, the faunistic dissimilarities, if any, may possibly be explained by climatic differences and need not contradict the hypothesis of a closer geographical connection between different continents in the past.

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