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Littoral myriapods: a review

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Abstract

Representatives of many terrestrial arthropods groups including myriapods (Pauropoda, Symphyla, Diplopoda and Chilopoda) have been recorded from sea shore habitats. The Chilopoda, notably the Geophilomorpha, have a relatively large number of species from different genera and locations around the world which have been recorded as halophilic. Silvestri (1903) referred to accidentali, indifferenti and genuini and these categories would seem to be useful although there are some species which appear to be halophilic in one region but found inland elsewhere**.** In a survey of relevant literature, problems have occurred in identifying species as halophiles because of lack of precision of habitat details. There seem to be features of geophilomorphs which pre-adapt them to a littoral habitat and to be able to survive transportation in seawater. This could lead both to wide distribution and the occurrence of isolated populations.

Keywords: Myriapoda, seashore, species, adaption

1. Introduction

The first record of a halophilic myriapod seems to be that of Leach (1817), describing *Strigamia maritima* (as it is now known) as 'Habitat in Britannia inter scopulos ad littoral maris vulgatissime'. Johnston (1835) reported *Strigamia accuminata* as common in Berwickshire (Scotland), 'especially on the sea shore' and it seems highly probable that in the latter case he may have actually been referring to *S. maritima*. Parfitt (1866) reported the rediscovery of the species at Plymouth; other early records are from Sweden, Helgoland, Norway, Denmark and Northern France (Hennings 1903) and from Ireland (Pocock 1893). Grube (1872) described a second littoral species, *Hydroschendyla submarina* from St. Malo on the French Channel coast; Thompson (1889) reported this from Jersey and Pocock (1889) drew attention to the existence of specimens from Cornwall in the Natural History Museum, London that had been collected in 1868 but not recognised. The first Mediterranean record of this species seems to be that of Silvestri (1903) from Portici, Italy. Silvestri (1903) also recorded the first halophilic diplopod, *Thalassisobates littoralis*, from the Italian Mediterranean and listed as halophiles the centipedes *Pachymerium ferrugineum*, *Tuoba poseidonis* and *Henia bicarinata* and the millipede *Polyxenus lapidicola*. By this time, Porat (1894) had described *Tretechthus uliginosus* from Cameroun.

Discussions or reports of experiments relating to littoral myriapods were given by Plateau (1890), Hennings (1903), Silvestri (1903), Laloy (1904), Bagnall (1917), Schubart (1929), Cloudsley-Thompson (1948), Crabill (1960), Pereira & Minelli (1993), Pereira (1999). John Lewis carried out work on British species, mostly in the 1960s, and this is referred to in his book (Lewis 1981).

2. Why do terrestrial organisms invade the littoral zone?

In addition to myriapods, a diversity of both insects and chelicerates are represented in the littoral fauna in various parts of the world as reference to Cheng (1976), Hayward & Ryland (1990), NEAT (North East Atlantic Taxa) (Hansson 1998), and ERMS (European Register of Marine Species) (Costello et al. 2001) will show. Since myriapods, insects and most chelicerates are regarded as essentially terrestrial groups and this apparent invasion of the seashore has happened a number of times (in at least six different families of geophilomorph centipedes, for instance) it is useful to consider the possible reasons for this.

Intertidal areas are themselves often highly productive from algal growth and may receive quantities of (mostly) plant material (algae, seagrass, etc.) brought in by the tides (also guano from seabirds). In various stages of decomposition this can provide nutrition for a range of organisms, which in turn, are predated upon by carnivores. There are a number of examples in the literature of what appear to be energy flow from littoral to terrestrial habitats. For instance, Polis & Hurd (1995) report on extraordinarily high densities of spiders on small islands in the Gulf of California which they attribute to energy flow from the marine to the terrestrial food webs and the absence of predation. Polis et al. (2004) discuss the whole issue of trans-boundary transfer between habitats, including that of sea to land. In an extreme case of this, Catenazzi & Donnelly (2007) report on the relationship between the terrestrial desert and the highly productive marine environment at Paracas Bay, Peru. Consumers in this intertidal and nocturnal food web include Collembola, Thysanura, Diptera, Coleoptera, Talitridae, Chilopoda, Solifugi, Aranea, Scorpionidae and Reptilia. Even if, in temperate habitats, there was to be no net energy transfer between marine-littoral and terrestrial food webs at the interface, nevertheless shoreline production broadens the possible resources base and could entice terrestrial animals into the littoral zone. The extremely high densities of the geophilomorph carnivore *Strigamia maritima* observed on some British seashores is very noticeable (personal observations).

Rocky shores provide crevices which could provide not only shelter but may trap air as can burrows in mud and sand. Shingle provides sheltered interstices and the drift line a possible rich, if more temporary, shelter and food resource. Such environments will provide a degree of protection against both weather and predators and a relatively humid environment. In addition, the sea itself will provide an ameliorating effect on climate in the littoral zone and the possible absence of parasites due to unfavourable conditions for their alternate hosts may be factors in favour of entry to this habitat (Lewis 1981). The organisms themselves need to be able to tolerate (or avoid by migration or survival in air spaces) the effect of inundation with its consequential respiratory and osmoregulatory implications.

3. Issues involved in delineating littoral species

Littoral habitats are not necessarily always easy to sample, whether shingle, sandy/muddy shores, salt marsh, mangal or transitory drift lines and in addition to the physical difficulties in extracting littoral species from their substrate some appear to have discontinuous distribution patterns and even within a particular location may, possibly because of varying environmental conditions, show a patchy occurrence. These together with tidal, seasonal or weather induced local migration can make it difficult to collect littoral species.

Other issues include taxonomic ones relating to variability within and between ‘species’ as in the case of *Geophilus gracilis*, *G. fucorum* and *G. algarum* (Lewis 1962) or of synonymy. In addition there is no consistent use of terms such as ‘littoral’ or ‘sea shore’ in different accounts. In practice, very many accounts of Myriapoda from around the world just do not have adequate habitat data to indicate whether they might be littoral or not even though reported from coastal regions or comparatively small islands; some of these are included in the account that follows.

Species that occur on the shore may include both typically terrestrial ones that happen also to occur sometimes on the shore, species that commonly occur on the shore but also inland and species that appear to be exclusively either intertidal or in living in the immediate supra-littoral. Silvestri (1903) distinguished ‘Miriapodi halofili accidentali’, ‘Miriapodi halofili indifferenti’ and ‘Miriapodi halofili genuini’ whilst Schubart (1929) referred to thalassobionte and thalassophile Arten. Silvestri’s categories are probably more useful for our purposes; his accidentals include species such as *Lithobius forficatus*, the indifferent ones such as *Pachymerium ferrugineum* or *Henia bicarinata* which are clearly members of the typical littoral fauna but also occur elsewhere and the ‘genuini’, the, apparently, obligate halophiles. Unfortunately, in many cases there are so few specimens with habitat data recorded to be sure into which category a species should be placed; there are also types which appear to be genuine halophiles in one region but also occur inland elsewhere. Examples of the latter include *Schendyla peyerimhoffi* and *Schendyla monodi*, both apparently exclusively halophilic in NW Europe but recorded inland in Portugal and Spain respectively.

4. The range of littoral myriapods

This survey is derived from the relevant literature and indicates also some species that could also possibly be halophilic but for which there is insufficient habitat data. Since many of these reports are based only on the original descriptions, it would seem unlikely that reference to type material with its location data would add significantly to our knowledge of the species concerned. However, it is quite likely that some references may have been missed. For both Pauropoda and Symphyla the number of species listed here must be more a reflection of the relatively small number of workers with these groups and the difficulties involved in studying them rather than their absence from littoral habitats.

4.1. Pauropoda

R. S. Bagnall (1935a, b) referred to *Allopauropus remyi* (Bagnall, 1935) from below high tide level in Scotland, described from France and probably not exclusively halophilic, *A. danicus* (Hansen, 1902), also from Scotland (also found in non-coastal sites) and *A. thalassophilus* Remy, 1935 from Mediterranean France and Scotland. Bagnall's *A. littoralis* and *A. stepheni* appear to be nomena dubia (Ulf Scheller pers. comm.). Remy (1954) listed three Mediterranean species, *Allopauropus milloti* Remy, *A. kocheri* Remy and *A*. cf. *remyi*. *Amphipauropus rhenanus* (Hüther, 1971) is reported from sand-dunes near the sea in Denmark, Norway and Sweden (Anderssen et al. 2005).

4.2. Symphyla

Bagnall (1911, 1912, 1915) reported *Scolopendrella notacantha* Gervais, 1840 near high water mark, Dee Estuary, *Symphylellopsis subnuda* (Hansen, 1903) on sea banks at Blackhall Rocks and *Symphylella horrida* (probably *S. vulgaris* Silvestri according to Edwards 1959) on sea banks at Hart, a little to the south of Blackhall Rocks, all in northern England and apparently not exclusively littoral. Roth & Brown (in Cheng 1976) list *Symphyella essigi* Michelbacher, 1939 from the beach at highest tide level at Point Reyes, California and Scheller & Stoev (2006) report *Symphylella vulgaris* (Hansen, 1903) from an halophilous habitat on the Black Sea Coast of Bulgaria.

4.3. Diplopoda

Thalassisobates littoralis (Silvestri, 1903) is reported from the western Mediterranean, around the British coast and from a single Swedish site (Kime 1990). The same author (Kime 1999) suggested that it may have been introduced to NW Europe. It also occurs on the coast of USA (Virginia, Massachusetts, Connecticut) to which it may have been introduced (Enghoff 1987). *Dolichoiulus tongiorgii* (Strasser, 1973) occurs on the Mediterranean coasts of France and Italy (Enghoff 1992). Both species would appear to be 'halofili genuini'. In addition, *Orinisobates soror* (Enghoff, 1985) is recorded from shingle and debris, Sakhalin and Kuril Islands (Russia) by Mikhaljova (1998) and the polydesmoid *Lissodesmus orarius* is described and reported as coastal down to high tide level (including being in company with intertidal crabs) in Tasmania by Mesibov (2005). The latter (pers. comm.) also describes the introduced *Ommatoiulus morletii* (Lucas, 1860) in large numbers walking over intertidal sand in NW Tasmania in 2007. Golovatch and Kime (2009) describe *Leptoiulus belgicus* (Latzel, 1884) as having been observed in large numbers in dunes and under stones on coastal beaches in the intertidal zone well below the high watermark in Wales. Silvestri (1903) had included *Polyxenus lapidicola* Silvestri, 1903 in his list of halophiles; subsequent records of this species are not exclusively littoral and apparently these actually refer to *Polyxenus macedonicus* Verhoeff, 1952 (R. D. Kime pers. comm.).

Presumably, in suitable conditions, millipedes occur in coastal habitats around the world but either because of their rarity or the difficulty in collecting them, few are recorded. Lawrence (1984) refers to a species of *Chilexenus* (Penicillata) at Port Alfred, South Africa which is 'probably able to tolerate a certain amount of salinity'. Shinohara (1961) lists 6 species of diplopod from the supralittoral at Manazuru, Japan and Takano (1980) includes 7 species, none intertidal, in an account of species from some Japanese seashores. In NW Europe, *Cylindroiulus latestriatus* (Curtis, 1845) is commonly but by no means exclusively found close to the sea shore but not, it seems, intertidally.

4.4. Chilopoda

4.4.1. Scutigeromorpha

Pallas (1772) writes of *Julus araneoides* (*Scutigera coleoptrata* Linné, 1758) as 'insectum pelagicum abamico mihi Navarcho quodam inter susceptos in Oceano Atlantico Fuci natatis fasciculos'. Scutigeromorphs are seen in coastal localities in various parts of the world. In Jersey *S. coleoptrata* has been collected amongst large pebbles above high water mark and seems to occur in similar situations on the French Channel coast (Barber 2006).

4.4.2. Lithobiomorpha & Scolopendromorpha

In the British Provisional Atlas (Barber & Keay 1988) some 10 lithobiomorphs and *Cryptops hortensis* (Donovan, 1810) are all recorded at least once from seashore sites. These include both the ubiquitous *Lithobius forficatus* (Linné, 1758) and also *Lithobius melanops* Newport, 1845, a species also common in gardens and similar disturbed sites. None of the species, however, appear to be truly halophilic. Takano (1980) shows *Lithobius ellipticus* Takakuwa, 1939 as intertidally recorded in his Fig. 4. In an account of myriapods from Nouvelle-Calédonie, Demange (1963) described a new species, *Campylostigmus plessisi*, a halophilic scolopendromorph, possibly the first one of these to be reported.

4.4.3. Geophilomorpha

At least six, possibly more, of the families of Geophilomorpha contain genera, one or more of whose species appear to occur in the littoral zone (Tab. 1).

Tab. 1 Geophilomorph families and genera containing littoral or possible littoral species.

Family	**Genera with littoral species**	**Genera with possible littoral species**
Mecistocephalidae	*Mecistocephalus*	
Oryidae		*Orphnaeus*
Himantariidae		*Gosothrix*, *Stigmatogaster*
Schendylidae	*Hydroschendyla*, *Nyctunguis*, *Pectiniunguis*, *Schendyla*, *Schendylurus*	*Bimindyla*, *Nesonyx*, *Thindyla*
Ballophilidae	*Ballophilus*, *Caritohallex*	*Ityphilus*
Lintotaeniidae	*Strigamia*	
Dignathodontidae	*Henia*	
Geophilidae	*Erithophilus*, *Geophilus*, *Lionyx*, *Mixophilus*, *Pachymerium*, *Polycricus*, *Tuoba*	*Diphonyx*
Aphilodontidae		*Aphilodon*

NW Europe: A number of halophilous geophilomorphs ('halofili genuini' or 'halofili indifferenti') have been recorded from North West Europe (Tabs 2a, 2b). *Schendyla monodi*, known as a littoral species only from France but from an inland site in Spain, may be the same as *Schendyla viridis* Verhoeff, 1951 from Mont Soratte (Demange 1961).

Of some interest is the geographical distribution of *Pachymerium ferrugineum*, a species widespread in Europe and recorded from many locations around the world. In Northern Europe coastal areas, especially seashores, are the preferred habitat but it is widespread inland elsewhere. An account of its life history and ecology were given by Palmen & Rantala (1954). In Scandinavia the species tends to have a more easterly distribution contrasted with the more western *Strigamia maritima* (Andersson et al. 2005) and there are only three British records, all from seashore shingle (Barber & Keay 1988). It has recently been recorded from the seashore in Brittany (Iorio 2005) and is known both from the French Atlantic Coast and inland in France (Iorio 2007, 2008) and the Netherlands (Berg 1995).

Barber & Keay (1988) recorded a further nine geophilomorphs (in addition to those listed) with some seashore records from the British Isles.

Tab. 2a Littoral Geophilomorpha (Geophilidae) recorded from NW Europe.

Species	**Distribution**	**Localities**	**Habits**	**Reference**
Geophilus algarum Brölemann, 1909 *	French Channel and Atlantic Coasts	Brittany, Chausey Is., Basse Normandie, Pays-de-la-Loire	Littoral	Brolemann (1930)
Geophilus algarum var. *decipiens* Brolemann, 1930	French Channel and Atlantic Coasts	Ponte-de-la-Roque, Manche;	Littoral	Brolemann (1930)
		Baie d'Arcachon, Gironde		Demange (1961)
Geophilus gracilis Meinert, 1898 (*Geophilus fucorum seurati* Brolemann, 1924)	Great Britain, Ireland, Brittany	S.W.England, Wales, Isle of Man, Ireland, Brittany	Littoral, stones on estuarine mud, etc.	Barber & Keay (1988), Iorio (2006)
Geophilus pusillifrater Verhoeff, 1898	Great Britain, Brittany	Sussex, SW England, Brittany	Few records, apparently littoral. Originally described by Verhoeff from an inland locality in Herzegovina	Barber & Keay (1988), Iorio (2006)
Geophilus flavus (De Geer, 1778)	Widespread in Europe	Various littoral records	An essentially terrestrial species which can occur on the sea-shore	Barber & Keay (1988)
Pachymerium ferrugineum (C. L. Koch, 1835)	Widespread	Coastal habitats preferred in Northern Europe	Widespread throughout Europe. 3 coastal shingle records only from the British Isles	Barber & Keay (1988)

* The *G. algarum* of Bagnall (1917) from Northern England were definitely not this species; possibly immature *Strigamia maritima* (Eason 1961)

Tab. 2b Littoral Geophilomorpha (Schendylidae, Lintotaeniidae, Himantariidae) recorded from NW Europe.

Species	**Distribution**	**Localities**	**Habits**	**Reference**
Hydroschendyla submarina (Grube, 1872)	Eastern Atlantic, Mediterranean, Bermuda	Scandinavia to North Africa	In crevices at or below high water mark	Barber (2009)
H. submarina var. *egregia* Latzel, 1890	Channel Islands	Described from Jersey	Littoral, rock crevices	Latzel in Moniez (1890)
Schendyla monodi (Brolemann, 1924 (? = *S. viridis*)	French, Channel & Atlantic Coasts, Spain	Nr Roscoff Baie d'Archeron	Estuarine, Salt marshes, Inland in Spain	Brolemann (1924), Demange (1961), Barace & Herrera (1980)
Schendyla peyerimhoffi (Brölemann & Ribaut, 1911)	Great Britain, Brittany, Portugal, Morocco, Canary Islands	South & West Britain, Brittany	Shingle, rock crevices & under stones on estuarine mud, Inland in Portugal	Barber (2009), Iorio (2006), Machado (1952)
Strigamia maritima (Leach, 1817)	Eastern Atlantic	Scandinavia, Germany, Netherlands, British Isles, Northern France	In shingle, under stones, in crevices, etc. Seems to be able to tolerate more or less freshwater conditions (Armitage 1982)	Andersson et al. (2005), Barber & Keay (1988), Berg (1995), Brolemann (1930), Hennings (1903), Rosenberg (1982), etc.
Stigmatogaster subterranea (Shaw, 1789)	NW Europe etc.	NW & Central Europe, Newfoundland	Widespread in woodland in Britain but has been recorded from littoral sites from Cornwall to W Scotland	Barber & Keay (1988) etc.

Mediterranean Sea and Adjacent Areas: The species described from Mediterranean, Black Sea and Dead Sea coasts are listed in Tabs 3a and 3b. Possible other Mediterranean halophiles include *Diphonyx conjungens* (Verhoeff 1898) where early records (Verhoeff, 1941) suggest it as a littoral species but it has been subsequently recorded at many inland sites, up to 1800 m (Bonato et al. 2008), *Geophilus naxius* Verhoeff, 1901, thallassobionte according to Schubart (1929) but found in Crete between 100 and 1500 m; mainly in altitudes above 1500 m (Simaiakis et al. 2004), *Schendyla mediterranea* Silvestri, 1898 frequently recorded from coastal localities (but it is not clear if actually in littoral habitats) but often found in inland in truly montane localities as well (L. Bonato pers. comm.). *Stigmatogaster dimidiata angusta* Latzel, 1886 (now regarded as synonymic with *Stigmatogaster dimidiata* (Meinert, 1870)), reported from Pyrénées-Orientales by Brolemann (1930), was described by Chamberlin (1960) as 'a form of known littoral habits' but there seems to be no other reference to such habits in this species. *S. dimidiata* is also recorded from Alpes-Maritimes (up to 400–450 m) and Algeria but is not a littoral species in the sense of being halophilous or halobiontic (E. Iorio pers. comm.).

Tab. 3a Littoral Geophilomorpha (*Geophilus, Tuoba*) recorded from the Mediterranean Region.

Species	Distribution	Localities	Habits	Reference
Geophilus fucorum Brölemann, 1909	Mediterranean	Littoral des Alpes Maritimes; Banyuls-sur-Mer,	Vit sur les grèves et dans les cordons de varech battus par les vagues	Brolemann (1930)
		Insular Greece, France, Italy, Corsica		S. Simaiakis pers. comm.
Geophilus gracilis Meinert, 1870 *(G. fucorum seurati* Brolemann, 1924)	Mediterranean	Algeria, La Pérouse		Brolemann (1930)
Tuoba poseidonis (Verhoeff, 1901)	Mediterranean	Circumméditerranéen et Nord-Africain	Sur les grèves et dans les cordons littoraux de vareche du littoral médterranéen de France	Brolemann (1930)
		France including Corsica, Italy (including Sardinia & Sicily), Slovenia, Greece, Malta	Under stranded remains of *Posidonia* sp	Zapparoli et al. (2004)
	Dead Sea	Dead Sea		Zapparoli et al. (2004)

Africa (Non-Mediterranean): Tab. 4 lists four species, two from the Red Sea Sudan, one from Cameroun and one probable halophile from South Africa. According to Lawrence (1984) no true semi-marine forms seem to live along the South African coasts but a likely halophile (based on name & location) had been described by that author (Lawrence 1963) as *Aphilodon maritimus* (Lawrence, 1963) and it seems highly improbable that there are no littoral geophilomorphs on the coast of this region.

Other possible halophiles from Southern Africa but with insufficient habitat data are *Geoperingueyia grandidens* Lawrence, 1963 (Qolora River Mouth, Transkei), *Mesoschendyla monopora* (Attems, 1909) (Possesion Is, S. of Luderitz Bucht, etc.), *Schendylurus australis* (Silvestri, 1907) (Port Elizabeth, Cape) and *Geoperingueyia conjugens* Attems, 1928 (Grahamstown).

South Atlantic Islands: *Tuoba ashmoleorum* Lewis, 1996 was collected amongst basaltic outcrops, Shelly Beach, Ascension Island (Lewis 1996). *Tuoba benoiti* (Matic & Darabantu, 1977) from St. Helena was found at above 300 m, i.e. not a littoral record (Ashmole & Ashmole 2004). Possibly it also occurs on the shore there**.** Although the genus *Tuoba* is often regarded as containing largely littoral forms this is certainly not the case for all species.

Tab. 3b Littoral Geophilomorpha (other genera) recorded from the Mediterranean Region.

Species	Distribution	Localities	Habits	Reference
Pachymerium ferrugineum	Mediterranean	Mediterranean Region etc.	Tout le littoral jusque dans les cordons de varech;	Caziot (1925)
			Se rencontre souvent sur les grèves en compagnie de *Henia bicarinata*	Brolemann (1930)
			Variety of habitats including seashore but seldom in woodlands in Italy	Minelli & Iovane (1987)
P. ferrugineum insulanum Verhoeff, 1902	Mediterranean	Crete & other Aegean Islands; Only one inland record from Crete	Sand dunes or typical coastal phryganic ecosystems (satellite islands of Crete). Associated with *Posidonia* and/or *Tamarix* sp. & *Phragmites* sp.	S. Simaiakis pers. comm.
	Black Sea	Bulgaria	Unter Steinen, unter angespülten Braunalgen *Cystosira barbata* und Seegrass (*Zostera marina*)	Kaczmarek (1969)
Henia bicarinata (Meinert, 1870)	Mediterranean	Algeria, Canary Islands	Espèce localisée sur les grèves, notamment les cordons littoraux de vareche	Brolemann (1930)
		Italy	Euriecious, sometimes recorded from the seashore, 0–700m	Minelli & Iovane (1987)
		Macaronesia, Maghreb, Croatia, Bosnia-Herzegovina, Greece, Malta	Coastal areas in stranded *Posidonia*; also inland	Zapparoli et al. (2004)
Hydroschendyla submarina	Mediterranean	France, Greece (Mainland & Islands), Italy (including Sicily & Sardinia), N. Africa	Under stranded remains of *Posidonia* sp. and near brackish marshes	Zapparoli (2002)

Tab. 4 Littoral Geophilomorpha recorded from Africa (other than the Mediterranean region) & India.

Species	**Distribution**	**Localities**	**Habits**	**Reference**
Tuoba poseidonis	Red Sea	Egypt Somalia		Zapparoli et al (2004)
Tuoba sudanensis (Lewis, 1963)	Sudan	Sudan	Described originally as a sub-species of *T. littoralis*	Lewis (1963)
Tretecthus uliginosus (Porat, 1894)	Cameroun	Bekolongo River near Bibundi	Under stones on sandbank, a site flooded by both fresh & salt water	Porat (1894)
Aphilodon maritimus (Lawrence, 1963)	South Africa	Umhalali, North Coast, Natal & Qolora River Mouth, Transkei	Presumed to be halophilic on basis of location & name given	Lawrence (1963)
Mixophilus indicus (Silvestri, 1929)	India	Madras; Cooum River	Animals found when searching for the annelid *Lycastis*; coiled within loose mud in the same way as these polychaetes	Silvestri (1929)

India: A single species. *Mixophilus indicus* (Silvestri, 1929) has been recorded (see Tab. 4).

East Asia: Eight species found in the littoral zone have been recorded for Japan, one of these also for Taiwan and South Korea (Tab. 5). Of these, *Mecistocephalus manazuensis* is probably synonymous with *M. nannocornis* Chamberlin, 1920, most records of which are non-coastal (Uliana et al. 2007). Shinohara (1961) and Takano (1980) also both also recorded a range of species from the supralittoral.

North America: Six species are recorded from littoral sites on the west coast of North America (Tab. 6a) but only half that number from the eastern and southern coasts and one from Bermuda (Tab. 6b). If this is not due to missed published material, it presumably reflects lack of collecting activity along that coast as it is difficult to conceive of there not being halophilic geophilomorphs along the eastern seaboard.

Geophilus vittatus (Raffinesque, 1820), is a very widespread terrestrial species, occurring in much of the United States including California (Crabill 1954). Chamberlin (1912a), amongst other records, included 2 specimens of this collected on a sandy beach at Pacific Grove, California (as *G. rubens*) whilst amongst the Crabill records is another Chamberlin one (1909) from a sea cliff at Long Island, New York (as *G .deducens*). It would thus seem likely to be a ‘halofil accidentali’.

There are a number of North American species from likely locations that could be halophilic but without habitat data including *Polycricus marginalis* (Meinert, 1866), *Nyctunguis montereus* (Chamberlin, 1904), *Polycricus floridanus* (Cook, 1899), *Ityphilus lilacinus* Cook, 1899*, Nyctunguis catalinae* (Chamberlin, 1912*), Pectiniunguis nesiotes* Chamberlin, 1923*, Pectinuiniunguis amphibius* Chamberlin, 1923, *Nyctunguis mirus* Chamberlin, 1923, *Nyctunguis danzantinus* Chamberlin, 1923, *Nesonyx flagellans* Chamberlin, 1923, *Gosothrix insulanus* Chamberlin, 1923, *Geophilus nicolanus* Chamberlin, 1940, *Pectiniunguis catalinesis* Chamberlin, 1941.

Tab. 5 Littoral Geophilomorpha recorded from Japan, Korea & Taiwan.

Species	**Distribution**	**Localities**	**Habits**	**Reference**
Strigamia japonica (Verhoeff,1935)	Japan Kuril Islands	Hokkaido, Honshu, Shikoyu, Kyushu, Ryukyus (Loochoo) Kuril Islands		Verhoeff (1935), Paik (1961a)
	South Korea, Taiwan	South Korea, Quelpart Is. Kwan Tze Ling		Paik (1961a), Paik (1958), (1961b), Wang (1959)
Tuoba japonicus (Fahlander, 1935)	Japan	Misaki	'im Littoraland oder darüber, unter Holzstücken gesammelt'	Fahlander (1935)
Tuoba kozuensis Takakuwa,1934	Japan	Kôzu (no data) Kanto Region	- Intertidal	Takakuwa (1934) Takano (1980)
Tuoba littoralis (Takakuwa,1934)	Japan	Manazuru	Seashore	Shinohara (1961)
Tuoba tiosanus Takakuwa, 1934	Japan	Tyosi & Micronesia(no data) Kanto Region	- Intertidal	Takakuwa (1934) Takano (1980)
Mecistocephalus manazurensis Shinohara,1961	Japan	Manazuru	Seashore	Shinohara (1961)
Mecistocephalus satumensis Takakuwa,1938	Japan	Kanto Region	Intertidal	Takano (1980)
Pachymerium ferrugineum	Japan	Kanto Region	Intertidal	Takano (1980)

Caribbean: Several species have been described from this region which appear to be halophiles (Tab. 7). Other possible littoral species whose descriptions lack habitat data include *Bimindyla gertschi* (Chamberlin 1952), which, in its description is suggested, might have a habitat similar to *Hydroschendyla submarina* (Chamberlin 1952b), *Ityphilus lilacinus* Cook, 1899 and other species of *Ityphilus*, *Pectiniunguis insulanus* (Brolemann & Ribaut 1911), *Polycricus marginalis* (Meinert 1866), *Schendylops varipictus*, (Chamberlin 1950), *Tuoba culebrae* (Silvestri 1908).

South America: Three definite littoral species are reported from the South American mainland and two species from the Galápagos Islands which have occurred in seashore sites (Tab. 8). There are also two possible halophiles from Juan Fernandez, *Tuoba baeckstroemi* (Verhoeff, 1924): *'*Zahlreiche Stücke von Santa Clara bei Masatierra unter Steinen, 6.VIII.17', *Tuoba laticollis* (Attems, 1903): 'Santa Clara, unter Steinen im Walde', 'auf Masatierra 6 St. in Baumstücken, 3.IV.17' (Attems 1903, Verhoeff 1924)**.** As already indicated, although the genus *Tuoba* as presently defined includes a number of apparently more or less exclusively littoral species it does appear that certainly not all species come in that category.

Tab. 6a Littoral Geophilomorpha recorded from North America (West Coast).

Species	**Distribution**	**Localities**	**Habits**	**Reference**
Geophilus admarinus Chamberlin, 1952	Alaska	Redd Bay, S. E. Alaska	Numerous specimens taken under stones near the low tide mark	Chamberlin (1952a)
Geophilus becki Chamberlin, 1951	California	Cabrillo Beach nr San Pedro	Under rocks & kelp at water's edge	Chamberlin (1951)
		Pacific Grove, Montery Bay		Haberman (1982, unpub.)
Lionyx hedgepethi Chamberlin, 1960	California	Nr Dillon Beach, Marin County	Under stones between tide levels	Chamberlin (1960)
Nyctunguis heathi (Chamberlin, 1909)	California	Montery County	Fairly common in some areas during the day or on surfaces of rocks at night during low tide. High Intertidal zone on rocky shores	Morris et al. (1980)
		Central California	Common	Ricketts et al. (1985)
	? British Colombia			Austin (2000)
Pectiniunguis americanus Bollman, 1889	Gulf of California	Described from Pichilungue Bay	Essentially littoral in habit though it has been taken some distance inland	Chamberlin (1923)
Pectiniunguis amphibius Chamberlin, 1923	Gulf of California	Danzante & Carmen Is.	Below high tide mark, 'resembling *Hydroschendyla* in its habits'	Chamberlin (1923)

Tab. 6b Littoral Geophilomorpha recorded from North America (Eastern & Southern Coast and Bermuda).

Species	Distribution	Localities	Habits	Reference
Erithophilus neopus Cook, 1899	USA	Florida	Described without habitat information but L.A.Pereira reports seeing it in a collection with *Pectiniunguis halirrhytus* indicating that it is a littoral species.	L.A.Pereira pers. comm.
Pectiniunguis americanus Bollman, 1889	USA, Mexico	Florida, Mexico (East Coast)	Littoral habits & prevalence about the Mexican coasts under piles of driftwood, etc.	Chamberlin (1913, 1914)
Pectiniunguis halirrhytus Crabill, 1959	USA, Mexico	Florida, Mexico	A number of records from under beach drift; some records from below HTM in seaweed	Pereira et al. (1999)
Hydroschendyla submarina	Bermuda	Bermuda	Upper Intertidal & low supra-littoral region in porous stone and in crevices; widespread but difficult to find	Sterrer (1986)

Tab. 7 Littoral Geophilomorpha recorded from the Caribbean area

Species	Distribution	Localities	Habits	Reference
Ballophilus riveroi Chamberlin, 1950	Tortola	Sea Cow Bay	Berlese sifting; one adult male closely agreeing with Chamberlin's description.	Crabill (1960)
Caritohallex minirrhopus Crabill, 1960	Tortola	Sea Cow Bay	Berlese sifting of beach debris	Crabill (1960)
Polycricus bredini (Crabill, 1960)	Tortola	Sea Cow Bay	Berlese sifting of beach drift	Crabill (1960)
Schendylops virgingordae Crabill, 1960	Virgin Gorda	Prickly Pear Island	Berlese samplings of beach drift	Crabill (1960)
	Martinique	Le Diamant	'Forêt domaniale, sur la plage'	Pereira (1999)

Tab. 8 Littoral Geophilomorpha recorded from South America.

Species	**Distribution**	**Localities**	**Habits**	**Reference**
Pectiniunguis bollmani (Pereira et al. 1999)	Venezuela	Cayo Sombrero, State of Falcón	Under inter-tidal rocks and under wood debris on a sandy beach	Pereira et al. (1999)
Schendylops virgingordae Crabill, 1960	Venezuela	Playa Mero, State of Falcón (Parc National Morrocoy)	'Dans une zone de mangroves, lagunes et îlots côtiers formés par accumulation de sable, coraux et coquilles molluscques'	Pereira (1999), Pereira & Minelli (1993)
Thindyla littoralis (Kraus, 1954), (= *T. pacifica* (Chamberlin, 1955))	Peru	Don Martin Is Departements of Lima, Ica & Arequina	Limited to littoral zone	Kraus (1954), Pereira & Hoffman (1995) & others
Pectiniunguis albemarlensis Chamberlin, 1914	Galápagos Is.	Bahia Darwin	*Cryptocarpus* [1], beach strand [1]; other sites to 600m	Shear & Peck (1992)
Pectiniunguis krausi Shear & Peck, 1992	Galápagos Is.	Isla Santa Cruz	Juvenile, Intertidal; other sites to 1100m	Shear & Peck (1992)

Australia New Zealand and Pacific Islands: Three species of *Tuoba* are recorded from the seashores of Australia, one of which occurs on Hawaii, and a further species from New Zealand (Tab. 9). In a pitfall study of the strandline fauna, large numbers of geophilomorphs (probably *Tuoba laticeps*) were collected from beaches all around Tasmania (Richardson et al. 1997, 1998). Chamberlin (1920) recorded a range of geophilomorph species, some of which might be halophiles, from New Zealand including 5 species of *Zelanion*, from such sites as Day's Bay and Lyell Bay but all without habitat data. Possible halophiles from Fiji but described without habitat data are *Ballophilus fijiensis* Chamberlin, 1920 and *Pectiniunguis fijiensis* (Chamberlin, 1920).

Tab. 9 Littoral Geophilomorpha recorded from Australasia & Hawaii.

Species	**Distribution**	**Localities**	**Habits**	**Reference**
Tuoba sydneyensis (Pocock, 1891)	Australia, New Caledonia, New Britain, Solomon Islands	Western Australia, New South Wales	Seagrass litter, under rocks, under crab exuviae, under logs. All littoral or on beach.	Jones (1998)
Honuaphilus alohanus (Chamberlin, 1926)	Hawaii	Kure Is, Laysan, Pearl & Hermes Reef, Midway (Eastern Is, under driftwood on beach)	'It occurs primarily in littoral habitats and is beach dwelling throughout its range; thus it may have reached the Hawaiian Islands without human assistance' [occurs up to 3200 ft = 950m]	Bonato et al. (2004)
Tuoba laticeps Pocock, 1901	Australia	Western Australia, Tasmania	Under rocks, high tide level, rocks on sand, stones on fine gravel, under stones (strand line), in small cave, etc.	Jones (1998)
Tuoba pallida Jones, 1998	Australia	Western Australia	Silver gull nest, Penguin Is, Rockingham; coast shrub litter 27 km south of Northcliffe	Jones (1998)
Tuoba xylophaga (Attems, 1903)	New Zealand	New Zealand: - North Island - South Island - Stewart Island	On dead bird, on seaweed washed ashore, supralittoral sand, logs on sand, driftwood on fine stony beach, etc.	Jones (1998)
			From sandhills on both islands and Stewart Island	Archey (1936)

4.4.4. Unidentified species

There have been a variety of seashore records of centipedes where the species was not identified e.g. Cape Verde Islands, Galapagos (Crossland 1929), Colombia, Panama, Costa Rica (Polhemus & Evans 1969). This would support the idea that there are further, as yet undescribed, littoral species of geophilomorph or a wider distribution of known species than here described.

5. Physiological adaptions

As indicated earlier, the main physiological issues for terrestrial animals moving into littoral habitats will relate to gaseous exchange and osmoregulation. Animals will be immersed in seawater twice daily for a shorter or longer time depending on their location on the shore-shore although not normally continuous 24 hour immersion. In estuarine conditions there will be changing salinity, generally below that of full sea-water. *Strigamia maritima* seems to be able to tolerate conditions well up river. In estuaries and Armitage (1982) reports it occurring in fresh water. Although there is some published work relating to geophilomorphs, most of this dates back 50 years or more and there seems to be little for other myriapods.

Gaseous exchange: Although there seems to be little published on the physiology of marine millipedes, there are some interesting reports of diplopods surviving immersed in fresh water (Golovatch & Kime 2009). *Serradium semiaquaticum* Enghoff et al., 1997 a troglobiotic species from northern Italy is remarkable in showing modified, broom-like mouthparts, combined with hydrophobic microtrichia in the spiracles and *Myrmecodesmus adisi* (Hoffman 1985) from Amazonia shows plastron respiration in its immature stages. *Aporodesminus wallacei* Silvestri, 1904 and *Cryptocorypha ornata* (Attems 1938) both have a cerotegument for plastron respiration and mouthparts adapted for food uptake under water. Plastron respiration as such has so far not been demonstrated in any marine littoral myriapods.

As an alternative to immersion, some littoral arthropods live in air filled burrows or with a bubble of air trapped in some way e.g. by a web. Although Bonnel (1929) reported that *Mixophilus indicus* trapped a bubble of air in a loop in the posterior end of the body, Sundara Rajalu (1972) was unable to confirm this and there is no clear evidence of littoral myriapods using trapped air bubbles. In any case, as Lewis (1962) pointed out, although newly immersed specimens of *Strigamia maritima* have bubbles of air on their surface these are likely to be rapidly dispersed by movement.

Other than these possibilities, littoral animals will need to be able to either tolerate temporarily lowered oxygen conditions, absorb oxygen directly from sea-water via their body surface or using some sort of ‘gills’, trap air in their tracheal system or in some other way.

Laloy (1903) described how *Strigamia* in sea water took refuge under stones and that bubbles of air could be seen in the openings of the stigmata which quite likely permitted the animals to resist submersion. When it was surprised by the water it floated and then used body movements to swim downwards and shelter under a stone. Suomalainen (1939) had suggested that spiracles of *Pachymerium ferrugineum* might act as physical gills and Lewis (1960 cited in Lewis 1981) described an experiment with nitrogen saturated water that indicated that this could be true for *Strigamia maritima*. Sundara Rajalu (1972) suggested the possibility of cutaneous respiration taking place in *Mixophilus indicus*.

In experiments with this latter species, the same author measured the blood pH of immersed *Mixophilus* which fell from pH 7.2 to pH 6.7 in small specimens of the species and to pH 5.8 in larger ones. After removal from water, oxygen uptake showed a temporary increase, peaking at 3 hours in smaller specimens and at 5 hours in larger ones. He had also looked at the main tracheal trunks of immersed animals which, after being returned to air, showed rhythmic pulsations, the rate being faster in animals immersed longer (Sundara Rajalu 1970). Although pulsation was present in animals that had not been immersed this was at a much slower rate (3–5 pulses min^{-2} compared with about 24 pulses min^{-2} for specimens from a 3-day immersion). The author also looked at a terrestrial species in which he failed to find tracheal pulsation and noticed differences in structure, the tracheal trunks of *Mixophilus* having much swollen trunks, resembling locust air sacs. This would suggest the build up of an oxygen debt as a result of some form of anaerobiosis and the tracheal pulsations being a feature of a recovery phase. Ivan Kos (pers. comm.) reports finding a similar phenomenon when measuring oxygen consumption in the terrestrial lithobiomorph *Lithobius agilis*.

Body Fluid Regulation: Littoral animals need to have mechanisms for regulating body water volume/composition or to be able to tolerate changes in the concentration of their body fluids. For myriapods these are likely to involve either removal of excess ions by some mechanism or tolerance of changing body fluid concentration.

Geophilomorphs have been shown to be more tolerant of both desiccation and immersion than lithobiomorphs. Plateau (1890) described experiments on terrestrial centipedes in which geophilomorphs (*Geophilus flavus*) survived in seawater for 12, 27, 65 hours and in freshwater for 6, 14 & 15 days. He argued that if a terrestrial species could survive in this way there would not be problems of submersion for maritime ones. Hennings (1903) described *Strigamia maritima* as becoming inactive after 24–30 hours and dying after 30–40 hours of total immersion in seawater. Nesrine Akkari (pers. comm.) described a live *Pachymerium ferrugineum* being taken directly from water in a landing net from a shallow lagoon in Tunisia by a colleague who was actually collecting mosquito larvae.

Binyon & Lewis (1963) reported on survival times for *Strigamia maritima* and *Hydroschendyla submarina* in seawater compared with *Stigmatogaster subterranea*. In 10 % seawater survival times were 36–72 hrs, 48–84 hrs and 30–46 hrs for the three species respectively whilst in 100 % seawater the times were 12–24 hrs, 12–36 hrs and 4–8 hrs. They described how the osmotic pressure of the body fluids of all three of these species were about 44–50 % of that of seawater but that when immersed in seawater the Na^+ concentration of *S. subterranea* rose by nearly 70 % whilst those of the others remained nearly constant even after 14 hours. They argued that the animals must have lost water by osmosis. In the case of marine teleosts, this problem of osmotic desiccation is overcome by drinking seawater and secreting excess salt back across the gills. If this is so in the two littoral centipede species, they suggested that enlarged salivary glands could be the site of salt secretion to remove excess Na^+ back into the water.

Interesting contrasts exist between *Strigamia maritima* and *Hydroschendyla submarina* (Lewis 1981). When immersed in seawater, after an initial period of immobility, *S. maritima* becomes active within 2 hours at 16–19 °C whereas *H. submarina* remains more or less stationary overnight. This reflects the fact that *S. maritima* is a mobile species, concentrating in areas that are climatically favourable and have a good food supply. Immersed in seawater, young eggs of *S. maritima* shrink rapidly although older eggs are more tolerant and egg-laying corresponds to minimum spring tides and least stormy part of year (May–June). Males migrate up the beach to deposit their spermatophores and all stadia migrate to the top of the shingle bank to moult. *H. submarina* eggs, on the other hand are impermeable to seawater and in this species egg laying and moulting can take place in the littoral zone (Lewis 1962).

6. Dispersal mechanisms

The present discontinuous distribution of species and genera, their occurrence on isolated islands and their presence on both sides of oceans could be accounted for by (a) Continental drift / Climate change (b) Transport by birds or other animals (c) Aerial dispersal (d) Transport as a result of human activity (e) Passive transport by water (rafting).

(a) Pereira et al. (1997) in discussing zoogeographical aspects of the Neotropical Geophilomorpha suggest that a few taxa have the traits of an old Gondwanian faunal element but describe the bulk of the Neotropical geophilomorphs as belonging to wide-ranging groups, possibly recent immigrants to South America.

Verhoeff (1935) in describing *Strigamia japonica* from Japan, suggested that there may have been a continuous occurrence of a population of *Strigamia* along the Siberian coast during the last warm period which was later broken up by climate change. This was then broken up to give the European and Asian maritime forms.

(b) Transport by birds (zoochory) has been suggested for the freshwater millipedes *Aporodesminus wallacei* Silvestri, 1904 (St. Helena, Sydney, Tahiti, Hawaii) and *Cryptocorypha ornata* (Attems 1938) (St. Helena, Hawaii, Cook Is., the Marquesas, Tahiti, Hong Kong) (Golovatch & Kime 2009). There is no definite evidence of this being a common mechanism for dispersing littoral myriapods but it certainly remains a possibility.

(c) Small organisms are always at risk of aerial transport as dust, etc. is picked up and carried in the atmosphere, possibly for long distances. Flying insects and balooning spiders will especially be likely to be carried aerially. This will not particularly favour seashore species or myriapods. However Megan Short, studying the penicillate millipede *Phryssonotus novaehollandiae* in coastal heathy woodland in Victoria (Australia) suggested (in litt.) that such small animals with their assortment of spines were so easily blown away by wind that aerial dispersal was a possibility.

(d) Dispersal by human activity (anthropochory) is always likely and almost certainly accounts for some of the dispersal of myriapods although animals associated with agriculture or similar practices would seem to be more likely to be spread this way than seashore organisms. A recent study looked at the possibility of transport of organisms to the sub-Antarctic (Whinam et al. 2005) and described various possibilities with cargo containers.

(e) Accidental dispersal by rafting of animals e.g. on plant debris (hydrochory) is seen as a likely dispersal mechanism for animals and littoral species are in an optimum situation for this. Crabill (pers. comm. cited by Roth & Brown in Cheng 1976) describes *Orphaneus brevilabiatus* (Newport, 1845) as found in protective cocoon-like structures in or on twigs floating or awash on beaches. It occurs throughout the larger landmasses and islands of the tropics and this can possibly be explained by tolerance of saltwater. Suomalainen (1939) reported on *Pachymerium ferrugineum* floating on seawater for as long as 31 days before sinking. Even after submersion the longest surviving individual survived 178 days in seawater at 6–12 °C; interestingly, *Pachymerium ferrugineum* is probably the most widespread centipede in the World.

Lewis (1996) drew attention to the fact that in *Tuoba* (Geophilidae), a genus with a number of littoral species around the world, that there is a long and spiniform pre-tarsal parunguis (spine) on the legs which, it is suggested, probably serves as a special hold-fast adaptation – which would also be useful during transportation. A similar structure is seen in *Pectinunguis*

(Schendylidae) (Pereira, Minelli & Foddai 1999). The millipede *Thalassisobates littoralis* has much longer setae fringing the metazonites and much longer tarsal claws than its terrestrial relative**,** *Nemasoma varicorne* C. L. Koch, 1847 (Blower 1985). It is interesting to speculate as to whether this could assist in dispersal.

There is, in fact, limited quantitative data on the extent to which insects (for instance) survive as drifters. Drifting vegetation has been found up to 16 km offshore which supported many insects although only 25 % of it had living terrestrial animals and no living insects were found in vegetation collected 160 km offshore. Colonies of ants have been reported in drifting wood (Bowden & Johnson in Cheng 1976). Even if the chances of survival are small, the possibility remains for transport in this way. The pseudoscorpion *Apocheiridium pelagicum* Redikorzev, 1938 was first collected 200 miles (320 km) at sea in plankton nets; its habitat is in reefs constantly submerged by the sea (Roth & Brown in Cheng 1976). The fact that species of the heteropterous bug, *Halobates* (ocean skaters) can live on the surface of the open ocean suggests also that there is no fundamental reason why arthropods of terrestrial origin should not be able to survive in this environment for a period of time and be dispersed over wide distances.

‘The scattered and often wide-ranging distribution of halophilous centipedes has been commented upon several times. Such species are very probably dispersed across very large distances, although in a very unpredictable way. It is possible to think of dispersion by rafting across the Atlantic Ocean for e.g. *Schendylops.* This was Crabill’s (1960) hypothesis and we see no reason to dispute it’ (Pereira & Minelli 1993). ‘There is a single specimen of *Schendylops* in the Natural History Museum in London, too damaged for allow for confident specific identification, but good enough to allow a confident identification as a member of a genus occurring, with many species, on both sides of the Atlantic. This specimen was collected long ago from Ascension Island, midway between Africa and South America, along the route of the westbound South Equatorial Current’ (Pereira et al. 1997).

7. Isolation of populations

The varied nature of coasts will tend to break up species into isolated populations which may favour genetic divergence. Dispersal across oceans and to isolated islands could accentuate this effect. This may be reflected in variations in characters between populations at different sites e.g. variation in segment numbers of geophilomorphs and in other characters as for instance described by Lewis (1962) for *Strigamia maritima* and Shinohara (1961) for *Tuoba littoralis*.

Arthur & Kettle (2000) demonstrated a latitudinal cline in segment number in *Strigamia maritima* in Britain. They suggested that climatic selection and local adaptation could be responsible; Vedel et al. (2008) showed that, in laboratory experiments, temperature regime influences the number of leg-bearing segments that develop and which could provide an explanation for this phenomenon.

8. Conclusions

The littoral marine appears to offer an appropriate environment for many arthropods, including members of the myriapod groups, to colonise despite osmotic and respiration problems. Possible reasons for this include an abundance of food, absence of parasites and predators and shelter.

Whereas some parts of the world have a number of species of littoral myriapods (mostly centipedes) recorded (e.g. Europe, West Coast of North America, Japan) others are very imperfectly known. There are few records of Pauropoda and Symphyla from littoral sites, many of these are quite old and we know little of how they are adapted to this environment; current state of knowledge of Diplopoda is of only a small number of 'genuine halophiles' from Europe, Far-Eastern Russia and Tasmania. The likelihood of other species elsewhere would seem high.

At least 40 species of Geophilomorpha (in at least six families) from different parts of the world appear to be permanent members of the marine littoral ('halofili genuini' or 'indifferenti') although some records are based on few specimens and could be 'accidentali'. Undoubtedly other species will be described and there are many areas of the world which would repay investigation for littoral centipedes. Littoral geophilomorphs appear to have a considerable capacity for survival submerged or floating on sea water. In at least some cases, their behaviour and life cycle assists in survival in the littoral zone but osmotic problems seem to have been solved (presumably by excretion of Na^+ ions, but the mechanism and location of this is not known) and respiration may be through the trachea, at least in part (possibly plastron structures around the stigmata and respiration by trachea), but there is also some evidence for anaerobic processes and the creation of an oxygen debt.

Whatever the mechanisms of survival, it seems possible that species might be dispersed, possibly across considerable distances, by rafting and this could account for the distribution of genera and families in different parts of the world. Isolated populations, however they came about, could show genetic differences.

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