

Global diversity of spelaeogriphaceans & thermosbaenaceans (Crustacea; Spelaeogriphacea & Thermosbaenacea) in freshwater

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Abstract Spelaeogriphaceans and thermosbaenaceans are two orders of eyeless, unpigmented peracarid crustaceans represented by very few species from subterranean waters. Spelaeogriphaceans occur only in continental waters, either running or still, in limestone or sandstone caves, or in calcrete aquifers. The four species known are limnic except one occurring in slightly brackish water loosely associated with an endorheic basin. The Thermosbaenacea are primarily marine, with only 18 species recorded in limnic conditions or in brackish inland waters whose salinity does not derive from dilution of seawater. They occur in limestone caves, the interstitial medium associated to alluvial deposits, or in thermo-mineral springs. Spelaeogriphaceans are found on the southern continents, in ancient cratons not affected by sea transgressions at least since the Early Cretaceous, when Gondwana started to break-

up. The former integration of these terranes into Gondwana suggests that the penetration of spelaeogriphaceans in continental waters took place previous to the fragmentation of this super continent (starting ca. 140 Ma), and that their current distribution pattern was driven by continental drift. The distribution of the Thermosbaenacea matches precisely the area covered by the ancient Tethys Sea or its coastlines. They are most probably relicts of a once widespread shallow-water marine Tethyan fauna stranded in interstitial or crevicular groundwater during marine regressions.

Keywords Freshwater · Global assessment · Species richness · Peracarida · Crustacea

Introduction

Spelaeogriphaceans and thermosbaenaceans are two orders of eyeless, unpigmented peracarid crustaceans represented by very few species from subterranean waters. The Spelaeogriphacea Gordon, 1957 occur only in continental waters, either running or still, in limestone or sandstone caves, or in calcrete aquifers. All species are limnic except one occurring in slightly brackish water loosely associated to an endorheic basin.

Thermosbaenacea Monod, 1927, in contrast, seem to be primarily marine although only 5 out of the 34 species known are euhaline, living in lava tubes or in

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the interstices between submersed coarse sand grains, volcanic tephra or coral rubble (Wagner, 1994). Most taxa occur in the anchialine environment associated with marine coastal areas, where water salinity varies sharply across the water column and derives from dilution of sea water. Only 18 species have been recorded in limnic conditions or in brackish inland waters whose salinity does not derive from dilution of seawater. They occur in limestone caves, the interstitial medium associated to alluvial deposits or in thermo-mineral springs.

The spelaeogriphacean body is roughly cylindrical, with the cephalothorax incorporating only the first thoracomere (which carries the maxillipeds) and with a short, posteriorly directed carapace covering only part of the second thoracomere dorsally (Fig. 1A). The pereion consists of seven free pereioneres, each with a pair of similar biramous stenopodial pereopods, and the pleon comprises six free pleomeres, each with a pair of well-developed biramous pleopods. The telson is free, articulated to the 6th pleomere. The most remarkable autapomorphy of the group is the transformation of the exopods of the posterior pairs of pereopods into non-setose, respiratory paddles.

Contrary to spelaeogriphaceans, whose inclusion in the Peracarida is undeniable since brooding females display a thoracic ventral marsupium formed by oöstegites (= foliaceous medial extensions of the pereopodal coxae), the inclusion of the Thermosbaenacea in this group is debatable since here the embryos are carried in a dorsal brood pouch derived from the carapace (Richter & Scholtz, 2001). Apart of this, the rest of features of the thermosbaenacean body plan is roughly similar to the spelaeogriphaceans (Fig. 1B); just notice that the pleopods are now

vestigial and present only on pleomeres 1 and 2, and that the condition of the posterior extension of the carapace varies from covering the second thoracomere only (in males and non-brooding females of Thermosbaenidae, Monodellidae and Halosbaenidae) to cover all thoracomeres (Tulumellidae). *Thermosbaena mirabilis* is a highly modified thermosbaenacean that separates from the ordinary morphology of the group in having a pleotelson (formed by the 6th pleomere and telson), and the display of only five pairs of pereopods.

The mouthparts of spelaeogriphaceans and thermosbaenaceans conform to a functional series of scrapers in an arrangement considered to fit for

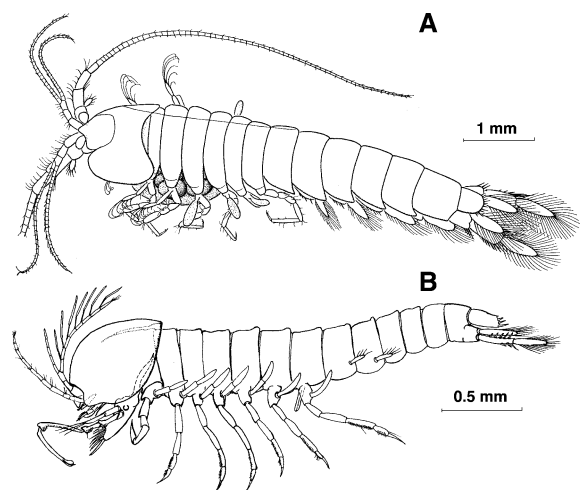


Fig. 1 General aspect of Spelaeogriphacea and Thermosbaenacea. (A) *Spelaeogriphus lepidops* Gordon 1957, a spelaeogriphacean from Table Mountain, South Africa (after Gordon, 1960). (B) male of *Tethysbaena atlantomaroccana* (Boutin & Cals, 1985), a freshwater thermosbaenacean from Morocco; notice that ornamentation of pereopodal exopods is omitted from figure (after Cals & Boutin, 1985)

Table 1 Global diversity of Spelaeogriphacea

	Distribution	Habitat	Salinity range
Spelaeogriphidae			
<i>Mangkurtu</i> Poore & Humphreys, 1998			
<i>mityula</i> Poore & Humphreys, 1998	NW Australia	Borehole wells	Limnic
<i>kutjarra</i> Poore & Humphreys, 2003	NW Australia	Borehole wells	Oligohaline
<i>Poticoara</i> Pires, 1987			
<i>brasiliensis</i> Pires, 1987	Brazil	Caves	Limnic
<i>Spelaeogriphus</i> Gordon, 1957			
<i>lepidops</i> Gordon, 1957	South Africa	Caves	Limnic

Table 2 Global diversity of non-marine Thermosbaenacea

	Distribution	Habitat	Salinity range
Thermosbaenidae			
<i>Thermosbaena</i> Monod, 1924			
<i>mirabilis</i> Monod, 1924	Tunisia	Thermo-mineral springs	Presumed oligohaline
Monodellidae			
<i>Tethysbaena</i> Wagner, 1994			
<i>juriaani</i> Wagner, 1994	Dominican Rep.	Anchialine limestone wells and spring	Limnic to oligohaline
<i>gaweini</i> Wagner, 1994	Dominican Rep.	Wells in alluvial sediments	Limnic to oligohaline
<i>haitiensis</i> Wagner, 1994	Haiti	Spring, wells and alluvial sediments	Limnic to oligohaline
<i>juglandis</i> Wagner, 1994	Haiti	Wells in alluvial sediments	Limnic
<i>lazarei</i> Wagner, 1994	Cuba	Cave and river interstitial	Limnic to oligohaline
<i>tinima</i> Wagner, 1994	Cuba	Wells in limestone	Limnic
<i>calsi</i> Wagner, 1994	Saint John; Tortola (British Virgin Islands)	Wells in alluvial deposits	Limnic to oligohaline
<i>relicta</i> (Pór, 1962)	Israel	Thermo-mineral springs	Oligohaline to hyperhaline
<i>somala</i> (Chelazzi & Messana, 1982)	Somalia	Wells in limestone	Oligohaline to polyhaline (evaporites)
<i>atlantomaroccana</i> (Cals & Boutin, 1885)	Morocco	Wells in alluvial deposits	Presumed limnic
<i>tarsiensis</i> Wagner, 1994	Spain	Well in alluvial deposit	Limnic
<i>texana</i> (Maguire, 1965)	Texas (U.S.A.)	Artesian wells	Limnic
<i>vinabayesi</i> Wagner, 1994	Isla Juventud (Cuba)	Cave	Limnic
Halosbaenidae			
<i>Limnosbaena</i> Stock, 1976			
<i>finki</i> (Mestrov & Lattinger-Penko, 1969)	Bosnia-Herzegovina; Italy	Interstitial of river alluvia; caves	Limnic
sp. Wagner, 1994	France	Well	Limnic
<i>Halosbaena</i> Stock, 1976			
<i>tulki</i> Poore & Humphreys, 1992	NW Australia	Calcrete aquifers	Oligohaline (evaporites)
<i>Theosbaena</i> Cals & Boutin, 1985			
<i>cambodjana</i> Cals & Boutin, 1985	Cambodia; Thailand	Caves	Limnic

Salinity tolerance ranges: Limnic: <0.5‰; Oligohaline: 0.5–5‰; Polyhaline: 18–30‰; Hyperhaline: >40‰

scraping small food particles from a substrate (Fryer, 1964).

Species diversity

The Spelaeogriphacea comprises a single family, the Spelaeogriphidae Gordon, 1957 with three genera: *Speleagriphus* and *Poticoara* (both monotypic), and *Mangkurtu*, with two species (Table 1). Three fossil forms from the Carboniferous of Canada, the

Upper Jurassic of China, and the Lower Cretaceous of Spain are treated also as spelaeogriphaceans by some authors (Schram, 1974; Shen et al., 1998; 1999). Nevertheless, none of these fossil forms preserves the diagnostic pereopodal exopods, and their body tagmosis and short carapace do not preclude their allocation to other peracaridan orders.

The Thermosbaenacea embraces four families, of which only three include non-marine species (Table 2). The family Thermosbaenidae is monotypic. The Monodellidae includes two genera:

Monodella (monotypic) and *Tethysbaena* (23 species), of which only 13 species of *Tethysbaena* are considered here as non-marine. The Halosbaenidae consists of the truly limnic genera *Limnosbaena* (two species, one of them not formally described) and *Theosbaena* (monotypic), plus the genus *Halosbaena*, with two marine species plus one from non-marine, brackish inland waters. The fourth thermosbaenacean family Tulumellidae, comprising the single genus *Tulumella* (three species), is fully marine. There is no fossil record of the Thermosbaenacea known to date.

Many species of thermosbaenaceans have been reported from oligohaline water in coastal aquifers or anchialine environments only, frequently around haloclines where water salinity changes abruptly from limnic-oligohaline to marine euhaline. These taxa (shown in Appendix Table 1) are not included in the total estimate of non-marine species since none has been reported from pure fresh waters, nor from marine euhaline water either.

Present distribution and historical processes

Living spelaegriphaceans appear associated with freshwater in southern continents, in ancient cratons not affected by sea transgressions at least since the Early Cretaceous, when Gondwana started to break-up (Fig. 2; Table 3; Appendix Fig. A). *Spelaegriphus lepidops* is known only from two caves in South Africa excavated in Ordovician quartzites (Gordon, 1957). *Potiicoara brasiliensis*, from two caves in Upper Proterozoic limestone at Mato Grosso do Sul (Brazil; Pires, 1987). And the two species of *Mangkurtu*, from borehole wells in calcrete of Middle to Late Tertiary age on north-western Australia, although these deposits overlie and are in direct contact with Early Cretaceous alluvial conglomerates (Poore & Humphreys, 1998; 2003). The former integration of these terranes in Gondwana suggests that the penetration of spelaegriphaceans in continental waters took place previous to the fragmentation of this supercontinent (starting ca. 140 Ma), and

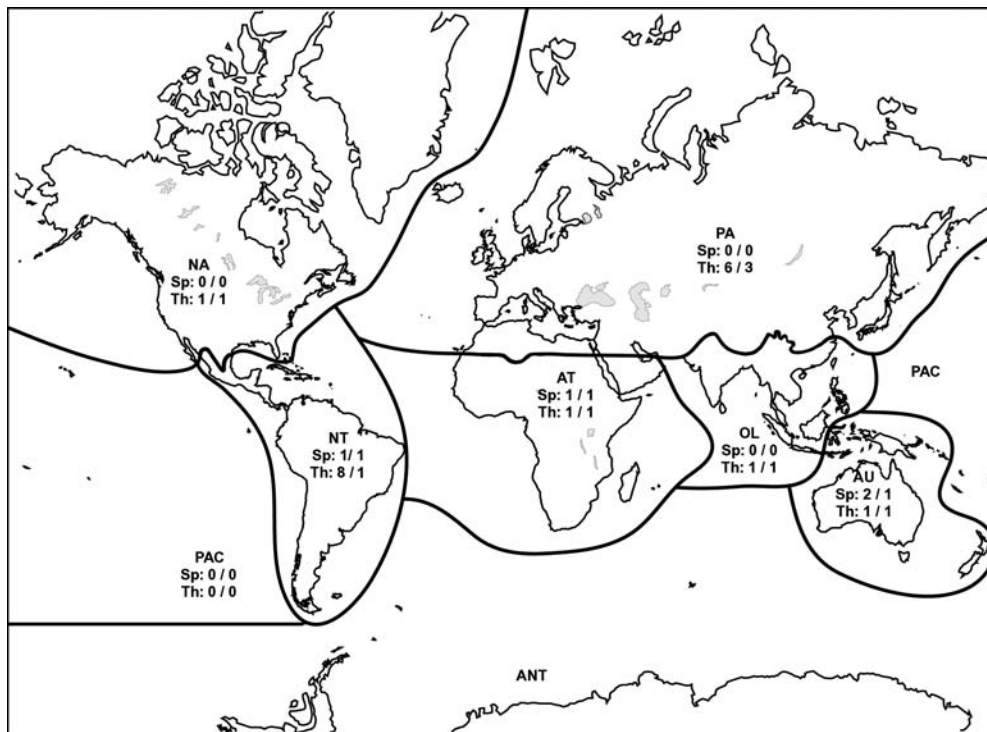


Fig. 2 Global distribution of Spelaegriphacea and continental water Thermosbaenacea (Species number/Genus number). PA—Palearctic, NA—Nearctic, NT—Neotropical, AT—

Afrotropical, OL—Oriental, AU—Australasian, PAC—Pacific Oceanic Islands, ANT—Antarctic

Table 3 Global and per biogeographic region diversity (species number) of Spelaeogriphacea and non-marine Thermosbaenacea

	PA	NA	NT	AT	OL	AU	PAC	World
Spelaeogriphacea								
Spelaeogriphidae	–	–	1 (1)	1 (1)	–	2 (1)	–	4 (3)
Thermosbaenacea								
Thermosbaenidae	1 (1)	–	–	–	–	–	–	1 (1)
Monodellidae	3 (1)	1 (1)	8 (1)	1 (1)	–	–	–	13 (1)
Halosbaenidae	2 (1)	–	–	–	1 (1)	1 (1)	–	4 (3)
Total Thermosbaenacea	6 (3)	1 (1)	8 (1)	1 (1)	1 (1)	1 (1)	–	18 (5)

In brackets, number of genera. No records of these groups exist from Pacific oceanic islands or Antarctica. PA: Palaeartic, NA: Nearctic, NT: Neotropical, AT: Afrotropical, OL: Oriental, AU: Australasian, PAC: Pacific Oceanic Islands, ANT: Antarctic

that their current distribution pattern was driven by continental drift.

The distribution of the order Thermosbaenacea matches precisely the area covered by the ancient Tethys Sea or its coastlines (Fig. 2, 3; Table 3; see also Appendix Figs A and B). They are most probably relicts of a once widespread shallow-water marine Tethyan fauna, stranded in interstitial or crevicular groundwater during episodes of marine regression. The amphi-Atlantic distribution of *Tethysbaena*, or the so-called “full Tethyan track” displayed by *Halosbaena* (with species in the Caribbean, Canary Islands and Australia) suggest the origin of these genera dates back to at least the final opening of the Atlantic (95 Ma) and the maximum extent of the Tethys sea (120 Ma), respectively. The timing of colonisation of continental waters by

thermosbaenacean lineages is probably more recent (all inland water stations fall within areas covered by the sea in Pliocene or more recent times), and the speciation process can have been peripatric.

The distribution of the Thermosbaenidae casts doubts on whether they represent a separate family from its closest relative, the Monodellidae. The single representative of the family dwells in a Tunisian thermo-mineral spring placed in a zone recently covered by the sea (Late Pliocene). This station falls within the area covered by the Monodellidae, which comprises a widespread amphi-Atlantic genus (indicative of the ancient origin for the family; see above) present also in N Africa (*Tethysbaena*), plus a second genus *Monodella*, monotypic and known only from a single-anchialine cave in Italy. The Thermosbaenidae are probably a young,

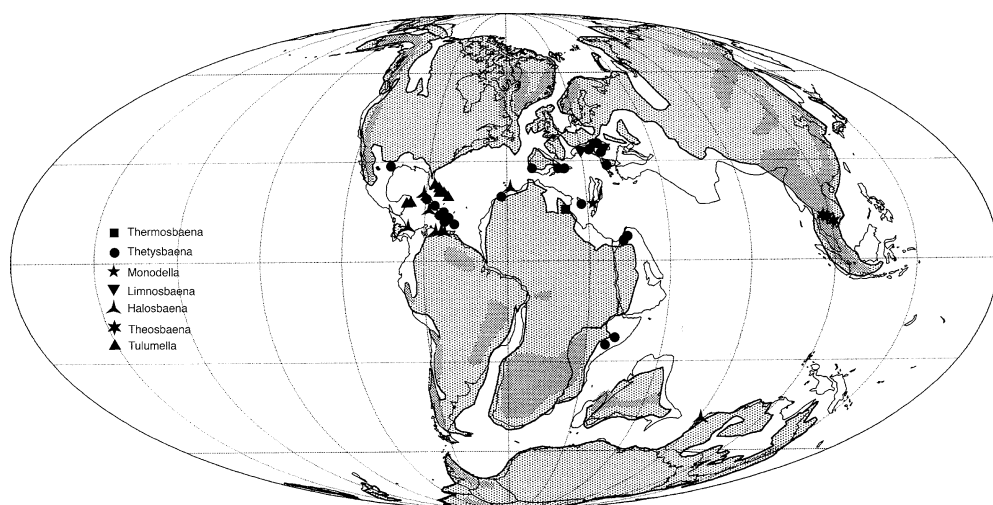


Fig. 3 Translocation of present distribution of Thermosbaenacea (including both marine and continental water taxa) to an Aptian (Lower Cretaceous; 120 Ma) palaeo-coastline map. Shaded areas denote emerged lands

highly modified member of the family Monodellidae adapted to an exceptional habitat (hot springs; see Wagner, 1994: 317).

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