# Gondwanan heritage in groundwater crustaceans of peninsular India

Initially, India was nestled in the supercontinent Pangaea at high southerly latitudes between Late Paleozoic and Early Permian ca. 255 Ma (ref. 1). The Pangaea was intact during the Late Triassic and Early Jurassic periods, but the first stage of its rifting took place in the middle Jurassic period ca. 180 Ma. Before its journey into northern latitudes, the Indian plate rifted from other Gondwanaland-masses at different times in the geological past[1] – from Africa along with Madagascar ca. 180–170 Ma, from Antarctica–Australia ca. 130 Ma and from Madagascar ca. 90 Ma. Eventually, the docking against Asia began ca. 55–65 Ma. During its tectonic evolution from the Pangaean times to the present day, the Indian plate being both as a biotic 'ferry' and a biotic sink[2], had experienced, *inter alia*, extensive exchange between peninsular autochthonous and Asian Tertiary biota[1,3–6]. As a result, the modern terrestrial and freshwater biota of India is 'overwhelmingly oriental' though it harbours but a few living relicts, both invertebrates and vertebrates, that might date back to the pre-drift period[4,5]. According to Mani[5], 'The Peninsula *per se* is biogeographically *India vera*, the largest and the oldest region of differentiation of the original floras and faunas of India'.

And yet, India as a whole has remained a *terra incognita* for groundwater fauna (stygofauna) till recently[7,8]. Regular stygofaunistic surveys in the country have begun since 2000, especially in the coastal deltaic belt of the rivers Krishna and Godavari, following the fortuitous discovery of two typical stygobiotic crustacean taxa: the copepod family Parastenocarididae[9] and the eumalacostracan order Bathynellacea[10]. As of now, over 3000 groundwater samples collected from river banks, borewells and caves in peninsular India have been examined. Detailed taxonomic study of the stygobiotic bathynellaceans and copepods (body length ca. 1 mm), has revealed 60-odd, mostly new species, half of which have been formally described till now. This note is mainly meant to report on the unequivocal Gondwanan heritage in these little-known taxa and also stress their importance in the overall evolutionary history of Indian biota.

Generally, all the obligate subterranean fauna (stygobionts) may be good candidates for historical biogeography[11]. However, the crustaceans as a group are better suited for this purpose because they are dominant and widespread in the ecosystems of both karstic and alluvial aquifers. Amongst crustaceans, the members of the order Bathynellacea, in particular, have long been recognized as suitable objects for understanding the history of the earth's crust and biological speciation, the reasons being: (i) Bathynellacea belong to an ancient lineage, dating back to Carboniferous; (ii) they live as unobtrusive ecological generalists; (iii) they occupy relatively inaccessible, cryptic habitats, i.e. interstitial spaces of sandy river banks, caves, etc., and (iv) have very limited powers of dispersal with no resting stages.

Incidentally, it may be mentioned here that the biogeographic studies based on stygobionts assume special importance at this juncture when the globalization of world's economy has brought about increasing effects of homogenization of the world's biota[12]. As a result, the study of biogeography, which was once 'a pillar of evolution', has now come to be greatly distorted by the presence of alien invasive organisms. An example is the biogeographic catastrophe that has befallen the San Francisco Bay, USA, which reportedly has some 234 invasive species, constituting about 90% of its aquatic population[12]. The enormous economic losses inflicted by the invasives are a different story.

The Gondwanan distribution of the stygobiotic bathynellacean and copepod genera of the peninsular India is summarized in Table 1. Amongst these crustaceans, the bathynellaceans, the ancestors of which inhabited the tropical seas during the Carboniferous times, display the Gondwanan lineage rather spectacularly. This group as a whole might have achieved its worldwide distribution prior to the breakup of Pangea, and its present-day geographic distribution can more plausibly be explained by the vicariance model rather than by the classic dispersal model[12–14]. Till now, only three genera of the family Parabathynellidae, i.e. *Chilibathynella*, *Habrobathynella* and *Atopobathynella*, and one genus each of the families Leptobathynellidae and Bathynellidae, i.e. *Parvulobathynella* and *Serbanibathynella* respectively are known from peninsular India. The specific biogeographic patterns of these genera and their implications are briefly dealt with here.

Genus *Chilibathynella*: Known only by two species, viz. the Chilean *C. clandestina* and the Australian *C. australiensis*, this genus was considered 'an entirely austral group', displaying transantarctic relationships[15]. Also, in terms of panbiogeography, this genus was believed to belong to the southern temperate track, which connects the southern South America, Australia, Tasmania and New Zealand with Pacific basin baseline[16]. However, following the discovery of the Indian cavernicolous *C. kotumsarensis*, the biogeographic range of the genus extends far north into the tropical belt of Northern Hemisphere[17]. This genus is rather rare in India as is elsewhere.

Genus *Habrobathynella*: Originally established for two Madagascan species (*H. milloti* and *H. jeanneali*), this genus

**Table 1.** Distribution of the Indian stygobiotic bathynellacean and copepod genera on other Gondwana landmasses

| Indian genera | Africa | Madagascar | South America | Australian region | Antarctica |
|---|---|---|---|---|---|
| *Chilibathynella* | – | – | + | + | – |
| *Habrobathynella* | – | + | – | – | – |
| *Atopobathynella* | – | + | + | + | – |
| *Parvulobathynella* | + | – | + | – | – |
| *Serbanibathynella* | * | – | – | – | – |
| *Siolicaris* | – | – | + | – | – |
| *Kinnecaris* | + | + | – | + | – |
| *Haplocyclops* | + | + | + | – | – |
| *Rybocyclops* | – | + | – | – | – |
| *Allocyclopina* | – | + | – | + | – |

**Nannobathynella*, the sister group of *Serbanibathynella*.

is most common in peninsular India where 11 species are recorded, of which eight species have been described. The active speciation process of the *Habrobathynella* in the river banks of peninsular India is noteworthy. Prior to its discovery in peninsular India, this genus was presumed to belong to northern tropical track, connecting tropical South America and tropical Africa, having an Atlantic Ocean baseline[16]. Given the fact that vast tracts of the global groundwater domain still remain unexplored, future studies are likely to unearth this genus from other Gondwana landmasses.

Genus *Atopobathynella*: Five species of this genus are recorded in peninsular India, of which only one species (*A. operculata*) has been described thus far[18]. Previously, one species each from Chile, New Zealand and Tasmania, and eight from mainland Australia have been established[19]. This genus is also known from an undescribed Madagascan species[14]. The geographical range of this genus extends to both East and West Gondwana continents. Prior to its Indian record, Lopretto and Morrone[16] assigned this genus and *Chilibathynella* to the southern temperate track, which is no longer tenable.

Genus *Parvulobathynella*: It is a most derived genus represented by two species each in India and South Africa, and one species each in Paraguay, Chile and Ivory Coast. It is yet another iconic case of Gondwanan lineage.

Genus *Serbanibathynella*: This monotypic Indian taxon has its closest sister relationship with the genus *Nannobathynella*, which is represented by a species each from São Paulo, Zimbabwe and Ivory Coast[20]. *Serbanibathynella* is only the third genus of Bathynellidae from the Gondwanan tropics, the other two being *Nannobathynella* and the monotypic Malawian *Agnathobathynella*.

Not surprisingly, the Indian bathynellaceans show no close phylogenetic affinity with their Asian counterparts. In fact, the Asian taxa are clearly plesiomorphic, which prompted Schminke[15] to presume that East Asia was the centre of evolution of Bathynellacea. Recently, some of the most primitive bathynellacean taxa have turned up in Australia[21,22].

Compared with Bathynellacea, Parastenocarididae is a much younger group, having originated possibly in the early Tertiary or even earlier[23]. Though neither the resting stages nor the means of dispersal is known for parastenocaridids[24], downstream dispersal in a water course seems probable[25]. Here also, like in the case of Bathynellacea, the vicariance events involving the continental drift rather than the subsequent dispersal events are believed to be responsible for their worldwide distribution[26]. In this scenario, the composition of parastenocaridid fauna in peninsular India also reflects the clear-cut Gondwanan heritage, as evidenced up till now by two parastenocaridid genera: *Kinnecaris* (Schminke) and *Siolicaris*. The former is represented in India by *K. godavari*[27], whereas its congeners occur all along the eastern side of Africa from Ethiopia down to South Africa, and also in West Africa, Madagascar, Western Australia and Papua New Guinea[28]. *Siolicaris*, which is under revision (P. H. C. Corgosinho, pers. commun.), is so far known in India by *S. sandhya*[9], whereas the other known species are neotropical.

Furthermore, two genera of the copepod family Cyclopidae, viz. *Haplocyclops*[29] and *Rybocyclops*[30] and one genus of another copepod family Cyclopinidae, viz. *Allocyclopina*[31], are represented in peninsular India by a single described species each. Interestingly enough, all these three genera have their type species in Madagascar. *Haplocyclops* also occurs in Brazil and Iran. Biogeographically, the reported occurrence in Iran of a species of *Haplocyclops* (here, *H. iranicus*[32]), is certainly incongruous. The morphology of this species and its generic affinities need to be re-examined. Madagascar apart, *Allocyclopina* has been reported from Reunion Island and South Australia.

What is surprising about the Indian groundwater Crustacea as a whole is that this widespread group does not have any peculiar genera despite the traditional assumption that India as an isolated continent existed far out in the Tethys Sea for about 100 Ma (ref. 3). Another conundrum thrown up by this group is the utter truancy of the likes of the basal bathynellacean taxa of Australia such as *Billibathynella* and *Brevisomabathynella* nor even the cosmopolitan *Hexabathynella*. Phylogenetically, this fauna is much less diversified in India vis-à-vis Australia[33].

All in all, the Indian stygobiotic crustaceans typify the Gondwanan heritage. These tiny ancient unique creatures in the hypogean realm are no less important than the epigean charismatic vertebrates in understanding the evolutionary history of the earth crust. However, their existence is now threatened, *inter alia*, by the indiscriminate sand-mining activity throughout the country. Sand miners are digging to a depth of 15 m or so with the help of machines and even extracting the earth after touching the river floor. The Andhra Pradesh state Government policy provides for banning the use of machinery and restricting the depth of sand extraction[33] to 2 m, though most of the hyporheic diversity exists in the upper one meter or so.

Undoubtedly, the vast, ancient and ecologically highly-diversified Indian aquatic subterranean domain is a veritable treasure trove of faunal wealth, to which little attention has been paid thus far. Subterranean biology as a thrust area of basic research deserves the rapid response of the funding agencies, researchers, policy makers and land managers.


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ACKNOWLEDGEMENT. I thank DST and UGC, New Delhi, for financial assistance.

Received 8 March 2011; accepted 29 June 2011

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# MEETINGS/SYMPOSIA/SEMINARS

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