AN EVALUATION OF MORPHO-TAXONOMIC CHARACTERS AND THEIR STATES

On the basis of the present study, an attempt is made to evaluate the taxonomic/ecologic significance of the whole gamut of the morphological characters and their diverse states within the Indian diaptomid taxa. Such an appraisal becomes all the more important, given the fact that at least some of the morphologic characters, which are generally ignored while characterizing new species, are now found to be useful in discriminating the species.

Body Size

It is well known that females are always more robust than males. A look at the body-size spectrum of the Indian diaptomids shows that *Megadiaptomus hebes* and *M. pseudohebes* are the largest species, the body length of both sexes being always above 2 mm (maximum of females 3.1 mm). Next comes *Spicodiaptomus chelospinus* with a mean length of 2 mm (maximum of females 2.69 mm), followed by *Paradiaptomus greeni* (females 2.0-2.6 mm). Rarely, 2 mm body length is attained by the females of *Heliodiaptomus viduus*, *Tropodiaptomus orientalis*, and *Arctodiaptomus parvispineus*. All other species are about 1 mm long. The minimum body size of 0.8 mm was observed in the males of *Allodiaptomus raoi* and *Eodiaptomus shihi*.

Body size is a decisive factor in governing the habitat preference of diaptomid copepods. All the species measuring 1.5 mm and above are obligatorily confined to small seasonal, generally turbid, fishless ponds and pools. Ecologically, all such taxa, as exemplified above, are *r*-strategists. In the present scenario of increasing habitat destruction, the *r*-selected species are under the serious threat of extinction. In contrast, the small-bodied forms inhabit a wide range of relatively stable, permanent habitats such as lakes, reservoirs, and rivers. These *K*-selected species are less vulnerable to the threat of anthropogenic activities. *A. raoi* and *E. shihi*, which
are the most slender Indian diaptomids, are generally adapted to lotic habitats, showing setal reduction on the natatory legs, as already described. Not surprisingly, both these predominantly rheophilic species are never found in completely isolated, rain-fed habitats (Ranga Reddy, 1983, 1994).

**Prosome**

The pre-antennular ventral filaments or rostral spines are larger in the females than in the males. These filamentous structures are rather blunt in *Paradiaptomus* but slender and pointed in the members of Diaptominae. The fourth and fifth pedigers in the females are generally completely fused to each other. At times the point of fusion of these segments is indicated by a lateral indentation or a short transverse septum. On the other hand, in the males of certain species, e.g. *A. michaeli*, *E. shihi*, and all the species of *Neodiaptomus*, the two somites are completely separated by a distinct septum. Rarely, a complete transverse row of fine spinules occurs between the two pedigers, as in the case of certain species of *Heliodiaptomus* (*H. viduus*, *H. contortus*, *H. cinctus*) and *Allodiaptomus* (*A. mirabilipes*, *A. intermedius* and *A. raoi*). Exceptionally, an additional transverse row of spinules has now been noticed between third and fourth pedigers in both sexes of *H. viduus*. But, no dorsal projections have been observed on the fourth pediger of any of the Indian species [cf. the Chinese *Sinodiaptomus (Sinodiaptomus) sarsi* (Rylov, 1923).

The fifth pediger is always produced postero-laterally into wing-like structures, which are more prominent in the females than in the males. The relative size of these lateral wings, their shape, and the size of the hyaline spines borne by them are of species-specific importance, especially in separating the females of closely allied species.
**Urosome**

As in all calanoids, urosome is limbless and separated from the fifth pedigerous (thoracic) somite by a major articulation (Giesbrecht’s Gymnoplea).

Female Urosome.—It consists of three somites in the females of all the species barring *Paradiaptomus greeni, Neodiaptomus meggitti* and all the species of *Tropodiaptomus* as well as *Megadiaptomus* in which it has only two somites owing to the fusion of the last two somites. The genital complex is formed by the fusion of the anterior two somites of the urosome. The genital double-somite is thus large and has paired ventral genital apertures, which are protected by a simple or scale-shaped operculum. General models of configuration of the genitalia in Calanoida have been presented by Huys & Boxshall (1991), Ohtsuka et al. (1994), Cuoc et al. (1997), Barthélémy et al. (1998) and Barthélémy (1999). Defaye et al. (2000) dealt with the taxonomic value of the female genital structures in Paradiaptominae and proposed the size, shape and position of the genital operculum as a new diagnostic character for this subfamily. Practically nothing is known about the female genital structures of the Indian diaptomid species except for *P. greeni*.

The morphological differentiation of the female genital double-somite is of immense taxonomic value but only for species-level decisions. This somite varies widely in its size and shape. The proximal part is generally dilated and provided with a hyaline spine on either side. The exact location, size and shape of these spines often help in distinguishing the closely allied congeners. Sometimes the somite is laterally drawn out into prominent lobes as in *P. greeni, H. kolleruensis*, etc. Rarely, the right distal corner is produced into a short lobe as in *T. defayaeae* n. sp. On the whole, the lateral contours of this somite are species-specific. Furthermore, this somite is generally longer than, or, rarely, as long as, the rest of urosome including caudal rami.
The only exception among the Indian diaptomids is *Heliodiaptomus contortus* in which the somite is shorter than the combined length of the next two somites. Interestingly, among all the Asian species, a similar character state is manifest only in the Chinese endemic, *Heliodiaptomus falxus* Shen & Tai, 1964. The second urosomite is telescoped into the genital double somite to a varying degree in different species and sometimes even fused with the anal somite, thus resulting in bimerous urosome. The second urosomite and anal somite are unornamented, except for sensilla, as in *P. greeni*.

Caudal Rami.—The female caudal rami in females are somewhat longer than wide in most species. Occasionally, they are nearly twice as long as wide in *A. raoi* and 2.7 times the width in *Arctodiaptomus michaeli*. The ornamentation consisting of hair on the lateral margins of the caudal rami is of taxonomic value. Generally, both margins are hairy, but sometimes only inner margins (e.g. *H. kolleruensis*, *N. schmackeri*, *N. physalipus*) and rarely only outer margins (*A. raoi*). Another useful criterion is that the right ramus is dilated proximally as in *N. physalipus* and *N. lindbergi*. But this dilation is discernible only in the lateral view. No chitinous structures occur on female caudal rami.

Caudal Setae.—The caudal setae have so far received but little attention in the diaptomid taxonomy. And yet, they are occasionally useful at species level. Let us take up the case of the Indian *Neodiaptomus* species, for example. The species can be easily told from each other thus: the setae are proximally dilated in *N. schmackeri*; the second seta (counted from inner side) always crosses over the third seta in *N. intermedius*; the third and fourth setae are fused the base in *N. meggitti*; the setae are relatively more curved in *N. physalipus* than in *N. lindbergi*. However, it is hard to find a similar degree of morphological differentiation of caudal setae in
other congener. That is why the setal characters are not precisely depicted for most species in
the world.

Male Urosome.— Unlike the female urosome, the male urosome without any exception
consists of five somites. Generally the anal somite together with the caudal rami is bent to the
right side to a varying degree in different taxa, perhaps to aid the male in grasping the female
during mating. Rarely, it is straight as in *H. kolleruensis*. The following characters and their
diverse states are important in the diaptomid taxonomy:

1. Ornamentation: the second and third urosomites are furnished with ventral hair. Rarely,
the third urosome alone has ventral hair, e. g. *P. blanci*, *P. annae*, and *P. sasikumari*. It
is noteworthy that urosome is consistently hairless in all the species of *Megadiaptomus*,
*Spicodiaptomus*, and *Tropodiaptomus*. The other ornamentation elements such as fine
denticles and sensilla are observed on urosomites in *N. meggitti* and *P. greeni*,
respectively.

2. The right distal corner of the pre-anal somite is often produced to a varying degree in
different species and thus can be useful in separating the congener.

3. The caudal rami are asymmetrical, the right ramus being different from the left one in
size, shape and/or ornamentation. More importantly, the presence of tooth-like chitinous
structure at the ventro-distal corner of the right ramus, according to Kiefer (1932), is a
generic criterion for *Neodiaptomus*. The size and shape of this tooth vary between
species. *Neodiaptomus* apart, the chitinous prominences on the right caudal ramus have
hitherto been documented only in two Indian species: *Allodiaptomus satanas* and *E.
shiih*. In fact, *A. satanas* was originally assigned to the genus *Neodiaptomus* by Brehm
(1952) based mainly on the above criterion. Subsequently, however, Ranga Reddy (1987)
transferred it to the genus *Allodiaptomus* by taking into account the armature of the second exopodal segment of male P5. The chitinous prominence in *E. shihi* is tiny and only visible in lateral view. In this study, I have found a small chitinous tooth in *H. pulcher*. This tooth, however, lies below the second outer caudal seta, but not at the inner distal corner of the ramus as in *Neodiaptomus* species. The setae on both rami are longer than in female and sometimes certain setae of the right ramus are transformed variously. For example, the lateral two setae of the right ramus are modified in *P. greeni*; all the terminal setae barring the innermost one are proximally dilated in *H. contortus*, and so on.

**Antennules**

It is well known that any appendage or body part that is involved, either directly or indirectly, in the reproductive process, is of great importance in taxonomy. The right male antennule is modified into a grasping appendage to aid the male in clasping the female during mating. The transformation is evident from the following points: the number of segments is reduced to 22; segments 13 to 18 (ancestral segments 15-20) are swollen with modified armature elements; geniculation occurs between segments 18 and 19 (ancestral segments 20 and 21). In this connection, it should be mentioned that, up till now, the presence of three and four post-geniculate segments has been regarded as a diagnostic of the subfamilies Paradiaptominae and Diaptominae, respectively (see Kiefer, 1932; Rayner, 1999; Dussart & Defaye, 1995, 2001). The sole Indian representative of Paradiaptominae, i.e. *P. greeni*, however, has four instead of three segments. Nevertheless, I think it is only appropriate at the present juncture to consider the situation of this taxon only as an exception and so I refrain from amending the antennular criterion in existing definition of Paradiaptominae.
Segments 8, 10, 11, and 12-16 bear a spine or spinous projection each on the frontal margin. The sensory spine on segment 8 as well as 12 is rudimentary and small. However, the spine on segment 8 is relatively large in the members of the genus *Arctodiaptomus* and in certain species of other genera such as *H. contortus, A. contortus, A. raoi*, and *E. shihi*. The spinous process on segment 13 is largest and variously modified. In some species of *Tropodiaptomus*, the same segment also has a small, hook- or tooth-like lateral spine at the base of the usual spinous process (e. g. *T. doriai, T. hebereri, T. vicinus* and *T. maduraiensis* n. sp.). Among the Indian taxa, segment 14 is devoid of spinous process in *Tropodiaptomus* alone, and that of segment 16, when present, is shortest. On the whole, the relative lengths of the spinous processes vary between species.

Another significant taxonomic character of the male right antennule is the size and shape of the lateral spinous process on the antepenultimate segment. This process is either shorter or longer than the next segment and often lined with narrow hyaline membrane on the outer margin. It is longest and staff-like in *E. shihi* but completely absent in *P. greeni* and several species of *Arctodiaptomus*. An array of intermediate conditions exist in other species. Occasionally, the spinous process is transformed into comb-like structure with varying number of teeth as in all the congeners of *Phyllodiaptomus* and *Sinodiaptomus*. A similar character state is also found in *H. pulcher* and *A. satanas*. Also, the ultimate segment ends in a fang in *P. greeni* and *Acanthodiaptomus denticornis*—probably a case of convergent evolution. All in all, the various other criteria of the grasping antennules can at best be regarded as important at species level only.

The left antennule of male is as in female. The basic chaetotaxy is as follows: (Arabic numerals = segments, Arabic numerals in parentheses = number of setae, ae = aesthetasc, sp
=spine): 1(1+ae), 2(3+ae), 3(1+ae), 4(1), 5(1+ae), 6(1), 7(1+ae), 8(1+sp), 9(2+ae), 10(1), 11(1), 12(1+sp+ae), 13(1), 14(1+ae), 15(1), 16(1+ae), 17 (1), 18(1), 19(1+ae), 20(1), 21(1), 22(2), 23(2), 24(2), 25(4+ae). No differences in the number of armature elements have been observed between the species of the same genus or different genera; the relative lengths of setae, however, show some variation between sexes as in A. michaeli.

A close study of the antennular length vs. body length among the Indian diaptomids shows that stout-bodied species (e. g. M. pseudohebes, P. greeni, S. chelospinus, all tropodiapomids, etc.) possess short antennules, hardly reaching the end of caudal rami whereas the slender-bodied ones (e. g. H. cinctus, all phyllodiaptomids, neodiaptomids, etc.) have long antennules extending beyond the tips of caudal setae by the last 2-4 segments.

**Antenna and oral parts**

From the viewpoint of taxonomy, antenna, mandible, maxillule, maxilla and even maxillipeds are highly conservative between the diaptomid genera and species. As observed by Ranga Reddy (1987), coxa-basis of mandible in A. raoi alone has three instead of four setae. According Rayner (1999), maxillipeds are ‘raptorial’ in the genus Paradiaptomus. Otherwise the armature details of all the appendages remain the same in various Indian taxa.

**Natatory legs (P1-P4)**

P1-P4, like the post-antennular cephalic appendages, are generally conservative, without throwing up helpful taxonomic clues. Nonetheless, some Indian species do exhibit certain interesting and useful taxonomic characters:

1. *A. raoi* has two derived features: 1) the outer marginal spine is lost on first exopodal segment of P1-P4, and 2) the third endopodal segment of P2-P4 has six instead of seven setae.
2. In *E. shihi*, as in *A. raoi*, P2-P4 have the reduced number of six setae on the third endopodal segment, but the spine on the first exopodal segment of P1-P4 is intact.

3. The outer marginal spines on exopodal segments of P2-P4 are characteristically modified into spinulose papillae in both sexes of the genus *Megadiaptomus*—an easily observable, important generic criterion.

4. An as yet undocumented character of *Tropodiatomus orientalis* is that one of the setae (third inner one) on the third exopodal segment of P4 is extraordinarily long and fringed with large setules.

5. The middle endopodal segment bears a distinct hyaline lobe (Schmeil’s lobe/organ) on the posterior surface in the species of *Tropodiatomus*, *Arctodiaptomus*, and *Acanthodiaptomus*. The nature of this lobe, too, is of some help in taxonomy.

6. The coxal seta on P4 of *Keraladiaptomus rangareddy* is longest, reaching almost the end of third endopodal segment. The next longest seta is noticed in *P. sasikumari* in which the seta extends up to the second exopodal segment.

**Fifth legs (P5)**

The diaptomid taxonomy as a whole may be said to have been founded chiefly on the various morphological trends associated with the highly transformed, sexually dimorphic fifth pair of legs. Such an extreme taxonomic importance of this appendage obviously stems from its role in grasping the female and transferring the spermatophore during copulation. The chief characters and their states of P5 are discussed hereunder.

**Right Male P5.**—always larger than and structurally much different from the left male P5.

Coxa: in its simplest form, this segment is somewhat spherical, bearing a hyaline spine of varying size near outer distal corner of posterior surface (e.g. *H. viduus*). Sometimes the spine
arises from a distinct lobe-like structure as in *H. contortus* and in various *Tropodiaptomus* spp. The segment tends to be enlarged at inner distal corner into a simple or bifid, rounded or triangular lobe. In *S. chelospinus*, the lobe is in the form of a pointed spinous structure, horizontally arching over the coxa of left P5 whereas it assumes upright posture in all the species of *Neodiaptomus* and *Phyllodiaptomus*, and particularly strongly developed in *Phyllodiaptomus* spp. Overall, its size and form are species-specific. But this lobe is completely absent in *E. shihi* and also in several species of *Tropodiaptomus* and *Arctodiaptomus*.

**Basis:** longer than wide (exception: as long as wide in *H. kolleruensis*) and always carries a weak sensory seta near outer distal corner and hyaline lamellae or lobes of different size and shape on the inner margin. These hyaline structures are highly useful in separating the individual species, especially of *Tropodiaptomus*. *H. contortus* has a single, exceptionally large, spherical hyaline lobe. The proximal inner corner at times carries a plug-like chitinous structure on the posterior face as in *A. similis similis* and *E. shihi*. Both the Indian species of *Sinodiaptomus* (*S. indicus* and *S. mahanandiensis*) have a massive, bifurcate chitinous outgrowth at proximal inner corner.

**Exopod 1:** this segment is wider than long and produced at outer distal corner into a spinous process of varying size in all the Indian species except those of *Megadiaptomus*. This process is most prominent in *E. shihi*. The presence of a triangular or trapezoidal, chitinous structure on the mid-posterior margin is highly characteristic of *H. viduus*. Similarly, the chitinous tooth present at the inner distal corner is diagnostic of *H. kolleruensis*, and it is massive in *Tropodiaptomus hebereri* and *T. keralaensis* n. sp.

**Exopod 2:** the armature pattern of this segment together with certain other features of the left male P5 and female P5 is often highly decisive at the genus level. The shape and size of this
segment also vary widely even between congeners. The most plesiomorphic state of this segment, as is manifest in *Paradiaptomus greeni*, consists of a nearly rectangular segment, bearing a small principal lateral spine near the outer distal corner. In the genus *Eodiaptomus*, too, the principal lateral spine is inserted close to the end claw, but the constellation of the other characters such as the endopod of the male right P5 and the essential details of the male left P5, *inter alia*, is distinctly different. The segment is thin and hollows out on the posterior surface and bears a digitiform lateral spine mostly in the distal position in *Phyllodiaptomus*. The position of the lateral spine is often useful in telling apart several genera except *Arctodiaptomus*. For example, this spine is typically proximal in all the species of *Heliodiaptomus* except *H. kolleruensis*, whereas it is inserted at about the mid-outer margin in *Neodiaptomus* spp. In *Alloodiaptomus*, though the principal lateral spine is proximal, the segment has one or two short accessory spinous processes near the outer distal corner. Also, the size and form of the principal lateral spine can shed light on the inter-species relationships. A hyaline structure of varied shapes occurs near the base of the principal lateral spine in all the species of *Tropodiaptomus* and *Arctodiaptomus* and at least in some species of other genera, but none such in *Neodiaptomus*.

End claw (exopod 3): the claw occurs in a wide variety of shapes amongst the diaptomid species. The proximal third or so of the claw is thickened and even produced into a lateral bulge as in *N. meggitti, N. physalipus, N. intermedius* and *H. viduus* and is typically twisted at its base in *H. contortus*.

Endopod: this rudimentary ramus is unisegmented in all the species except *P. greeni*, but its size and shape are subject to much variation between congeners. According to Kiefer (1932), the genus *Neodiaptomus* is characterized by flask-shaped endopod, but it is not so in *N. meggitti* and in several other Southeast Asian species. Primitively, the endopod is armed with two apical
setae, as in all the species of Paradiaptomus and Tropodiaptomus whereas it spinulose in all other taxa. As a generic criterion, the endopod is much elongated in Arctodiaptomus.

Left Male P5.—The taxonomic content of this appendage is no less important than that of the right male P5 at both genus- and species-level interpretations. It consists of a two-segmented protopod (coxa and basis) as well as exopod in all the Indian taxa except for the genus Tropodiaptomus in which both exopodal segments are fused together into a broad plate-like structure (see below). Generally, this leg extends up to the end of the first exopodal segment or rarely the midlength of the second exopodal segment of the right P5 and ends in a pair of terminal structures—an outer roughly thumb-like process and an inner ornamented or bare, normal or modified seta.

Coxa: generally rectangular or oval in outline, bearing a weak hyaline spine or seta, which is inserted at about the distal outer or inner corner either on a lobe or directly on the posterior surface. N. meggitti is unique in that the coxa has a thumb-like chitinous structure, studded with very tiny denticles.

Basis: it is as long as or somewhat longer than coxa and has a weak sensory seta at outer distal corner and a single hyaline lobe or lamella on the inner margin (exception: two lobes in H. pulcher). The lamella is more extensive in Arctodiaptomus. The inner margin is without any hyaline structure in only a few species such as P. greeni, E. shihi, T. doriai, etc. Further, the length/width ratio can be help in discriminating the species.

Exopod 1: this segment is always larger than exopod 2 and is particularly long and slender in Neodiaptomus spp., straight or somewhat incurved, with a pad of sensory hairs on the inner margin. No hyaline structures occur on this segment.
Exopod 2: this segment is small, rounded or oval, with a pad of sensory hairs on the inner margin and with an apical thumb and inner seta. The apical structures are prominently developed into pincers—an outstanding feature of the genus *Arctodiaptomus*. A comb-like hyaline ‘fan’ is present between the thumb and seta in the *annae*-group of the *Phylodiaptomus*, which has been raised to the status of subgenus, viz. *Ctenodiaptomus* (see Dumont et al. 1996). In *P. greeni*, the second exopodal segment and thumb are fused into a flange, carrying a lateral spine in addition to the seta, which is slender and backwardly directed. This situation is almost typical of the subfamily Paradiaptominae. As already pointed out, the transformation resulting from the fusion and differentiation of exopod is unique to the genus *Tropodiaptomus*. The plate-like structure thus formed is variously denticulate or dentate on the inner margin much like a saw among the congeners. The terminal thumb and seta are greatly reduced in this genus.

Endopod: the size and shape of the endopod are highly variable among the various taxa. It is especially elongate and vaguely two-segmented in *Neodiaptomus*; the tip is pointed with a subapical row of fine spinules. In some species, the endopod is rather short, e. g. *A. raoi*, *H. contortus*, etc.

Female P5

The fifth pair of legs in the female is much less differentiated; both legs are symmetrical except for basis and end claw of right leg being relatively stout. And yet, the appendages do provide taxonomic clues to identify the individual species and some genera as well.

Coxa: usually bears a spine of varying size near outer distal corner. In *Megadiaptomus* spp., however, the spine arises from the middle of the posterior surface—perhaps a plesiomorphic state. Both coxal spines are either equal (*N. meggitti*, *E. shihi*, *Tropodiaptomus* spp., *Arctodiaptomus* spp., etc.) or strongly unequal with the left spine being always larger than
the right one as in *A. raoi*, *N. intermedius*, etc., thus suggesting the plesiomorphic and apomorphic states, respectively. Exceptionally, the lateral half of the posterior surface of coxa in both legs is ornamented with fine spinules in *M. hebes*.

**Basis**: this is roughly triangular, rectangular or spherical in outline and has a lateral sensory seta the seta. The seta is generally short, but, in its derived state, very long, extending beyond the end of the first exopodal segment as in *P. blanci*, *P. sasikumari*, etc. In *T. maduraiensis* n. sp., a small hyaline lobe occurs near the middle of posterior margin, and in *N. meggitti*, a small papilla is present at midlength of inner margin.

**Exopod 1**: elongate and unarmed in all the Indian diaptomids, but bears sensilla in some species of *Arctodiaptomus*. As already mentioned, this segment is slightly stouter on right P5. At times the length/width ratio of this segment is handy enough for separating the congeners as in the case of *Megadiaptomus*. In *Keraladiaptomus*, the first exopodal segment, as a rule, is very long and slender.

**Exopod 2**: the transformation of this segment into a strong claw-like structure is characteristic of all diaptomids. In fact, Bradford-Grieve et al. (2010), following Ferrari & Ueda (2005), considers the ‘attenuation’ of the inner distal corner of this segment as a synapomorphy for the superfamily Centropagoidea as whole. The dilated proximal region of the second exopodal segment bears a short lateral spine close to the third exopodal segment in most taxa. This spine is stout in *H. contortus* and *H. cinctus*, relatively long in *A. michaeli* but completely absent in *E. shihi*. The claw is finely spinulose along both outer and inner margins, or, at times, only on inner margin. In all the Indian *Neodiaptomus* spp., the claw has denticulated margins; the denticles on the outer margin are always fewer than on the inner margin. As an exception within the genus *Heliodiaptomus*, *H. viduus* also has denticulate claw. Based on SEM studies, Dumont
& Ranga Reddy (1993) opined that the claw is secretory, containing a gland, which opens via a pore at its tip. For the first time, they also reported on the presence of a distinctive ‘conveyor canal’ on the anterior surface of the claw and discussed the nature of this canal and its usefulness in identifying the congener of *Phyllodiaptomus*. According to the above authors, we cannot rule out the possible existence of a similar structure in allied genera, but it is non-existent in *Tropodiaptomus*.

Exopod 3: this segment is largest in *K. rangareddyi*. Similarly, in other primitive genera such as *Megadiaptomus* and *Spicodiaptomus*, it is somewhat large and distinct from the second exopodal segment and armed with a long, setiform spinulose spine and short, naked spine or spinous process. The inner spine in *K. rangareddyi* is unusually strong and long and, in fact, unique in the whole of the family Diaptomidae. In *P. annae* the spine is setiform and long as compared with its congener. This segment is partially or completely fused with the second exopodal segment in *Tropodiaptomus* spp. It is greatly reduced in size but distinct in various other Indian species, and completely absent in all the species of *Allodiaptomus* (exception: *A. satanas*), *H. contortus*, and *H. cinctus*, thus representing the most derived state.

Endopod: slender, elongate, and mostly 1-segmented (exception: 2-segmented in *Phyllodiaptomus* spp.). Its length relative to the first exopodal segment is often useful in discriminating the species. Similarly the tip is rounded, pointed or truncate in various taxa and ornamented with one or two rows of spinules. In *N. meggitti*, the tip is acutely pointed, with a subapical row of spinules. While rounded in *Arctodiaptomus* species, it is obliquely truncate in most *Neodiaptomus* spp., some *Heliodiaptomus* spp., etc. Among the Indian taxa, it is only in *Paradiaptomus*, *Tropodiaptomus*, *Acanthodiaptomus* that the endopod is armed with two setae, one apical and one subapical.
On the whole, the diaptomid morpho-taxonomy hinges mainly on the various character states of the fifth legs and habitus (especially thoracic wings and double-genital somite) in both sexes and the male right antennule. Rarely, the size, number and/or arrangement of setae on natatory legs/caudal rami do provide important clues, but these are not known for most species.
BIOGEOGRAPHIC EVOLUTION AND SPECIES RICHNESS

The land area of India (20°00'N, 70°00'E) is about 3,287,263 km², which is 2.4% of the total surface of the world, has three biodiversity hotspots, viz. Western Ghats, Eastern Himalayas, and India-Myanmar border (hilly ranges). The evolution of any group of biota is always intricately linked to the geomorphological evolution of the area. Hence, a proper comprehension of the salient features of the historical biogeography of India is essential for analyzing the origin, evolution, and species richness of the Diaptomidae.

TECTONIC EVOLUTION OF THE INDIAN PLATE AND ITS AFTERMATH

Current plate tectonic theory postulates that India was nestled in the supercontinent Pangaea at high southerly latitudes between Late Paleozoic and Early Permian ca. 255 Ma (Chatterjee & Scotese, 1999). 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 Gondwana landmasses at different times in the geological past—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.

Apart from serving as Noah’s Ark to transport a variety of animals from Africa to Asia (Briggs, 1995), the Indian plate had apparently experienced extensive exchange between peninsular autochthonous and Asian Tertiary biota (Briggs, 1989, 2003; Mani, 1974; Ali & Aitchison, 2008). Out-of-India dispersal consequent upon India-Asia collision is evidenced by the fossil records of diverse taxa such as freshwater ostracodes, ranid frogs, agamid lizards, grasses, diatoms and whales (Bajpai & Gingerich, 1998; Thewissen et al., 2007). It must also be
noted that the dramatic latitudinal and climatic changes that affected the peninsular India during its northward drift caused substantial extinction in its original biota (Mani, 1974; Raven & Axelrod, 1974). Moreover, the massive Deccan Traps volcanism had a devastating impact on peninsular India biota, including the extinction of dinosaurs at Cretaceous-Tertiary boundary (Bajpai, 2009). On the whole, the researches carried out in stratigraphy, palaeomagnetics, and palaeontology provide a substantial body of knowledge about India’s past (Briggs, 2003).

CURRENT SCENARIO OF BIOGEOGRAPHY IN INDIA

Though nearly half of the country lies outside tropics, in the middle latitudes and within the temperate zone, it is customary to describe India as tropical, mainly because it is shielded off by the Himalaya in the north from the rest of Asia and has nearly uniform tropical monsoon climate. Nevertheless, the variety in elevation and the local climate is extremely remarkable and includes transitions from the nearly rainless Thar Desert in Rajasthan to the rainiest place on earth, i.e. Mawsynram in the East Khasi Hills district of Meghalaya state in north-eastern region (annual rainfall 11,872 mm), from Sriganganagar in Rajasthan, one of the hottest places on earth (54°C) to alpine and arctic conditions on the Himalaya, and from the geologically stable and ancient areas of the Peninsula with senile topography to geologically unstable and recent areas of youthful topography on the Himalaya. Except for the high-altitude Himalayan habitats, which are characteristically temperature-dominated, vast areas of monsoon-mediated ecology support tropical flora and fauna, but contain also numerous remarkable pockets of temperate biota. The uplift of the Himalayan Mountains exercised far-reaching influence on the climate and the
composition of the flora and fauna of the whole of India. In one word, the Himalaya presides over the ecology and biogeography of India.

As a result of the spectacular tectonic and historical biogeographic upheavals outlined above, the modern terrestrial and freshwater biota of India is “overwhelmingly oriental” though it does harbour but a few living relicts that might date back to the pre-drift period, e.g. the bivalve mollusk *Mullaria*, two genera of land snails, an earthworm species of the family Pheodrilidae, and some millipeds of the family Sphaerotheriidae, etc. (Briggs, 2003; Mani, 1974). And in zoogeographic approaches, India is generally placed in the Oriental Realm of Wallacea (1876). According to Mani (1974), however, parts of the Punjab and the higher Himalaya should be included within the Palearctic, and also the western parts of the Indo-Gangetic Plains of north India are related more to the Ethiopian-Mediterranean than to the Malayan area. It cannot be overemphasized that the peninsular India is quite distinct geomorphologically and biogeographically from the rest of India and its primary faunistic affinities are to be traced back more to the Madagascan Region than to the Oriental or even the Malayan area. Thus, while the Peninsula *per se* is biogeographically *India vera*, the largest and the oldest region of differentiation of the original floras and faunas of India, the Himalaya and the other Extra-Peninsular parts are merely “biogeographical appendages of secondary importance” (Mani, 1974). It was further emphasized by Mani (1974) that the greatest bulk of the true Indian flora and fauna had differentiated and evolved in the Peninsula, throughout the Palaeozoic, Mesozoic and Tertiary, right nearly up to Pleistocene times, and spread extensively into the Extra-Peninsular areas during the late Tertiary. The fauna and flora that had differentiated in the Peninsula should be regarded as the original flora and fauna of India. However, as mentioned above, for the sake of biogeographical convenience, the peninsular part
and the Eastern Borderlands of India, despite their fundamental differences in history, flora and fauna, are regarded as parts of the Oriental Realm of Wallace.

**BIOGEOGRAPHIC EVOLUTION OF THE INDIAN DIAPTOMIDAE**

A perusal of the existing literature shows that it was Tollinger (1911) who first mapped the distribution of the few early known Indian diaptomid species. Kiefer (1932), after establishing a new system of classification for the Eastern Hemisphere (Old World) diaptomids, recognized in his 1939 paper, two broad biogeographic groups, viz. “Arctic” (Europe and Asia) and “Gondwana” (Africa, India, and Australia). Subsequently, Sewell (1956) dealt with the biogeographic distribution of Copepoda based on the Continental Drift Theory and put all the then known diaptomid genera of the world into two subgroups each of Laurasia and Gondwanaland. The other useful references in which the distribution of certain Indian taxa is recorded include Brehm (1953a, b) and Ranga Reddy (1994). Dussart & Defaye’s (2002) World Directory provides updated biogeographic information on the continental calanoid copepods of the world as a whole.

To date, the family Diaptomidae comprises about 470 species in four subfamilies; the two largest subfamilies comprising 24 species (Paradiaptominae) and about 440 species (Diaptominae), of which 24% are endemic to the Oriental region (Boxshall & Defaye, 2008). The Indian tally is 45 valid species (inclusive of 4 new species) in 13 genera of both the major subfamilies. Of these, 29 species are endemic to India (Table 25) whereas the remainder are distributed mostly in other Asian countries (Table 24).
Clearly, four major amphitheatres have contributed to the origin, diversification and radiation of the Indian Diaptomidae (Fig. 115).

1. The Peninsular amphitheatre (Deccan Plateau) encompasses most of central and southern India and is bounded by the Arabian Sea in the west, the Indian Ocean in the south and the Bay of Bengal in the east.

2. The Indo-Chinese amphitheatre, which lies outside the limits of India, but extending westwards as a narrow belt on the forest-covered ranges of the Himalaya, and overlapping the Peninsular amphitheatre in the northeast in Assam.

3. The Malayan amphitheatre overlapping the Indo-Chinese amphitheatre in the north; and

4. The Himalayan Amphitheatre is a part of the Palearctic Realm and represents indeed the southernmost limits of the Turkmenian Subregion in the west and to some extent the Manchurian Subregion in the extreme east. The fauna consisting of temperate or partly European elements was differentiated mostly during Pliocene-Pleistocene and partly also in recent times.

Given India’s tectonic history and its physical and biotic links with Asia following its break-up from the Gondwana Supercontinent, one would expect the Indian Diaptomidae to present a mix of phylogenetic (Gondwanan) and geographical (Asiatic) elements, the latter greatly outnumbering the former, as in other groups of Indian biota (see Mani, 1974). Indeed, the Indian diaptomid genera represent four distinct biogeographic groups:

1. The **Gondwana derivatives**. These are exemplified by *Paradiaptomus* (Paradiaptominae) and *Tropodiaptomus* (Diaptominae), representing the oldest component-elements (phylogenetic relicts) of the character fauna of the Peninsula (see below).

2. The **Oriental elements**. *Sinodiaptomus, Eodiaptomus, Phyllodiaptomus, Heliodiaptomus, Neodiaptomus*, and *Allodiaptomus* dominate the Indian diaptomid
fauna; these are largely isolates and outliers of the Tertiary Asiatic forms of the Indo-Chinese and Malayan subregions. The species represented by these genera are the dominant geographical relicts in the Peninsula and characterised by more or less pronounced discontinuity in their distribution.

3. The Pleistocene relicts (Palaearctic elements) are represented by *Acanthodiaptomus* and *Arctodiaptomus*, which are restricted to the Himalayan Amphitheatre. Most probably these lineages radiated into India from the northwestern rather than the northeastern corridor. It must also be mentioned here that there is no trace whatsoever of these Pleistocene relicts in any of the elevated pockets of the Peninsula including the Nilgiri Hills (altitude above 2000 m).

4. The Indian endemics include *Spicodiptomus*, and *Keraladiaptomus*, which are represented by large-bodied (c. 2.5 mm), temporary-water dwellers in the southern part of the Peninsula. Another closely related genus *Megadiaptomus* also lives in the above region as well as the neighboring Sri Lanka, which has land connections with Peninsular India.

Boxshall & Jaume (2000) hypothesized that the ancestral stock of the Diaptomidae inhabited freshwater and hence the family represents a single colonization event; also, the two major subfamilies Paradiaptominae and Diaptominae, which markedly differ from each other in biology, diversity and evolutionary histories, colonized freshwater independently. The same authors further speculated that the original colonization of continental waters by the subfamily Diaptominae occurred in the northern supercontinent of Laurasia sometime after the break-up
Pangaea around 160 Ma and that the ancestors of the Paradiaptominae were the first to colonize freshwater on the African plate.

Now that we have a fairly good knowledge of the species composition and distribution of the diaptomids of India, the Gondwanan fragment, and of the Extra-Peninsular Laurasian part of the present South East Asia, it would be interesting to consider how far the above hypotheses hold good in this context. One important point can be made straightway. Without question, the present-day distributional patterns of the Indian Diaptomidae have come about more by dispersal than by historical tectonic events. Incidentally, it would be instructive to recall here that the exactly opposite situation holds good for the Indian groundwater crustaceans. While these stygobiont crustaceans have very little, if any, in common with their Asian counterparts, they display spectacular phylogenetic affinities with their counterparts on other Gondwana landmasses in the Southern Hemisphere (Ranga Reddy, 2011). It is thus abundantly clear that unlike in the case of the epigean fauna (here, the diaptomid copepods), the present-day distribution patterns of the typical hypogean fauna (stygobionts) are due to vicariance than to dispersal (Holsinger, 1991; Stock, 1993; and others).

Now let us examine in detail the biogeographic trends within each of the Indian diaptomid genera in the Oriental region.

**The Gondwana derivatives**

Genus *Paradiaptomus*.— The subfamily Paradiaptominae, to which this genus belongs, has only four genera and 24 species (Rayner, 2000). These taxa are restricted to Africa, with some isolates and outliers in southern Europe and the Middle East. Ecologically, the taxa are mostly confined to marginal habitats such as temporary, semi-permanent or inland saline waters, supposedly because of the competitive superiority of Diaptominae (Dumont & Verheye (1984).
In India, *Paradiaptomus greeni* is the sole representative of the Paradiaptominae, occurring almost throughout the country, but always confined to highly turbid, rain-fed, seasonal ponds and pools. It has not colonized the water bodies in the elevated zones, and is yet to be recorded in south-western State of Kerala. Outside India, it is known from Pakistan, Sri Lanka, and Madagascar (Dussart & Defaye, 2002). The non-diversification in India of *Paradiaptomus*, unlike the other ancient Gondwanan derivative, *viz. Tropodiaptomus*, is intriguing.

As for the Paradiaptominae, the complete absence from India of the other African lineages such as *Lovenula* and *Metadiaptomus* could be due to local extinctions experienced by the Indian plate during its northward drift. Given their habitat preference, morphology, and evolutionary history, the Paradiaptominae appear to have predated the Diaptominae in colonizing the African plate, as speculated by Boxshall & Jaume (2000). However, the alternative pathway suggested by the same authors, i.e. the entry of paradiaptomines into African plate from Laurasia via the Iberian peninsula during the Late Eocene (37Ma) is questionable, given the fact that the African plate itself is the home of the Paradiaptominae as a whole (only 4 of the 24 African species are outliers).

Genus *Tropodiaptomus*.—This is the most speciose of diaptomid genera, containing over 60 species, of which as many as 45 are confined to Africa, whereas the remainder with the sole exception of the Australian *T. australis* are distributed in Asia. Eleven species including four new species occur in India. (The validity of *T. lakhimpurensis* Reddiah, 1964 and *T. chauhani* Roy, 1984 is in serious doubt.) Of these, five species are endemic to India, whereas others have an extended range of distribution, but mostly within the Asian boundaries. On the whole, the species have disjunct or short-range distribution, inhabiting permanent ponds and lakes. In India,
tropodiaptomids are fairly large-bodied, rare in their occurrence and always with sparse populations, and they never occur in temporary, rain-fed pools and ponds. The radiation of these genera into Southeast and East Asia might have occurred from the northwestern Australia and/or through the Assam-gateway of India, but the timing of this event is not known. The impoverishment of tropodiaptomids in Australia is probably due to the greater competitive abilities of the sympatric Boeckella group of Centropagidae. In any case, there is little doubt about the Gondwanan origin of the tropodiaptomid lineage with Africa as its epicenter.

The Oriental elements

As already mentioned, the present-day Indian flora and fauna are predominantly oriental because of the extensive biotic interchange between India and Asia following the India-Asia collision around 55 Ma. Mani (1974) underscored the formation Assam-gateway in the northeastern India as the most important phase in the biogeographical evolution of India. This corridor opened up extensive interchanges between peninsular autochthonous and Asiatic Tertiary-mountain flora and faunas, the movements being equally strong both from the west to the east and vice versa. The peninsular elements spilled over into the Extra-Peninsular area and differentiated in the Tertiary mountains of south China, Indo-China and Thailand and Malaya. What is also noteworthy is the westward intrusion along the Himalaya right up to the great defile of the River Sutlej as well as the southward intrusion into Peninsula and Sri Lanka, which still formed part of the Peninsular mainland of India (Jacob, 1949). The distribution patterns of the Indian Diaptomidae also bear this out (see below).
Genus *Sinodiaptomus*.—This genus has three valid species, viz. *S. chafannoni* (Richard, 1897), *S. sarsi* (Rylov, 1923) and *S. valkanovi* Kiefer, 1938 in Asia (Ueda & Ohtsuka, 1998), and two endemic species, viz. *S. indicus* and *S. mahanandiensis* in India. All these species are generally confined to small ponds and pools. Of the three Asian taxa, while *S. valkanovi* is endemic to Japan and perhaps the oldest one among known introductions of freshwater by human activities (Ueda & Ohtsuka, 1998), the others have a wide range of distribution in Asia. In India, *S. mahanandiensis* is yet to be found outside its type locality, whereas *S. indicus* is widely distributed, especially in the Peninsula.

Clearly, the Asian species are plesiomorphic compared with their Indian congeners, and the Asian lineage radiated into India some during Eocene through Assam-gateway.

Genus *Eodiaptomus*.—While reviewing the biogeography of the then known seven species of this genus, Ranga Reddy & Dumont (1998) recognized South-east Asia as their epicenter, with only one outlier each in central India (*E. shihi*) and tropical northern Asia and New Guinea (*E. lumholtzi*). The recent addition of three more good specie, viz. *E. phuphanensis* Sanoamuang, 2001 and *E. phuvongi* Sanoamuang & Sivongxay, 2004, from Thailand and *Eodiaptomus indawgyi* Dumont & Green, 2005 from Myanmar, corroborates the above viewpoint. On the whole, the species are somewhat rare in freshwaters, displaying restricted or endemic distributions. According to Bayly (1966), the Indonesian *E. wolterecki* forms a biogeographic like between the Southeastern and East Asian *E. sinensis* and *E. japonicus* in the north and *E. lumholtzi* in the south right up to northern Australia.
Genus *Phylodiaptomus*.—Following the reappraisal of this genus by Dumont & Ranga Reddy (1993), three species have since been described, all from Thailand: *P. christineae* Dumont, Ranga Reddy & Sanoamuanga, 1996, *P. surinensis* Sanoamuang & Yindee, 2001, and *P. thailandicus* Sanoamuang & Teeramaethee, 2006, thus making a total of nine valid species. (*P. irakiensis* Khalaf, 2008 is just another synonym of *P. blanci*.) All the species except *P. blanci* have restricted or endemic distribution. *P. blanci* is the most widespread species (see Fig. 73, Table 24).

The species show highly interesting distribution trends in India where three short-range endemics, viz. *P. annae*, *P. wellekensae* and, *P. sasikumari*, occur together with *P. blanci*. *P. blanci* occurs almost throughout the country except the southernmost States of Tamilnadu and Kerala. In Tamilnadu State on the east coast, bounded by the Bay of Bengal, *P. blanci* is replaced by either *P. annae* or *P. wellekensae* whereas in Kerala State on the west coast, bordering the Arabian Sea, it is replaced by *P. sasikumari*. According to Dumont & Ranga Reddy (1994), this distribution pattern is suggestive of an event of adaptive ration in the extreme south of the Peninsula, in the recent past. The ranges displayed by the species are typical of allopatric, or perhaps parapatric speciation. The specific geomorphologic features that are responsible for this phenomenon are not yet known.

Here again, the Southeast Asian species not only outnumber their Indian congeners but also appear to be plesiomorphic, as evident from the large, rounded second exopodal segment along with a thick end claw of the male P5, multi-ridged conveyer canal in Chinese *P. tunguidus*, etc. We can speculate that the Indian species might have derived from a common Southeast Asian ancestor.
Genus *Heliodiaptomus*.—This is the second most speciose diaptomid genus in the Oriental, having 12 valid species, of which six are recorded in India, viz. *H. viduus, H. contortus, H. cinctus, H. pulcher, H. kolleruensis*, and *H. elegans*. While *H. viduus* and *H. elegans* have extended distribution within the Asian continent, the rest are endemic to India. *H. viduus* is the most common diaptomid species on the Indian subcontinent; it is also recorded in Thailand and Myanmar. *H. elegans* is a typical oriental species, widely distributed in Southeast Asia including southern parts of China. On the Indian subcontinent, it has recently been recorded in Assam State; it is already known from Bangladesh, which is very close to the Assam-gateway, but completely replaced in the peninsular India by *H. cinctus*. Between *H. pulcher* and *H. kolleruensis*, the latter is rather rare and confined only to Andhra Pradesh State whereas the former, also rare, is somewhat better represented in the peninsular India. Incidentally, the position of *H. kolleruensis* within this genus still continues to be unsettled not only because of the uncharacteristic median position of the lateral spine on the second exopodal segment of the male right P5, as pointed out by Ranga Reddy & Radhakrishna (1981), but also because of the peculiar metasomal wings and the lateral arms of the genital double-somite in the female. In this context, it is interesting to note that *H. contortus*, what with its pincers-like terminal processes on the left P5 and proximally twisted end claw on the right P5 of the male together with the exceptionally short genital double-somite of the female, indicates its spectacular morphologic and biogeographic affinity with its Chinese congener, *H. falxus* Shen & Tai, 1964.

Genus *Neodiaptomus*.—Though we find 13 nominal species, all of the Oriental region, having been listed in databases such as [http://www.marinespecies.org/copepoda](http://www.marinespecies.org/copepoda) and [http://invertebrates.si.edu/copepod/index.htm](http://invertebrates.si.edu/copepod/index.htm), it must be mentioned that the validity of the
Indian *Neodiaptomus madrasensis* Roy, 1999, and the Vietnamese *Neodiaptomus curvispinosus* Dang & Ho T.H., 2001, *Neodiaptomus vietnamensis* Dang & Ho, 1998 cannot be accepted because of their poor characterization. Hence it is advisable to treat them as *species inquirenda* pending future studies. Furthermore, the phylogenetic relationships between the Indian and the Asian species are not very clear as in the case of other diaptomid genera. Nevertheless, some distinct biogeographic patterns are easily discernible.

It is beyond doubt that *N. schmackeri* is most widely distributed and common in the Oriental (Table 24). On the other hand, *N. meggitti* is rare and has a rather restricted range in Southeast Asia (Ranga Reddy, 2000), extending from Malaysia and Myanmar to South Andaman Islands. Geomorphologically, though Andaman Islands have a lot in common with the neighboring Myanmar, one cannot rule out the possibility of *N. meggitti* having been introduced into the Andaman Islands by man through various activities of trade, transport, etc. On the mainland of India, this species is apparently replaced by its ecological equivalent and sister species, *N. intermedius*. Both these congeners inhabit stagnant water bodies such as pools, ponds, reservoirs, etc.

Of the three South Indian endemics, *N. physalipus* inhabits ponds and lakes at high altitudes (2000 m or above) whereas its closest congener, *N. intermedius* prefers low-land areas. *N. lindbergi*, which is widely distributed in the southern peninsula, and can co-occur with *N. schmackeri* (Ranga Reddy, 1994).

Morphologically and biogeographically, the Indian endemics together with *N. schmackeri* form a homogenous group. However, these taxa are apparently different from their Southeast Asian congeners, viz. the Indonesian *N. lymphatus* (Brehm, 1933), the predominantly Chinese *N. yangtsekiangensis* Mashiko, 1951, the Malaysian *N. laii* Kiefer, 1974, and the Thai *N.*
songkhramensis Sanoamuang & Athibai, 2002, and N. siamensis Proongkiat & Sanoamuang, 2008, in several respects such as nearly non-denticulate end claws of the female P5 and the form of endopod, the position of the lateral spine on the second exopodal segment of the right P5 and the armature of right caudal ramus in the male. At any rate, in order to have a better picture of the biogeography of the genus, the morphological relationships of the Southeast Asian species vis-à-vis the Indian congeners need to be reexamined critically.

Genus Allodiaptomus.—Following the amended delimitation of Mongolodiaptomus against Neodiaptomus and Alloidiaptomus and the resultant reallocation of their species (see Ranga Reddy et al. 2000), the genus Allodiaptomus presently contains only five species, viz. the Indian A. raoi, A. mirabilipes, A. satanas, and A. intermedius, and the Thai A. rarus. (The Vietnamese A. mieni Dang & Ho, 1985, is treated here as a species inquirenda) (see also Dussart & Defaye, 2002). Sanoamuang (2001) transferred A. rarus to the genus Mongolodiaptomus, but without explaining the rationale behind this decision. Hence its status quo ante is maintained here.

Of the five species of Allodiaptomus, A. raoi alone has widespread distribution in Southeast Asia (Ranga Reddy, 1994; Dussart & Defaye, 2002). Most probably, this species radiated in to Southeast Asia through Assam-gateway (see below). Brehm (1953) reported it from the Tapti River near Mandi in the northwestern Indian State of Himachal Pradesh. In the Peninsula, this species is confined to the Andhra Pradesh State except for the southern part where is replaced by its sister species, A. intermedius (Fig. 23). A. raoi is common in two peninsular rivers of Krishna and Godavari and canal-fed ponds in the coastal belt of Andhra Pradesh. All other Indian species have a rather very restricted range. While A. mirabilipes is strictly confined to southwestern State of Kerala, A. satanas occurs in northeast State of Meghalaya, and A. intermedius lives in
southern pockets of Andhra Pradesh. Both *A. raoi* and *A. intermedius* have remarkable rheophilic habits.

**The Pleistocene relicts (Palaeartic elements)**

As already mentioned, the fauna, in general, comprises temperate or partly European elements, which were differentiated mostly during Pliocene-Pleistocene and partly also during recent times. Both *Acanthodiaptomus* and *Arctodiaptomus*, which are widely distributed in the Palaeartic region as candidates of postglacial invasion, are restricted in India only to the Himalayan Amphitheatre. While *Acanthodiaptomus* is represented by a single well-known species, *A. denticornis*, *Arctodiaptomus*, which is the second most speciose genus in the Diaptomidae after *Tropodiaptomus*, has seven species, five of which are endemics (Table 25), most of them occurring in lakes and ponds at an altitude of about 3000-5000 m. As far as the Indian Diaptomidae are concerned, the Himalayan Amphitheatre is least investigated. Therefore, future faunistic investigations in this area are likely to bring to light several interesting Palaeartic taxa.

**The Indian endemics**

Of the 13 genera so far known from India, the monotypic *Spicodiaptomus* and *Keraladiaptomus*, and the bitypic *Megadiaptomus* alone are endemic to India. (*Megadiaptomus* also occurs in Sri Lanka, which is only a part of the Peninsula.) Coincidentally, the species of these three genera are confined to the fast vanishing marginal habitats such as the temporary, rain-fed ponds and pools of the southern peninsular States of Tamilnadu, Kerala, and Andhra Pradesh, and all of
them are large-bodied (c. 2.5 mm) and rare in the occurrence. And of the 46 valid species, 29 (63%) are Indian endemics. Not surprisingly, the evolution of all the Indian endemics barring *A. satanas* and *Arctodiaptomus* spp. took place in the southern part of the Peninsula, which indeed is *India vera*, as already mentioned.

Nevertheless, the traditional view that India, given its remarkable tectonic evolution from the Pangaean times to the present day, had undergone an extended period of isolation (millions of years) before its contact with Eurasia is not borne out by the differentiation and evolution of any peculiar genera or higher taxa (Brigs, 1989). And this is true of the Indian diaptomid and stygobiont fauna as well. Furthermore, as with most Indian fauna and flora (see Mani, 1974), the diaptomid fauna also seem to have attained maximum level of differentiation of species in relation to the available habitats (ecological niches), thus attaining ecological and geographical saturation and evolutionary stagnation. Initially, the evolutionary stagnation of the original fauna of the Peninsula, thanks to its well-known geological stability and mature topography, paved way for rapid and complex changes with the influx of exotic elements, when Assam—contact with Asia was established, as an early phase of the Himalayan uplift. The taxonomic work on the Indian diaptomids began right from the start of 20th century, but, as of now, only about 50 species are known. Even granting that certain regions, especially the Himalayan water bodies, are still undersampled, the poor diversification (= speciation) of Diaptomidae over a landmass of India’s size and highly differentiated geomorphology and climate is baffling. And this is in stark contrast to the situation in Southeast Asia, which is the true epicenter of, and most species-rich in, the Oriental diaptomid fauna. For example, Thailand, which lies in the middle of the mainland of Southeast Asia, has an area of 514,000 km$^2$, constituting only 15.6% of the land area of India, but supports 40 diaptomid species (Sanoamuang, 2011).
All in all, the distribution trends in the Indian diaptomids are in support of the hypothesis put forward by Boxshall & Jaume (2000) that the original colonization of continental waters by the subfamily Diaptominae occurred in the northern supercontinent of Laurasia sometime after the break-up of Pangaea around 160 Ma.

**SPECIES RICHNESS**

The formation of the Assam-gateway at the northeastern corner is “the most important phase in the biogeographical evolution of India” (Mani, 1974). As already mentioned, this vital biogeographic corridor facilitated extensive interchanges between the Indian and Asian biota, thus changing the modern biotic composition of the epigean ecosystems of India into one of “predominantly oriental” nature. The importance of the Assam-gateway can be understood in relation to species richness of the Diaptomidae as well.

Recent sampling of Deepor Beel, an important floodplain lake (area 1000-4000 ha, depth 1-4 m, altitude 53 m) and a Ramsar site in Brahmaputra Valley of northeastern India near the Assam-gateway, has revealed eight diaptomid species in a single plankton sample. These include four congeners of the genus *Heliodiaptomus* (*H. cinctus*, *H. contortus*, *H. viduus* and *H. elegans*), three congeners of the genus *Neodiaptomus* (*N. schmackeri*, *N. meggitti* and *Neodiaptomus* sp.) and a sole representative of the genus *Tropodiaptomus* (*T. orientalis*). The coexistence of eight diaptomid species in any given water body is not yet known in the world (Reid and Dumont, pers. commun). This brings to mind the famous, fundamental, ever-green question in plankton ecology: “Paradox of the plankton” by Hutchinson (1961). This originally phytoplankton-triggered paradox is an apparent massive violation of the Gause’s principle of
competitive exclusion or the “one species, one niche” requirement for coexistence. Several mechanisms have been proposed for species coexistence (see Wilson, 1990). However, a quantitative answer to this basic description question is still elusive, and this is an important gap in our understanding of community dynamics (Fox et al., 2010).

As for the Deepor Beel paradox, no long-term data of this habitat, which coincidentally lies within the biodiversity hotspot of India-Myanmar border, are available. Hence it is not known whether the observed high diaptomid diversity is maintained near equilibrium throughout the year or fluctuates seasonally and what the causative mechanisms of this rare phenomenon are. However, the available long-term observations on the diaptomid species diversity patterns in the Peninsula help in comparing the variation in richness across the geographical space of the country. Momentarily, the great majority of the zooplankton communities in the Peninsula contained 1 to 3, as anywhere else, or, rarely, 4 to 5 species. The coexistence of eight species in Deepor Beel is obviously due both to historical and ecological factors. The very geographical location of this water body right at the Assam-gateway— a rendezvous, as it were, for Southeast Asian and Indian biota— appears to be the overriding historical factor for this extraordinary species consortium. This is evidenced by the nature of the species involved and their overall biogeographic affinities. As already pointed out (see Oriental elements), of the four congeners of *Heliodiaptomus*, *H. cinctus* and *H. contortus* are Indian endemics, whereas *H. viduus* is widespread in India and Southeast Asia, and *H. elegans* is a typical Southeast Asian element. Similarly, while *N. schmackeri* and *T. orientalis* are widespread, *N. meggitti* and *Neodiaptomus* sp. are predominant oriental elements. Outside the northeastern region, it is hard to expect such a species constellation anywhere on the Indian subcontinent. During the present study, five diaptomid species co-occurred on a single occasion in a sample from Bangladesh, which is not
far from Deepor Beel (Ranga Reddy, pers. commun). In addition to the historical factors, habitat heterogeneity, high primary productivity, reduced predation pressure as well as environmental stress, niche diversification of the species, shallow depth of the water body, the climatic factors (this habitat is located within the world’s rainiest belt), etc., must have also been involved in favouring such high species richness.

Interestingly enough, the species richness is high whereas the endemism low in the northeastern India. The converse is true of the Peninsula. In other words, the species richness shows a declining biogeographic gradient from the northeastern point of Deepor Beel to the southernmost point (Kanayakumari) of the Peninsula—a distance of about 3400 km.
ASSESSMENT OF CONSERVATION STATUS

Conserving biodiversity involves addressing three categories: species and their sub-populations; genetic diversity; and ecosystems. Conservation measures and biodiversity studies depend on good and up-to-date taxonomic data. General faunistic lists are the result of long periods of sampling. How many species on a global list are actually living in an area can only be answered by updating inventories. The value of any biodiversity analysis and the adequacy of conservation measures thus depend on the quality of basic data.

From the standpoint of conservation, freshwater copepods, in general, have so far received scant attention in the world (Reid et al., 2002). As for the diaptomid copepods, which are successful in all kinds of freshwater habitats, their existence has now come under the threat of a host of anthropogenic activities all over the globe. For example, the widespread hypertrophication process of inland waters, owing to increased nutrient enrichment, can easily eliminate most of the sensitive species. This is because diaptomids, unlike cyclopids, cannot tolerate the extremes of physico-chemical variables in hypertrophicated systems. So, their decline or disappearance can be interpreted as an early symptom of ecosystem stress (Tavernini et al., 2003). The fauna is also under threat from agricultural practices, urbanization, pollution and pesticides (Hammer & Brendonck, 1997). Habitat destruction is yet another alarming cause of depletion of diaptomid species, especially those inhabiting intermittent or episodic freshwater bodies like ponds and pools (Williams, 2002). As a result, as many as 62 known diaptomid species in the world, which include 11 Indian species, are included in the 2000 International Union for the Conservation of Nature and Natural Resources (IUCN) Red List of threatened animals, as recommended by the Species Survival Commission (SSC). Hence, based on the present data together with the already available distribution records of all the valid Indian
diaptomids in the literature, the current conservation status of each species is evaluated in accordance with the IUCN criteria.

1. Critically Endangered (CR A-E)

Three species, viz. *Spicodiaptomus chelospinus*, *Keraladiaptomus rangareddyi*, and *Megadiaptomus pseudohebes*, need to be placed in the Critically Endangered category because they fulfill the IUCN-stipulated criteria. The rationale behind this proposal is discussed below.

*Spicodiaptomus chelospinus* (CR)

*S. chelospinus* is the one of largest Indian diaptomid species, inhabiting turbid ephemeral waters (Ranga Reddy, 1985). Rajendran (1973), the original author of this species, reported its occurrence in 22 localities in the districts of Madurai, Ramanathapuram, and Tirunelveli of the Tamilnadu State in southeastern of India. Later, this species was redescribed by Ranga Reddy (1985) based on the specimens collected by late Denton Belk from seven habitats in Madurai district and two habitats in Ramanathapuram between 14 and 18 October 1980. Indubitably, this species is endemic to the southern districts of Tamilnadu State (Rajendran, 1973; Ranga Reddy, 1985). It was included in the 2000 IUCN Red List of threatened animals under the Endangered B category (EN B). But this status needs to be revised in the light of the present findings.

A sampling survey done in Madurai and Dindigul districts during December 2005 revealed the presence of this species in only one of the 26 habitats sampled, i.e. a roadside temporary pond near Sedapatti village, 17 km from Dindigul. There was no trace of this species in any other locality where this species was previously reported. Even in the Sedapatti sample, the species was represented by only two male and two female specimens. During the above survey, it was also observed that several of its previous habitats had physically disappeared due
to quarrying, road-widening and housing activities plus increasing industrialization. Washing of clothes was also observed in some ponds and reservoirs besides pollution caused by domestic sewage and pesticides used in the nearby agricultural farms. Thus, going by the direct observation of the reduction in the extent of occurrence and the remarkable decline in the population size, as stipulated in the IUCN criteria, it can be safely concluded that *S. chelospinus* is indeed a Critically Endangered species.

Furthermore, because of its large body size, *S. chelospinus* is prone to fall an easy prey to both invertebrate and vertebrate predators. At the present rate of indiscriminate habitat destruction, it would not be surprising if this species goes completely extinct in the coming decades.

*Megadiaptomus pseudohebes* (CR A-E)

The conservation status of this species has not yet been assessed. This largest species among the Indian diaptomids was previously known in good numbers from several quarry pools at Nallapadu village in Guntur district, besides its type locality a temporary pond at Kondakarla in Visakhapatnam district, all in Andhra Pradesh State of southeastern Peninsula (Ranga Reddy, 1988; Ranga Reddy and Devi, 1985). Repeated sampling in Nallapadu quarry pools in nine consecutive years (2002-2010) revealed not even strays of this species. However, this species was found in a hitherto unknown habitat, i.e. Vejendla quarry pond, 15 km from Guntur town in Andhra Pradesh State, consistently during 2002-2008, but with progressively reduced population size. These quarries have since disappeared owing to the establishment of hollow-brick industry. Construction of railway quarters in 2006 accounted for the complete destruction of Nallapadu habitats. It is not known whether *M. pseudohebes* is still persisting at its type locality. The
present observations show that the area of occupancy of this species is less than 10 km². Hence, according to the IUCN criteria, it is assigned to the Critically Endangered, CR B1 category.

*Keraladiaptomus rangareddy* (CR A-E)

As yet nothing is known of the conservation status of this species. For sure, this taxon is endemic to Kerala, as rightly observed by its original authors, Santos Silva et al. (1994). It was described on the specimens collected on August 9, 1991 from its type locality, i.e. Kuttappan Kulam pond in the village of Mattam, and Monastery Pond near Christ College in Iranjalakuda town, both in Trichur district of Kerala State. In the present study about 100 plankton samples were collected from Kerala State in 2004 and 2005, including six samples from Monastery Pond. None of them contained even strays of this species. According to the original collector of this species, F. K. Kakassery (pers. commun.), this species was not found even at its type locality despite his several subsequent samplings. Before concluding and reporting to the IUCN that this species is Extinct (EX) or Extinct in the Wild (EW), I think it advisable to make some more sampling surveys for this rare species. As far as Monastery Pond is concerned, it was almost completely invaded by the luxuriant growth of marginal and floating vegetation—which is only symptomatic of hypertrophication. For the time being, *K. rangareddy* can be considered as yet another Critically Endangered (CR) species, fulfilling at once all the IUCN criteria, A to E.

*Heliodiaptomus kolleruensis* (CR A-E)

In the 2000 IUCN Red List, this species was assigned to VU D2 category. This status must perforce be revised now.

This is a rare species endemic to Andhra Pradesh State. Previous records of *H. kolleruensis* by Ranga Reddy & Radhakrishna (1981) and Ranga Reddy (1994) point to its occurrence in Lake Kolleru, Bhadrakali tank at Warangal, a turbid reservoir on the Nagarjuna
University campus, and a pond at Jeedimetla, a suburb of Hyderabad city. During the last 30 years, these habitats have been severely affected by various anthropogenic activities, especially increasing industrialization and the concomitant pollution.

Initially, this species was reportedly occurring in good numbers in Lake Kolleru (Ranga Reddy & Radhakrishna, 1981). However, it was non-existent in all the subsequent collections from this habitat and also from the reservoir on the Nagarjuna University reservoir. I cannot say anything about it in Bhadrakali Tank for want of subsequent samples from this habitat. But the Jeedimetla habitat had completely vanished owing to fast-paced, heavy industrialization. Thus, all the present observations leave no doubt that *H. kolleruensis* belongs outright to the Critically Endangered (CR) category, fulfilling almost all the stipulated criteria A to E.

**Vulnerable (VU D2)**

The 2000 IUCN Red List contains the following Indian endemic species under the Vulnerable D2 category on the basis of “acute restriction in [their] area of occupancy”: *Heliodiaptomus pulcher*, *Neodiaptomus physalipus*, *N. intermedius*, *Eodiaptomus shihi*, *Arctodiaptomus euacanthus*, and *A. michaeli*. The present findings strongly favour the status quo ante, VU D2, for all these species. In addition, going by the same IUCN criterion, the following eight other Indian species must also be included in the same category:

1. *Tropodiaptomus euchaetus*
2. *Tropodiaptomus defayeeae* n.sp.
3. *Tropodiaptomus venkataramani* n.sp.
4. *Tropodiaptomus raoi* n.sp.
5. *Tropodiaptomus keralaensis* n.sp
6. *Phyllodiaptomus wellekensae*
7. *Phyllodiaptomus sasikumari*
8. *Sinodiaptomus mahanandiensis*

Of these seven species, the species listed at 1 to 5 and 8 are yet to be found outside their respective type localities. While *Tropodiaptomus* species are somewhat large-bodied species and live not in isolated ephemeral pools and ponds, but in river- or canal-fed permanent or semi-permanent ponds and even lakes, the other species prefer ephemeral waters. In due course, these species are likely to be qualified for Critically Endangered category.

**Lower Risk (LR)**

“A taxon is Lower Risk when it has been evaluated, does not satisfy the criteria for any of the categories Critically Endangered, Endangered or Vulnerable.” The Indian diaptomids can be separated into two subcategories as follows:

a. **Near Threatened (nt):** “Taxa which do not qualify for Conservation Dependent, but which are close to qualifying to for Vulnerable.” The following eight species may be assigned to the category:

1. *Neodiaptomus lindbergi* (LR nt)
2. *Neodiaptomus meggitti*
3. *Tropodiaptomus orientalis*
4. *Tropodiaptomus doriai*
5. *Tropodiaptomus hebereri*
6. *Tropodiaptomus mutatus*
7. *Tropodiaptomus vicinus*
8. *Tropodiaptomus nielseni*

Of these, *N. lindbergi* alone is endemic to the Andhra Pradesh and Karnataka States in the Peninsula whereas the rest are distributed in other parts of Asia.
b. Least Concern (lc): “Taxa which do not qualify for Conservation Dependent or Near Threatened.” The following ten species fall into this category:

1. *Paradiaptomus greeni* (LR lc)
2. *Heliodiaptomus viduus*
3. *Heliodiaptomus contortus*
4. *Heliodiaptomus cinctus*
5. *Allodiaptomus mirabilipes*
6. *Allodiaptomus raoi*
7. *Neodiaptomus schmackeri*
8. *Phyllodiaptomus blanci*
9. *Phyllodiaptomus annae*
10. *Sinodiaptomus indicus*
11. *Arctodiaptomus similis similis*
12. *Arctodiaptomus salinus*
13. *Acanthodiaptomus denticornis*

Data Deficient (DD)

The species that come under this category have been listed below.

*Arctodiaptomus stewartianus* (Brehm, 1924) **DD**

*Arctodiaptomus altissimus altissimus* Kiefer, 1936 **DD**

*Arctodiaptomus parvispineus* Kiefer, 1935 **DD**

*Megadiaptomus hebes* Kiefer, 1936 **DD**
It must be noted that all the DD species following their original description, have not been reported either from their respective type localities or from anywhere else. As regards *M. hebes*, Kiefer (1936) described it from an unspecified locality in Karnataka (erstwhile Mysore) State. However, this species was unseen in any of the 54 samples collected from diverse habitats including temporary ponds from this State. Ranga Reddy (1988) redescribed it based on Sri Lankan specimens deposited in the Smithsonian Institution by C. H. Fernando under the name, *Zeylonodiaptomus papillopedis* Fernando & Hanek, 1976, the synonym of *M. hebes* (see Radhakrishna & Ranga Reddy, 1977). Thus, the occurrence of this species in India is still puzzling whereas there is hardly any information about its present distribution in Sri Lanka. Given the fact that *M. hebes*, like its Critically Endangered congener *M. pseudohebes*, is an inhabitant of the ephemeral water bodies, its conservation status may not be different.

Paradoxically, it is clear from the standpoint of conservation that the endemics of the peninsular India cause greater concern than the Oriental, Palaearctic and Pleistocene elements in India. The reason is that the intermittent and episodic habitats, which constitute the home of these endemic taxa, are subject to increasing devastation. It is true that these obligate temporary pool dwellers lay diapausings eggs to tide over the dry phase of the habitats, but such an adaptive strategy of any species is of little avail in the face of large-scale habitat destruction caused by man. Many ponds and pools and their indigenous biota have been lost forever, and those that remain face increasing pressure due to agriculture, pollution, and urbanization. Unfortunately the microcrustacean fauna is not taken into account in the existing laws concerning the environmental protection in India. Today the biodiversity conservation efforts in the country are focused on such charismatic megafauna as tiger, lion, panda, crocodile, etc., but not on the lower invertebrates. So, at this juncture, any discussion on the conservation of the lower invertebrates can at best be a subject of academic interest only.