

Keynote paper

## CLADISTICS OF THE *ANTHESSIUS* DELLA VALLE, 1880: A MAJOR GENUS OF POECILOSTOME COPEPODS PARASITIC IN MOLLUSCA

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### ABSTRACT

The result of a cladistic analysis of the genus *Anthessius* Della Valle, 1880 failed to support Nair's (1988) proposal to create a new genus *Tridacnophilus* to accommodate four species of *Anthessius* living in the mantle cavities of the giant clams (Tridacnidae). Nevertheless, the obtained most parsimonious cladograms (phylogenetic trees) indicate that coevolution occurred between certain species of *Anthessius* and their notaspidean (Gastropoda: Opisthobranchia) hosts.

### INTRODUCTION

Up to the present, 246 species of parasitic copepods have been reported from 458 species of Mollusca. They belong to five orders of Copepoda (Harpacticoida, Misophorioida, Cyclopoida, Poecilostomatoida, and Siphonostomatoida), with Poecilostomatoida as the dominant group embracing 73.2% (180 out of 246 species) of the known copepod parasites of Mollusca. The hosts of these copepod parasites are distributed in five classes of Mollusca as follows: one species of Aplousobranchia, three species of Polyplacophora, 181 species of Gastropoda, 252 species of Pelecypoda, and 21 species of Cephalopoda. Poecilostomatoida is a major order of Copepoda occurring in symbiosis with all major animal groups living in the ocean (Ho 1991). Currently, 53 families of copepods are classified under this order and 18 of them have all or some of their members living in or on the molluscs. Among these 18 families of mollusc-parasitizing poecilostomes, Anthessiidae is the major one with 41 of its members utilizing either bivalves or gastropods as their hosts. Currently, 48 species of poecilostome copepods are classified under five genera of the Anthessiidae, namely, 41 species in *Anthessius* Della Valle, 1880; four species in *Panaetis* Stebbing, 1900; and one species each in *Katanthessius* Stock, 1960;

*Neanthessius* Izawa, 1976; and *Rhinomolgus* Sars, 1918. While the species of *Rhinomolgus* are planktonic and those of *Katanthessius*, *Neanthessius*, and *Panaetis* are parasitic in prosobranchs, the members of *Anthessius* are variable in their occurrence (Table 1). In 1988, B. Unnikrishnan Nair proposed to remove four species of *Anthessius* (Table 2, Fig. 1) occurring in the giant clams (Tridacnidae) to a new genus, *Tridacnophilus*. Since the arguments for this taxonomic treatment are questionable, I decided to use a cladistic analysis to test the feasibility of Nair's (1988) proposal.

Cladistics is essentially a method of phylogeny reconstruction. In reconstruction, the taxa are grouped by using the shared derived characters (= synapomorphies), and the obtained cladogram (phylogenetic tree) is treated as a phylogenetic hypothesis and served as the basis for setting up a system of classification. Thus, a cladistic analysis of the 41 known species of *Anthessius* would aid in finding the justification for Nair's (1988) creation of *Tridacnophilus*. Furthermore, the result of this phylogenetic analysis can also be applied to check for the possible coevolution between the copepod parasites and their molluscan hosts.

Table 1. Known species of *Anthessius* arranged in alphabetical order in each occurrence.

Occurrence	Number	Name of species
in weed washings	1	<i>brevifurca</i>
in plankton	4	<i>concinus, dilatatus, groenlandicus, investigatoris</i>
in bivalves	19	<i>alatus, amicalis, arenicola, atrinae, brevicauda, discipedatus, distensus, fitchi, araciliunguis, kimlenis, minor, mytilicolus, pinctadae, pectinis, pinnae, prolectus, saecularis, solenocurti, solidus</i>
in prosobranchs	4	<i>leptostylis, longipedis, sensitivus, teisseri</i>
in opisthobranchs	12	<i>arcuatus, delabellae, hawaiiensis, light, navanacis, nortoni, obtusispina, ovalipes, pleurobrancheae, proximus, stylocheili, varidens</i>
in fish	1	<i>lophiomi</i>

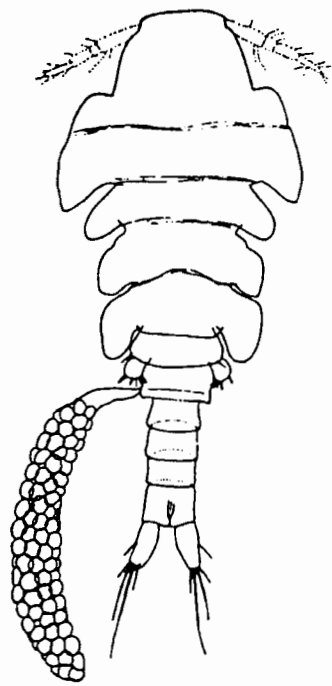
### SPECIES OF *ANTHESSIUS*

The most distinctive features found in the copepods of the genus *Anthessius* are: (1) possessing a pair of raptorial antenna tipped with 2, 3 or 4 claws; (2) bearing a pair of piercing, rasping mandibles; and (3) equipped with a pair of strong and abrasive maxillae carrying a row of various number of teeth. In spite of being equipped with such distinctively transformed cephalic and oral appendages for feeding on their host's tissue, species of *Anthessius* are indifferent from free-living, planktonic copepods in having four pairs of biramous and trimerous legs armed with a full set of plumose setae for swimming. Thus, it is not unusual to find some individuals of *Anthessius* on or in marine animals other than their normal hosts - bivalves and gastropods. For instance, *Anthessius alatus* Humes & Stock, 1965 is a parasite of giant clams in the Indo-West Pacific, but it has been reported to occur on a sea star (*Acanthaster planci*) and in a sponge (*Acanthella auranta*) in the Red Sea (Humes & Stock 1965). Further, *Anthessius obtusispina* Ho, 1983 was first found in the gill cavity of a surfperch before it was described from a notaspidean sea slug in California (Ho 1983).

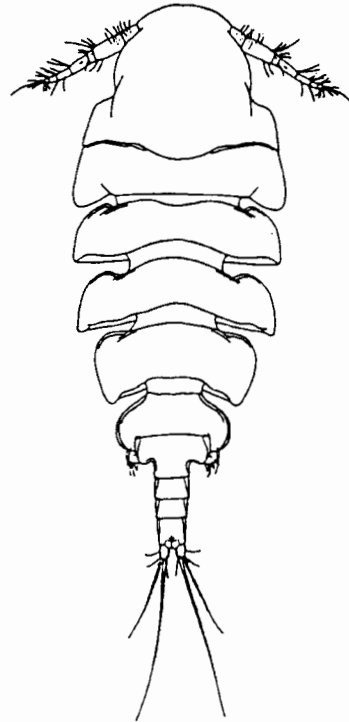
Although six species of *Anthessius* were not reported from molluscs (Table 1), based on the above information and judging from the facts that they are known from a single finding and found with only one or few individuals from weed washings (Sewell 1949), plankton samples (Scott 1909; Sars 1918; Hansen 1923; Sewell 1949) and in the gill cavities of a fish (Avdeev & Kazatchenko 1985), they are most

likely nothing but some straying individuals wandered off their normal molluscan hosts. Thus, it is assumed that members of *Anthessius* are all parasitic on or in the gastropods and bivalves.

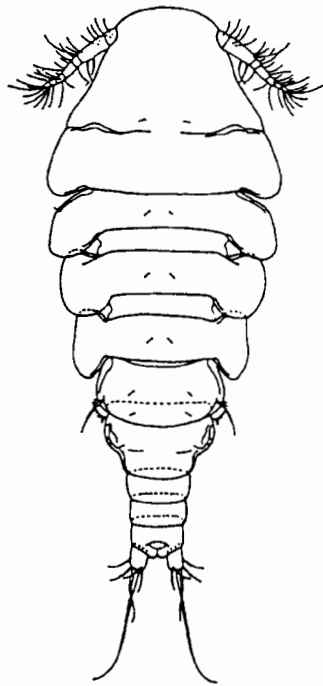
In his proposal to create a new genus *Tridacnophilus* to accommodate the four species of *Anthessius* occurring in the mantle cavities of the giant clams (Table 2), Nair (1988) argued that these four species differ from the rest of the congeners in (Figs. 1-3): (1) the marked indentation of the cephalosome, (2) the development of large epimeral lobes on pedigers one to four, (3) the unusual shape of the fifth pediger and genital complex, (4) the relatively short but stout antennule and antenna, and (5) the nearly rounded free segment of leg 5 with strong armature. However, a close examination of the external anatomy of the 41 species of *Anthessius* revealed that the five points enumerated by Nair (1988) do not apply to all four species concerned or confined to only these four species. For examples, as shown in Fig. 1, *A. discipedatus* Humes does not bear the features of (1), (2) and (3); and there are three species of *Anthessius*: *A. nortoni* (Illg 1960), *A. obtusispina* (Ho 1983) and *A. longipedis* (Ho & Kim 1992), bearing an antenna being shorter and stouter than the one found in *A. solidus* (Fig. 2), and the structure of leg 5 in *A. solidus* (Fig. 3) does not fit with point (5) enumerated by Nair (1988). Therefore, I opt for the use of cladistic analysis to examine if these four species of tridacnid parasites are monophyletic in the phylogeny of the *Anthessius*. If they are, then, Nair's (1988) proposal is to be upheld.



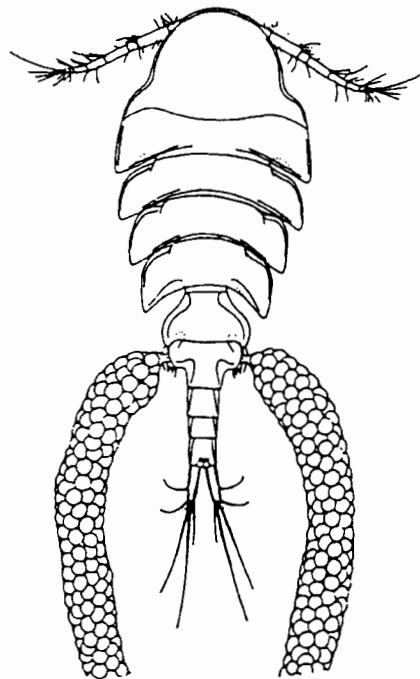
*alatus* Humes & Stock, 1965



*amicalis* Humes & Stock, 1965



*discipedatus* Humes, 1973

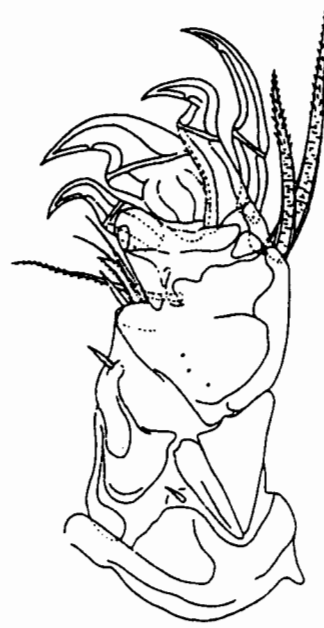


*solidus* Humes & Stock, 1965

Figure 1. Habitus of the four species of tridacnid-parasitizing *Anthessius* (after Humes 1973; Humes & Stock 1965).



*alatus* Humes & Stock, 1965



*amicalis* Humes & Stock, 1965



*discipedatus* Humes, 1973



*solidus* Humes & Stock, 1965

Figure 2. Antenna of the four species of tridacnid-parasitizing *Anthessius* (after Humes 1973; Humes & Stock 1963).

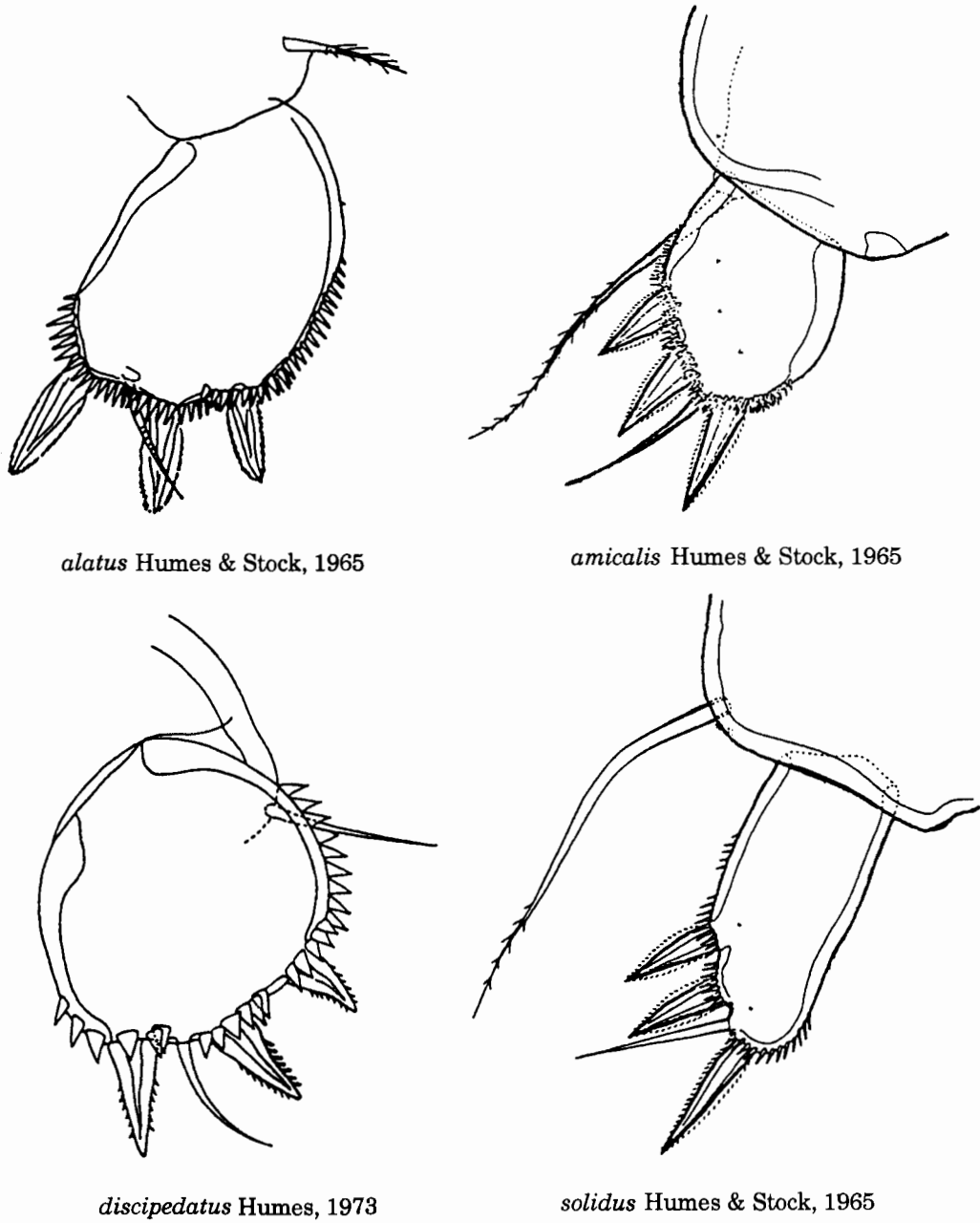


Figure 3. Leg 5 of the four species of tridacnid-parasitizing *Anthessius* (after Humes 1973; Humes & Stock 1963).

Table 2. Host-Parasite list for four species of *Anthessius* parasitic in the giant clams (Tridacnidae)

Host	<i>Anthessius</i>	Locality	Author
<i>Hippopus</i>			
<i>hippopus</i>	<i>amicalis</i>	Eniwetok Atoll	Humes (1972)
	<i>discipedatus</i>	Moluccas	Humes (1976)
<i>Tridacna</i>			
<i>gigas</i>	<i>alatus</i>	Eniwetok Atoll	Humes (1972)
<i>maxima</i>	<i>alatus</i>	Red Sea	Humes & Stock (1965)
		Eniwetok Atoll	Humes (1972)
		New Caledonia	Humes (1973)
	<i>amicalis</i>	New Caledonia	Humes (1973)
<i>squamosa</i>	<i>alatus</i>	Madagascar	Humes & Stock (1965)
		Eniwetok Atoll	Humes (1972)
		New Caledonia	Humes (1973)
		Moluccas	Humes (1976)
	<i>amicalis</i>	Red Sea	Humes & Stock (1965)
		Madagascar	Humes & Stock (1965)
		Eniwetok Atoll	Humes (1972)
		New Caledonia	Humes (1973)
	<i>solidus</i>	Madagascar	Humes & Stock (1965)

### CHARACTER ANALYSIS

To perform a cladistic analysis, it is required first to conduct a close examination of the various states of the homologous characters exhibited by the members of the ingroup (= *Anthessius*), then compare them with the counter parts found in the outgroup to determine the direction of the character transformation (= polarization). In this study, since many species of *Anthessius* are unknown of their male, the following character analysis can only be confined to the adult females. Moreover, since more than one-third of the reported species of *Anthessius* are unknown for their details of the appendages, it is, regrettably, impossible to find more than five characters for carrying out the wanted analysis.

In as much as *Anthessius* is the most primitive genus of the Anthessiidae, the outgroup needs to be selected from the sister taxa of this family and not within the family. Based on Ho's (1991) recent phylogenetic analysis of the families of Poecilostomatoida, Anthessiidae is the most primitive family of a clade (Branch 79) containing 11 families of copepods parasitic on fish or associated with various kinds of marine invertebrates. Since sister taxa of the Anthessiidae on

Branch 79 of Ho's (1991) cladogram are all highly modified, it is necessary to seek the outgroup from the other basal clades.

*Hemicyclops* Boeck, 1873 is generally considered to be the most primitive genus of the Poecilostomatoida (Ho 1984), it is accordingly adopted as the outgroup to polarize the character states transformation within the *Anthessius*. In the following analysis, (0) indicates plesiomorphic (ancestral) state; (1), apomorphic (derived) state; and (2) or (3), still further apomorphic state:

1. Antenna without terminal claw (0), with 2 terminal claws (1), 3 terminal claws (2), or 4 terminal claws (3).

*Anthessius pinnae* Humes is the only species bearing a pair of antennae tipped with two claws (Humes 1959). Comparing with those species bearing four terminal claws, it became clear that the innermost terminal and the subterminal elements in *A. ninnae* are in the form of a seta and in those 13 species with three terminal claws, it is the subterminal element which remained as a seta. Since the more the number of claws the better is the parasite equipped to hold on to the host tissue, the evolution of this attachment organ is thus considered to be conversion of more terminal elements into claws.

2. Mandible unarmed at outer lash base (0), armed with a hyaline plate (1) or armed with a pectinate process (2).

The mandible of *Hemicyclops* is quite different from that of *Anthessius*, it is tipped with two setae and two stout, denticulate or spinous processes. However, comparing with other poecilostomes, it is not difficult to speculate that in the course of evolution, the two setae in the ancestral form became atrophied and the remaining two processes developed into two long lashes like those found in the modern *Anthessius*. Thus, the addition of a hyaline plate or a pectinate process at the base of the outer lash is considered as a further development toward the parasitic mode of life. Since the mandible is utilized by the species of *Anthessius* in piercing and rasping host tissue for collecting food, the development of a pectinate process is considered to be more specialized than the development of a hyaline plate.

3. Maxillar terminal process without a row of teeth (0), with less than 10 teeth (1), or with more than 10 teeth (2).

As in the case of the mandible, the maxilla of *Anthessius* appears very different from that of *Hemicyclops*. This is simply due to the development of parasitic adaptation in the ancestor of *Anthessius*. Examination of the 41 species of *Anthessius* shows that this appendage differs from species to species only in the number of teeth on the terminal process, with the highest number (16 teeth) occurring in *A. arcuatus* (López-González *et al.* 1992) and the lowest number (3 teeth) occurring in *A. lophiomi* (Avdeev & Kazatchenko 1985), *A. saecularis* (Stock 1964), and *A. sensitivus* (Stock *et al.* 1963). Since there is not a species of *Anthessius* bearing nine teeth on its maxilla, "ten" is selected as a number to distinguish between the two states of maxillar character: high number of teeth versus low number of teeth. In this case, the former is considered to be more specialized.

4. Terminal segment of leg 4 exopod armed with 3 spines (0) or 4 spines (1).

The formula for the exopod of leg 4 in *Hemicyclops* is I-0;I-1;II,I,5. In *Anthessius*, 16 species show this formula of armature and the rest (25 species) have a formula of I-0;I-1;III,I,5, with an addition of one outer spine on the terminal segment. Since a character state identical with the outgroup's is considered as a plesiomorphic state, those 25 species bearing four spines on the terminal segment of leg 4 is considered to be more specialized.

5. Caudal ramus shorter than anal somite (0) or longer than anal somite (1).

Although species of *Hemicyclops* exhibit the same two states of character mentioned above, many planktonic poecilostomes carry a pair of short caudal rami which, in many cases, are shorter than the anal somite. Thus, in this study, those species of *Anthessius* with a pair of caudal rami longer than the anal somite are considered to be bearing an apomorphic state.

In the above analysis of the five selected characters, only nine apomorphies (three for character 1, two each for characters 2 and 3, and one each for characters 4 and 5) were identified. This number of character transformation is certainly too low to expect for obtaining a fully resolved cladogram (phylogenetic tree); but, nevertheless, since the intent for conducting the present study was to find the phylogenetic groupings of the 41 species of *Anthessius* so as to test Nair's (1988) creation of *Tridacnophilus*, construction of cladogram based on this limited amount of data was attempted.

#### TREE (CLADOGRAM) CONSTRUCTION

In order to employ the available computer programme to perform phylogenetic reconstruction, the above analysis of the homologous characters was reduced into a data matrix shown in Table 3. Since the mandible of *A. groenlandicus* Hansen, *A. investigatoris* Sewell, and *A. navanacis* (Wilson) are unknown, it is indicated with a "?" in the matrix. The same symbol applies

Table 3. Data Matrix. Names under "Taxa" show the first six letters of each species in *Anthessius*, except for "outgrp" which stands for outgroup. For the name of each species refer to Table 1.

Taxa	Character 1 2 3 4 5	Taxa	Character 1 2 3 4 5	Taxa	Character 1 2 3 4 5
outgrp	0 0 0 0 0	gracil	3 0 1 0 1	ovalip	2 2 2 1 0
alatus	3 1 2 1 1	groenl	3 ? 1 1 1	pectin	2 0 2 1 1
amical	3 1 1 1 0	hawaii	2 2 1 1 1	pincta	2 1 1 1 1
arcuat	2 2 2 1 0	invest	3 ? ? 1 ?	pinnae	1 0 1 0 1
arenic	3 0 1 1 1	kimjen	2 1 1 0 0	pleuro	2 2 2 1 1
atrina	2 1 1 0 1	leptos	3 0 1 0 1	projec	2 1 1 0 1
brevic	2 1 1 1 0	lighti	3 1 1 1 0	proxim	3 1 1 0 0
brevif	0 0 1 1 0	longip	3 1 1 0 1	saecup	3 1 1 0 1
concin	2 2 2 1 1	lophio	3 0 1 0 1	sensit	3 1 1 0 0
dilate	2 0 1 0 1	minor	3 0 1 1 0	soleno	3 0 1 1 1
discip	3 1 1 1 0	mytili	3 1 1 1 1	solidu	3 1 1 1 1
disten	3 1 2 1 0	navana	3 ? 1 0 0	styloc	3 1 1 1 1
dolabe	3 1 1 0 0	norton	3 1 1 0 1	teisse	3 0 1 1 1
fitchi	3 1 1 1 1	obtusi	2 2 2 1 0	varide	3 0 1 0 0

also to the maxilla and the ratio of caudal ramus to the anal somite for *A. investigatoris* Sewell, because these information are not available from Sewell's (1949) report of this species.

The phylogenetic computer package HENNIG86 Version 1.5 was used to analyze the data summarized in Table 3. The algorithm employed was IE\* (implicit enumeration). This algorithm allows one to find all shortest (most parsimonious) trees (cladograms) for the ingroup which show the least number of character state changes in the course of their evolution. Four such trees were obtained (Fig. 4), with a Tree Length of 24, a Consistency Index of 0.37, and a Retention Index of 0.79.

#### RESULTS AND DISCUSSION

The four trees shown in Fig. 4 are not fully resolved. This is expected because only a limited number of characters were available for analysis.

In the obtained four trees, *A. brevifurca* Sewell is shown to be the most primitive living *Anthessius*, followed by *A. pinnae* Humes and then by *A. dilatatus* (Sars). After this initial cladogenesis, there is no consensus branching among those four cladograms, except for a group of five species occurring in a monophyletic situation on Branch 43 in

Trees 1, 3, and 4; and on Branch 47 in Tree 2. These five species are: *A. arcuatus* López-González, Conradi, Naranjo & García-Gómez; *A. concinnus* (Scott); *A. obtusispina* Ho; *A. ovalipes* Stock, Humes & Gooding; and *A. pleurobrancheae* Della Valle.

It is clear from this cladistic analysis that the four species of tridacnid-parasitizing *Anthessius* are not in a monophyletic group. The occurrence of these four species on the four obtained trees are summarized in Table 4 for an easy inspection. Clearly, a quick examination of Table 4 shows that *A. amicalis* and *A. discipedatus* are closer to each other than either of them is to *A. alatus* or *A. solidus*, and, further, the latter two species never occur on the same branch in any of the four obtained trees. Thus, Nair's (1988) contention to create *Tridacnophilus* for accommodation of these four species of *Anthessius* occurring in the mantle cavities of giant clams does not have a support from this cladistic analysis. In other words, creation of *Tridacnophilus* should be abolished. In 1988, Ho reported that there were five species of *Anthessius* [*A. oncinnus* (Scott); *A. hawaiiensis* (Wilson); *A. obtusispina* Ho; *A. ovalipes* Stock, Humes & Gooding; and *A. pleurobrancheae* Della Valle] showing close affinity with each other. After discussing some synapomorphies, close affinities, and



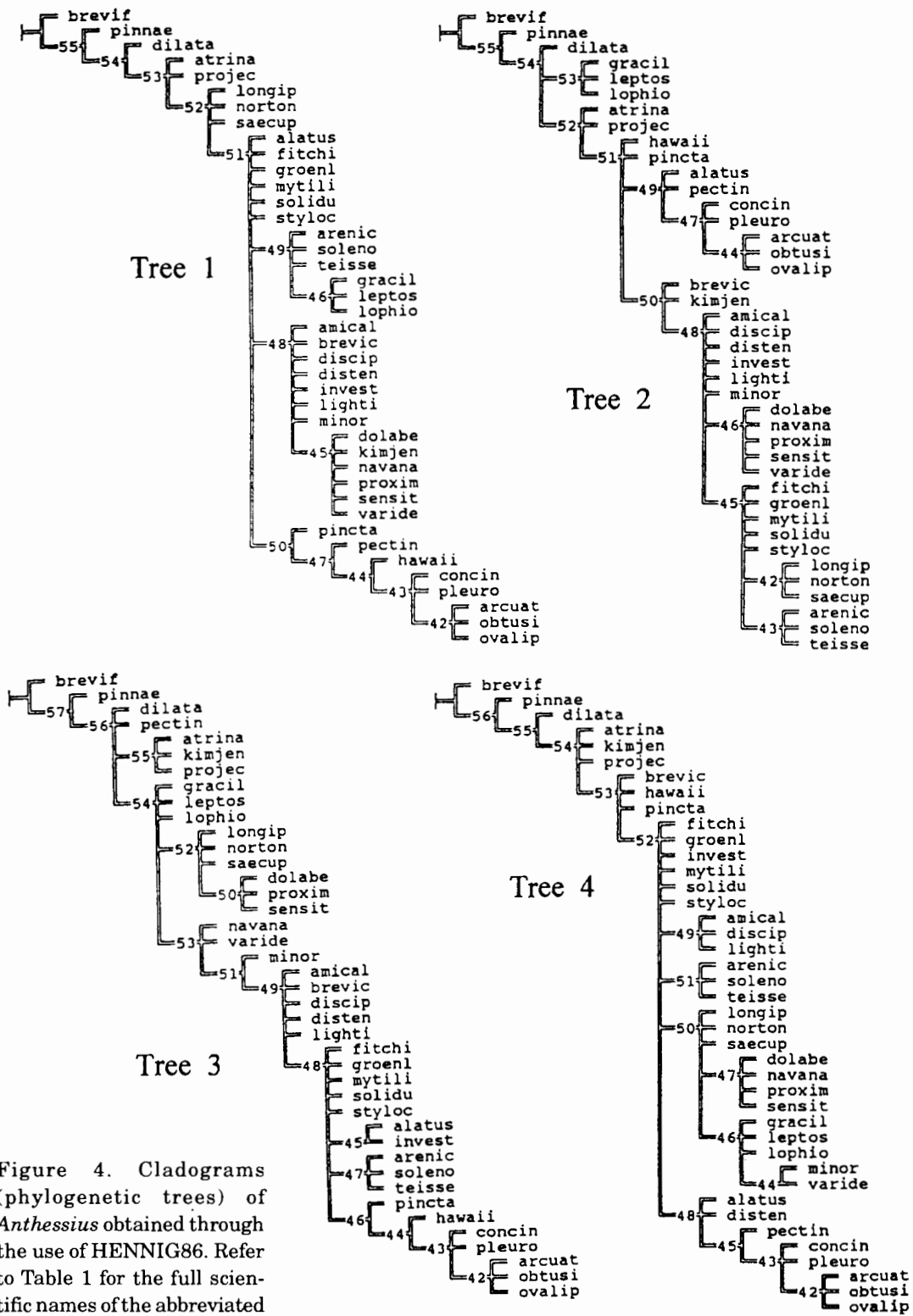


Figure 4. Cladograms (phylogenetic trees) of *Anthessius* obtained through the use of HENNIG86. Refer to Table 1 for the full scientific names of the abbreviated names.

Table 4. Location of the four species of Tridacnid-parasitizing *Anthessius* on the four obtained cladograms.

<i>Anthessius</i>	Tree 1	Tree 2	Tree 3	Tree 4
<i>alatus</i>	Branch 51	Branch 49	Branch 45	Branch 48
<i>amicalis</i>	Branch 48	Branch 48	Branch 49	Branch 49
<i>discipedatus</i>	Branch 48	Branch 48	Branch 49	Branch 49
<i>solidus</i>	Branch 51	Branch 45	Branch 48	Branch 52

host-parasite relationships of those five species, Ho suggested that they evolved from *Anthessius*-like copepods that were once associated with bivalves but had subsequently shifted to live on the notaspidean sea slugs. It is interesting to point out that those five species pointed out by Ho (1983) are clustered in a monophyletic group on Branch 44 in Tree 1 and Tree 3 (Fig. 4) with an addition of *A. arcuatus*, which was reported by López-González *et al.* (1992) from a notaspidean gastropod, *Berthella stellata* (Risso), in Spain. Thus, Ho's (1988) contention is supported by the present cladistic analysis.

#### CONCLUSION

Based on the present cladistic analysis, the four species of *Anthessius* occurring chiefly in the mantle cavities of giant clams (Tridacnidae) in the Indo-West Pacific are not so closely affiliated as to warrant a separate genus, *Tridacnophilus* Nair, 1992. However, the obtained cladograms uphold Ho's (1983) suggestion that coevolution occurred

between some species of *Anthessius* and their notaspidean hosts.

Andrew Scott (1909) reported *A. concinnus* (= *Hermanella concinnus*) from a plankton sample taken during Siboga Expedition to the East Indies. However, according to the obtained cladograms (on Branch 43 in Trees 1, 3, and 4; and Branch 47 in Tree 2), *A. concinnus* is a parasite of notaspidean sea slug, if one accept Ho's (1983) suggestion. Therefore, a discovery of *A. concinnus* from a notaspidean sea slug in the Malay Archipelago will serve as a further support to Ho's (1988) suggestion and also corroborate the phylogeny of the *Anthessius* depicted in Fig. 4.

#### ACKNOWLEDGEMENTS

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