CHAPTER 6
GENERAL DISCUSSION

6.1 Introduction

This Chapter attempts to synthesize the information from the different chapters for an overview of how the monogeneans interact with each other (Section 6.3.1) and with their hosts (Section 6.3.2) in order to define the characteristics of the monogeneans on the siluriforms of Thailand (Section 6.3).

Issues raised in Chapters 4 and 5 which are pertinent to the taxonomy and systematics of the monogeneans such as the validity of Ancyrocephalidae Bychowksy, 1937 will be discussed in Section 6.2. The expected outcome of any taxonomic investigations is to define an evolutionary trend for the group in question and this will be attempted in Section 6.4. The pathogenic potentials of the monogeneans will be elaborated in Section 6.5.

6.2 Taxonomic status of Ancyrocephalidae Bychowsky, 1937

The present 83 monogenean species of the Order Dactylogyridea Bychowsky, 1937 (Appendices 3.1-3.8) belong to seven genera in two subfamilies Ancylodiscoidinae and Ancyrocephalinae of the family Ancyrocephalidae. The seven genera include three genera (*Bifurcohaptor* Jain, 1958, *Cornudiscoides* Kulkarni, 1969 and *Thaparocleidus* Jain, 1952) from the Ancylodiscoidinae and four genera (*Bychowskyella* Achmerow, 1952, *Hamatopeduncularia* Yamaguti, 1953, *Mizelleus* Jain, 1957 and *Quadriacanthus* Paperna, 1961) from the Ancyrocephalinae. There are 18 dactylogyridean genera of monogeneans on the siluriforms of the Old World. In Thailand there are seven genera on the freshwater siluriform fishes compared to seven genera in Africa, nine in India, five in Peninsular Malaysia and four genera in the Palearctic region (Section 4.3.5). The dactylogyridean monogenean genera of the siluriforms do not infect fish hosts belonging to other orders such as the Cypriniformes. The exception is the presence of *Thaparocleidus* Jain, 1952 on the notopterids (Section 4.3.1 (i)). The siluriforms are also only hosts to specific monogeneans (listed in Table 6.1) other than the ubiquitous gyrodactylids (Table 6.1).

The taxonomic status of the family Ancyrocephalidae raised in Section 4.3.1 will be discussed in Section 6.2.2. A relevant issue is the class name of the monogeneans (Section 6.2.1). The issue of whether the Monogenea is monoplyletic or not will not be dealt with in this thesis. This issue is well discussed by Justine (1998) and it is not within the scope of this thesis to discuss this issue and at the moment it is also too premature to take a stand.

6.2.1 Monogenea van Beneden, 1858

There are several classification schemes for the Class Monogenea based mainly on morphological characteristics (Boeger & Kritsky, 1993; Bychowsky, 1937, 1957; Gussev, 1978, 1985; Lebedev, 1988; Justine, Lambert & Mattei, 1985; Malmberg, 1990). In 1937 Bychowsky divided the Class Monogenoidea (as he called it) into two subclasses, Polyonchoinea and Oligonchoinea, while Price (1937) followed Odhner (1912 in Price, 1937) in dividing the monogeneans into two groups, Monopisthocotylea and Polypisthocotylea. Lebedev (1988) divided the monogeneans into three orders, viz., Polystomatoinea, Oligonchoinea and Polyonchoinea. The Oligonchoinea of Bychowsky (1937) corresponds to the Polystomatoinea and Oligonchoinea of Lebedev (1988) and Monopisthocotylea Odhner, 1912.

The yet unresolved dispute over the use of the names Monogenoidea and Monogenea has been reviewed by Wheeler and Chisholm (1995) who noted that the monogeneans have been recognised as a distinct group, the ***Monogeneses***, as early as 1858 by van Beneden within the class Trematoda, although the name Monogenea was used by Carus (for ***Monogeneses***) in 1863. Bychowsky (1957) referred to the group as Monogenoidea (van Beneden, 1858), while other authors had used the name Monogenea Carus, 1863. According to the review of Wheeler and Chisholm (1995), Bychowsky (1957) was correct in attributing the authorship to van Beneden (1858) but incorrect in referring to the group as Monogenoidea since the word ***Monogeneses*** as used by van Beneden was correctly translated as Monogenea by Carus. Hence, following the rule of nomenclature the proper name for the monogenean is Monogenea van Beneden, 1858.

Table 6.1 Classification of the monogeneans found only on the siluriforms
(fw = freshwater ; m = marine)

Class: Monogenea van Beneden, 1858
Subclass: Polyonchoinea Bychowsky, 1937
Order: Dactylogyridea Bychowsky, 1937
Suborder: Dactylogyrinea Bychowsky, 1937
Family: Ancyrocephalidae Bychowsky, 1937
- **Subfamily:** Ancylodiscoidinae Gussev, 1961
  - **From siluriform hosts**
    - *Anchylodiscus* Johnston & Tiegs, 1922 (m)
    - *Ancylodiscoides* Yamaguti, 1937 (fw)
    - *Bifurcohaptor* Jain, 1958 (fw)
    - *Cornudiscoides* Kulkarni, 1967 (fw)
    - *Protoancylodiscoides* Paperna, 1969 (fw)
    - *Pseudancylodiscoides* Yamaguti, 1963 (fw)
    - *Thaparocleidus* Jain, 1952 (syn. *Silurodiscoides* Gussev, 1976) (fw)
  - **From non-siluriform hosts**
    - *Malayanodiscoides* Lim & Furtado, 1986 (fw)
    - *Notopterodiscoides* Lim & Furtado, 1986 (fw)
- **Subfamily:** Ancyrocephalinae Bychowsky, 1937
  - **From siluriform hosts:**
    - *Bagrobdella* Paperna, 1969 (fw)
    - *Bychowskyella* Achmerow, 1952 (fw)
    - *Chauhanellus* Bychowsky & Nagibina, 1969 (m)
    - *Hamatopeduncularia* Yamaguti 1953 (m)
    - *Mizelleus* Jain, 1957 (fw)
    - *Paraquadriacanthus* Ergens, 1988 (fw)
    - *Quadriacanthus* Paperna, 1961 (fw)
    - *Schilbetrema* Paperna & Thurston, 1968 (fw)
    - *Schilbetrematoides* Kritsky & Kulo, 1992 (fw)
  - **From non-siluriform hosts:**
    - *Ancyrocephalus* Creplin, 1839 (m) (type genus of the Ancyrocephalinae)
    - *Ancyrocephalus (s.l.)* Gussev, 1976 (fw)
    - *Bravohollisa* Bychowsky & Nagibina, 1970 (m)
    - *Cabellaria* Bychowsky & Nagbina, 1970 (m)
    - *Haliotrema* Johnston & Tiegs, 1922 (m)
    - *Metahaliotrema* Yamaguti, 1953 (m)
    - *Parancyrocephaloides* Yamaguti, 1938 (fw)
    - *Pseudohaliotreamtoides* Ymaguti, 1953 (fw)
    - *Pseudohaliotrema* Yamaguti, 1953 (m)

Family: **Neocalceostomatidae Lim, 1995**
- *Neocalceostoma* Tripathi 1957 (m)
- *Neocalceostomoides* Kritsky, Mizelle & Bilqees, 1978 (m)

Subclass: Polyonchoinea Bychowsky, 1937
Order: Gyrodactylidea Bychowsky, 1937
Family: Gyrodactylidae Cobbold, 1864
- *Gyrodactylus* Nordmann, 1832
- *Macrogyrodactylus* Malmberg, 1957

6.2.2 Validity of Ancyrocephalidae Bychowsky, 1937

The monogenean subfamilies found on Thai catfish are the Ancylodiscoidinae Gussev, 1961 and Ancyrocephalinae Bychowsky, 1937 in the family Ancyrocephalidae Bychowsky, 1937 (Section 4.3.1). The heterogeneity of the group (especially of the Ancyrocephalinae) has been noted (Gussev, 1978; Kritsky & Boeger, 1989; Lim, 1994, 1995a, 1995c, 1996a, 1998). In reviewing the status of Ancyrocephalidae, Kritsky & Boeger (1989) proposed two possible solutions concerning this issue, favouring their option of making Ancyrocephalidae a junior synonym of Dactylogyridae and including all the subfamilies of the Ancyrocephalidae as subfamilies of Dactylogyridae. This was the status of the four-anchored monogeneans prior to the proposal of Bychowsky and Nagibina (1978) to separate the four-anchored monogeneans from the Dactylogyridae into the family Ancyrocephalidae. The other proposal of Kritsky and Boeger (1989) was to sink Ancyrocephalidae and raise all the subfamilies to family status within the Order Dactylogyridea.

There are presently three options: (1) to accept the proposal of Kritsky and Boeger (1989) of reducing the Ancyrocephalidae as a junior synonym of Dactylogyridae, (2) to retain the Ancyrocephalidae without any changes, or (3) to raise status of the subfamilies currently within the Ancyrocephalidae.

Kritsky and Boeger's (1989) proposal to synonymise Ancyrocephalidae and to include all the subfamilies into Dactylogyridae will result in making the Dactylogyridae heterogeneous. The Dactylogyridae at the moment contains monogeneans with two anchors with needles and 14 marginal hooks. The ancyrocephalids, on the other hand, have four anchors, 14 marginal hooks and lack needles. While agreeing that the Ancyrocephalidae is heterogenous and in need of revision, the present conservative approach is to retain Ancyrocephalidae (accept Option 2) until more information become available on the interrelationships between the different groups of the Order Dactylogyridea. Option 3 is also probable as noted by the relative homogeneity amongst the members of the Ancylodiscoidinae (see later). The Ancyrocephalinae, however, is heterogeneous containing both marine and freshwater genera (see Sections 4.3.1 & 6.3.3).

The monogeneans found on the siluriform fishes of the Old World (summarised in Table 6.1) belong to two orders Dactylogyridea and Gyrodactylidea and three families Ancyrocephalidae, Neocalceostomatidae and Gyrodactylidae with a total of 20 genera. Also included in Table 6.1 are related groups of dactylgoyrideans from non-siluriforms to indicate the heterogeneity of the subfamily Ancyrocephalinae. The generic components of the subfamilies have undergone changes since 1978 (see Gussev, 1978; Lim, 1998). The two subfamilies of the Ancyrocephalidae are differentiated based on the types of seminal vesicles and the characteristics of the haptoral elements (Table 6.1). The subfamily Ancylodiscoidinae differs from the Ancyrocephalinae in having blind sac-like (saccate) seminal vesicle, while dactylogyrid-type seminal vesicles (dilation on vas deferens) are present in the Ancyrocephalinae. However the subfamily Ancyrocephalinae is made up of genera from both freshwater and marine environments. (Table 6.1; see also Section 6.3.3). The Ancyrocephalinae has been a catch-all group and may include unrelated genera. A revision of the Ancyrocephalidae should also address the status of the genera within the Ancyrocephalinae (Table 6.1). Future revision may see a return of all the genera formerly listed by Gussev (1961) (some of which are now in the Ancyrocephalinae) to the Ancylodiscoidinae (see Section 6.4).

6.3 Characteristics of monogeneans on siluriforms in Thailand

To understand how a ecosystem works it is necessary to know the characteristics of the community and the factors affecting the characteristics. The characteristics of the monogeneans community is the product of the strategies adopted by the interacting species to diversify and to survive together (Section 6.3.2) and the associations with their hosts which enable the monogeneans to survive and evolve on and with the hosts (Section 6.3.3).

In this Section, the implications of the diversity of monogeneans on catfish as revealed in Chapters 4 and 5 will be discussed herein to elucidate the characteristics of monogeneans on a community of siluriforms in a tropical ecosystem. The observed diversity of monogeneans is probably the results of diversification of the host species (Section 3.3.2) and subsequent co-evolution and speciation of the monogeneans (Sections 3.4; 4.3.4 & 5.4.3).

Prior to this it is also necessary to determine the expected diversity of monogeneans on the Thai catfish to provide some idea of the number of species yet to be described from the freshwater catfish (Section 6.3.1).

6.3.1 Expected Diversity of species on Siluriformes of Thailand

The diversity of a community is important since diversity is an indication of the stability of a community. The greater the diversity the more stable the community. The diversity of a community of organisms is composed of two components, the number of species present in the community (species-richness of the community i.e. the number of species present in the community) and the relative abundance of the species (or evenness or equitability) (Lim, 1998; Solomon, 1979). To compare the diversity of different communities, it is necessary to determine the diversity indices for the different communities. Several indices of diversity exist but these usually take into account the relative abundance. In this study relative abundance data is not available since it was not possible to sample the same number of host species (see Section 2.5), therefore, only one component of the diversity (the species-richness) could be considered.

The 83 dactylogyridean species obtained in the present study are not representative of the expected diversity on freshwater siluriform fishes of Thailand, since these 83 species were collected from only 40 of the 44 host species investigated and there are 98 species of freshwater catfish in Thailand (see Section 3.3.2 & Table 6.2). The expected number of monogenean species on catfish in Thailand could be estimated by considering the number of monogenean species per host species and the number of freshwater siluriforms.

Lim (1998) estimates the species-richness or species diversity of freshwater monogeneans in the Malaysian Peninsular to be 816 species based on the assumptions that (a) all host species will possess monogenean species, (b) monogeneans are host-specific, with no overlap of monogenean species on the different fish host species, and (c) the number of monogeneans per infected fish host species is about three species.

In Thailand there are seven genera on the freshwater siluriform fishes compared to seven genera in Africa, nine in India, five in Peninsular Malaysia and four genera in the Palearctic region (Section 4.3.5).

Table 6.2 Diversity of monogeneans on freshwater catfish of Thailand

Fish families	No. of fish species recorded	No. of fish species examined	No. of fish species infected	No. of monogenean species collected	Average No. of monogenean species per host
Amblycipitidae*	1	0	-	-	-
Akysiidae*	5	0	-	-	-
Ariidae	4	1	1	1	1
Bagridae	25	12	10	30	3(1-8)
Chacidae*	1	0	-	-	-
Clariidae	7	7**	7	9	2(1-4)
Heteropneustidae	1	1	1	1***	1
Pangasiidae	12	10	9	19	4(1-6)
Schilbeidae	5	1	1	2	2
Siluridae	23	9	9	19	3(1-4)
Sisoridae	14	3	2	2	1(1-1)
Total 11 families	98	44	40	83	2-3

Remarks: * not examined; ** with two non-indigenous species; ***have same monogenean species as *Clarias* spp.

Assumption a and empty niches

The assumption that all fish species will possess monogenean species could be argued to be incorrect as shown by the absence of monogeneans on four of the 44 species of catfish (9 %) examined. However the absence of monogeneans from these fish species could be due to the low number of hosts investigated (Section 2.2.2) and/or that the samples were collected from too few localities (Section 2.2.1). Locality differences have also been shown to be a factor affecting distribution (Lim, 1987a). If the present observation is a true presentation of what is expected in nature, then it follows that 9 % of the siluriform fish species in Thailand would be without monogenean. This means that 9 % of 98 species of siluriforms, that is nine catfish species, will be completely devoid of monogenean species (Table 6.3). This will be considered in the estimation of diversity.

Assumption b and wide specificity

The second assumption is also not always true in all cases since there are monogenean species with wide host specificity which are capable of infecting a large number of related host species (Section 4.3.4). In this study there are 20 species of monogeneans which could be found on two or more host species (Section 4.3.4.2). For example, *Thaparocleidus caecus* could be found on six host species (Section 4.2.5 & Table 4.11). Of the monogeneans collected 76 % of the monogenean species could be found on one host species, while only 24 % could be found on more than two or more host species. The number of host species sharing the same monogenean species vary depending on the fish families concerned: within the Clariidae there are five *Clarias* species sharing one or more species (Table 6.2), for example *Clarias batrachus* shares two monogenean species with *C. macrocephalus* and one species with *C. cataractus* and *C. meladerma* (Section 4.2.3 & Table 4.1), within the Pangasiidae the number is higher, nine pangasiids are found to share one or more monogenean species (see Section 4.2.5 & Table 4.1).

In the estimation of diversity the number of overlapping species will not be considered in view of the low number of overlapping species.

Assumption c and diversity per host species

This present study notes that the monogeneans per fish host species range from one to eight species. The range is consistent with that observed for the Cyprinidae (one to 14) and Siluriformes (one to ten) in Peninsular Malaysia (Lim, 1987a, 1998). This study reveals that 28 % of the catfish possess two monogenean species, while 18 % and 11 % of the catfish have three and four monogenean species, respectively (Table 4.10). The average monogenean species per catfish host species is thus between two to three (Section 4.3.3.3; Table 6.2).

This agrees with the predicted number of three monogenean species per host species used in estimating the total diversity of monogenean species on freshwater fish in Peninsular Malaysia (Lim, 1998). This assumption of three monogenean species per host species is justified since 38 % of the fish examined (17 host species) have three or more monogenean species compared to 9 % of the siluriforms (four species) without monogeneans, 25 % of host species (11 species) with one monogenean species and 28 % of the fish species (12 species) with two monogenean species (Table 4.10).

Estimation of diversity

By multiplying the average number of monogenean species per fish host species by the number of host species, the expected diversity on Thai freshwater catfish is estimated to be 196 to 294 species based on the assumed presence of two monogenean species per host species and three monogenean species per host species, respectively. This means that the present 83 species represents only 33 % to 50 % of the probable monogenean diversity on catfish, and that there are about 113 to 211 species (or 50 % to 67 %) yet to be described (Table 6.3).

If empty niches are considered and assuming that the present observation reflects what is in nature, then 9 % of the siluriforms will be without monogeneans. This means nine species of siluriforms (9 % of 98 species) will be without monogeneans while 89 siluriforms will be expected to possess two or three monogenean species per host species giving an estimated expected diversity of 178 to 267 monogenean species, respectively (Table 6.3). These figures can only be confirmed or refuted when all the catfish species of Thailand have been sampled.

Table 6.3 Estimated number of monogeneans on Thai freshwater catfish

No. of fish species	1 monogenean species / host species	2 monogenean species/ host species	3 monogenean species/ host species	No. of monogenean yet to be described
98 species (total catfish species)	98	196	294	113-211
89 species (based on predicted 9 % of fish species being uninfected)	89	178	267	95-184

6.3.2 Monogenean species diversification

It has already being established that the monogenean fauna on the Thai catfish is diverse (Chapters 4 and 4). This section will discuss how the diversifications of monogeneans at species and morphological levels enable the host species to accommodate the diverse monogenean species on the gills. For species to survive and thrive they must be able to find their hosts as well as to adapt to their changing environments (macro and micro-environments). This section will discuss the impact evolutionary strategies or processes have on the interacting monogeneans to maintain species integrity and species diversity for survival.

6.3.2.1 Significance of morphological diversity and rates of change

The siluriform monogeneans are morphologically diverse. The amount of morphological diversity exhibited by a monogenean group is dependent on the structures analysed. For example the members of the ancylodiscoidins are 84 % similar in terms of sclerotised hard parts, while the members of the ancyrocephalins are only 68 % similar in terms of sclerotised parts (Section 5.3.1; Figs. 5.1 & 5.19). The ancyrocephalins thus exhibit more morphological diversity indicating that the ancyrocephalins are a more morphologically diverse group (see also Section 6.2.). In terms of haptoral armament the ancylodiscoidins are 74 % similar, while the ancyrocephalins are 64 % similar (Sections 5.3.1 & 5.3.7; Figs. 5.2 & 5.20). The copulatory organs and vaginal armaments are morphologically more diverse amongst the *Thaparocleidus* of the silurids than amongst the *Thaparocleidus* of the pangasiids (Sections 5.3.3 & 5.3.4; Figs. 5.7-5.12). The *Thaparocleidus* from the silurids have greater diversity in haptoral armaments compared to the *Thaparocleidus* from the bagrids: the haptoral armaments of *Thaparocleidus* species on the silurids are only 25 % similar compared to 56 % similarity in haptoral armaments exhibited by the *Thaparocleidus* from the bagrids.

The difference in morphological diversity of the different structures exhibited by the different monogeneans indicates that rates of change of the different sclerotised parts are different in different groups of monogeneans on different host groups or even on the same host species. The sclerotised parts in co-existing congeners are more diverse when compared to congeners from different host species indicating that co-existing congeners have a more rapid rate of change (Section

5.4.2). There are no patterns in the differential rates of change of the different sclerotised parts of the monogeneans in relations to monogenean genera or families and to host groups. Elucidation of the factors affecting the rate of change of morphologies in different groups of monogeneans will provide a better understanding of how speciations occur. Elucidation of the factors governing the diversity within the gills will assist in explaining the difference in diversity observed in different host species. The factors are probably multi-faceted involving the hosts, parasites and the macro-environment. There seems to be more questions than answers at the moment.

6.3.2.2 Significance of morphological diversity and co-existing species

Table 4.2 indicates that the bagrid and the pangasiid species have the highest monogenean species diversity compared to the other families. In fact *Hemibagrus nemurus* and *H. wyckoides* have eight and seven monogenean species which belong to three and two genera, respectively (Table 4.2). While *Pangasius larnaudii* and *Pteropangasius pleurotaenia* have six *Thaparocleidus* species each. Being morphologically different, the different co-existing non-congeners on the *H. nemurus* and *H. wyckoides* probably inhabits different parts of the gills and in doing so use the resources on the gills differently. This leads indirectly to resource partitioning on the gills and hence avoid interspecies competition. Pathologically diverse monogenean fauna on the gills will inflict less damage to the gills than when many individuals of one species are present (Lim, 1987a) and hence it is advantageous to the host species to have a diverse parasitic fauna.

The similarities amongst congeners (co-existing as well as non co-existing) (Section 5.4.1) could be explained by similar ancestry (Section 6.4). The difficulty is in explaining the observed differences amongst co-existing congeners (Section 5.4.2). Most of these co-existing congeners are not grouped together in the dendrograms generated during the morphological analysis (Section 5.3.2) (Figs.5.4-5.6) indicating that in most cases the co-existing congeners are morphologically different. This non-grouping of congeneric species of a given host species seems to support Lim' s (1987a) observations that co-existing congeneric species are more different than congeneric species from related host species.

The co-existing congeners with different haptoral armaments probably inhabit different parts of the gills (which have been shown to be heterogeneous by Hughes, 1984) to prevent competition and also to increase distances between different species to avoid interspecies breeding in order to preserve species integrity. This strategy is probably employed by the co-existing congeners on *Pangasius conchophilus* (the four *Thaparocleidus* species are separated into three groups according to the haptoral armaments: see Fig. 5.8; Section 5.3.3). Co-existing congeners with different sclerotised reproductive structures (as exemplified by three *Cornudiscoides* species on *Hemibagrus nemurus* which are scattered into different clusters when the reproductive structures are considered: Fig. 5.18; Section 5.3.6) probably employed this means to prevent cross-breeding and to preserve species integrity.

Lim (1987a) suggests that the co-existing congeners are different due to evolutionary processes which enable only monogeneans with different morphologies to co-exist by (a) inhabiting different parts of the gills (resource partitioning), hence reducing negative interspecific interactions, and (b) limiting interspecies breeding. Very similar co-existing congeners are probably not observed since they are not able to survive physically.

The number of co-existing congeners (25 % and 38 % of the siluriforms have two, or three and more co-existing species: Table 4.10) indicate that there are enough genetic variations within the monogenean community to allow for speciations to occur. Hence within the monogenean community there are enough processes to reduce spatial competition especially interspecies competition, to ensure species integrity (too much gene flow) and at the same time to maintain enough generic variations within the monogenean community for species diversification. This hypothesis should be tested.

6.3.3 Association between host and monogenean

About 76 % of the monogenean species on the Thai siluriforms are host specific (Section 4.3.4.2; Table 4.11). This concurs with the observation of Bychowsky (1957) that about 74 % of the known monogenean species occur on a single host species and 84 % on a single host genus. This observed specificity also conforms with the characteristics of the monogeneans from other fish groups in other regions (Llewellyn, 1956; Gussev, 1976; Kennedy, 1975; Rohde, 1979). On the other hand, about 24 % of the monogeneans on the 40 catfish species infect more than one host species (Table 4.11) which are usually related at least at generic if not at family level. For example *Quadriacanthus kobiensis* is found on four *Clarias* species (Clariidae). *Thaparocleidus caecus* is found on six species of of Pangasiidae in four genera which are closely related, in fact, except for *Helicophagus* the other three genera (*Pangasionodon*, *Pteropangsius* and *Pangasius*) were classified as *Pangasius* until recently (Section 4.2.5). Another example is *Bychowskeylla tchangi* which could be found on three related clariid species (two *Clarias* species and *Heteropneustes* species) .

Specificity may have either a physiological or ecological basis or both. In monogeneans, specificity is usually pronounced as are the monogeneans in the present study where 76 % of them are found on one host species (Table 4:11). The reasons put forward for this distribution pattern of monogenean species are varied. The most quoted reasons for host specificity (see Section 4.3.4) is that the host and monogeneans co-evolved suggesting that the relationships have been long and intimate and that specificity has a phylogenetic significance.

The absence of monogeneans from the four host species (Sections 4.2 & 6.3.1) could be due to non-conducive macro-environmental factors (Lim, 1987a). Another probable reason is based on the observed over-disperse distribution patterns (negative binomial distribution) of monogeneans on a host population (Lim, 1987a) which implies that within a given host populations there are a few individuals without parasites as well as few with many parasites. It is thus possible that in the case of the four species that the fish individuals sampled did not contain any monogeneans (Section 4.2). This means that more fishes should be examined.

The presence of *H. longicopulatrix* on the marine ariid, *Arius venosus* and freshwater ariid, *Hemipimelodus borneensis* of Peninsular Malaysia and Thailand, respectively (Section 4.3.1 (ii)) suggests that in some cases the host species plays a more important role than the macro-environment in determining species existence. A possible explanation for the presence of a particular monogenean species on different but related host species (*T. caecus* on six pangasiid species) and unrelated hosts (*Bychowskyella tchangi* on two species of clariids and on *Heteropneustes fossilis*) could be the ability of the monogenan species to adapt and to overcome host immune system. This phenomenon is known as host-capture or host-transfer (see Lim, 1987a). This phenomenon has been put forward to explain presence of species in unrelated hosts (see Leong & Holmes, 1981). It is difficult in many of these cases to determine the original host species. It could be speculated that *H. longicopulatirx* could have been transferred to *H. borneensis* from *A. venosus* because of the fact that there are more individuals of *H. longicopulatrix* on *A. venosus*. However there are no evidence to refute the converse.

6.3.3.1 Significance of faunistic links

Morphologically the monogenean species on Thai catfish do not differ from the monogeneans found on catfish from Peninsular Malaysia (Lim, 1986a, 1987a, 1987b, 1991b; Lim & Furtado, 1983), Vietnam (Ha, 1968), South China (Long, 1981; Ma *et al.*, 1983) and India (Gussev, 1976; Jain, 1952b, 1958; Kulkarni, 1969b; Majumdar & Agarwal, 1988; Tripathi, 1957). This indicates that the monogenean fauna of Thailand is closely related to the Malaysian monogenean fauna and hence that the host species of these two regions are closely related.

In Thailand there are seven monogenean genera on the freshwater siluriform fishes compared to seven genera in Africa, nine in India, five in Peninsular Malaysia and four genera in the Palearctic region (Section 4.3.5 & Table 6.1). The Indian monogeneans are more similar to the Thai monogeneans than to the Malayan fauna: *Mizelleus* is found on Indian and Thai *Wallago* but not the Malayan *Wallago*. The significance of the presence of *Mizelleus* in Thailand and India will be discussed in Section 6.3.3.2.

Faunistically different regions possess their own unique of monogenean fauna (Tables 4.12 & 4.13) although there are some overlapping genera and even species (see *Quadriacanthus kobiensis* on *Clarias batrachus* of India, Peninsular Malaysia and Thailand, and *Bychowskyella tchang* on *Clarias batrachus* of India, Indo-China, Peninsular Malaysia and Thailand). The presence of similar types of monogeneans on related hosts in apparently unconnected faunistic regions suggests some affinities between these biogeographical regions (Lim, 1997, 1998; Paperna, 1979) (Section 4.3.5). The presence of *Quadriacanthus* on African, Indian and Southeast Asian clariids (Section 4.2.3; Tables 4.12 & 4.13) implies geological links between the Southeast Asian region, India and Africa (see also Lim, 1998). The geological links of the Southeast Asian region to Gondwana has already been established (Metcalfe, 1993). The lack of catfish fossils makes it difficult to ascertain when and where the fish evolved and their route of dispersion. The fishes could have being present on the Southeast Asian terranes (See Metcalfe, 1993) prior to the break up of Gondwana or they could have been brought to Southeast Asia when India collided with mainland Asia (Section 3.6) (Lim, 1997) (see also Section 6.3.3.3). The relatedness of the different fish species from the different regions and as well as the relatedness of their monogeneans could be detected using molecular biology and biochemical techniques.

6.3.3.2. Endemicity of monogenean and transition zone

With a few exceptions (Section 6.3.3.1), the siluriforms in different regions have their own distinct endemic monogenean fauna. The genera *Schilbetrema* and *Schilbetrematoides* are only found on the Schilbeidae in Africa, while *Bifurcohaptor* and *Cornudiscoides* are endemic to India, Peninsular Malaysia (Lim, 1987b) and Thailand (present study) and restricted to the Bagridae (Section 4.3.5).

The presence of *Mizelleus* on the *Wallago* of India and Thailand but not on the *Wallago* of Peninsular Malaysia (see Section 4.3.5) indicates that Thailand could be a transition zone for monogenean (and host) distribution (see Lim & Lerssutthichawal, 1996). The fauna of Thailand will thus be interesting from the point of view of species dispersion. Thailand could thus harbour, *Ancylodiscoides*, which are found on Chinese and Indian siluriformes but not on Malayan fauna thus far.

6.3.3.3. Centre of origin of the monogeneans

Southeast Asia has been postulated to be the centre of origin for the Bagridae, Pangasiidae and Siluridae (see Section 3.7). Bagridae, Clariidae and Schilbeidae were postulated to be present in three plates of China, India and Southeast Asia prior to their break away from Gondwana (Kottelat, 1989). The issue here is whether the monogenean distribution patterns concur with the aforementioned hypothesis that Southeast Asia is the centre of origin of at least some of the catfish.

The primitive genera *Bifurcohaptor*, *Cornudiscoides*, *Quadriacanthus* and *Bychowskyella* (see Section 6.4.1) are distributed in India, Thailand and Peninsular Malaysia and in the case of *Quadriacanthus* also in Africa, while *Mizelleus* is found only in India and Thailand. The assumption that species are usually distributed closest to their centre of origin (Gussev, 1976) would therefore suggests that Southeast Asia could be the centre of origin for the *Bifurcohaptor* and *Cornudiscoides* and their hosts the bagrids. As for *Quadriacanthus* the centre of origin could have been in Gondwana: the clariids could have been on the Southeast Asian terranes prior to their break away from Gondwana or brought to Southeast Asia when India collided into Asia. While continental Southeast Asia and/or India could be the centre for *Mizelleus* and its host, the silurid. The monogenean distribution data seems to concur with the hypothesis about the place of origin for some of the siluriforms.

Presently it is not possible to confirm or refute if Southeast Asia is the centre of origin of the monogenean genera mentioned above. In order to determine the centre of origin for the ancestral monogenean of the siluriforms it is necessary to determine which of the 18 genera found on the Old World siluriforms is the most primitive. The above issues could only be resolved when molecular data from all the siluriform hosts and their monogeneans become available.

6.4 Evolution and phylogeny of monogenean fauna of Thai catfish

The establishment of a phylogenetic relationship will enable us to understand how the monogeneans differentiate (speciate), survive and co-evolve with their hosts and how they are 'recruited'. Such information is not only of academic interest but necessary for a better understanding of disease conditions and transmission in order to institute effective control measures.

There are several hypotheses on phylogenetic relationships of the monogenean groups at family and higher levels based on morphology (Boeger & Kritsky, 1993; Kritsky & Boeger, 1989; Kritsky & Lim, 1995) (see Sections 5.1 & 6.3.2) and lately on DNA (see Rohde, Hefford, Ellis, Baverstock, Johnson, Watson & Dittmann, 1993; Justine, 1998). There are however few attempts to determine the phylogenetic relationships amongst members of related monogenean genera on a specific group of fish (Sections 4.3.1 & 5.4). A hypothesis on the interrelationships of the dactylogyridean monogeneans of the siluriforms based on the haptors and seminal vesicles has been given (see Lim, 1991c). Prior to the establishment of the hypothesis it is necessary to determine the primitive monogenean (see Section 6.4.1). The hypothetical evolution of the monogeneans will be compared with the phylogeny of the hosts to evaluate the correctness of the hypothesis (Section 6.4.)

6.4.1 The primitive monogeneans

The search for primitive monogeneans is an on-going endeavour (Gussev, 1976; Lim, 1987a) because the primitive catfish monogenean, when known, will provide clues to phylogeny of the parasites and their hosts. Since there are no records of monogenean fossil the determination of the primtive monogeneans is usually done indirectly through assumptions. The primitive monogeneans have been postulated to possess certain characteristics: (a) primitive monogeneans are usually found on primitive hosts, (b) primitive genera have fewer members i.e. lower diversity, and (c) primitive genera or species are usually very host specific (see Gussev, 1976). *Mizelleus* suits the bill and so do *Quadriacanthus*, *Bifurcohaptor*, *Cornudiscoides* and *Ancylodiscoides* (Section 4.3.1). *Bychowskyella* is found on six fish families in the Oriental and the Amur-Chinese region (Palearctic) (Sections 4.3.1(i); 4.3.5 & Appendix 3.2), hence does not have all the characteristics of a primitive monogenean compared to *Quadriacanthus* which is found only on the clariids of Southeast Asia, India and Africa and on the bagrids of Africa (Section 4.3.1(ii)). *Thaparocleidus* with the highest species diversity and found in all the families of siluriforms except on the Clariidae, Ariidae and Heteropneustidae (Section 4.3.1(i), is considered to be the most advanced. The order of antiquity of the dactylogyridean genera is as follows: *Mizelleus* > *Quadriacanthus* = *Bifurcohaptor* = *Cornudiscoides* = *Ancylodiscoides* > *Bychowskyella* > *Thaparocleidus*.

Based on the above discussion the ancestral monogenean of the catfish should have characteristics which are common to all the dactylogyridean genera. The traits common to all the dactylogyrideans are (a) a simple dactylogyrid seminal vesicle and (b) a haptor with four anchors, two bars, 14 marginal hooks and no patches (since patches are found in some and absent in others). The dactylogyrid seminal vesicle is considered a common trait because it is found in most dactylogyridean except for the ancylodiscoidins with saccate seminal vesicles, while the *Anchylodiscus* has both types of seminal vesicles (see Lim, 1992c).

6.4.2 Evolutionary pathways of the ancyrocephalins and ancylodiscoidins

It has already been noted that the monogeneans of the siluriforms of the subfamilies Ancyrocephalinae and Ancylodiscoidinae are related (Section 6.2). According to Kritsky and Boeger (1989) the saccate-seminal vesicle (blind sac-like seminal vesicle of the ancylodiscoidin) is apomorphic while the dactylogyrid-type of seminal vesicle is symplesiomorphic. It is also probable therefore that the two dactylogyrid seminal vesicles and the dactylogyrid and saccate seminal vesicles combination are apomorphic of the dactylogyrid type.

Fig. 6.1 depicts and summarises the hypothethical evolutionary changes in the haptoral armaments and seminal vesicles in the dactylogyridean monogeneans of the siluriforms as postulated by Lim (1991c). The ancestral monogenean of the catfish is postulated to have a simple dactylogyrid seminal vesicle and haptor with four anchors, two bars, 14 marginal hooks and no patches (see Section 6.4.1). Two possible evolutionary routes from the ancestral form to the present-day forms are denoted in RED (Route 1) and GREEN (Route 2).

The ancestral form gives rise to the ancyrocephalid of the Ariidae and the ancyrocephalin of the freshwater siluriforms very early in the evolution. The pre-ancyrocephalid form of the Ariidae retains all the characteristics of the ancestral forms (section 6.4.1), while the pre-ancyrocephalin form retains the primitive haptor and primitive distal dactylogryid seminal vesicle and evolving a second proximal dactylogyrid seminal vesicle. Subsequent evolution of the ancyrocephalids on the Ariidae has already been postulated in Lim (1996a) and will not be discussed here. The evolution to the other monogenean genera from the pre-ancyrocephalin form (with ancestral haptoral armaments & two dactylogyrid seminal vesicles) could occur in two ways.

In Route 1, the pre-ancyrocephalin form gives rise to two sister groups: the pre-*Bychowskyella* form (with two dactylogyrid seminal vesicles & evolving patches on the dorsal anchors) and the pre-*Anchylodiscus* form (ancestral haptor, distal dactylogyrid seminal vesicle, proximal seminal vesicle becoming saccate).

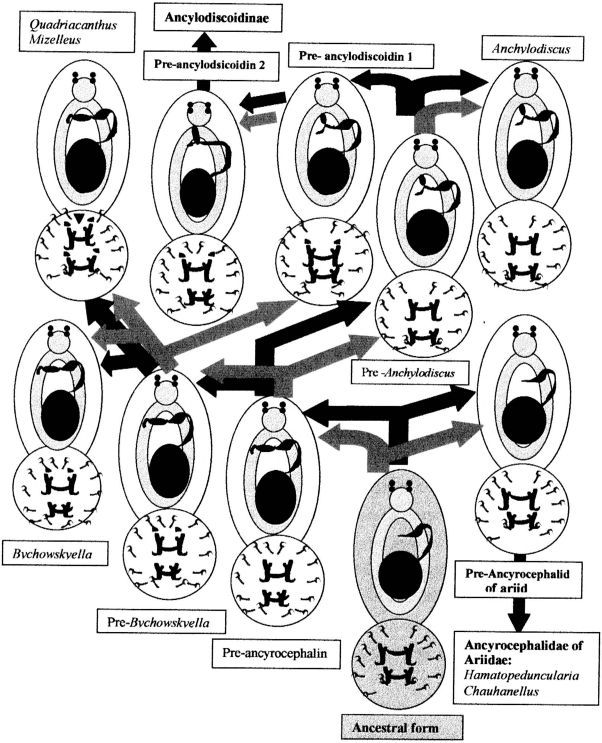

Fig. 6.1. Hypothetical evolutionary pathways (Route 1 & Route 2) of the dactylogyridean monogeneans found on the siluriforms of the Oriental region (adopted from Lim, 1991) (Figure is used here with the persmission of Lim LH.S.).

The pre-*Anchylodiscus* form gives rise to the first pre-ancylodiscoidin form (loses distal dactylogyrid seminal vesicle, retaining proximal saccate seminal vesicle and ancestral haptor) and the *Anchylodiscus* form (with all the characters of the pre-*Anchylodiscus*). The first pre-ancylodiscoidin form then acquire patches on its dorsal anchors transforming into the second pre-ancylodiscoidin form (with saccate seminal vesicle & dorsal anchors with patches) which evolves to form the other ancylodiscoidins (see Table 6.1). The subsequent evolution of the ancylodiscoidins will be discussed later (Section 6.4.3). The pre-*Bychowskyella* form gives rise to two sister groups: the *Bychowskyella* which retains all the characters of the pre-*Bychowskyella* form and the *Quadriacanthus-Mizelleus* group which acquires another set of patches while retaining the two dactylogyrid seminal vesicles. Subsequent evolution of the *Bychowskyella-Quadriacanthus-Mizelleus* group needs more studies before their evolutionary status could be determined.

In Route 2 (GREEN) the pre-ancyrocephalin form (with ancestral haptor & two dactylogyrid seminal vesicles) gives rise to two sister forms: the pre-*Anchylodiscus* form (ancestral haptoral armaments & distal dactylogyrid seminal vesicle & proximal seminal vesicle becoming saccate) and the pre-*Bychowskyella* form (two dactylogyrid seminal vesicles & acquiring patches on dorsal anchors). The pre-*Anchylodiscus* evolves unchanged to the present-day *Anchylodiscus*. The pre-*Bychowskylla* form gives rise to two other sister groups: the first pre-ancylodiscoidin (with dorsal patches and distal dactylogyrid seminal vesicles, while proximal seminal vesicle changing into saccate form) (this pre-ancylodiscoidin form is similar to the pre-*Anchylodiscus* in the seminal vesicles and differing in having dorsal patches) and the *Bychowskyella* form (retaining all the characteristics of pre-*Bychowskyella* form) and finally to the *Quadriacanthus-Mizelleus* group (with the acquisition of another set of patches).

It should be noted that the two routes discussed are by no means the only possibilities. The structure of the haptors remained basically unchanged as the monogeneans co-evolve with their hosts differentiating into the different genera, except for the acquisitions of patches in the ancylodiscoidins (one dorsal pair) and ancyrocephalins (one or two pairs), onchia and other minor parts and changes to bars and patches in the ancyrocephalins (Section 5.3.1.2). At the present time the above pathways are just postulations and should be tested with more information especially from developmental biology and molecular biology DNA.

The implications of this hypothesis on the evolution of the dactylogyrideans of the siluriforms is that the ancylodiscoidins with blind sac-like seminal vesicle is the advanced form, while the ancyrocephalins with two dactylogyrid-type seminal vesicles are related to the primitive form. Lim (1992c) suggested that the *Anchylodiscus* species (with one dactylogyrid type seminal vesicle and one blind sac-like seminal vesicle) could be the link between the ancyrocephalin forms and ancylodiscoidin forms.

6.4.3 Evolution of the ancylodiscoidins

The second pre-ancylodiscoidin form develops from the first pre-ancylodsicoidins with the loss of the distal dactylogyrid seminal vesicles and retention of proximal saccate seminal vesicle and patches on the dorsal anchors (Routes 1 & 2; Fig. 6.1) giving rise to the other ancylodiscoidins (*Ancylodiscoides, Cornudiscoides, Bifurcohaptor, Thaparocleidus*) on the siluriforms and on non-siluriforms, the notopterids (Table 6.1).

The ancylodiscoidins could be derived from either the pre-*Anchylodiscus* (Route 1) or the pre-*Bychowskyella* forms (Route 2), depending on whether the patches are developed prior to the development of the saccate seminal vesicles or after. It is difficult to ascertain this presently. In Route 1 (RED) the dactylogyridean monogeneans of the siluriforms only have to lose the distal dactylogyrid seminal vesicle and to acquire the saccate seminal vesicle only ONCE. While in Route 2 (GREEN) the development of the saccate seminal vesicle must occur twice in the evolution of the catfish monogeneans i.e. in the pre-*Anchylodiscus* form and the pre-ancylodiscoidin form. However in Route 2, the monogeneans have only to acquire the patches ONCE while in Route 1, the patches are acquired by the catfish monogeneans TWICE (Fig. 6.1) unless the pre-*Anchylodiscus* actually have patches which was lost enroute to the present-day *Anchylodiscus*.

The next stage in the development of the pre-ancylodiscoidins into different genera (Table 6.1) is not easy to postulate presently until more information especially on host phylogeny, developmental biology data of the ancylodiscoidins and DNA data become available.

6.4.4 Phylogeny of monogeneans versus phylogeny of hosts

The rationale for the detailed documentation of the hosts is so that the information could be used to elucidate the evolutionary standing of their monogeneans.

If according to the parasitophyletic rule (Table 6.4) that ancient hosts have ancient monogeneans: then it follows that ancient monogeneans are found on ancient hosts. The evolution of the dactylogyrideans suggests that the monogenean genera *Mizelleus*, *Quadriacanthus* and *Bychowskyella* are primitive (Sections 6.4.1 & 6.4.2) this would then imply that their hosts silurids, clariids and sisorids are ancient siluriforms. However the silurids are also hosts to the advance *Thaparocleidus* as well as to *Mizelleus* and *Bychwoskyella*, while the sisorids are hosts to *Bychowskyella* and *Thaparocleidus*, and the clariids hosts to 'the two primitive genera, *Bychowskeylla* and *Quadriacanthus*.

Lim (1991b) considers the *Bychowskyella* with onchia to be more primitive than the *Bychwoskyella* without onchium. This implies that sisorids possessing *Bychowskyella* with two onchia could be more primitive than the silurids with *Bychowskyella* with one onchium. However the converse (*Bychowskyella* with onchium is more advance) can also be true. The implication of this is that the sisorids and silurids are evoluionary more advanced than the clariids which possess *Bychowskyella* without onchium. The only way to resolve this is to determine the DNA of the dactylogyrideans of the siluriforms.

The highly diversified *Thaparocleidus* is considered an advanced genus (see also Section 6.4.1) since it is found on almost all the siluriform groups except the clariids, the plotosids and the ariids. The poorly diverse but highly specific *Ancylodiscoides*, *Bifurcohaptor* and *Cornudiscoides* are found on silurids (a primitive siluriform) and the bagrids (which according to Berg, 1947, is also a primitive group) suggests these three monogenean genera could be related to the primitive monogeneans (see later) (see also Section 6.4.1). However bagrids are also regarded as an advanced group (Mo, 1991).

Table 6.4 The parasitophyletic rules (adopted from Lim, 1987a)

Rules	Concepts	Implications
1. Fahrenholz's rule:	The classification of parasitic groups parallels that of their hosts.	Ancestors of extant parasites must have parasitised the ancestors of extant hosts and both groups must have evolved in parallel (co-evolution).
2. Szidat's rule:	The primitive hosts are parasitised by the primitive parasites, and specialised hosts have specialised parasites.	The degree of specialisation may serve as a clue to relative phylogenetic ages of the hosts.
3. Eichler's rule:	Large host groups have more genera of parasites than small groups, or isolated groups of hosts often do not harbour many kinds of parasites.	The diversity of parasites in isolated groups is less than the diversity of groups with many species or with groups with near affinities to other groups.
4. Manther's rule:	i) Parasites evolve more slowly than their hosts. ii) The longer association with a host-group, the more pronounced the exhibited by the parasite group. iii) A host species harbours the largest number of parasite species in the area where it has resided longest.	i) Parasites are usually of a lower phylogenetic group than their hosts and usually older. iii) Overspecialized parasites may be found in some specialized host. This suggests that parasites can adapt to infect the fish which inhabit the same areas for a long time. iii) if the same or two closely-related species of host exhibit a disjunct distribution and posses similar parasite fauna, the areas in which the hosts occur must have been contiguous at a time in the past.

The bagrids and pangasiids are probably the most advanced siluriforms since they have greater *Thaparocleidus* diversity. Pangasiids could be considered more advanced than the bagrids since bagrids are hosts to primitive monogeneans, the *Bifurcohaptor* and *Cornudiscoides*. However the possibility that the pangasiid could have lost their primitive monogeneans through the course of evolution cannot be discounted at the present time.

The present information on the phylogeny of the siluriforms seems to support the above observations on antiquity patterns of the monogeneans: (a) silurids are more ancient than the other groups (Berg, 1947; Chardon, 1968; Mo, 1991), (b) bagrids are more advanced than silurids, and (c) silurids are more primitive than the clariids which are in turn more primitive than the sisorids (Fig. 3.1: Chapter 3).

According to the hypothetical evolution (Fig. 6.1) the monogeneans of the ariids evolved separately from the monogeneans of the other siluriforms having parted from the freshwater catfish dactylogyrideans very early in the evolution of this group of monogeneans. Ariidae has been postulated to be most related to the freshwater siluriform, the Diplomystidae (see Berg, 1947) which is found in South America. A review of the literature revealed that no monogeneans have been recorded from this host family (Kohn & Cohen, 1998).

The evolutionary pathways in Fig. 6.1 also suggests that the plotosids are more related to the freshwater siluriforms than the marine siluriforms, the ariids. The monogenean on the plotosids (like the pre-ancyrocephalids on the ariids) branched from the other freshwater ancyrocephalids early in the evolution of the freshwater dactylogyridean monogenean of the siluriforms. This is a likely scenario since the plotosids could have separated from the freshwater catfish early in the evolution of the siluriforms. The relationships of the plotosids to the freshwater silurids (Section 3.4.1) (Berg, 1947) and also to the schilbeids (Mo, 1991) have been postulated (Section 3.4.1). According to some authors the plotosids are supposed to have migrated from freshwater environment to the sea (see Kobayakawa, 1991). The relationships of the plotosids to freshwater siluriforms is also supported by the presence of *Anchylodiscus* which has been postulated to be related to the ancylodiscoidins because of the saccate seminal vesicle (Lim, 1991c).

Within a given host group and based on the parasitophyletic rules (Table 6.4) that the primitive monogenean species could be found on primitive fish host species, the primitive species could be postulated. Within the pangasiid, *Helicophagus waandersii*, which is considered to be a primitive species would **theoretically possess** primitive monogeneans or monogeneans with primitive traits. The primitive *Thaparocleidus* species (based on this assumption) will resemble *Thaparocleidus caecus*, *Thaparocleidus* n. sp. 16 and *Thaparcleidus* n. sp. 17 (see Figs A51, A54, A56). Within the bagrids, *Batasio tengara* is considered a primitive species and its monogenean species, *Thaparocleidus* n. sp. 1 could also possess primitive traits (Fig. A21).

However difficulties in determining the antiquity of the siluriform groups because of differing opinions of the ichthyologists (Section 3.4.1) makes it difficult to use the hosts' phylogeny to ascertain the phylogeny of the monogeneans (see later). The absence of certain monogeneans could be due to environmental effects as is the acquisition of monogeneans hence it is difficult to use host phylogeny to suggest parasite evolution without collaborating evidence although the hosts do provide clues to the phylogenetic interrelationships of the monogeneans.

Whether Fig. 6.1 is reflective of the true evolutionary status of the catfish monogeneans could only be evaluated on the basis of indirect evidence since there are thus far no records of fossilised monogneans. However there are some discrepancies and the non-congruence of the information with that of the host evolutionary patterns is due to the incomplete host information. The discrepancies noticed may be due to the way the monogeneans are acquired by the hosts. The hosts could have acquired their monogeneans by direct inheritance (co-evolution) or via transfer from one host species to another through contact especially in the use of the same habitats by the different hosts. Parasites could also be lost through dispersion and subsequent evolution. For example ancyrocephalins could have been acquired by the evolutionary more advanced clariids and the sisorids from the primitive silurids through contacts.

If Fig. 6.1 does reflect the true status of the **monogenean phylogenetic** relationships it could be used to suggest possible hosts relationships based on the evolution patterns of their monogeneans.

6.5 Disease causing potentials of monogeneans

The role of monogeneans as disease causing agents has already been reviewed in Section 1.2.1. One of the rationale given for the present study of the monogenean fauna on the siluriform fishes which are earmarked for culture in Thailand is that it will document parasites which might be pathogenic under intensive culture situations (Section 1.3). In fact of the 44 fish species investigated, 16 have being identified by the Thai authorities as potential culture species (Section 1.4) and prior to this study there are practically no reliable information on the monogenean fauna on these fish species (Sections 1.1 & 1.3). An important contribution of this study is that it provides the basic information on the interacting and co-existing species on the 40 catfish species.

The absence of disease signs on feral fish and the high species diversity encountered, suggest that there are factors controlling any drastic increase in any of the co-existing species within the community thereby keeping the population of the different species to a level within the carrying capacity of the environment. These factors help to maintain species diversity resulting in ecosystem stability. From the parasitological and pathological point of view diversity is important since damages to the gills caused by one type of invading species is minimised (see Buchmann, 1988, 1997). Monogeneans have been shown to be greatly enhanced in numbers under intensive culture conditions (Section 1.2.1). In most cases there seems to be an increase in abundance of one particular species of the co-existing species, as exemplified by the increase in *Thaparocleidus siamensis* on cultured ***Pangasianodon hypophthalmus*** (Section 4.2.5).

The important issue here is to determine which of the co-existing species would become potential pathogen(s) under intensive culture. It is difficult presently to ascertain whether a specific species or a species with wide host range could become the potential pathogen. There are two co-existing congeners on *Pangasianodon hypopthalmus*, interestingly though it is not *Thaparocleidus caecus* (the species with wide host range) which shows an increase in abundance under culture but the highly host-specific, *T. siamensis* (Table 4.1 & Section 4.2.5). There are eight species of *Quadriacanthus* on *Clarias gariepinus* in Africa but on the *Clarias gariepinus* imported into Thailand for culture only *Q. bagrae* is found (Section 4.2.3 & below) as well as on the hybrid of *Clarias gariepinus* and probably the local *C. macrocephalus*.

Although monogeneans have been implicated to cause mortality of fish under culture it is not certain whether in most cases the monogeneans are direct or indirect causes (Lim, pers. com.). This aspect needs investigations.

Fishes are translocated for aquarium trade as well as for culture. Most of the freshwater fish of Thailand in particular and Southeast Asia in general are important aquarium fishes and this translocation can provide a means for the spread of parasites (in fact *T. caecus* was first described from an aquarium fish by Mizelle and Kritsky (1969)). Translocation of fish species for aquaculture has also brought about dispersion of parasites. This is documented in the presence of the *Quadriacanthus bagrae* on *Clarias gariepinus* imported from Africa for culture in Thailand as well as its presence on the hyrbid off-spring of the cross between *C. gariepinus* and *C. macrocephalus* (Section 4.2.3). Another example is the translocation of tilapias and their monogeneans to the Philippines (Lumanlan *et al.*, 1992) and to Peninsular Malaysia (Lim, unpublished data). The specificity of monogeneans limits their spread to local fish species. However, the danger of exotic monogeneans invading related local fish hosts is real. This is shown by the spread of *Pseudodactylogyrus bini* and *P. anguillae* from imported *Anguilla japonicum* to local *A. anguilla* population in Europe in the late 1970s (see Buchman *et. al*, 1987, 1997; Molnar, 1984) resulting in mass mortality in the local *A. anguilla* populations. Better quarantine measures must be instituted to ensure that *Quadriacanthus* species from the translocated *C. gariepinus* do not spread to local indigenous *Clarias* species.

Although it is beyond the scope of this thesis to identify the actual pathogen(s) in culture situations, this study has documented the monogenean species on feral fish species and any one of these monogeneans could have serious impacts on the fish under culture conditions. A follow-up of this study should be done to investigate the distribution patterns of monogeneans on culture siluriforms.

6.6 Concluding remarks

As a pioneering study, this study has contributed significantly (Appendices 3.1-3.8) to the basic knowledge of the parasite fauna on the siluriform fishes in Thailand (Sections 1.3 & 1.5). The main objective of this study (Section 1.5) has been achieved, given the limitations encountered (Section 2.5) even though the present collection only represent at best 30 % to 50 % of the monogeneans expected to be available on the Thai freshwater siluriforms (Sections 3.3.2 & 6.3.1). A complete documentation of the monogeneans on the other freshwater siluriforms not investigated in this study should be given priority. This investigation is important in view of the role of Thailand as a transition zone for the different adjacent biogeographical regions, the declining fish population due to rapid rate of aquatic environment degradation in Thailand (Sections 1.1 & 1.5) and the importance of siluriform fishes in aquaculture (Section 1.4). As a transition zone Thailand may encounter greater generic diversity than presently observed (Sections 4.3.5 & 6.3.3.2). *Ancylodiscoides* which is found in India and China (Tables 4.12 & 6.1) and not on the Southeast Asian catfish might be found in Thailand.

Morphological data supports the hypothesis put forward by Lim (1987a) that the co-existing congeners use different morphological strategies to survive and to preserve species integrity (Section 6.3.2.2), but this hypothesis needs to be tested. The monogeneans could also be using different biochemical strategies to survive and this aspect needs investigations. The factors affecting the evolutionary balance between maintaining species and genetic diversity, and species integrity are not known and the elucidation of these factors will certainly enable a better **understanding of the** evolutionary processes currently taking place.

As noted previously (Section 6.3.3.1) there are no monogenean fossils and hence any hypotheses on the evolution of the monogeneans would have to be discerned from their hosts especially since the evolution of the monogeneans are closely associated with the evolution of their hosts (co-evolution) (see Brooks, 1986; Lim, 1987a; Rohde, 1993) (Sections 3.4, 4.3.4 & 6.4.4). Hypotheses concerning the primitiveness of the monogeneans are also useful in determining the characteristics of the primitive monogenean. Currently information on host interrelationships and their centres of origin are still unclear and in some cases unavailable (Sections 3.6 & 3.7) making it difficult to predict the probable centre of origin for the siluriform monogeneans and to properly evaluate hypothesis of evolution of monogeneans.

A revision of the monogeneans on the siluriforms is urgently needed (Section 6.2.2). Future taxonomic investigations on the monogeneans would have to incorporate information from light microscopy, transmission electron microscopy and molecular biology for a better understanding of the phylogeny and evolution of the monogeneans (Sections 6.2 & 6.4). There is a paucity of information on the developmental biology of the monogeneans which is necessary to understand how the different genera are derived. The ecology of the monogeneans in the tropics which will provide information on how the monogeneans are recruited and how the population maintained, is poorly understood.

This study has revealed gaps in our knowledge on the monogeneans and identified several pertinent issues on the monogeneans, which would form the basis for future investigations. There is also a need to incorporate the various techniques available not only for a better classification system but also for a better understanding of how the monogeneans survive and thrive on the hosts.

SUMMARY

This study focussed on the documentation of the monogeneans on freshwater Siluriformes in Thailand to establish the characteristics of the monogeneans of the siluriforms. Thailand has about 98 species of freshwater Siluriformes. Forty of the 44 species examined for gill monogeneans are infected. Eighty-three monogenean species belonging to seven genera (*Bifurcohaptor, Bychowksyella, Cornudiscoides, Hamatopeduncularia, Mizelleus, Thaparocleidus* and *Quadriacanthus*) in two subfamilies (Ancylodiscoidinae and Ancyrocephalinae) in the family Ancyrocephalidae were described. Assuming an average infection of three and two monogeneans per host species, the expected monogenean diversity on Thai freshwater siluriforms is 294 and 196 species, respectively. The present observed diversity represents only 33% - 50% of the expected diversity.

The majority of the monogeneans on Thai siluriforms (76 %) are host-specific, while 24 % are found on two or more related host species (at generic or family levels). The Thai freshwater Siluriformes harbour only freshwater ancyrocephalins and ancylodiscoidins. The exception is *Hemipemilodus borneensis* (Ariidae) which harbours two species of the marine genus, *Hamatopeduncularia*. Such specific host-monogenean distribution patterns are also observed for the monogeneans on the siluriforms of Peninsular Malaysia and Africa.

Each biogeographical region has its own unique siluriform monogenans. The African fauna is distinct from the Oriental fauna with few exceptions. The Thai siluriform monogeneans are closely related to the Malayan and Indian fauna, and distantly related to the fauna of South China and Africa. Exchange of species occurs between adjacent areas. Southeast Asia and Africa were geologically linked. Lack of fish fossils makes it difficult to ascertain whether siluriforms were present on the Southeast Asian components prior to drifting from Gondwana or were brought to Southeast Asia when India collided into mainland Asia. The hypothesis of Southeast Asia as the centre of origin for many siluriforms and their monogeneans cannot

presently be verified. The presence of *Mizelleus* in Thailand and India and its absence in Peninsular Malaysia attest to the possibility of Thailand as a transition zone.

About 9 % of the fish hosts are without monogeneans, while 25 % have one, 28 % have two, 18 % have three, and 20 % with four or more co-existing species: indicating that co-existing species are common. Co-existing species can be congeners or non-congeners and the number vary from one to eight depending on host species: *Hemibagrus nemurus* has eight species belonging to three genera, *H. wyckoides* harbours seven species from two genera, while *Pangasius larnaudii* and *Pteropangasius pleurotaenia* have six species of *Thaparocleidus* each.

Morphological analysis reveals that co-existing species are morphologically different (not cluster together). These observed differences are evolutionary strategies for species survival by minimizing interspecific interactions (competitions) and interspecific mating (preservation of species integrity).

Evolutionary trend of the dactylogyridean monogeneans based on seminal vesicles and haptoral armaments implies that monogeneans of the ariids are related to the primitive ancyrocephalid. The ancyrocephalin genera (*Bychowskyella, Mizelleus* and *Quadriacanthus*) are morphologically similar to the ancient form, while the ancylodiscoidins are comparatively more advanced. *Thaparocleidus* is postulated to be the most advanced genus. The evolutionary hypothesis concurs to some extent with hosts' phylogeny.