

## Taxonomy: A Precursor to Understanding Ecological Interactions among Schistosomes, Snail Hosts, and Snail-Eating Fishes

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*Abstract.*—We have observed a dramatic decrease in the abundance of snail-eating fishes and an increase in the prevalence of schistosomiasis among village residents and expatriate tourists at Lake Malawi, Africa, over the past two decades. We hypothesized that these observations were linked by a cause-and-effect relationship and that the observed decrease in fish molluscivores permitted an increase in the abundance of snails that are intermediate hosts to schistosomes; we proposed a sampling protocol to determine these relationships. Initially, we thought that intensive study of the interactions among fish, intermediate-host snails, and human schistosomes in southern Lake Malawi could be applied to other areas throughout the lake. More than two-thirds of the cichlid species in Lake Malawi are undescribed, the taxonomy of the *Bulinus* snails is poorly known, and not all strains of *Schistosoma hematobium* have been identified. Before we can identify the interactions among these components of the system and effectively manage snail-eating fishes, we must be able to accurately delimit the taxonomic units (e.g., species, populations, and demes) within each of the above groups.

Lake Malawi is the southernmost of Africa's large rift lakes (Figure 1). Overharvest of cichlids in Lake Malawi has resulted in a dramatic decrease in the abundance of snail-eating fishes and concomitant increases in the prevalence of snails acting as intermediate hosts to schistosomes and in the prevalence of schistosomiasis among village residents and

expatriate tourists (Stauffer et al. 1997a, 2006). Data collected in 1978 showed that at Chembe Village (Figure 1), the density of the cichlid *Trematocranus placodon*, a facultative molluscivore, ranged from 10 to 26 fish<sup>-1</sup>·200 m<sup>-2</sup> at depths between 1.5 and 9.1 m. In 1991, the densities at the same location and depths ranged from 0 to 2 fish<sup>-1</sup>·200 m<sup>-2</sup>. The prevalence of schistosomiasis in school-age children at Chembe Village was 36.0% in 1978 and 87.4% in 1991 (Stauffer et al. 1997a, 2006). Stauffer et al. (1997a) stated that a lakewide strategy of using fish for

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controlling schistosome hosts should be initiated to reduce the prevalence of this disease. Through funding by the joint National Science Foundation and National Institutes of Health (NSF-NIH) Program in Ecology of Infectious Diseases (DEB0224958), we have begun to study the relationship between human schistosomes, intermediate-host snails, and fishes in the hope of devising and implementing such a strategy in Lake Malawi. Samples have been taken throughout Lake Malawi from Chilumba in the north to Nankumba Peninsula in the south (Figure 1). To date, we have shown that the increase in infection rate of schistosomiasis in southern Lake Malawi between 1978 and 1991 was coincident with the reduction in numbers of snail-eating fishes (Stauffer et al. 1997a, 2006).

Our efforts to determine the causative agents of this increase in disease prevalence are hampered by the lack of knowledge of the taxonomy of the schistosomes, snails, and fishes. If, in fact, it is possible to use molluscivorous fishes in the biological control of intermediate-host snails and thus lower the transmission rates as postulated by Stauffer et al. (1997a, 2006), then identification of these fishes is imperative to the implementation of any management strategies. Thus, we have become cognizant of the importance of correctly identifying and delimiting populations or species of the above fauna. The purpose of this paper is to discuss and identify the urgency for detailed taxonomic information at all levels for the development of effective management and biological controls of a human disease that affects 200 million people in the tropics (Stauffer et al. 1997a).

### Schistosomiasis in Lake Malawi

Human schistosomiasis is caused by trematodes of the genus *Schistosoma*. These trematodes use humans as the definitive host and use certain snails as intermediate hosts to complete their life cycle. Humans in primary contact with water are infected by cercariae, the first larval stage (Figure 1 in Stauffer et al. 1997a). After infecting humans, the schistosome, depending on the species, migrates to the vascular system around either the bladder or the bowels, where it matures. If both sexes are present, fertilized eggs are produced and can be released into the aquatic environment when the human host defecates or urinates in the water. The eggs hatch, and the second larval stage (miracidium) infects specific snails, including planorbid or prosobranch species (Warren and Mahmoud 1990); the miracidia develop into sporocysts within the snails. Subsequently, cercariae (Figure 2) are released from the snail host to infect bathing or submersed humans, thus completing the life cycle.

*Schistosoma mansoni*, *S. hematobium*, and *S.*

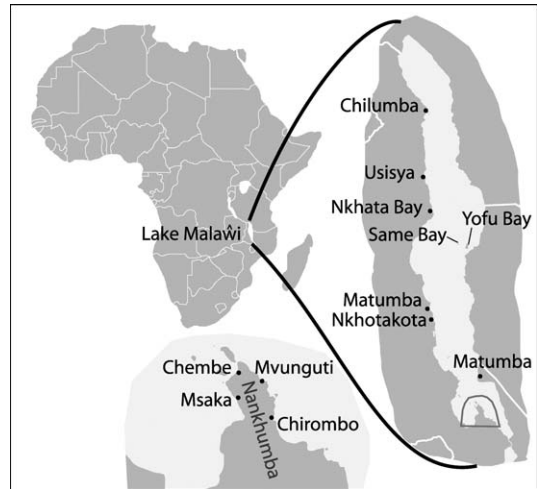


FIGURE 1.—Location of Lake Malawi, and the study area where the ecological interactions of schistosomes, snails, and fish were assessed.

*japonicum* are the most widespread of the five known schistosomes that parasitize humans; *S. intercalatum* and *S. mekongi* have a more restricted distribution (Rollinson and Simpson 1987). Schistosomiasis can cause considerable pathological changes (e.g., impaired physical and mental activity) in many infected individuals of a given population (Foster 1967; Jordan and Webbe 1969). Although *S. mansoni* is found in Malawi, in this paper we will concentrate on *S. hematobium*, the urinary schistosome found in Lake Malawi. In Malawi, novel central nervous system manifestations have been reported (CDC 1993), and gynecological lesions added to overall morbidity (Wright et al. 1982) could theoretically facilitate the transmission of AIDS (Feldmeier et al. 1994; Harms and Feldmeier 2002). The widespread occurrence of schistosomiasis in Malawi has been recognized for over 70 years (Dye 1924; Cullinan 1945; Ransford 1948); however, the open waters of Lake Malawi were considered to be schistosomiasis-free (Evans 1975) until the late 1980s (Stauffer et al. 1997a).

In 1999, the Danish Bilharzias Laboratory investigated the human epidemiology of schistosomiasis and intestinal worm infections in 28 villages and 19 primary schools on the Nankumba Peninsula (Danish Ministry of Foreign Affairs 2000). They were particularly interested in the prevalence of the disease in Chembe Village on Nankumba Peninsula, for which historical data were available. Urine samples from 4,232 school children (ages 6–14) and from 4,324 villagers (children and adults) living in randomly selected households were filtered and examined for



FIGURE 2.—Schistosome cercariae released from the snail *Bulinus nyassanus* (photo by H. Madsen).

eggs of *S. hematobium*. Additionally, stool samples from a randomized subgroup of the same individuals (609 school children and 421 villagers) were examined for eggs of *S. mansoni* and other intestinal worm infections. The findings indicated that the average prevalence of infection with urinary schistosomiasis (for lakeshore and inland communities combined) was 39% (range, 10.2–72.7%; Chembe Village, 57.7%) among villagers and 64.5% (range, 15.3–94.0%; Chembe, 87.5%) among school children. In terms of morbidity due to urinary schistosomiasis, an average of 41.1% (range, 9.8–78.0%; Chembe, 49.3%) of the villagers and 49.9% (16.9–89.2%; Chembe, 69.7%) of the school children had microhematuria. Furthermore, an average of 11.3% (range, 0.0–28.0%; Chembe, 17.8%) of the villagers and 31.6% (range, 1.7–68.4%; Chembe, 55.9%) of the school children had more than 50 eggs/10 mL of urine (i.e., a heavy infection). The prevalence of infection with intestinal schistosomiasis was low (total village average, 2.1%; range, 0.0–20.0%), whereas the average rate of infection with hookworm (the only other intestinal worm infection of significance in the area) was 28.0% (range, 0.0–66.7%). Based on historical information, it was difficult to interpret the high prevalence of urinary schistosomiasis on the Nankumba Peninsula, in light of sporadic treatment campaigns in the area.

#### Snail Intermediate Hosts in Lake Malawi

During the 1980s, the snail *Bulinus globosus* was the only known intermediate host of *S. hematobium* in the Lake Malawi basin, where it was confined to heavily vegetated areas and backwaters. Chiotha et al. (1991) showed that *B. globosus* had a thinner shell and was more easily crushed than other shallow-water mollusks (e.g., *Melanooides* and *Lanistes* spp.) and postulated that it would be a preferred food of molluscivorous fishes. We hypothesized that the snail-eating fishes inhabiting the open waters of the lake prevented *B. globosus* from invading these areas, and thus we postulated that in the absence of adequate numbers of snail-eating fishes, *B. globosus* would invade the shallow open waters of the lake (Stauffer et al. 1997a).

Contrary to Stauffer et al.'s (1997a) hypothesis about the ability of *B. globosus* to colonize open waters, data collected by our group and the Danish Bilharziasis Laboratory since 2003 showed that *B. nyassanus* and *B. succinoides* are the only *Bulinus* species inhabiting the open waters of Lake Malawi; only the former species has been shown to act as a host for *S. hematobium*. An experimental study in which *B. nyassanus* were exposed to miracidia of *S. hematobium* obtained from infected Chembe villagers revealed that 3 of 19 snails shed human schistosome cercariae at 6–8 weeks postexposure (Madsen et al. 2001). Hamsters

*Mesocricetus auratus* exposed to cercariae obtained from field-collected, schistosome-infected *B. nyassanus* had eggs of *S. hematobium* in their livers at 12 weeks postexposure; at 21 weeks postexposure, they showed hepatomegaly with granuloma formation (Madsen et al. 2001). Furthermore, *S. hematobium*-infected *B. nyassanus* have been found regularly in routine collections at Chembe Village from 1999 to present, particularly from June to October. Prevalence of infection is generally below 1% but can be higher locally.

Similar monthly surveys carried out on the eastern (Mkope Village) and western (Malembo Village) shores of the Nankumba Peninsula reported only small numbers of *B. nyassanus* in the lake and none in the peninsula's inland waters (Phiri et al. 1999). In contrast, *B. globosus* was very common in inland waters but not in the lake itself. Thus, coexistence of the two species was not observed. The highest average infection rate of *B. globosus* with human schistosomes was 24% (Malembo, August 1999). Major differences in the bottom substrate at the surveyed sites may explain why *B. nyassanus* was uncommon at Mkope and Malembo (Phiri et al. 1999). At Chembe Village, the substrate primarily consists of very coarse sand to gravel, whereas at Mkope and Malembo fine silt is predominant. In the lake, *B. nyassanus* inhabits coarse sand (with or without vegetation), whereas *B. globosus* typically appears in small streams and ponds with vegetation (Marti et al. 1985).

### Fishes of Lake Malawi

Lake Malawi harbors the most diverse ichthyofauna of any freshwater lake in the world, containing as many as 850 species (Konings 2001). The rich fauna of this lake is primarily attributable to the explosive adaptive radiation and speciation of the haplochromine cichlids (Regan 1921; Trewavas 1935; Greenwood 1979).

The diversity of the fishes inhabiting Lake Malawi was recognized by Günther as early as 1893 (Eccles and Trewavas 1989). Regan's (1921) revision of the fishes of Lake Malawi encouraged several collecting expeditions, which provided the material for Trewavas' (1935) classic synopsis of the fauna. The cichlids of Lake Malawi are characterized, in part, by their interlake and intralake endemism. The status of many of the groups described as genera, however, remains questionable because precise locality information is lacking for 32 of the 38 type species used to define these genera. In some cases, the validity of the type species of the genus is questioned. For example, the type species of *Ctenopharynx* is *C. intermedius* (Günther), and the type collection of *C. intermedius*

consists only of the holotype, which is a relaxed skin with broken fins (Eccles and Trewavas 1989).

Although they produce new facts and speculation as to the different forms, surveys of Lake Malawi cichlids (Ribbink et al. 1983; Lewis et al. 1986; Konings 1990) have not resulted in comprehensive and formal descriptions of new taxa. The explosive radiation of the Lake Malawi cichlids has resulted in a paucity of characters needed to distinguish taxa. This dearth of information about unique characters is at odds with the need to be able to delimit species for the conservation and utilization of these fishes for food, tourism, disease control, and scientific investigations. Certainly, there is an inherent obligation for all the species in a World Heritage Site, such as Lake Malawi, to be documented and recognized. Examples of taxonomic confusion that inhibits the delineation of Lake Malawi fish species follow.

Original investigators of the Lake Malawi species flocks failed to recognize the tremendous intralake endemism of these fishes. For example, Iles' (1960: 258) account of *Copadichromis eucinostomus* is based on the two cotypes and specimens "from both ends of Lake Nyasa." Eccles and Trewavas (1989) provided additional morphometric and meristic information based on the lectotype and paralectotype specimens from Karonga, Chilumba, Vua, and unknown localities in Lake Malawi. Our observations of the breeding behaviors of these populations indicated that they build differently shaped bowers (Stauffer et al. 1993). We therefore postulated that more than one species existed within the populations historically identified as *C. eucinostomus*. These fishes are an important food source for the Malawians, and without correct identification we are not able to relate observed life history, behavioral, and ecological observations to a particular species so as to devise management plans that maximize yield of these fishes.

The males of many sand-dwelling cichlids build bowers (McKaye et al. 1990), which they aggressively defend and use as display sites during courtship. These bowers vary significantly among species, allowing us to differentiate various species based on bower shape (McKaye and Stauffer 1988; McKaye 1991). During the past decade, extensive research has been completed on the ecology and behavior of sand-dwelling fishes in southern Lake Malawi (McKaye 1991). As part of these studies, we observed that males fitting the description of *C. eucinostomus* (see Trewavas 1935; Iles 1960) constructed three different bower forms, suggesting that the different populations were distinct species. As a result, Stauffer et al. (1993) described these forms as three new *Copadichromis* species, which were

referred to in the literature formerly as *C. eucinostomus*. Unfortunately, we were unable to analyze the bower-shape of topotypes of *C. eucinostomus*, because the type locality information was not precise but simply "Lake Nyasa." A comparison of the behavioral information of the three new species from southern Lake Malawi with the published accounts of *C. eucinostomus* was futile. Consequently, the name *C. eucinostomus* is restricted to the two syntypes cataloged into the British Museum of Natural History.

Original species descriptions of the Lake Malawi fishes relied heavily on pigmentation patterns. For example, species of the genus *Protomelas*, locally known as "kambuzi," are characterized by a series of pleisiomorphic characters, including the presence of longitudinal bands on the flanks. Previously, the distinct vertical and horizontal lateral markings of *Protomelas fenestratus* were thought to distinguish it from *P. taeniolatus*, which has predominantly transverse stripes (Eccles and Trewavas 1989). In contrast, Ribbink et al. (1983) delimited these two species based on the fact that *P. fenestratus* blows into the sand and exposes aquatic insects when feeding, whereas *P. taeniolatus* feeds principally on algae and plankton. Observations by Konings (2001) indicate that other species representing both melanin patterns blow into the sand. Stauffer (1993) has already suggested that this entire group is in need of extensive study.

#### Interactions among Schistosomes, Snail Hosts, and Snail-Eating Fishes

Stauffer et al. (1997a) postulated that the reduction in the number of snail-eating fishes in the waters surrounding Chembe Village was linked to an increase in number of schistosome intermediate-host snails, which in turn was associated with the high prevalence of schistosomiasis in school-aged children. From 1978 to 1987, the open waters of Lake Malawi were free of human urinary schistosomes. Our current studies show that at sampling sites throughout Lake Malawi (Figure 1), *B. nyassanus* is the only intermediate host of human urinary schistosomes inhabiting the open waters of the lake; moreover, the only place where we collected samples containing infected *B. nyassanus* was at the Chembe Village side of Nankumba Peninsula (Madsen et al. 2004). No *B. nyassanus* that shed human urinary schistosomes were found anywhere else in the lake. We believe that the occurrence of high numbers of schistosome-infected school-age children at Chembe Village is linked to transmission of *S. hematobium* through both *B. nyassanus* in the open waters of the lake and *B. globosus* in the backwaters and streams.

#### Schistosome and Snail Host Interaction

*Schistosoma hematobium* is transmitted by the intermediate-host snail *B. truncatus* in northern Africa and by snails belonging to the *B. africanus* species group (primarily *B. globosus*) in southern Africa (Brown 1994). A review by Brown (1994) revealed that the North African *S. hematobium* was compatible with *B. truncatus* but not with snails of the *B. africanus* group. In West Africa, the existence of two strains of *S. hematobium* was demonstrated, one transmitted by *B. globosus* and the other by *B. truncatus* (= *B. rohlfsi*). Conversely, in East Africa, *S. hematobium* apparently is transmitted only by the *B. africanus* group and is noninfective to local strains of *B. truncatus* (Brown 1994). This information suggests that either (1) the *B. truncatus* in East Africa is a different species or strain from that found in West Africa or (2) the *S. hematobium* strains in East and West Africa differ.

From the above evidence, *S. hematobium* appears to be a single species comprising many local strains that differ according to their most compatible species of snail host (Brown 1994). The main divisions seem to lie between strains adapted most closely to *B. truncatus* (northern Africa, West Africa, and the Middle East), *B. globosus* (Africa south of the Sahara), or in smaller geographical areas, members of the *B. forskalii* group (Brown 1994). The parasite seems genetically heterogeneous and capable of developing compatibility with a variety of intermediate hosts, depending on local circumstances. Some species of snails (e.g., *B. wrighti* on the Arabian peninsula) have proven to be excellent hosts experimentally but are rarely found infected in natural habitats (possibly because these are not contaminated with schistosome eggs or because the intermittent habitats where the snails live do not persist sufficiently long to support transmission).

Within the *B. truncatus*-*B. tropicus* complex, most diploid species seem resistant to infection in nature (Brown 1994); however, *B. truncatus* is tetraploid. The fact that *B. nyassanus*, which is diploid, has been found to be infected (Madsen et al. 2001) is therefore an interesting exception to the rule. In parts of West Africa (e.g., Senegal), *B. senegalensis* is also involved in transmission of *S. hematobium*, as are *B. truncatus* and *B. globosus* (Southgate et al. 2000). *Schistosoma hematobium* from the Middle Valley of the Senegal River basin was found to be compatible with *B. senegalensis*, whereas *S. hematobium* from Mbodiène (Lower Valley), which is naturally transmitted by *B. globosus*, was incompatible with *B. senegalensis* and *B. truncatus* (Southgate et al. 2000). These data demonstrate that different strains of *S. hematobium* from different regions of the Senegal River basin

exhibit distinct intermediate-host specificities, which in turn will have an effect on the epidemiology of the disease, including the periods of transmission (Southgate et al. 2000). *Bulinus truncatus* from the Lower Valley of the Senegal River basin was shown not to be compatible with *S. hematobium* from the Middle Valley (Sene et al. 2002). Webster et al. (2004) recently provided the first empirical support of coevolution of a schistosome and its snail host, thus supporting our contention that different strains of schistosomes will have differential success in infecting different *Bulinus* species. Conversely, perhaps the populations of *S. hematobium* are relatively similar and the snails that are currently identified as a single species may instead represent several undescribed taxa.

The fact that some snail species do not transmit infection in the field and yet are good intermediate hosts experimentally suggests that they would transmit disease if introduced into new habitats. With increased human travel, the spread of parasite strains could increase if suitable intermediate hosts are present, and new transmission foci might be established. Thus, prediction of which local populations or species of *Bulinus* spp. are potential hosts to the different populations or strains of *S. hematobium* is essential.

Molecular genetic studies have greatly assisted our understanding of snail–schistosome interactions at various evolutionary levels. Molecular phylogenies have resolved evolutionary relationships of host snails at the family (Morgan et al. 2002), genus (Stothard and Rollinson 1996; Stothard et al. 1996), species (Stothard and Rollinson 1997; Jones et al. 2001), and population (Davies et al. 1999) levels. For schistosomes, molecular studies have resolved species–group relationships (Bowles et al. 1992; Barker and Blair 1996; Lockyer et al. 2003), identified new species, revealed population structure, and tracked gene flow between populations (Davies et al. 1999). By comparing these various host–parasite phylogenies, we have gained a better understanding of the overall biogeography and evolutionary origins of these groups and have found apparent cases of host extensions, host specificities, and coevolution across planorbid snails and schistosome species (Morgan et al. 2002; Lockyer et al. 2003; Webster et al. 2004).

Although highly informative for the historic evolution of schistosomiasis in a broad evolutionary sense, these cophylogenetic studies do little to explain the current dynamics of specific host–schistosome outbreaks in natural populations. Recent severe foci of schistosomiasis, such as the one in Chembe Village, are more likely to be understood by comparative population genetic studies of both host and parasite from the same sample localities (Preston and Southgate 1994).

To date, only one study has examined genetic population structure of both a specific schistosome (*S. hematobium*) and its snail host (*B. globosus*) from natural population samples distributed across two unconnected river systems in the Zimbabwean highveld (Davies et al. 1999). This 20-km<sup>2</sup> region is known for its geographical variation in parasite infectivity and snail susceptibility, as was previously revealed by reciprocal cross-infection studies (Manning et al. 1995). The randomly amplified polymorphic DNA genetic profiles revealed extensive population structure between each *Bulinus* population sample, whereas schistosome structure was partitioned between river systems (Davies et al. 1999).

The preceding information, coupled with the fact that infected *B. nyassanus* are apparently limited to the Chembe Village region (Figure 1), led us to hypothesize that either (1) the snails we identified as *B. nyassanus* throughout the lake were really a complex of species or (2) there were two distinct strains of *S. hematobium*—one using *B. globosus* as an intermediate host and the other using *B. nyassanus*. We further postulate that any new schistosome strain, if present, could have been introduced from northern Africa by tourists visiting Nankumba Village. Given that *B. truncatus* is an intermediate host indigenous to northern Africa, we want to examine the relationship among *B. globosus*, *B. nyassanus*, and *B. truncatus*.

In an attempt to further analyze these relationships, we obtained (from GenBank) partial nucleotide sequences for the mitochondrial cytochrome oxidase subunit 1 (*CO-I*) gene for each taxon of *Bulinus*. To ensure that the sequence analysis occurred in the proper reading frame, we obtained a full copy of the *Pupa strigosa CO-I* gene from the mitochondrial genome (GenBank accession number NC002176). Multiple sequence alignments were performed with ClustalX (Thompson et al. 1997). All trees were constructed in MEGA version 3, using neighbor-joining, minimum-evolution, and maximum-parsimony methods (Kumar et al. 2004). Analysis parameters were the default MEGA settings. The bootstrap test of phylogeny was used to assess the statistical validity of the trees. Bootstrap values were based on 1,000 replications. Nodes with bootstrap values less than 50% were condensed. The resultant neighbor-joining, minimum-evolution, and maximum-parsimony trees are shown in Figures 3–5, respectively.

In all cases, *B. nyassanus* is more closely related to *B. truncatus* from Malawi and northern Africa than it is to *B. globosus*. Thus, we deem it reasonable to assume that the schistosome infecting *B. truncatus* in northern Africa, if introduced into the Lake Malawi basin,

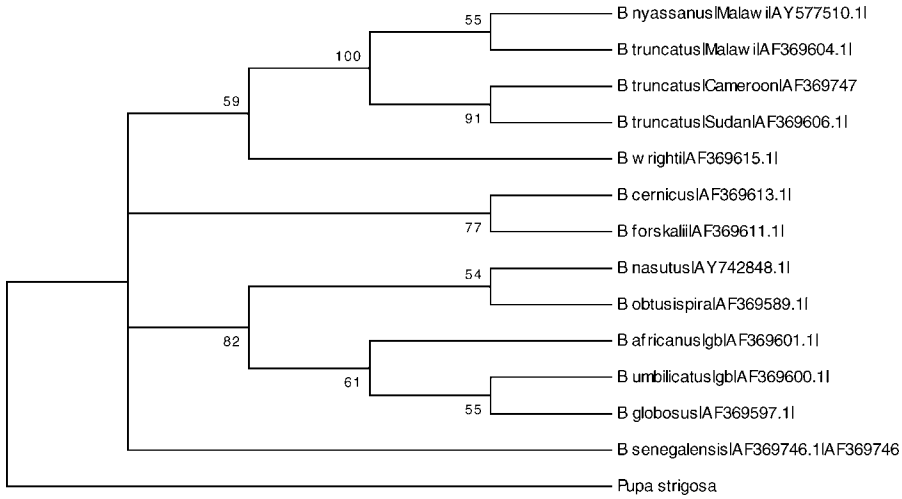


FIGURE 3.—Condensed (bootstrap cutoff value, 50%) neighbor-joining tree of published cytochrome oxidase subunit 1-coding DNA of *Bulinus* spp. Bootstrap values are based on 1,000 replications.

would be preadapted to use *B. nyassanus* as an intermediate host.

**Fish as Biological Controls**

Stauffer et al. (1997a) demonstrated the relationship between the decline in the number of snail-eating fishes and the concomitant rise in the prevalence of schistosomiasis in school-age children. We hypothesized that if we could implement management strategies to restore molluscivorous fish populations to their pre-1980 levels, the prevalence of the disease would decrease. The current poor understanding of the

alpha-level taxonomy of the indigenous fishes, however, retards the formation of such management plans.

Lake Malawi harbors the most speciose ichthyofauna of any freshwater lake in the world. More than 450 species of fish have been described there, and there may be as many as 850 species. In many cases, fishes that were thought to have a lakewide distribution were found to be made up of several distinct species (Stauffer et al. 1997b). Thus, it is essential to identify each species and collect life history and behavioral data for molluscivorous fishes that inhabit the lakeshore areas within Lake Malawi. Life history information of

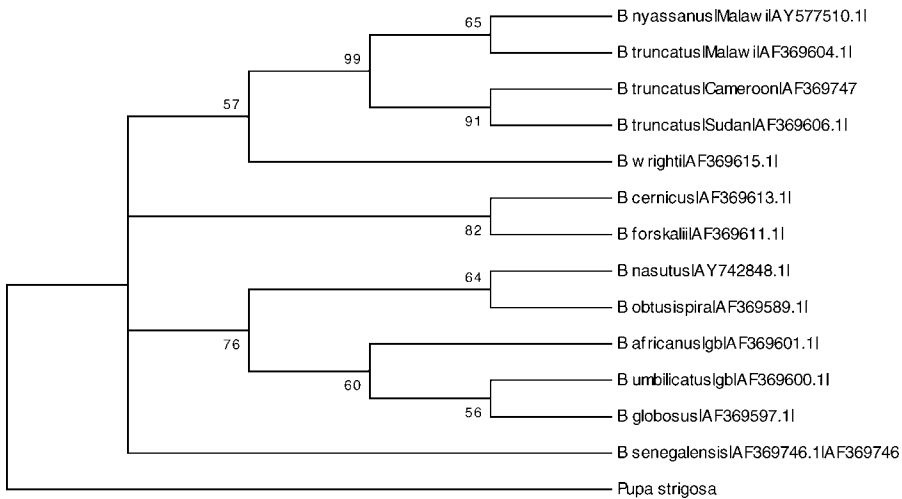


FIGURE 4.—Condensed (bootstrap cutoff value, 50%) minimum-evolution tree of published cytochrome oxidase subunit 1-coding DNA of *Bulinus* spp. See Figure 3 for additional details.

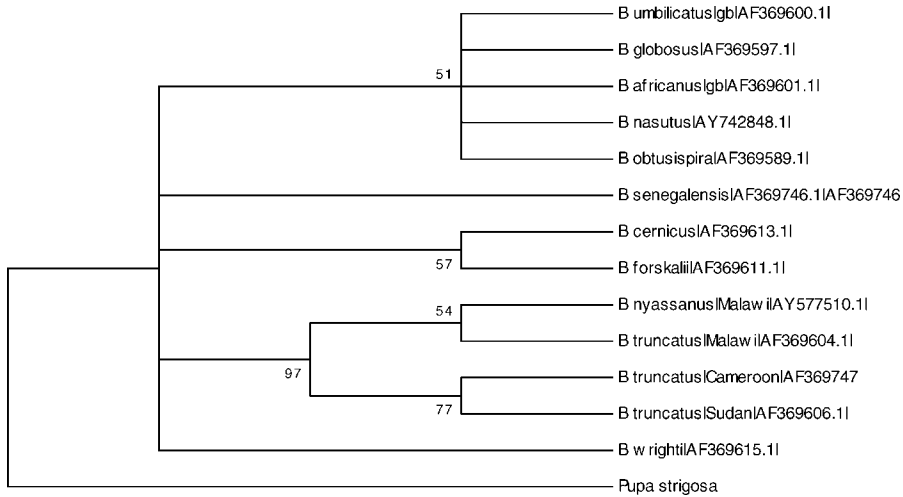


FIGURE 5.—Condensed (bootstrap cutoff value, 50%) maximum-parsimony tree of published cytochrome oxidase subunit 1-coding DNA of *Bulinus* spp. See Figure 3 for additional details.

the fish species is essential for developing management plans to restore populations to historical levels. Information on spawning season, fecundity, growth rate, age structure, and age at maturity is necessary for such plans.

The phenotypic plasticity of the Lake Malawi cichlids (Stauffer and van Snik Gray 2004) further confounds the development of management strategies. To a certain extent, the development of molariform teeth on the pharyngeal bones determines the effectiveness of these cichlids to crush and consume snails. Greenwood (1965) determined that the pharyngeal jaw apparatus of the Old World cichlid *Astatoreochromis alluaudi* is phenotypically plastic. Individuals that fed on thick-shelled snails developed stronger pharyngeal bones with larger molariform teeth than did those feeding on thinner-shelled mollusks. Thus, even if the species are known, environmental conditions may affect the efficacy of these fishes in acting as biological controls for intermediate-host snails.

### Conclusions

The lack of enforcement of the fishing laws of Malawi has resulted in a drastic decline in the harvest of needed food fish and in the number of molluscivorous fishes which in turn has enhanced the spread of schistosomiasis. If, in fact, the increased prevalence of schistosomiasis in Chembe Village is directly linked to overfishing, this is the first example of overharvesting leading directly to the spread of a human disease. A comprehensive understanding of any ecosystem requires a basic knowledge of the species that occur within such a system. In Lake Malawi, more than two-

thirds of the cichlid species are undescribed, the taxonomy of the *Bulinus* snails is poorly known, and the strains of *S. hematobium* have not all been identified. Before we can identify the interactions among these components of the system, we must be able to accurately delimit taxonomic units (e.g., species, populations, and demes) within each of the above groups. Ecological and behavioral studies (Jackson et al. 1963; Fryer and Iles 1972) have been responsible, in part, for focusing attention on the large number of fish species occurring within Lake Malawi. These research efforts have been slowed and results often confused by the uncertain systematic status of the cichlids being examined. The coevolutionary patterns of intermediate-host snails and schistosomes cannot be discerned without adequate descriptions of the individual species involved.

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