Evolution in ancient lakes: radiation of Tanganyikan atyid prawns and speciation of pelagic cichlid fishes in Lake Malawi

Geoffrey Fryer
Institute of Environmental and Biological Sciences, Lancaster University, Lancaster, LA1 4YQ, UK

Abstract

Atyid prawns from Lake Tanganyika are still poorly understood. There are at least 11 species sharing an exceptionally small size and a reduction in the number of branchiae. The majority are benthic although some are pelagic. This is reflected in different morphologies of the body and walking legs. Morphological adaptions of the denticles on the chelipeds are adaptive as they relate to different ways of feeding. Pelagic fish from Lake Malawi do not represent an example of sympatric speciation as suggested by Shaw et al. (2000). It is more likely that several, independent radiations started from inshore generalists, which gradually adapted to the openwater.

Introduction

This paper presents biological information on two very different groups of animals in the two great rift lakes of Africa that has a bearing on the two key evolutionary phenomena of adaptive radiation and speciation.

A neglected example of adaptive radiation: the atyid prawns of Lake Tanganyika

That L. Tanganyika is home to an assemblage of endemic species of atyid prawns has been known for almost a century, but these animals have been largely neglected. Calman (1899, 1906) described 11 species from material collected during the expeditions of Moore and Cunnington, allocated them to 3 endemic genera, *Limnocardina, Caridella* and *Atyella*, and made some brief but pertinent comments relevant to their evolution. Bouvier (1914) discussed their characters, origin and affinities, and recapitulated some of these matters in his monograph of the Atyidae of the world (1925) in which he added some details to Calman's descriptions, and subsequently Calman (1928)

further described a species and Roth-Woltereck (1958) another. Coulter (1991) gave a brief summary of what little has been recorded about them, but there has been no serious study of these animals, and their potential to contribute to our understanding of evolutionary phenomena has been neglected. More species may yet be discovered, and it even remains to be proven that they comprise a true species flock. Although they display what may be convergent resemblances to specialised forms elsewhere, they share a unifying characteristic – a reduction in the number of branchiae. However, resemblances between *Limnocaridina* and the non-endemic *Caridina*, and between *Atyella* and the non-endemic *Atya*, led Calman (1906) to suggest that reduction of the gills may have taken place twice among the endemic species. Molecular investigation should resolve this question. Work on other atyids gives some inkling of the ways in which the Tanganyikan species may have exploited the opportunities offered by this ancient lake and indicates their potential interest.

A phenomenon repeated in other animals that have radiated in ancient lakes is that, although the common and widespread atyid, *Caridina nilotica*,

occurs in the vicinity it is apparently absent from the lake itself. This is particularly striking as it is common in Lakes Malawi and Victoria, where it is the only atyid. In L.Victoria, it has greatly increased in abundance since the arrival of the Nile Perch and subsequent ecological changes and is now a key component of the fauna where it serves as the main food of the small Nile Perch and is therefore of immense importance to the fishery of that lake.

The Tanganyikan genera *Limnocaridina, Caridella* and *Atyella*, have eight, three, and two species, respectively. All are relatively, some very, small.[1] Little is recorded about their ecology. What is clear, e.g. from the summary of Hori (1997), is that atyid prawns are extremely important components of littoral food webs in L. Tanganyika. As noted below, they are equally important in the pelagial zone.

Most atyids are benthic, and several Tanganyikan species are clearly such. They are extensively eaten by various littoral fishes, several of which have indeed been designated as "shrimp-eaters" that feed largely or almost exclusively on these prawns (e.g. Hori et al., 1983; Yuma & Kondo, 1997; Yuma et al., 1998). Yuma and Kondo say that on rocky shores "shrimp-eaters are numerically dominant among the benthivorous cichlids both in species and individuals." They record that *Altolamprologus compressiceps, Gnathochromis pfefferi, Neolamprologus furcifer,* and *N. toae* feed almost exclusively on atyids, and that *Lamprologus callipterus, Neolamprologus leloupi,* large *Lobochilotes labiatus* and subadult *Lamprologus elongatus* do so extensively. Not only are the "shrimp-eating" propensities of these and other cichlids well documented but the ways in which atyids are captured by some of these fishes have been described by Yuma (1994), Yuma and

---

[1] Large atyids (*Atya*) occur in W. Africa and the Americas and (other genera) the Indo-Pacific region. There are single records of *Atya africana* and *A. scabra* from "Mbuma dans le Mayombe" that are indicated (in different places) deep in the Congo basin on maps in the splendid monograph of Hobbs & Hart (1982). I cannot locate this site. If it refers to a location in the Mayombe near the Congo mouth it is more easily understood. Otherwise large atyids appear to be absent from eastern, central and southern Africa.

Kondo (1997), Hori (1997) and Hori et al. (1983). These different methods of capture suggest that prawns of different species are targeted by different fishes and it is tantalising to realise how much information on the habits and ecological preferences of atyids might have been gleaned had the specific identity of the prey of these fishes been ascertained instead of being characterised simply as "shrimps". It has even been recorded that *N. furcifer* picks up atyids from micro-depressions of rocks where they conceal themselves (Yanagisawa, 1997) but the prawn concerned was not identified. Prawns from other substrata are collected in other ways and presumably involve different species. For example *Grammatotria lemairii* digs for them in sand (Hori, 1997). More recently Yuma et al. (1998) identified some of the prawns – one species of *Caridella* and six species of *Limnocaridina* – eaten by cichlids. *Limnocaridina latipes*, plentiful on rock surfaces, was much the most frequently, and sometimes the only, species eaten by several cichlids. *L. spinipes* and *L. socius* were eaten by *Lamprologus lemairii* and, in smaller numbers, by *L. labitus* and *Neolamprologus toae*, and *Caridella minuta* by *N. tretocephala* and *L. labiatus*. They believe that prawns may provide a superabundant source of food, especially at night, and make the interesting observation that some species appear to lurk beneath rocks by day and emerge at night.

Hemibates stenosoma, one of the most abundant benthic species, that penetrates deep water, is also a prawn eater. At depths of up to 50 m prawns constitute about 50% of its diet. Their importance diminishes with depth, but even at 120 m they make up about 20% of the stomach contents (Coulter, 1991). Various benthic non-cichlid fishes also feed extensively on atyids, e.g. several species of *Chrysichthys*, of which *C. graueri* is predominantly a prawn-eater which feeds heavily on prawns at depths of up to 50 m. Prawns have also been found in its gut at 150 m. Whether these were collected at this depth remains to be proved.

A noteworthy feature of the adaptive radiation of the Tanganyikan atyids is that some of them spend time in the plankton. Here, they are a preferred food of the abundant, shoaling, pelagic clupeid *Stolothrissa tanganikae*, and are also eaten by the larger clupeid *Limnothrissa miodon*. They are also eaten by species of *Lates*, especially by *L. stappersi*, and have even been found in the guts

of *L. mariae*, which also feeds on them extensively, captured at depths approaching 200 m (Coulter, 1991). Happily, Marlier (1957) identified the species consumed by *Stolothrissa*. These are predominantly *Limnocaridina parvula* and *L. retiarius*, but *L. similis* was recorded occasionally. The significance of the identity of the most frequently consumed species will soon become apparent. Marlier notes that these prawns "vivent en bandes énormes", another significant observation, but adds that their biology "est encore mal connue", which is still the case.

All atyids collect food by use of two pairs of chelipeds. In the most primitive species, the West Indian *Xiphocaris elongata*, these appendages seize and pick up discrete items, for which purpose both the propus and dactylus bear distal denticles, illustrated by Bouvier (1925) and by Fryer (1977) who describes the feeding mechanism. While the chelipeds of other atyids may or may not retain one or more distal denticles, all are armed with a complex array of spines and/or setae with which they very effectively sweep particles from surfaces or employ in other ways. Particle-sweepers include the closely related African species *Caridina nilotica* and *C. africana*, whose feeding mechanism is described by Fryer (1960). Neither of these retains distal denticles though such are present in certain other members of the genus.

While a basically similar method of food collection to that used by *Caridina*, that is scraping and sweeping particles from surfaces, is probably employed by most of the Tanganyikan species of *Limnocaridina*, all of the latter bear one or more distal denticles on both the propus and dactylus of the chelipeds. In *L. tanganyikae* (length c.25 mm, Fig. 1) and *L. similis* (c.17 mm, Fig. 2) there are from three to five stout denticles on the first pair, somewhat flattenened and curved at the tip in *L. similis*, flanked in each case by robust scrapers. This suggests that, as well as sweeping up particles, the chelipeds can pick up individual items or, in *L. similis*, perhaps pluck them from surfaces. The second pair of chelipeds is less heavily armed; e.g. in *L. tanganyikae* each bears only a single, rather spine-like, denticle (Fig. 3). This indicates that each pair is specialised for somewhat different functions, which must broaden the range of food sources that can be exploited. The chelipeds of other species of *Limnocaridina* bear some-

what different denticles e.g. *L. socius* (c.12 mm Figs. 4–6); *L. latipes* (c.10 mm, Fig. 7), *L. spinipes* (c.7 mm, Fig. 8). In *L. socius*, some of the denticles are curiously twisted. Only observations on the living animal can reveal their function.

The presence of distal denticles on the chelipeds of species of *Limnocaridina* led Bouvier (1925) to suggest that this is a primitive character that links that genus to *Xiphocaris*. Whether this is so or whether the exploitation of such denticles is a specialisation that has evolved in L. Tanganyika remains to be investigated. Certainly, however, two species of *Limnocaridina*, *L. retiarius* and *L. parvula*, whose chelipeds show a unique departure, retain a small distal denticle on both propus and dactylus, which are perhaps vestigial remnants of the primitive armature. These two species differ greatly in cheliped armature from those of other species of the genus.

In *L. retiarius* (c. 14 mm) and *L. parvula* (c.7 mm) both fingers of the chelae bear, along the whole length of their opposed edges, a row of long flexible setae, longer in *L. retiarius* (Fig. 9) than in *L. parvula* (Fig. 10). In the former, they are armed with what are clearly rows of filtering or sieving setules (Fig. 11); in the latter they are almost smooth. Distal sensory setae in *L. parvula* are shown in Figure 12. Calman (1906) percipiently suggested that in *L. retiarius* the whole ensemble served as a "kind of double casting net", and this may indeed be so. Thanks to the observations of Marlier (1957) we know that these two species, if not permanently pelagic, certainly spend much time in the plankton and must collect much, if not all, of their food in open water – itself an interesting departure. Atyids are generally benthic in habits. In the light of what is known of other atyids, a device whereby the chelipeds are spread, then 'thrown' forward, towards the end of which action they close, securing anything encountered during the process, appears to be a feasible means of food collection. This would represent a novel, and so far as I am aware unique, departure for an atyid. By comparison with, for example, the setules on the filters of filter-feeding branchiopods, those on the cheliped setae of *L. retiarus* are widely spaced (Fig. 11). This presumably reflects both the size of the particles captured and the mechanical constraints (water resistance) on the use of a fine-meshed cast net.
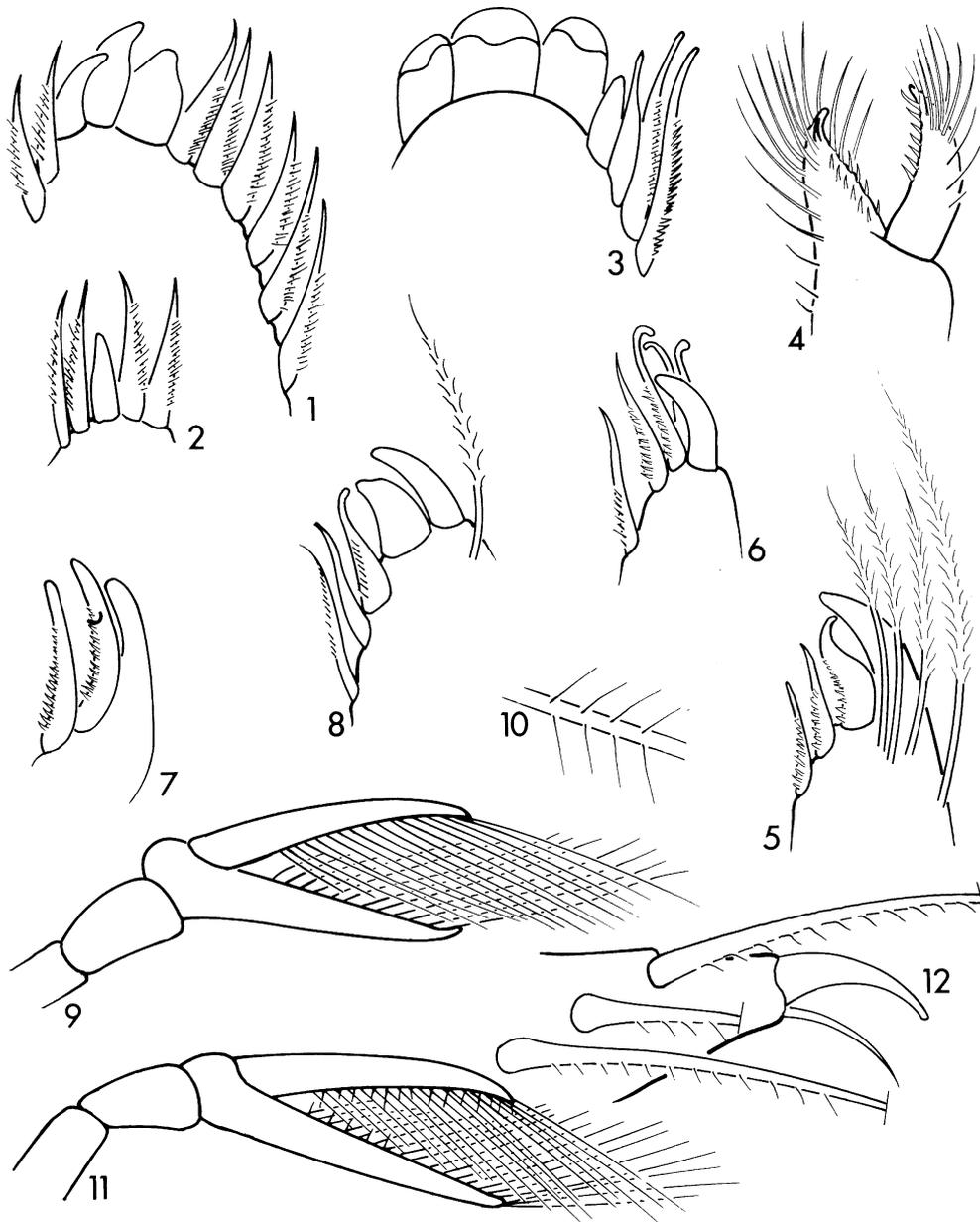
Figures 1–12. Details of species of *Limnocaridina*. Mostly re-drawn from Calman and Bouvier. Because it was not always possible accurately to check the size of the structures shown, it was deemed safest simply to indicate the size of the species concerned, which gives some indication of the size of the chelipeds. 1. *L. tanganyikae.* Length of adult c. 25 mm. Inner face of tip of dactylus of cheliped 1 showing stout distal denticles and adjacent scrapers. 2. *L. tanganyikae.* Inner face of tip of dactylus of cheliped 2. 3. *L. similis.* L. c. 17 mm Inner face of the tip of dactylus of cheliped 1 showing its flattened distal denticles. 4. *L. socius.* L. c. 12 mm Distal portion of cheliped 1, lateral. 5. *L. socius.* Tip of dactylus of cheliped 1, lateral. 6. *L. socius.* Tip of dactylus of cheliped 2, lateral. 7. *L. latipes.* L. c. 10 mm Tip of dactylus of cheliped 1, lateral. 8. *L. spinipes.* L. c. 7 mm Tip of dactylus of cheliped 1 lateral. One sensory seta only shown. 9. *L. retiarius.* L. c. 14 mm Chela of cheliped 1. Lateral setules of the long setae omitted (See Fig. 10). 10. *L. retiarius.* Details of one of the setae of the chela. 11. *L. parvula.* L. c. 7 mm Chela of cheliped 2. The setae lack setules. 12. *L. parvula.* Tip of dactylus of cheliped 1. Lateral view.

In keeping with their frequenting of the pelagial zone, these species are slender and have more slender, lightly built walking legs than other members of the genus. The slender dactyli of these legs contrast particularly strongly with their robust homologues in *L. latipes*. They also have large propulsive pleopods.

All three species of *Caridella* are very small: *C. paski* is only about 10 mm in length, *C. cunningtoni* 9 mm and *C. minuta* about 4 mm. This suggests that they may be able to frequent crevices in rocks or among the mollusc shells that form debris in some places in L. Tanganyika. *C. cunningtoni* was indeed dredged from among shells at depths of about 8 and 15 fathoms (14 and 27 m); in plenty at the latter depth – and *C. paski* was found plentifully beneath stones on a rocky shore. The food collecting cheliped setae of *Caridella minuta* are very short (Fig. 13), those of *C. cunningtoni* longer (Fig. 14), and those of *C. paski* still longer (Fig. 15). As this trend is in the same direction as that of absolute size, the differences between the three species are considerable, which points to different feeding habits, and perhaps different habitats and food sources. In *C. cunningtoni* and *C. paski* in particular, the first pair is markedly more robust than the second (Fig. 16), which presumably allows the different pairs to exploit slightly different situations (or the same situations in different ways) and thereby improve overall efficiency. All three species have short, very finely denticulated scrapers, and longer sweeping setae, arranged in a *Caridina*-like manner, but the number of elements is much fewer, their structure is less diverse, and their armature sparser. They clearly sweep up material in a *Caridina*-like way, but all are so small that the food is probably restricted to very small particles. In *C. minuta*, the setae are so short that the area swept at each application of a cheliped to the substratum must be very small. (Only observation of the living animal will show whether, for example, this is compensated for by very rapid activity by the chelipeds.) Many details remain to be elucidated. For example, some of the long setae of *C. cunningtoni* have a slender distal hook (Fig. 17) of unknown function.

All three are clearly benthic species. This is reflected particularly by the short walking legs of *C. minuta*, probably the world's smallest atyid,

with their stout dactyli armed with massive spines, and the similarly armed third maxillipeds.

The manner in which the chelipeds of the two species of *Atyella* are employed can be deduced with considerable confidence by comparison with those of the large *Atya* and smaller *Micratya* to which they bear a striking similarity in structure. The remarkable cheliped fingers of the latter genera bear very long setae and the carpus is deeply excavated to form a basin in which the proximal part of the propus can rest. Members of both genera often frequent streams, can use their long cheliped setae for sweeping up particles from surfaces, but can also extend those of each cheliped into a fan that can be held against the current and which filters passively, the four filtering baskets together making up a large filtering area (photographs in Fryer, 1977). From time to time the fans are closed and the captured contents passed to the complex mouthparts. This remarkable process was evidently seen and very briefly mentioned by Müller (1881), briefly but succinctly described (in *Atya*) by Cowles (1915), and described and illustrated in detail by Fryer (1977) and Abele (1983). The Tanganyikan *Atyella brevirostris* (L.c.13.5 mm) and *A.longirostris* (c. 15 mm) display such remarkable parallelisms to *Atya* and *Micratya* in cheliped structure and armature (Figs. 18, 19) that it may be surmised that they employ them in a similar manner. Like those of *Atya* and *Micrataya*, the two pairs of chelipeds are very similar, which is necessary if, during passive filtration, all four sets of cheliped setae have to combine to form a basket. Both species of *Atyella* were described from individuals collected among rocks in shallow water (Calman, 1906). Here, they probably sweep up detritus as *Atya* and *Micratya* do (see the fine comb borne by a few of the setae of *A. brevirostris*, Fig. 20), but it seems distinctly probable that they can also employ passive filtration, (see structure of the majority of the setae, Fig. 21) to which their chelipeds are well suited. The diversity of form of the cheliped setae is, however, somewhat less than that of at least some species of *Atya* (see Fryer, 1977). Among rocks in shallow water, there are regular surges that often flow in one direction sufficiently long to permit the entrapment of suspended particles by a fixed net. Some marine crustaceans do this using other appendages. The chelipeds are highly
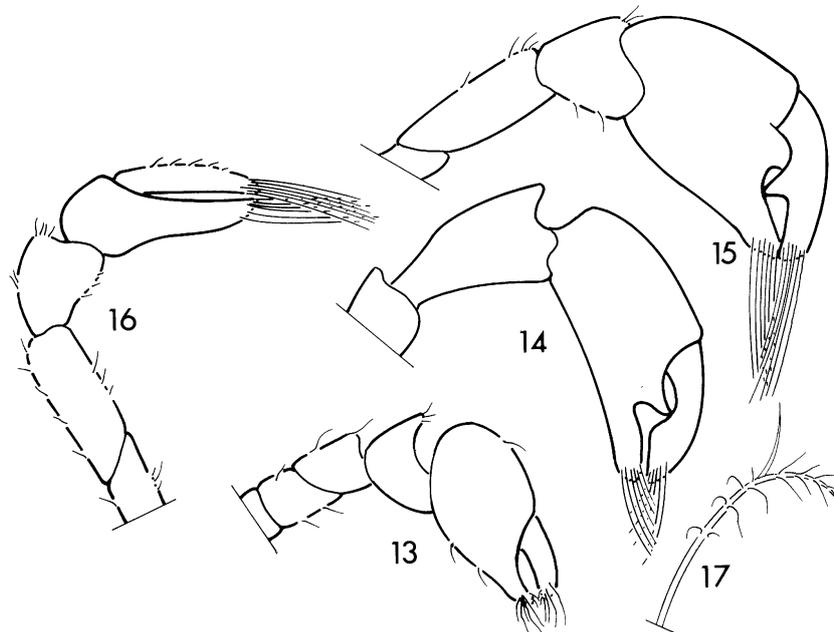
Figures 13–17. Details of species of *Caridella*. Mostly re-drawn from Calman and Bouvier. 13. *C. minuta*. (L. c. 4 mm) Cheliped 1. 14. *C. cunningtoni*. (L. c. 9 mm). Cheliped 1. 15. *C. cipaski*. (L. c.10 mm). Cheliped 1. 16. *C. paski*. Cheliped 2. 17. *C. cunningtoni*. Details of one of the sweeping setae of the chelipeds.

manoeuvrable and are well suited to continuous adjustment to variations in the direction of flow. Only observations on the living animals will resolve the matter but, as Calman (1906) pointed out before passive filtration by *Atya* was known, the morphological similarities between *Atya* and *Atyella* are striking. Now that we know how *Atya* uses its chelipeds, the parallels in structure suggest parallels in function.

The chelipeds of Tanganyikan atyids have undergone adaptive radiation in a manner analagous to that of the jaws and oral teeth of cichlid fishes. Moreover, just as convergence is to be seen in the food-collecting apparatus of the latter – as in the rock-frequenting Mbuna of L. Malawi and in their equivalents in the tropheine lineage of L. Tanganyika and the Mbipi of L. Victoria, so do the atyids of Tanganyika show convergence in food collecting mechanisms with atyid genera of other parts of the world. Whether the complex gastric mill of different species (the functional equivalent of the lower pharyngeal bone of cichlid fishes) differs much in relation to the nature of the food remains to be investigated.

Why the pelagic cichlid fishes of Lake Malawi do not provide evidence of sympatric speciation

There is abundant evidence that allopatric speciation has played the predominant role in the multiplication of species of cichlid fishes in the Great Lakes of Africa. More controversial has been whether sympatric speciation has occurred. Models of the process, however interesting, lack a vital element – proof. Shaw et al. (2000) now believe that they have demonstrated the phenomenon, among the pelagic species of Lake Malawi.

Most of the vast number of Malawian cichlids – possibly as many as a thousand species – are essentially littoral and/or benthic, and there is general agreement that their multiplication was via allopatric speciation, of which indeed they provide classic examples. A few are, however, pelagic and Shaw et al. reasonably argue that it is among such species, with wide distributions in continuous habitats and with no apparent barriers to dispersal, that the requirements for sympatric speciation are most likely to be met. They say that there are "at least 21 species of pelagic cichlids" in the
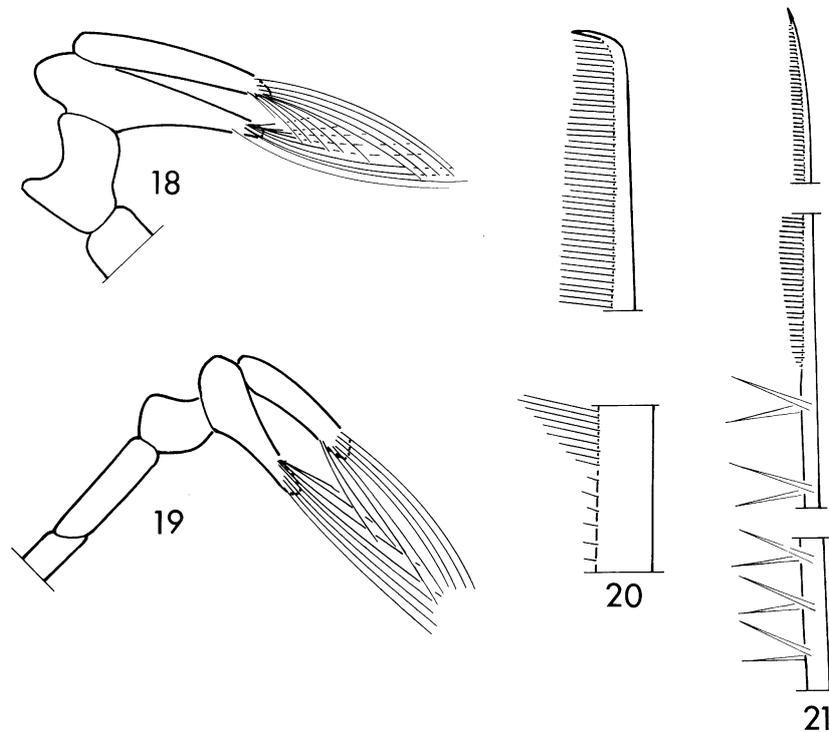
Figures 18–21. Details of *Atyella brevirostris*. L. c. 14 mm. Mostly re-drawn from Calman and Bouvier. 18. Cheliped 1. 19. Cheliped 2. Only a few of the long setae shown in each case. 20. Details of one of the few 'comb setae', distal and proximal. 21. Details of a filtering seta, distal to proximal.

lake – 9 *Rhamphochromis*, 11 *Diplotaxodon* and 1 *Pallidochromis* (at that time thought to be a monotypic genus). By use of molecular genetic markers they attempted to find out whether sub-structuring of the population occurs among some
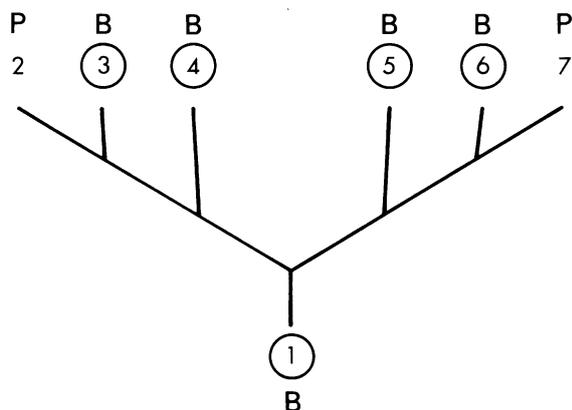

Figure 22. How two pelagic species (*L. tanganyikae* and *L. latipes*) may become each other's closest relatives as a result of the extinction of even closer relatives. P = pelagic, B = benthic. Extinct species circled.

of these species. They also sought to ascertain whether the pelagic species make up a monophyletic group, believing that such a demonstration "would suggest that radiation of the pelagics has occurred within the pelagic realm, and therefore that speciation most likely occurred under conditions of population structure concurrent with present populations, i.e. in sympatry". They established that three species of *Diplotaxodon* are "essentially single panmictic units" within the lake and do not display "the structuring prerequisite for allopatric genetic divergence during speciation." Moreover, their molecular data indicate that *Rhamphochromis*, *Diplotaxodon* and *Pallidochromis* constitute a single clade. They suggest that this indicates "strong, if indirect," evidence of sympatric speciation. There are several reasons for rejecting this claim. The fatal flaw in the argument, which depends explicitly on all the species involved being pelagic, is that this is not the case. Far from being pelagic, some of them are benthic. This is like including flightless birds in a study supposedly devoted exclusively to flying species.

By no means, all species of *Rhamphochromis* and *Diplotaxodon* referred to as pelagic are such: like *Pallidochromis,* some are benthic. *P. tokolosh* was categorized by its describer as "a deep water demersal" species (Turner, 1994), and later as "a deep-water benthic-feeding piscivore" (Turner, 1996). Subsequently, it was unambiguously referred to as a "benthic species" (Turner et al., 2001, p. 290) which lives predominantly at depths of between 75 and 150 m. Konings (2001) reports an undescribed species of *Pallidochromis* caught by fishermen in inshore waters and therefore probably not pelagic.

Although *Rhamphochromis* and *Diplotaxodon* undoubtedly form the bulk of the pelagic fish fauna, they also make up "a substantial portion of the demersal fish biomass" and their juvenile stages "appear to be a significant component of the littoral fish community in sandy areas" (Allison et al., 1995). Species of *Rhamphochromis* are essentially elongate piscivores. Their taxonomy is confused. Turner (1996) suggested that there are between 12 and 20 species, not all described, and later Turner et al. (2001), tentatively identified nine species of which four were considered to be undescribed. Irrespective of problems of identification, Turner (1996) stated categorically that most of the described species "seem to be absent ... from the pelagic zone." He also recorded that the habitat preferences of different species, which certainly include "the surface of open waters", also include "inshore waters" and that "some appear to be largely demersal." Indeed, of these listed in 1996, some as cheironyms, only *Rhamphochromis* 'big mouth', actually *R. woodi* (Turner et al., 2001) was unequivocally considered to be pelagic. Even *R. longiceps*, regarded as the most pelagic member of the genus by Eccles & Trewavas (1989), is said by Turner et al. (2001) "most likely to be encountered in sheltered muddy areas", Chia Lagoon and L. Malombe (connected to L. Malawi) being specifically cited. This taxon is, however, believed to be a species complex (Shaw et al., 2000). Others, such a *R.* 'short tooth brown', also qualify for pelagic status, and others have been collected in both midwater and bottom trawls. Several are however, usually collected only in bottom trawls or seine nets, which implies benthic habits. Examples are *R. esox* which, according to Turner et al. (2001), is never found in the eupelagic zone,

and *R. macrophthalmus* (categorised as demersal by Eccles and Trewavas), which occurs in the shelf zone at 50–100 m and occasionally in water as shallow as 30 m (Turner et al., 2001). *R.* 'stripe' frequents benthic habitats on rocky shores at all stages of its life, and Turner (1996) remarked that the morphology of other species "suggests that they are benthic forms" and "are probably confined to inshore waters." Some species are certainly to be seen and caught there.

Not all species of *Diplotaxodon* are pelagic. Although Eccles & Trewavas (1989) listed only three described species, Eccles was aware of the existence of at least seven others, which had been recognised earlier, but not described, by T.D. Iles. They noted that several species were regularly taken by demersal trawls "and appear to be part of the demersal community," and Allison et al. (1995) report that a number of species are found in the demersal community in the southern part of the lake. This is confirmed by Turner (1996) who reported several species from bottom trawls and who notes, for example, that *D.* 'deep' is "probably not a pelagic species." More details were provided by Turner et al. (2001) who recognised 11 species, of which 5 appeared to be undescribed. Of these, *D. similis* was said to be "found throughout the lake, apart from the eupelagic zone", *D. greenwoodi*, which is in part a paedophage and whose morphology is scarcely that of a pelagic form, is known from "a variety of benthic habitats at depths of 50–150 m," and *D. macrops* is abundant in the southern arms of the lake where it comprises 10–12% by weight of bottom trawl catches at 100–125 m, to which *D. apogon*, also caught in bottom trawls, contributes 3–4%. Thus, by no means, all species of *Diplotaxodon* are pelagic. Several are indisputably benthic.

Such facts clearly contradict the statement that there are at least 21 species of pelagic cichlids in the lake that belong to these three genera. They also have a cogent bearing on their probable evolutionary history.

The claim of Shaw et al. (2000) to have demonstrated sympatric speciation in the pelagial zone is emphatically negated by the fact that one of the three allegedly pelagic species of *Diplotaxodon* that formed the core of their study is indisputably benthic. *D. macrops*, for which they present data from the southern end of the lake, is caught in

abundance in bottom trawls, which is a clear reflection of its benthic habits, and there is no indication in their paper that the individuals used were collected in the pelagial zone. All three samples of *D. macrops* used for molecular studies were obtained within a linear distance of c.75 km. Two were from the SE arm from depths of <100 m, the other from further north at <200 m and almost certainly no more than 150 m. There are often no greater restrictions on the movements of benthic species over relatively uniform substrata than there are on pelagic species (which can in fact face rigorous barriers – see below) and one would therefore expect little molecular evidence of such restriction in these three samples. This was indeed the case but, if only as a result of isolation by distance, one might expect minor differences, and such are shown in the histograms of Shaw et al. (2000). For example, the frequency of allele 19 at the Pzeb 4 locus was, from south to north, about 20, 37, and 52 in the three samples, the last being the most distantly separated.

Moreover, it is a myth that there are no barriers to universal movements by pelagic/open-water species. This is convincingly demonstrated in L. Malawi by the findings of an extensive survey of the fishery potential of its pelagial regions (See Menz, 1995). What Allison et al. (1995) there called *Diplotaxodon* 'big-eye', actually includes at least two species, which makes the evidence even more convincing. *D.* 'big-eye' embraced the most open-water cichlids in the lake, and was reported as "absent from shallow waters including the S.E. arm" (Thompson et al., 1995). These authors emphasise that neither fry, juveniles nor adults "appear to have an inshore or even shallow water phase" and that the entire life cycle is completed far from shore. The southern parts of the lake from which these fishes are absent are <100 m deep but embrace a large expanse of offshore open water that is open to pelagic species that frequent areas of deep water to the north. *D. limnothrissa*, one of the three species studied by Shaw et al. (2000), which shares vast areas of open water with the species embraced by the name *D* 'big-eye', freely enters these waters, but *D* 'big-eye' does not. Although the latter ascends even to the surface waters by night, it descends by day below 100 m, and even to about 220 m, below which the permanently de-oxygenated hypolimnion is a barrier.

A need to descend below 100 m by day appears to be what rigorously excludes it from the S.E. arm to which there are no obvious barriers to entry.

It may also be that some wide-ranging pelagic species congregate at particular sites for breeding, which offers the opportunity for isolation, and ultimately for allopatric speciation. This is the case in the pelagic *Copadichromis quadrimaculatus*.

Shaw et al. (2000) demonstrate that *Rhamphochromis, Diplotaxodon* and *Pallidochromis* constitute a single clade (RDP), *Rhamphochromis* (R) representing one lineage, *Diplotaxodon* (D) plus *Pallidochromis* (P) the other (DP). Earlier work, using less abundant material, had suggested different phylogenetic relationships (Moran et al., 1994). Having shown that there are two lineages, Shaw et al. (2000) say that a major finding of their study is that no pelagics fall outside these lineages and no non-pelagics fall within them. Neither claim is correct. To take the second claim first, as demonstrated above, both lineages include benthic species. This alone effectively destroys the suggestion that "radiation leading to the current group of pelagic species has taken place within the pelagic realm." The close relationship of *D. macrops* (benthic) and *D* 'offshore' (pelagic) indicates an entirely different pattern of (non-sympatric) speciation, as does the presence in the same lineage of such a thoroughly benthic species as *Pallidochromis tokolosh* and completely pelagic species of *Diplotaxodon*.

Indeed, the existence of non-pelagic members of both *Rhamphochromis* (R) and *Diplotaxodon* (D), and of the benthic *Pallidochromis* (P), points clearly to a pattern of radiation exhibited by various other Malawian haplochromines. The early stages of radiation of the RDP clade, which is made up of highly derived forms, whose ancestors may have separated early from the basal stock, must have taken place in inshore littoral regions. Their earliest lacustrine ancestor certainly did not colonise the lake as a pelagic species. The primitive haplochromine coloniser was an inshore generalist. Initial differentiation and speciation clearly occurred in the littoral zone, almost certainly by allopatric speciation. Some, but by no means all, of the derivative species of the RDP clade would gradually become adapted to an open-water existence and some of them eventually colonised the pelagial zone.

It is easy to see how several pelagic species could have evolved independently from inshore ancestors. Ancestral forms would be distributed along shorelines with fragmented habitats where differentiation would be easy, and indeed inevitable. Examples abound among the present day cichlids of the lake. Being close to the basal stock, the ancestors of *Diplotaxodon* would perhaps be the first to exploit inshore zooplankton. Such isolates as began to venture offshore and to exploit more open water would, initially, still return to the littoral region to breed, and some speciation may have occurred, by allopatric means, *after* this stage had been reached. This is no hypothetical scenario: some 26 described, and perhaps as many undescribed, species of *Copadichromis* – the Utaka – one of which, *C. quadrimaculatus* has become truly pelagic, exhibit precisely this state of affairs today. Species of *Diplotaxodon* have taken adaptation to a pelagic existence even further and some of them appear to be independent of the ancestral littoral region. Such species of *Rhamphochromis* as are pelagic, or semi-pelagic, repeat the pattern, having done so in part by exploiting open water species of *Diplotaxodon* as prey.

Even if two pelagic species within the RDP clade should prove to be each other's closest relatives, this would be phylogenetically ambiguous. Such relationship could be the result of a benthic common ancestor, having given rise to two lineages, each of which produced a pelagic and several benthic descendants before it and all its benthic descendants suffered extinction. This would leave the two pelagic species as each other's closest relatives simply because closer relatives, with different lifestyles, became extinct (Fig. 22). Constructors of phylogenies often forget that we usually know nothing about species that became extinct.

To say (Shaw et al., 2000) that there are no pelagic cichlids in L. Malawi outside the RDP clade is also incorrect. Such species are not only represented but also illustrate various stages of adaptation to a pelagic lifestyle. Species of *Copadichromis*, that make up the zooplankton-eating Utaka, have acquired open-water habits, and *C. chrysonotus* spawns there, but most remain largely confined to near-shore waters. *C. quadrimaculatus*, however, extends into the pelagic zone where it occurs in vast numbers and is rightly included among the pelagic species by Allison et al.

(1995) and by Konings (2001) who describes how adults form shoals several kilometres offshore. Likewise, species such as *Champsochromis spilorhynchus* and *C. caereuleus* exhibit progressively convergent similarity to *Rhamphochromis* but remain inshore species largely confined to shallow water though *C. caerulus* penetrates to 55 m (Eccles & Trewavas, 1989). Particularly informative of this process are the species of *Cynotilapia*. This genus belongs to the group known as the Mbuna, whose members are specialised littoral fishes, for the most part closely associated with rocky habitats. Although still associated with rocks, species of *Cynotilapia* (most still undescribed) feed mostly on zooplankton collected above, and to the lakeward side of, the rocks (Fryer, 1959; Ribbink et al., 1983). These examples show how pelagic habits have arisen among littoral, benthic cichlids several times during the history of the flock. In no case is it necessary to postulate sympatric speciation and a pattern of allopatric speciation is sometimes crystal clear.

The three allegedly pelagic species of *Diplotaxodon* that received detailed attention from Shaw et al. (2000), were screened at six microsatellite loci. The results were said to "indicate that there is no substantial genetic substructuring within populations." There were in fact statistically significant differences among the five sampled populations of *D. limnothrissa*, and allele frequencies in the other species are by no means invariant, but the picture is nevertheless one of relative uniformity. What this tells us about speciation is not clear. If, in fragmented littoral habitats, populations in separated localities display conspicuous genetic differences, this indicates a potential for allopatric speciation: a potential for sympatric speciation cannot, however, be inferred from a uniform genetic structure. Such a situation simply indicates no incipient tendency to speciation. Certainly, for reasons given above, it gives no support to the suggestion that pelagic species evolved in the lake by sympatric speciation within this environment.

While there are no obvious barriers to gene flow in the pelagial zone, and populations of pelagic fishes (especially large, powerful swimmers) are often more or less genetically homogeneous (review: Hauser & Ward, 1998), there is always the possibility of genetic differences arising in allopatry

as a result of isolation by distance, and hydrological or ecological boundaries may present barriers. The absence of some pelagic species of *Diplotaxodon* from open water at the south end of L. Malawi is an excellent example. The elongate configuration of L. Malawi lends itself to the separation of northern and southern populations, a situation that is accentuated by its morphometry. Conditions that are more eutrophic than elsewhere prevail at the shallow southern end which is the recipient of nutrients that are from time to time squeezed into it from the deep-lying hypolimnion of the main basin as a consequence of longitudinal rocking of the thermocline. (For a simple explanation of this process see Fryer & Iles, 1972.) Adaptation to different conditions can reinforce isolation by distance and promote allopatric, not sympatric, speciation.

Consideration of the facts presented here leads to the conclusion that not only has sympatric speciation among the pelagic cichlid fishes of L. Malawi not been demonstrated, but that such speciation in the pelagial zone is inherently unlikely.

Acknowledgements

References

Allison, E. H., B. P. Ngatunga & A. B. Thompson, 1995. Indentification of the pelagic fish. In Menz, A. (ed.), The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa. Nat. Resour. Inst., Chatham, UK, 159–178.

Bouvier, E. L., 1914. Sur les characterès, less affinités et les origines de la faune atyiene du lac Tanganyika. Proceedings of the 9the International Congress of Zoology, 572–578.

Bouvier, E. L., 1925. Recherches sur la morphologie, les variations et la distribution géographique des crevettes d'eau douce de la famille des Atyides Encyclopedie Entomologique 4 Paris.

Calman, W. T., 1899. On two species of macrurous crustaceans from Lake Tanganyika. Proceedings of Zoological Society of London 1889: 704–712.

Calman, W. T., 1906. Zoological results of the Third Tanganyika Expedition conducted by Dr W A Cunnington 1904–1905. Report on the Macrurous Crustacea. Proceedings of Zoological Society of London 1906: 187–206.

Calman, W. T., 1928. On prawns of the family Atyidae from Tanganyika. Proceedings of Zoological Society of London 1928: 737–741.

Coulter, G. W., 1991. Lake Tanganyika and its Life. (Coulter, G. W. ed.). Nat. Hist. Mus. and Oxford University Press, London.

Cowles, R. P., 1915. The habits of some tropical Crustacea: II Feeding habits of *Atya molluccensis* and *Caridina* species. Philippine Journal of Science 10: 11–18.

Eccles, D. H. & E. Trewavas, 1989. Malawian cichlid fishes. The classification of some haplochromine genera. Lake Fish Movies, Herten, Germany.

Felgerhauer, B. E. & L. G. Abele, 1983. Ultrastructure and functional morphology of feeding and associated appendages in the tropical fresh-water shrimp *Atya innocous* (Herbst) with notes on its ecology. Journal of Crustacean Biology 3: 336–363.

Fryer, G., 1959. The trophic interrelationships and ecology of some littoral communities of Lake Nyasa with especial reference to the fishes, and a discussion of the evolution of a group of rock-frequenting Cichlidae. Proceedings of Zoological Society of London 132: 153–281.

Fryer, G., 1960. The feeding mechanism of some atyid prawns of the genus *Caridina*. Proceedings of the Royal Society Edinburgh Section 64: 217–244.

Fryer, G., 1977. Studies on the functional morphology and ecology of the atyid prawns of Dominica. Philosophical Transactions of the Royal Society of London Series B 277: 55–129.

Fryer, G. & T. D. Iles, 1972. The Cichlid Fishes of the Great Lakes of Africa. Their Biology and Evolution. Oliver & Boyd, Edinburgh, UK.

Hauser, L. & R. D. Ward, 1998. Population identification in pelagic fish: the limits of molecular markers. In Carvalho, G. R. (ed.), Advances in Molecular Ecology. IOS Press, Amsterdam, Netherlands, 191–224.

Hobbs, H. H. Jr. & C. W. Hart Jr, 1982. The shrimp genus *Atya* (Decapoda Atyidae). Smithsonian Contributions to Zoology 364: 1–143.

Hori, M., 1983. Feeding ecology of thirteen species of Lamprologus (Teleostei; Cichlidae) co-existing at a rocky shore of Lake Tanganyika. Physiol. Ecol. Japan 20: 129–149.

Hori, M., 1997. Structure of littoral fish communities organised by their feeding activities. In Kawanabe, H., M. Hori & M. Nagoshi (eds), Fish Communities in Lake Tanganyika. Kyoto University Press, Kyoto, 277–298.

Hori, M., K. Yamaoka & K. Takamura, 1983. Abundance and micro-distribution of cichlid fishes on a rocky shore of Lake Tanganyika. African Studies and Monographs 3: 25–38.

Konings, E., 2001. Malawi Cichlids in their Natural Habitat (3rd ed.). Cichlid Press, El Paso.

Marlier, G., 1957. Le Ndakala, poisson pelagique du lac Tanganika. Bulletin Agricole Congo Belge 48: 409–422.

Menz, A., 1995. The Fishery Potential and Producitivity of the Pelagic Zone of Lake Malawi/Niassa. Nat. Resour. Inst., Chatham, UK.

Moran, P., I. Kornfield & P. N. Reinthal, 1994. Molecular systematics and radiation of the haplochromine cichlids (Teleostei: Perciformes) of Lake Malawi. Copeia 1994: 274–288.

Müller, F., 1881. *Atyoida potimirim* eine schlammfressende Süsswassergarneele. Kosmos 9: 117–124.

Ribbink, A. J., B. A. Marsh, A. C. Marsh, A. C. Ribbink & B. J. Sharp, 1983. A preliminary survey of the cichlid fishes of rocky habitats in Lake Malawi. South African Journal of Zoology 18: 147–310.

Roth-Woltereck, E., 1958. *Limnocaridina iridinae* n.sp., eine interessante Garnele aus dem Tanganjikasee (Decapoda, Atyidae). Zoologischer Anzeiger 161: 187–192.

Shaw, P. W., G. F. Turner, M. R. Idid, R. L. Robinson & G. R. Carvalho, 2000. Genetic population structure indicates sympatric speciation of Lake Malawi pelagic cichlids. Proceedings of the Royal Society of London Series B 267: 2273–2280.

Thompson, A. B., B. P. Allison, B. P. Ngatunga & A. Bulirani, 1995. Fish growth and breeding biology. In Menz, A. (ed.), The Fishery Potential and Productivity of the Pelagic Zone of Lake Malawi/Niassa. Natural Resource Institute, Chatham, UK, 279–306.

Turner, G. F., 1994. *Pallidochromis tokolosh*, a new genus and species of deep water cichlid. (Teleostei: Cichlidae) from Lake Malawi, Africa. Ichtyological Explorations in Freshwater 5: 377–383.

Turner, G. F., 1996. Offshore Cichlids of Lake Malawi Lauenau. Cichlid Press, Germany.

Turner, G. F., R. L. Robinson, B. P. Ngatunga, P. W. Shaw & G. R. Carvalho, 2001. Pelagic cichlid fishes of Lake Malawi/Nyasa. Journal of Aquaculture and Aquatic Science 9: 287–302.

Yanagisawa, Y., 1987. Social organisation of a polygynous cichlid *Lamprologus furcifer* in Lake Tanganyika. Japanese Journal of Ichthyology 34: 82–90.

Yuma, M., 1994. Food habits and foraging behaviour of benthivorous cichlid fishes in Lake Tanganyika. Environmental Biology of Fishes 39: 173–182.

Yuma, M. & T. Kondo, 1997. Interspecific relationships and habitat utilisation among benthivorous cichlids. In Kawanabe, H., M. Hori & M. Nagoshi (eds), Fish Communities of Lake Tanganyika. Kyoto University Press, Kyoto, 85–103.

Yuma, M., T. Narita, M. Hori & T. Kondo, 1998. Food resources of shrimp-eating cichlid fishes in Lake Tanganyika. Environmental Biology of Fishes 52: 371–378.