The predator of guppies on Trinidad is the pike cichlid *Crenicichla frenata*, not *Crenicichla alta*: A caution about working with cichlids

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ABSTRACT

One of the most prominent predators of the guppy, *Poecilia reticulata* Peters, in its native habitat on the Island of Trinidad is a pike cichlid. This cichlid has been referred to in the guppy literature of the past twenty five years as *Crenicichla alta*. However, *C. alta* is the name currently given to a different fish, not found on Trinidad. The pike cichlid on Trinidad is *C. frenata* and should be identified as such by guppy researchers. The broader issue here is that researchers in other fields must be made aware that cichlids are extremely diverse and that our knowledge of cichilds is dynamic. The problem is exacerbated by the confusing state of cichlid nomenclature.

PIKE CICHLIDS ARE GUPPY PREDATORS

Numerous papers over the past decades have reported on the interactions between guppies *Poecilia reticulata* Peters and their predators in the freshwaters of Trinidad and the adjacent parts of the South American mainland. Indeed, this system has become widely cited as a textbook case of life history evolution (Starr and Taggart, 1995; Krebs and Davies, 1993; Wootton, 1990). For example, Stearns (1992) in his book "The Evolution of Life Histories" writes of "an exemplary case study: the Trinidad guppies" about how predators have shaped the life histories of guppies. One of these predators is a pike cichlid which has traditionally been referred to in this literature as "*Crenicichla alta*" (e.g., Rodd and Reznick, 1997; Houde, 1997, Weetman et al., 1999; and numerous references cited therein). Sites with these pike cichlids are called "*Crenicichla* localities" to indicate areas of high potential mortality to guppies (Rodd and Reznick, 1997). Mortality due to pike cichlids figures strongly in guppy evolution (Houde, 1997) and Endler (1983) ranked pike cichlids as the most dangerous of the piscine predators of the guppy. Given the prominence of pike cichlids in this research, we feel it is important to clarify the identity of the pike species that is/are affecting the guppies. More than a simple case of misidentification that has been perpetuated for decades, the guppy-pike cichlid system illustrates the dangers of working tangentially with cichlids but not being aware of developments in the dynamic field of cichlid research.

BUT WHICH PIKE CICHLID IS IT?

The natural range of the guppy (referred to in the older literature as *Lebistes reticulatus*) appears to have included parts of Venezuela, south through the Guianas to northern Brasil as well as Trinidad, Tobago, Margarita, Barbados and some of the Windward Islands as far north as St. Lucia (Haskins et al., 1961). This range overlaps the ranges of a number of species of pike cichlids of the genus *Crenicichla*. Crenicichlines are a diverse group from South America encompassing at least 75 valid species with another 25 undescribed (Kullander, 1997).

Identification of pike cichlids is compounded by the high degree of variation within some species. For example, Warzel (1996) illustrates extensive variation in *Crenicichla regani* from a wide range of sites throughout the Amazon Basin.

Different authors have applied various names to the pike cichlids on Trinidad, including *C. alta*, *C. frenata* and *Crenicichla saxatilis*. Haskins et al. (1961) identified the pike cichlid on Trinidad as *C. saxatilis*. Boeseman (1960) identified it as *C. alta*. Seghers (1974) and Liley and Seghers (1975), in their pioneering work on guppy behaviour and ecology, followed Boeseman. Use of the name *C. alta* in the guppy literature typically can be traced either to Seghers (1974) or Liley and Seghers (1975), or to Endler (1978, 1983) in which the author names *C. alta* as the pike cichlid on the Island of Margarita and south-draining streams of the Paria Peninsula of northeastern Venezuela. Since those studies, the name *C. alta* has been applied universally without question in the extensive guppy literature, the researchers apparently unaware of the diversity of crenicichlines or changes in crenicichline systematics.

The name used by guppy researchers, namely *C. alta*, is currently applied to a pike cichlid found some distance to the south of Trinidad on the South American continent (Ploeg, 1986, 1987). Ploeg (1991) concluded that the pike cichlid on Trinidad is *C. frenata*, distinct from other pike cichlids on the mainland. Because of the abundance of research on guppy-pike cichlid interactions using *C. frenata*, we think it important that the data being gathered be attributed to the fish being used, not to *C. alta*.

To clarify, *C. frenata* Gill and *C. alta* Eigenmann are both members of the saxatilis-like group of pike cichlids (Ploeg, 1991). *Crenicichla frenata* was described by Gill (1858) and is restricted to the waters of Trinidad. *Crenicichla alta* was described by Eigenmann (1912) and is found in the near-coastal freshwaters of northeastern South America. Specifically, Eigenmann described *C. alta* as coming from the lower Essequibo River, and the upper and lower portions of its tributary the Potaro River, Guyana. This is 400 km to the southeast of Trinidad and on the other side of the mouth of the Orinoco River, a major drainage system.

The situation on the mainland is far more complex, however, because of the presence of several other species of pike cichlids that could be confused with *C. alta*. For example, in Guyana, Eigenmann (1912) found *C. alta* to be a more inland form while *C. saxatilis* was coastal. Lowe-McConnell (1969) suggested the difference is more ecological: *C. alta* is found in heavily forested areas, whereas *C. saxatilis* is found in more open country. Other similar pike cichlids in Guyana include *Crenicichla johanna* Heckel, *Crenicichla lugubris* Heckel, and several undescribed species (Lowe-McConnell, 1969). To the east, in Surinam, Kullander (1997) identified seven species of pikes, namely *Crenicichla multispinosa* Pellegrin, *C. saxatilis* (Linnaeus), *C. lugubris* Heckel, *Crenicichla albopunctata* Pellegrin, *Crenicichla coppenamensis* Ploeg, *Crenicichla nickeriensis* Ploeg and *Crenicichla sipaliwini* Ploeg, but not *C. alta*. In western Venezuela, Winemiller et al. (1990) found *C. saxatilis* and *Crenicichla geayi* Pellegrin preying on guppies, though the latter is a smaller species and much less piscivorous than *C. saxatilis*. At this point, we cannot determine which pike cichlid is found on the Island of Margarita, nor on the mainland regions of Venezuela near Trinidad -- this requires further study of the pike cichlids found there.

We emphasize that identification of pike cichlids is not a simple matter, and the fishes in question are closely related and similar in appearance. Identifications have sometimes been made on few specimens, for example, Boeseman (1960) had two specimens to work with. Many cichlids are easiest to identify by the coloration of live specimens; however, these colours are variable and do not preserve well. Despite these problems, certain features of the pattern are useful for distinguishing some pike cichlids, including the position of the humeral blotch, the presence/absence or peculiarity of suborbital markings and/or postorbital markings, dorsal fin ocelli and caudal ocelli.

The postorbital stripe (or lateral band) and humeral blotch are particularly useful for distinguishing *C. alta* from *C. frenata*. The postorbital stripe extends from the eye posteriorly to the opercle and in some species (or individuals) continues posteriorly to the caudal region. In adult female *C. frenata*, the portion of the stripe between the orbit and the operculum is black, but edged in white above and below (Figure 1). In male

Figure 1. A female *Crenicichla frenata* illustrating the distinctive post-orbital stripe edged in white above and below characteristic of females of this species.

C. frenata and both sexes of *C. alta* the stripe is black with no edging.

The humeral blotch is a patch of black scales located on the flank posteriorly to the operculum, ventral to the base of the anterior portion of the dorsal fin, and dorsal to the base of the pectoral fin. In *C. alta* "the humeral spot [is] above the lateral band in all but the smallest (from Amatuk) [individuals], in which its center is on the lateral band" (Eigenmann, 1912; p. 517). Eigenmann goes on to say "In specimens from Trinidad of so-called *saxatilis* [*frenata*] the humeral spot is sometimes continuous with the lateral band and sometimes distinct, but always on the lateral line."

There is likely a similar identification problem with another cichlid predator of guppies on Trinidad, namely the blue acara. Haskins et al. (1961) referred to this fish as *Aequidens latifrons*. '*Aequidens*' *latifrons* is actually found in northern Colombia (Steindachner 1878); the *Aequidens*-like fish in Trinidad and coastal Venezuela is '*Aequidens*' *pulcher* Gill (Leibel, 1993).

PROCEED WITH CAUTION

We do not yet know if differences between the pike cichlid species affect how they interact with guppies or vice versa, but if there are ecological differences between species of pike cichlids, as has been suggested by Lowe-McConnell (1969), and as we may reasonably expect, this may be important to guppies.

We suggest that researchers working on guppies be aware that there are different pike cichlid species in the various localities where guppies are found and that this may be important in designing and interpreting experiments. Researchers in other fields that utilize cichlids (e.g., aquaculture, endocrinology, conservation biology) should be aware of the diversity of cichlids and that many species closely resemble each other. We also suggest that cichlid researchers make an effort to inform other researchers about these potential problems.

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