Hybrids, not a new rheophilic morph of Vieja hartwegi

Preprint · March 2018

DOI: 10.13140/RG.2.2.14727.09123

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Hybrids, not a new rheophilic morph of *Vieja hartwegi*

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Gómez-González et al. (2018) have presented specimens which they identify as a new rheophilic morph of *Vieja hartwegi* (Taylor & Miller, 1980). Below we question this species determination and instead demonstrate that they are most likely natural hybrids of *Vieja hartwegi* and the syntopic *Chiapaheros grammodes* (Taylor & Miller, 1980). First, we present evidence from the reported specimens, then we compare the evidence with a documented case of hybridization of these two species (Buchhauser, 1999) and other hybrids, and finally we provide additional discussion.

The first and most striking observation regarding the reported specimens is that none can be determined as *V. hartwegi*. The specimen in their Fig. 4A has no attributes of *V. hartwegi* whatsoever and looks like a small-mouthed *C. grammodes* and has a much larger head than any of the other shown specimens. The other three specimens (their Fig. 4B-D) and those in their Fig. 6 are indeterminable to species level and thus cannot be unequivocally determined as *V. hartwegi*.

The second striking observation is the high amount of shape and coloration-pattern variation between the supposedly rheophilic specimens. The specimens in their Figs. 4A, C, D and Fig. 6 are elongated while the specimen in Fig. 4B is rather deep-bodied. The specimen in their Fig. 4A reminds closely of *C. grammodes* in overall coloration, showing a midlateral and caudal blotch as well as the *Chiapaheros*-typical rusty spots on body and vermiculations on head, which are, however, much coarser than in *C. grammodes* and do not extent onto upper snout and forehead. Similar markings are found in all specimens in their Fig. 4 and are the only unifying feature of them; these spots and vermiculations are intermediate between the corresponding markings of *C. grammodes* and *V. hartwegi* (which has relatively coarse, irregular spots on head and body). Moreover, none of the specimens (their Figs 4, 6) has the *Vieja*-typical course of the midlateral stripe (in a lowered position; Říčan et al., 2005, 2016; their Figs 3, 5 and 9), but all have the plesiomorphic position (ancestrally shared with *C. grammodes).* None of the specimens (their Figs 4 and 6) has the apomorphic neomorphic condition of the midlateral blotch of *Vieja* (diffuse, elongated by fusion from two or more vertical bars, shifted in position dorsally; Říčan et al., 2005, 2016; their Figs 3, 5 and 9) but all have the plesiomorphic condition also found in *C. grammodes*. None of the specimens has the *Vieja*-typical elongated caudal fin-base blotch (extending onto caudal peduncle and often continous with the midlateral stripe). Instead all specimens have the plesiomorphic blotch (rounded and exclusively on caudal fin; their figs 4 and 6) found also in *C. grammodes*. To sum up, the melanin coloration patterns of the specimens are thus not those diagnostic of *Vieja* but are all as found in *C. grammodes*.

The high amount of shape variation and notable differences between *Vieja* species and the reported specimens here suggested as of hybrid origin is evident in the reported proportional values (Table 2 in Gómez-González et al., 2018). In all genera of the *Theraps-Paraneetroplus* clade of herichthyines, the head is (irrespective of their ecomorphology) short and deep, and especially foreshortened in the rheophilic genera. The reported specimens have none of these characteristics of the rheophilic herichthyines and instead have long heads and comparatively large mouths (not evident from the jaw length in Table 2 because there given only in relation to head length), a unique combination among their containing group. Table 2 in Gómez-González et al. (2018) reports a notable difference in head length (34.3% SL vs. 28.3) between the examined specimens of the normal morph of *V. hartwegi* (vs. 28.3–30.4 in the two examined *Vieja* species), but the table contains errors that make these and other values hard to trust, because the mean 34.3 for the putative hybrids is listed as derived from a range of 30.7–31.1 (in Table 2 also the minimum and maximum values are switched for the paratypes of *V. hartwegi*, their head length and head depth stray much from the examined specimens, and the Max-column for the 'rheophilic morph' repeats the data for the normal morph for all values). Also, the listed SD (5.4) is much higher than the SDs in the normal species (1.2, 1.3, 1.5) demonstrating a much higher variability among the specimens of the putative hybrids (see above). The mean head length of the reported specimens (34.3% SL) is intermediate between the short-headed *Vieja* species values (28.3–30.4) and those of the long-headed *C. grammodes* (based on Taylor and Miller, 1980) (39.6% SL).

The reported specimens also have a much narrower head (as judged from the interorbital distance) of 25.4% HL vs. 40.8 in *V. hartwegi* and 39.6–45.4 in the other two reported *Vieja* species. Again, the interorbital distance of the reported specimens (25.4% HL) is thus completely outside the values of *Vieja* (39.6–45.4) but very similar to *C. grammodes* (based on Taylor and Miller, 1980) (about 25.0% HL).

The optically much larger mouth of the reported specimens has not been addressed in the study but it does not fit to a rheophilic morphology. All rheophilic species of herichthyine cichlids of the *Theraps-Paraneetroplus* clade have small, subterminal mouths, in size thus comparable to the lentic *Vieja*, differing only in their inferior position on the head (Říčan et al., 2016).

In light of the above observations the much larger head, mouth and much more sharp heads of the reported specimens (their Figs 4 and 6 and Table 2) than found in *V. hartwegi* and in other *Vieja* (their Figs 3, 5 and 9) are easily explained as averaged values of the extreme morphologies found in the two proposed parental species, *V. hartwegi* and *C. grammodes*.

Additional arguments for the hybrid origin of the reported specimens are found in their meristic characters. *Vieja* species have a combination of modally 15 abdominal and 15 caudal vertebrae (a total of 30; Říčan et al., 2016). This diagnosis of *Vieja* has been questioned by Gómez-González et al. (2018) but on the wrong assumption. The ancestral count of vertebrae in Middle American cichlids is overwhelmingly robust and is modally 13 abdominal plus 16 caudal (13+16). The diagnosis of *Vieja* by 15+15 thus states that there was an increase in modal number of abdominal vertebrae from the ancestral condition to at least 15 and a decrease of caudal vertebrae to at least 15 (modally 15, extreme range 14–16), and this combination is unique among Middle American cichlids. That e.g. *V. bifasciata* has only 14 caudal vertebrae as reported by Gómez-González et al. (2018) is thus not a negation of the diagnosis, but is fully in agreement with it. The 15+15 vertebrae counts thus agree with those reported for *V. hartwegi* by Gómez-González et al. (2018). The specimens here interpreted as hybrids have 15 abdominal and 15(1)–16(2) caudal vertebrae, total 30(1)–31(2) according to Gómez-Gonzáles et al. (2018). The specimen in their Fig. 8B actually has 17 caudal vertebrae. *Chiapaheros grammodes* has modally 13+17(18) vertebrae. The elevated number of caudal vertebrae can thus again be explained by hybridization with *C. grammodes*, since the specimens have *Vieja*-like numbers of abdominal vertebrae (15) and *Chiapaheros*-like numbers of caudal vertebrae (up to 17). Middle American cichlids with a combination of 15+17 include only three species (Říčan et al., 2016 based on x-ray examination of >1100 heroine specimens): *Rheoheros*, *Talamancaheros* and *Tomocichla tuba*; all easily distinguishable from the reported specimens; a combination of 15+16 is found addtionaly only in *Amphilophus citrinellus*, *Cincelichthys*, *Chuco*, and *Vieja bifasciata*.

A likely decisive difference between the reported specimens and *Vieja* species is evident in Fig. 8 of Gómez-González et al. (2018). The difference concerns the oral teeth. The specimen of normal *V. hartwegi* in Fig. 8A shows typical *Vieja* teeth (type F or E sensu Říčan et al., 2016) that are characteristically flattened anteroposteriorly, while the specimen in Fig. 8B, the likely hybrid, has clearly visible conical, pointed teeth, additionally with an enlarged pair of teeth along the symphysis of the upper jaw and much smaller remaining teeth, a tooth morphology sensu Říčan et al. (2016) of type B or C, typical of predatory heroines (including *C. grammodes*) and not a rheophilic-morph tooth morphology of species in the *Theraps-Paraneetroplus* clade of herichthyines (type F or E; see Říčan et al., 2016 for photos and a review of all tooth-types in heroine cichlids and their association with feeding and habitat ecology). This important difference between the oral teeth in Fig. 8A and B has not been addressed in the paper and the teeth are not described as markedly different, which they are even from what is visible in the two photographed specimens in Fig. 8. No herichthyine in the *Theraps-Paraneetroplus* clade has type B or C oral teeth (Říčan et al., 2016).

Another important difference is also visible in Fig. 8 of Gómez-González et al. (2018). The anguloarticular bone of the lower jaw in the two specimens in Fig. 8 has a completely different shape and proportions that are beyond variation found conspecifically in Middle American cichlids (Říčan, unpublished data). The anguloarticular bone acts as two opposing lever systems in the cichlid lower jaw, one opening the jaw, and the other closing it, and these are governed by the sizes and shapes of the retroarticular process and the coronoid process of this bone (see Albertson & Kocher, 2006 for a review). The putative hybrid specimen in Fig. 8B has a long ventral base of the retroarticular process and a very sharp coronoid process, the specimen of *V. hartwegi* in Fig. 8A has a short ventral base of the retroarticular process and a robust coronoid process. These two types of the anguloarticular bone are based on examined material of Middle American cichlids (Říčan, unpublished data) basically on the opposite ends of the spectrum of variation. The more a species is predatory/piscivorous the longer is the ventral base of the retroarticular process and the sharper and shorter its coronoid process (the extreme is found in the highly specialized piscivores, i.e. *Parachromis, Petenia*, *Kronoheros* and *Caquetaia*) while on the opposite end herbivorous species have a short ventral base of the retroarticular process and a robust and long coronoid process (see Fig. 8 in Říčan et al., 2016 for the variation in length of the ventral base of the retroarticular process). The likely hybrid specimen in Fig. 8B thus has a shape of the anguloarticular bone resembling generalized predatory species, while the one in *V. hartwegi* in Fig. 8A agrees with other *Vieja* species and other detritivorous/herbivorous genera.

Based on their oral teeth and jaw morphology, head and mouth shape and size the reported specimens cannot be placed among the rheophilic guild (ecomorph) since all rheophilic herichthyines have a markedly different morphology as explained above. The reported specimens also cannot be placed in the rheophilic guild based on field data. The specimens have been collected in syntopy with *V. hartwegi* and the streams have not been surveyed along an elevational gradient. The whole argument for interpretation of the specimens as a rheophilic morph is thus completely without any evidence.

Gómez-González et al. (2018) have tried to demonstrate the conspecifity of the supposed rheophilic morph by molecular phylogeny, but unfortunately have only used a uniparentally inherited mtDNA marker. Recombinant nuclear DNA multilocus markers are now widely used in Middle American and Neotropical cichlid studies (e.g. Říčan et al., 2016; Ilves et al., 2017; Burress et al., 2018a,b) and should be used on these specimens in question to provide the definitive test of their origin.

We now turn to documented cases of hybrids in Middle American cichlids which further underscore our interpretation of the reported specimens as of hybrid origin. The high amount of shape and coloration-pattern variation between the reported specimens (see above) is a typical feature of low generation-specimens of hybrid origin. Based on this large variation in the reported specimens by Gómez-González et al. (2018) we deduce that the specimens are of a recent hybridization event(s). Říčan et al. (2005) reported specimens from a cross between a female *Parachromis managuensis* and male *Amatitlania nigrofasciata*. The hybrids remained fertile at least to generation F4 (after which the experiment was discontinued) and already since generation F1 showed a large amount of shape and coloration variation that could be grouped into two forms, each more resembling one of the parental species. Similar large variation in shape and coloration of specimens has also been obtained in e.g. hybrids of *Vieja* x *Parachromis*, or in hybrids of *Amatitlania nigrofasciata* x *Thorichthys meeki*. In all these hybrids there is a large amount of shape and coloration variation that can again be grouped into two forms, each more resembling one of the parental species. This type of variation closely matches the variation shown in Fig. 4 in Gómez-González et al. (2018), where specimen A is very similar to *C. grammodes* and the three other specimens are a mix of body shapes between the two putative parental species, with coloration patterns predominantly of *C. grammodes*.

The likelihood of hybrid origin for the reported specimens by Gómez-González et al. (2018) reaches virtual certainty due to reported hybrids (Buchhauser, 1999; Fig. 1) of the two purported parental species (*V. hartwegi* x *C. grammodes*; Fig. 1). The hybrid specimens of Buchhauser (1999) and the specimens of Gómez-González et al. (2018) share similar intermediate (between *V. hartwegi* and *C. grammodes*) body, head and mouth shape, mouth size and coloration patterns, chiefly characterized by the *C. grammodes*-typical rusty spots and body and head and especially the coarse vermiculations on the cheek and preorbital region, and by the absence of apomorphic *Vieja*-typical coloration patterns (see above, i.e. course of the midlateral stripe, condition of the midlateral blotch, condition of the caudal fin-base blotch).

Rheophilic morphs (or forms) of cichlid species are not known to differ so utterly in coloration patterns as to render the specimens indeterminable to species level as in the case of the specimens reported by Gómez-González et al. (2018). Typically such rheophilic forms are just more streamlined but easily recognizable variants of their species. To demonstrate our case we provide an example (see Musilová et al., 2015) of a rheophilic (lotic) form of *Mesoheros festae* in comparison with the typical lowland (lentic) form (Fig. 1). These two forms really differ in their occupied habitats but share the same coloration patterns unlike the situation reported in Gómez-González et al. (2018). Similar variation of morphology with habitat (e.g. water-flow, turbidity, bottom type) is common in many herichthyine species and is not worth of describing as special morphs, since the variation has the form of a cline and there are no sharply delineated distinct and habitat-segregated morphs. As an example, Říčan et al. (2016) and Pérez-Miranda et al. (2017) have reported an ecomorphological dichotomy in the herichthyine species *H. pantostictus* that however on a more detailed examination will also likely prove to be a smooth cline.

We believe to have convincingly demonstrated that the description of the supposed rheophilic morph of *Vieja hartwegi* by Gómez-Gonzáles at al. (2018) is based actually on natural hybrids between *V. hartwegi* and *C. grammodes*. Since the data concerning the ‘rheophilic morph’ are given separately in diagnosis, description and table, they do not distort the information on the ‘normal form’ and its distinction from related species. Therefore, the redescription of *V. hartwegi* (safe for the partly flawed table) is nevertheless a useful contribution to the knowledge of the species.

We would like to thank Peter Buchhauser (Tegernheim, Germany) for providing photos and additional information on the aquarium hybrid specimens of *V. hartwegi* x *C. grammodes* and their parents.

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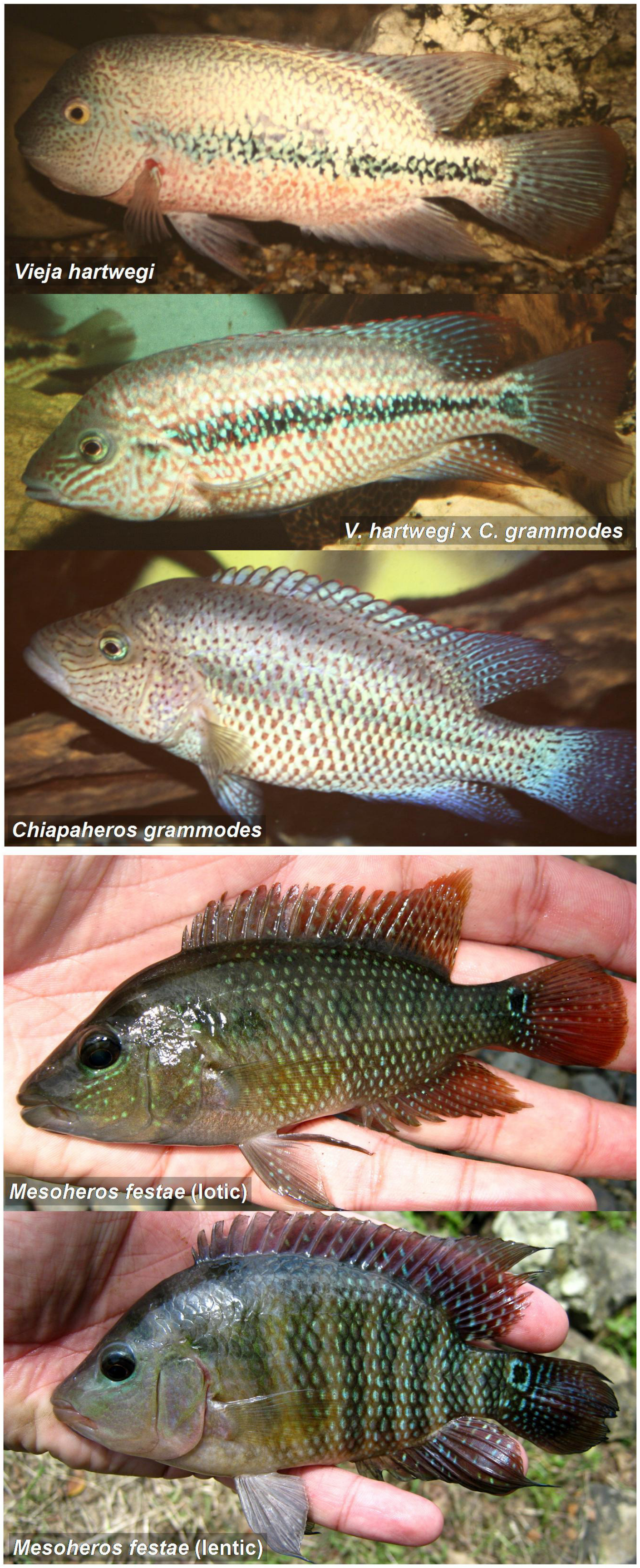

Figure 1. The figure demonstrates one of the hybrids obtained from a cross between *Vieja hartwegi* and *Chiapaheros grammodes* (Buchhauser, 1999); the two parental species are also shown (photos courtesy Peter Buchhauser). Further, a real situation of intraspecific ecomorphological dichotomy is demonstrated in an example from *Mesoheros festae* (collected by Říčan, 2009; see Musilová et al., 2015) from a highland lotic locality with corresponding morphology (0 23 21.8 S, 79 14 35.5 W; 336 m a. s. l.) and a lowland lentic locality with corresponding morphology (1 12 29.7 S, 80 21 34.6 W; 70 m a. s. l.).