

Feeding efficiency and food competition in coexisting sexual and asexual livebearing fishes of the genus *Poecilia*

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Abstract Considering its immediate costs of producing dispensable males, the maintenance of sexual reproduction is a major paradox in evolutionary biology. Asexual lineages that do not face such costs theoretically should replace sexuals over time. Nonetheless, several systems are known in which closely related sexual and asexual lineages stably coexist. In the present study, we studied a sexual/asexual mating complex of a sperm-dependent parthenogenetic fish

(amazon molly, *Poecilia formosa*) and its sexual congeners, the sailfin molly *P. latipinna* and the Atlantic molly *P. mexicana*. We asked whether differences in feeding behavior could contribute to their stable coexistence. We conducted a laboratory experiment to compare feeding efficiencies and also measured the competitive abilities between the two reproductive forms. Additionally, we measured gut fullness of fishes caught in natural habitats. Contrary to our predictions, we could not find *P. formosa* to be less efficient in feeding. We argue that food competition in mollies plays a minor role in mediating coexistence between closely related asexual and sexual mollies.

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Introduction

Sexual reproduction prevails in nature, and especially in vertebrates only very few asexual forms have been described (about 50 species in 22 genera: Vrijenhoek et al. 1989). The few systems in which asexual and closely related sexual lineages coexist offer a unique opportunity to examine the costs and benefits associated with both reproductive strategies (Moore and McKay 1971; Vrijenhoek 1979; Case and Taper 1986; Jokela et al. 2009). The system investigated here includes the amazon molly, *Poeci-*

lia formosa, which is a unisexual, livebearing fish (family Poeciliidae) with a reproductive mode called gynogenesis (Kallman 1962; Hubbs 1964; Balsano et al. 1972). In this special form of parthenogenesis, sperm of a host species is used to trigger the onset of embryonic development (Schlupp 2005), but fusion of the gametes does not occur (Hubbs 1964; Balsano et al. 1985). Consequently, paternal genetic material is not usually incorporated during zygote formation, and offspring are simple clones of the mother (Rasch et al. 1982; Turner 1982). The amazon molly arose as a hybrid between the Atlantic molly (*P. mexicana*) and the sailfin molly (*P. latipinna*), which also serve as sperm donors in the natural habitats (Hubbs and Hubbs 1932; Schlupp et al. 1998). The sperm-dependency of the amazon molly has important ecological consequences, forcing it to coexist with closely related sexual species in the same habitat (Niemeitz et al. 2002), where they actually form mixed-species shoals (Schlupp and Ryan 1996). In the coastal areas of Texas and the Mexican state of Tamaulipas, *P. formosa* occurs sympatrically with *P. latipinna*, while it is sympatric with *P. mexicana* in rivers and streams in northeastern Mexico (Darnell and Abramoff 1968; Miller 1983; Schlupp et al. 2002).

The apparently stable coexistence of the two different reproductive modes is not easily explained considering the costs of sexual reproduction: asexuals, being all-female, have a much faster population growth rate, because they do not produce dispensable males contributing nothing but sperm to reproduction (Maynard Smith 1978). Sexuals also pay the cost of meiosis; due to recombination only half of their genes are passed to the next generation, and successful genotypes can be destroyed in every reproductive cycle (Williams 1975). Consequently, asexual reproduction should be a more successful strategy at least in the short term, and everything else being equal, asexuals should outcompete sexuals over time (Maynard Smith 1978; Bell 1982; Lively and Lloyd 1990; Ladle 1992; Barton and Charlesworth 1998). In mixed sexual/gynogenetic systems like the amazon molly system, local extinction of the sexual forms should inevitably be followed by the local extinction of the asexuals due to the lack of sperm donors (Schlupp 2005; Kokko et al. 2008).

While metapopulation dynamics theoretically can explain the coexistence of the different reproductive

modes (Kokko et al. 2008), most models of coexistence assume some disadvantages for asexuals that balance the costs of sex (West et al. 1999; Agrawal 2001). In addition, (slight) ecological differentiation or specialization between reproductive forms may also mediate coexistence (see the Frozen Niche Variation Model; Vrijenhoek 1979; Wetherington et al. 1989; Vrijenhoek and Pfeiler 1997; Vrijenhoek 1998). For example, in a similar system of asexual and sexual fish (*Poeciliopsis monacha-lucida*) that mainly consume algae and detritus, the reproductive modes exhibited a reduced dietary overlap (Gray and Weeks 2001) and differed in the efficiency of handling different prey items (Weeks et al. 1992).

In studies of food consumption, *P. formosa* were found to have a higher feeding rate when exposed to winter conditions than *P. latipinna* (Fischer and Schlupp 2010). Furthermore, neonates of *P. formosa* were shown to be more sensitive towards food stress (Tobler and Schlupp 2010). These differences in feeding ecology may contribute to the stable coexistence of both reproductive modes in the *Poecilia*-system.

The present study was initiated to test further factors that may differ between the two reproductive modes. For example, costs of sexual reproduction could be balanced if asexuals were inferior in acquiring resources. Hence, we tested whether asexuals and sexuals differ in their feeding efficiency and competitive abilities. In previous studies, *P. formosa* was found to spend less time feeding than their sexual congeners (Heubel and Plath 2008; Padur et al. 2009). However, the focus of those studies was on feeding time reduction by male harassment, and the experimental design did not allow for an assessment of competition between different females. To examine whether asexuals have reduced competitive abilities as compared to sexuals, we designed a similar experiment allowing individual females (sexual or asexual) to feed in company of either a conspecific or heterospecific female, and we scored the time spent foraging as well as aggressive interactions. If asexuals have a disadvantage in foraging, this could also be reflected in lower gut fullness in the field. With a second approach, we therefore augment our data set by measuring gut fullness of asexual (*P. formosa*), and sexual (*P. latipinna* and *P. mexicana*) females collected from various natural populations.

Material and methods

Laboratory experiments

For the experiment on feeding efficiency and competition, *P. formosa* and *P. latipinna* were caught from the Guadalupe River in central Texas (Table 1) and transferred to the laboratory at Texas A&M University in College Station. To avoid any effects caused by sexual harassment (Plath et al. 2003; Heubel and Plath 2008), only females were used in the feeding experiment. Fish of both species, including males, were maintained in 120×30×40 cm aerated holding tanks at 24°C and an illumination cycle of 12 L:12D. Fish were fed twice a day with “Hikari tropical algae wafers” food tablets. Test subjects could acclimatize to the laboratory for at least 2 weeks before the feeding experiments and thus had enough time to familiarize with the food source. All fish involved in a trial were starved for 24 h prior to the start of the experiment, making sure that they were motivated to feed throughout the feeding tests. We measured all fish for standard length (SL) to the nearest mm after experiments were ended.

To test the feeding efficiency and competitive ability of the two species, focal fish were successively allowed to feed with a conspecific and a heterospecific competitor. The order of the two treatments was balanced and alternated between trials. The experimental tank (49×27×24 cm) was equipped with two clear Plexiglas cylinders (diameter 9.5 cm), one on each side. A food tablet was placed on the bottom in the front portion of the tank. The focal fish was introduced in one cylinder and the competitor in the

other cylinder. After 5 min of acclimatization, the cylinders were gently removed. We then recorded the time passed until the focal female started to feed on the food tablet (latency time). Trials in which individual fish did not start to feed were terminated after 20 min and fish were given a ceiling value of 1,200 s. If the focal fish started to feed, a 5-min observation period began, during which we recorded the time the focal female spent feeding on the food tablet. Furthermore, aggressive behaviors, including biting, chasing, and tail-beating (see Parzefall 1969; Parzefall 2001), were quantified, and we distinguished between aggressive behaviors directed from the focal female toward the competitor and vice versa. In total, we tested 62 individuals (33 *P. formosa* and 29 *P. latipinna*).

Gut fullness in natural populations

Data on gut fullness were reanalyzed from a previous study investigating patterns of trophic niche segregation by analyzing gut contents (Scharnweber et al., in prep.). We investigated three mixed populations of *P. formosa* and *P. latipinna* in Texas, USA, including an introduced population in the Guadalupe River (Hubbs et al. 1953), and three populations of *P. formosa* coexisting with *P. mexicana* in Tamaulipas and Nuevo León, Mexico (Table 1 for collection sites). To eliminate potential confounding effects of sex differences, only females were included in the analyses. In total, we investigated 394 individuals (227 *P. formosa*, 100 *P. latipinna*, and 67 *P. mexicana*). Collections took place between March and August 2009. Fishes from the sites Barretal, Central Texas, Weslaco, and Brownsville were collected twice, with at least 2 months in between (i.e., during spring and summer). All specimens were caught using a seine (length 4 m; mesh-width 4 mm). Immediately upon capture, fish were euthanized using MS222 (Tricaine Methanesulfonate) and fixed in a 10% formaldehyde solution for subsequent analyses in the laboratory. Whenever available, 15 individuals of each species and from each site were measured for gut fullness. To do so, fish were dissected, and the volume of the tubular intestine (including its content) was determined by introducing it into a measuring cylinder filled with tap water and measuring the volume of water replacement. Then gut contents were carefully removed and the volume of the empty intestine was measured again as described above. The difference between the two

Table 1 Study sites of coexisting asexual (*P. formosa*) and sexual mollies (*P. latipinna*, *P. mexicana*)

Study site	River basin	Latitude	Longitude
Sites with <i>P. latipinna</i>			
Central Texas	Guadalupe river	29.857	−97.868
Lincoln Park	Rio Grande (Bravo)	25.900	−97.479
Weslaco	Rio Grande (Bravo)	26.121	−97.962
Sites with <i>P. mexicana</i>			
Mante	Río Guayalejo	22.705	−99.001
Barretal	Río Soto La Marina	24.079	−99.123
Rio Juanillo	Río San Fernando	24.608	−98.299

volumes was used a measure of gut fullness. We assumed that individuals that were more efficient foragers would have more food in their intestines.

Statistical analyses

To analyze differences in feeding efficiency, General Linear Models (GLM) with repeated measures design were performed with latency time or total feeding time of the focal fish as dependent variable (with either a conspecific or heterospecific fish present as the repeated measures) and species identity of the focal fish as independent variable. Likewise, for the analysis of aggressive behavior, numbers of aggressive behaviors (sum for all three behavior categories) directed against or received from the competitor were subjected to similar rmGLM.

To assess differences in gut fullness, fish collected from the same site but different sampling periods were pooled for data analysis. The volume of gut contents was square root-transformed and subjected to analysis of covariance (ANCOVA), in which gut content volume was used as the dependent variable, and reproductive mode, host species (*P. latipinna* or *P. mexicana*), and study site (nested within host species) were treated as independent variables. Standard length was used as a covariate.

For further analysis of temporal variation of gut fullness, we included only sites that had been sampled twice. We ran a second ANCOVA, using the square root-transformed volume of gut contents as dependent variable and reproductive mode, host species (*P. latipinna* or *P. mexicana*), and study site (nested within host species) as well as time (spring/summer) as independent variables. Standard length was used as a covariate. In both analyses effect sizes were approximated using partial eta squared (η_p^2).

Results

Laboratory experiments

No overall differences between sexual and asexual mollies were detected in latency or feeding times (see between-subjects effects in Table 2). However, we found a significant interaction effect between ‘repeated measurement’ (conspecific versus heterospecific competitor) and ‘focal fish species’. *Poecilia*

Table 2 Results of repeated measures General Linear Models (rmGLM) using (a) latency and (b) feeding times of individual focal females interacting with a conspecific and heterospecific partner female as dependent variables (repeated measures, rm). In (c) numbers of aggressive behaviors directed toward the partner female and in (d) numbers of aggressive behaviors received from the partner female when competing for food were the dependent variables

Effect	df	F	P	η_p^2
(a) Latency time until feeding commenced				
Within-subjects effects				
Rm	1	2.763	0.102	0.044
Rm×focal fish species	1	5.777	0.019	0.088
Error	60			
Between-subjects effects				
Focal fish species	1	0.077	0.782	0.001
Error	60			
(b) Feeding time				
Within-subjects effects				
Rm	1	0.172	0.679	0.003
Rm×focal fish species	1	0.107	0.744	0.002
Error	60			
Between-subjects effects				
Focal fish species	1	0.964	0.330	0.016
Error	60			
(c) Aggressive behavior directed against competitor				
Within-subjects effects				
Rm	1	2.843	0.097	0.045
Rm×focal fish species	1	4.186	0.045	0.065
Error	60			
Between-subjects effects				
Focal fish species	1	1.236	0.271	0.020
Error	60			
(d) Aggressive behavior received from competitor				
Within-subjects effects				
Rm	1	0.879	0.352	0.014
Rm×focal fish species	1	0.001	0.971	<0.0001
Error	60			
Between-subjects effects				
Focal fish species	1	1.098	0.299	0.018
Error	60			

latipinna needed significantly more time to start feeding when tested with a conspecific than with a heterospecific competitor (paired *t*-test: $t_{28}=2.21$, $P=0.035$; Fig. 1a), but no such effect was found in *P. formosa* ($t_{32}=0.78$, $P=0.44$).

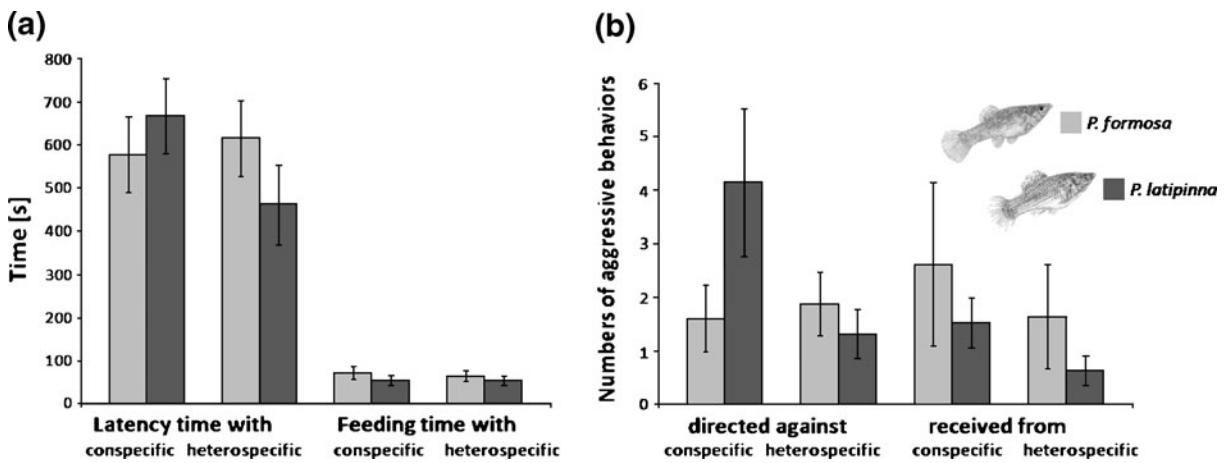


Fig. 1 a Mean (\pm SE) latency times until feeding commenced and total feeding times of *P. formosa* (light gray) and *P. latipinna* females (dark gray) while interacting with either a conspecific or a heterospecific competitor. **b** Aggressive

behaviors directed against and received by focal females [*P. formosa* (light gray) and *P. latipinna* (dark gray)] when competing with a con- or heterospecific female

Table 3 Results of ANCOVAs examining the gut fullness (a) and gut fullness while considering temporal variation at sites that were sampled twice (b) of sexual and asexual females

Effect	df	F	P	η^2_p
(a) Gut fullness				
SL	1	115.621	<0.001	0.261
Reproductive mode	1	0.587	0.444	0.002
Host species	1	1.026	0.312	0.003
Study site (host species)	4	0.705	0.589	0.009
SL×reproductive mode	1	0.445	0.505	0.001
SL×host species	1	0.089	0.766	<0.001
SL×study site (host species)	4	1.862	0.117	0.022
Reproductive mode×host species	1	0.344	0.558	0.001
Reproductive mode×study site (host species)	4	2.718	0.030	0.032
Error	327			
(b) Temporal variation of gut fullness				
SL	1	74.589	<0.001	0.231
Reproductive mode	1	1.402	0.237	0.006
Host species	1	0.480	0.489	0.002
Study site (host species)	2	0.231	0.794	0.002
Time	1	11.554	0.001	0.045
SL×reproductive mode	1	0.529	0.468	0.002
SL×host species	1	0.281	0.597	0.001
SL×study site (host species)	2	0.812	0.445	0.007
SL×time	1	8.422	0.004	0.033
Reproductive mode×host species	1	8.267	0.004	0.032
Reproductive mode×study site (host species)	2	0.131	0.877	0.001
Reproductive mode×time	1	4.948	0.027	0.020
Host species×time	1	13.241	<0.001	0.051
Study site (host species)×time	2	8.593	<0.001	0.065
Error	248			

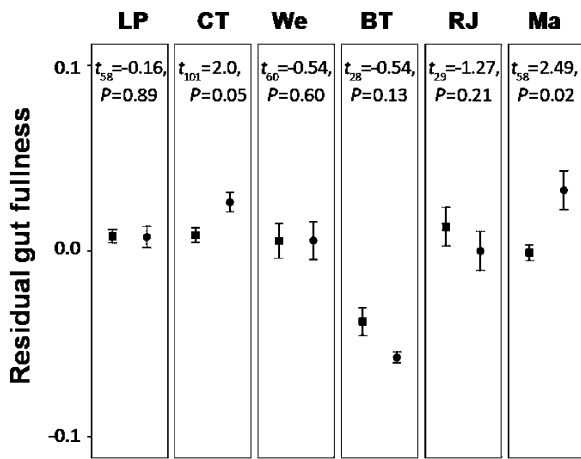


Fig. 2 Mean (\pm SE) gut fullness (residuals from GLM, corrected for body size) of sexual (*P. latipinna* or *P. mexicana*) (•) and asexual *P. formosa* (◦) females, from each study site. LP: Lincoln Park; CT: Central Texas; We: Weslaco; BT: Barretal; RJ: Río Juanillo; Ma: Mante. Results of post hoc independent samples *t*-tests comparing reproductive modes are shown

The analysis of aggressive behaviors revealed a significant interaction effect between ‘numbers of aggressive behaviors directed against the opponent’ and ‘focal fish species identity’ (Table 2). *Poecilia latipinna* was by far more aggressive towards conspecific than heterospecific competitors (Fig. 1b). None of the considered variables had a significant effect on numbers of aggressive behaviors received by the focal fish (Table 2).

Gut fullness in natural populations

Comparing gut fullness between reproductive modes and populations, ANCOVA did not detect a significant effect of reproductive mode per se, but there was a significant three-way interaction with the factor ‘host species’ and ‘study site’ (nested within host species;

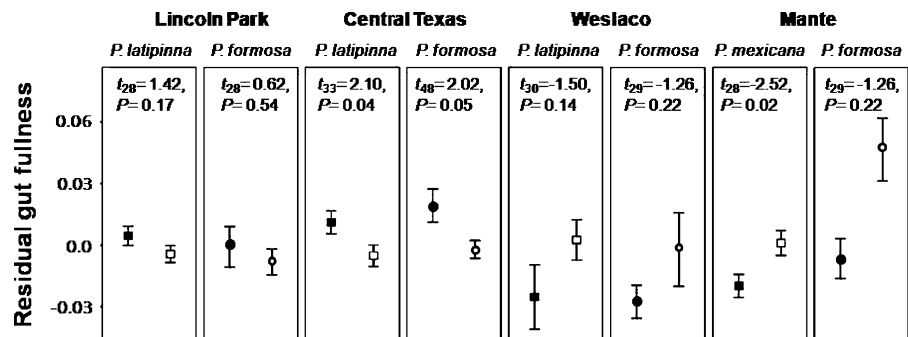
Table 3a). At two sites (Mante, and Central Texas) gut fullness differed significantly between the reproductive modes (Fig. 2), whereby *P. formosa* had significantly fuller guts than their sexual congeners. Interestingly, both reproductive modes overall showed a very low gut fullness in Barretal (Fig. 2). Most variation in gut fullness was explained by body size (SL), as larger fish naturally had more food in their guts. One might argue in this context that fish with empty intestines were not motivated to feed, and therefore should be excluded from the analysis, as they are not suitable for an investigation of feeding efficiency. However, the results did not change qualitatively when we reanalyzed the data while excluding individuals with empty guts (48 out of 394 individuals; analysis not shown).

The second ANCOVA detected a significant main effect of temporal variation of gut fullness as well as significant interaction effects including temporal variation and the other factors included in the analysis (Table 3b). As can be seen in Fig. 3, neither temporal differences nor differences between reproductive modes were consistent across sites.

Discussion

Contrary to our predictions, asexuals were not less efficient foragers in our feeding experiments. *Poecilia formosa* generally did not start to feed later on the food source and also showed similar feeding times as the sexual *P. latipinna*. Apparently, results from previous studies (Heubel and Plath 2008; Padur et al. 2009), where *P. formosa* was found to feed for shorter periods of times than *P. mexicana*, cannot be generalized. Results of the examination of gut fullness further supported the notion that asexual and sexual mollies do not consistently differ in feeding efficiency.

Fig. 3 Temporal variation of mean (\pm SE) gut fullness (residuals from GLM, corrected for body size) of sexual (*P. latipinna* or *P. mexicana*) (•) and asexual *P. formosa* (◦) females. Closed symbols represent gut fullness in spring, open symbols indicate gut fullness in summer. Results of post hoc independent samples *t*-tests comparing seasons are shown



We suggest that a considerable degree of the variation in gut fullness among sites as well as within sites over time may be explained by site-specific differences in resource availability. Notably, mollies from Barretal had a significantly lower overall gut fullness compared to all other study sites. It can only be speculated whether this is due to habitat differences or attributable to an earlier collection time (fish were caught in the morning as compared to afternoon at all other sites). Alternatively, variation in gut fullness across sites may also be constrained by intestinal length, which varies considerably across sites but not reproductive modes (Scharnweber et al., in prep). Intestinal length in these fish is highly plastic and seems to reflect local resource use. The underlying causes of variation among sites remain speculative and clearly warrant more detailed future investigation.

Contrary to our second prediction, asexuals were not less competitive than sexual mollies in the feeding experiment, i.e., their feeding rates were not more affected by heterospecific than conspecific competitors. On the contrary, we even found latency times of *P. latipinna* focal females to be longer when a competitor of the same species was around, and *P. latipinna* fought more with conspecific competitors. Nonetheless, caution is required when interpreting the latter result, as the results for received aggressive behavior did not follow the same pattern. It might be possible that species-specific cues necessary to trigger aggressive behavior lead to amazon mollies evoking less aggression. Several studies have shown that both species can distinguish between heterospecific and conspecific fish (Ryan et al. 1996; Gabor and Ryan 2001).

Pronounced differences in resource use and feeding behavior were found in the asexual *Poeciliopsis*-system (Weeks et al. 1992; Gray and Weeks 2001), which in terms of resource use is similar to the fish investigated here. The two systems, however, differ in resource availability and also in clonal diversity within asexual lineages. Whereas *P. formosa* appears to be of single origin and genetic diversity is low (Schartl et al. 1995; Lampert and Schartl 2008), asexuals in *Poeciliopsis* evolved multiply and thus exhibit higher clonal diversity (Weeks et al. 1992). Furthermore, fishes in the *Poeciliopsis* system are subject to shortages in resource availability during the dry season, leading to strong competition for food between sexuals and asexuals (Vrijenhoek 1978).

Overall, differences in foraging behavior and feeding competition do not appear to constitute a disadvantage to asexuals in the *Poecilia formosa* system. As the main food source of mollies is detritus (Darnell 1962; Winemiller 1993; Tobler 2008; Scharnweber et al. unpubl. data), which is rarely limiting (Moyle and Light 1996), it is likely that food competition generally plays a minor role in mollies. Other aspects of feeding ecology (e.g., microhabitat preferences or daily shifts in activity between sexuals and asexuals) within this system are thus far poorly understood and might still contribute to ecological differentiation. Also, asexuals and sexuals might differ in the efficiency of energy use and have different metabolic rates, as experiments have shown that *P. formosa* neonates are more susceptible to food stress than neonates of *P. latipinna* (Tobler and Schlupp 2010). To date it is unclear what selective forces are balancing the twofold advantage of asexual mollies. Ecological factors, such as resource use (Scharnweber et al. unpublished data; this study) and selection from parasites (Red Queen hypothesis: Tobler and Schlupp 2005; Tobler et al. 2005), appear to play a minor role, and male mating behavior remains to be one of the few documented mechanisms that consistently puts asexuals at a (slight) disadvantage (reviewed in Schlupp 2005; Schlupp 2009). Consequently, we are still lacking a comprehensive understanding of the mechanisms underlying the coexistence in this unusual mating complex.

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