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Standardized Classification of Poeciliid Development for Life-History Studies

JODY L. HAYNES

Complete life-history characterizations are available for only a few of the nearly 200 poeciliid species. A comprehensive synthesis of the evolution and phylogenetic distribution of life-history patterns within the family will require the characterization of numerous additional species. This process would be facilitated by the standardized quantification of life histories. Reznick et al. (1992) presented eight traits that characterize poeciliid life history. Because accurate assessment of all but one of these traits is dependent upon categorical classification of development, a standardized developmental classification is needed. The classification proposed herein is generally applicable to poeciliids exhibiting a variety of developmental modes. Eleven distinct stages are delineated: (1) immature ovum; (2) early-yolked ovum; (3) mature ovum; (4) blastodisc embryo; (5) embryonic shield/primitive streak embryo; (6) optic cup embryo; (7) early-eyed/limb bud embryo; (8) middle-eyed embryo; (9) late-eyed embryo; (10) very late-eyed embryo; and (11) mature embryo.

IN a review of poeciliid life histories, Reznick and Miles (1989) explained that, because of the scarcity of species characterizations, no previous attempt had been made to formulate a synthesis. At that time, life histories of only eight out of the nearly 200 named species had been adequately characterized. Strauss (1990) suggested that characterization of life-history traits be standardized within groups. For poeciliids, Reznick et al. (1992) took a step in this direction by listing eight traits that “fully characterize a poeciliid’s life history”: (1) superfetation, (2) maternal provisioning, (3) frequency of reproduction, (4) brood size, (5) offspring size, (6) age at maturity, (7) size at maturity, and (8) reproductive allotment. The accurate assessment of all of these traits except reproductive frequency is in some way dependent upon the categorical classification of development. Consequently, a standardized developmental classification is a next logical step in the standardization process.

On the development of *Fundulus heteroclitus*, Oppenheimer (1937) stated that the embryologist’s preferred method of classifying development is the distinction of stages by characters that are easily visible without histological study and that vary at different stages of development. Such stages must be of “sufficient duration,” however, to minimize minor differences between embryos in the same developmental phase (Oppenheimer, 1937). The classification proposed herein uses such criteria to provide a standardized system of categorizing the development of poeciliid fishes for life-history studies, in which it is necessary to stage ova and embryos from many females expeditiously.

Definitions and systematics.—The term “propagule,” as used herein, refers to the reproductive elements in the ovary, including both ova and embryos. Lecithotrophy is the nourishment of embryos by yolk deposited prior to fertilization

TABLE 1. DEVELOPMENTAL STAGES OF PREVIOUS CLASSIFICATIONS ALIGNED WITH THE STAGES OF THE PROPOSED CLASSIFICATION.

Author and date	Proposed developmental stages												
	1	2	3	4	5	6	7	8	9	10	11		
Bailey, 1933	10	← 20 →	30	40	50	60	70	80	90	100			
Self, 1937				1	2	3	4	5	6				
Turner, 1938			0	←				1-4	→		5		
Self, 1940	← 2 →	3	←					4	→		5		
Hopper, 1943	← 1 →		2-5	←				6	→				
Tavolga and Rugh, 1947			1	2-4	5-8	9-13	14-15	16-18	19-22	23-24	25		
Tavolga, 1949			1	2-4	5-7	8-10	11-14	15-17	18-21	22-25	26		
Hubbs, 1971 (#1)			←	1	→	←	2	→	←	3	→		
Hubbs, 1971 (#2)	←	1	→	←	2	→	←	3	→	←	4	→	
Schoenherr, 1977	1	2	3	←			4	→	←		5	→	
Stearns, 1978	1			2	←		3	→	←	4	→	5	
Reznick, 1981	←	1	→	2		3	←	4	→	←	5	→	6
Milton and Arthington, 1983	←	1	→			2	←	3	→	←	4	→	5
Monaco et al., 1983				←	1	→	2-3	←	4	→	5	→	6
Meffe, 1985		1	← 2 →	3	←			4	→	←	5	→	6
Brown-Peterson and Peterson, 1990	1-3	4	5	← 6 →	←		7	→	←	8	→	9	

(Wourms, 1981); lecithotrophic embryos lose 30–40% dry mass during development because of the costs of metabolism (Reznick and Miles, 1989). Matrotrophy is when embryos derive the majority of nutrients directly from the mother via modified follicular structures (Wourms, 1981); matrotrophic embryos either remain constant or increase in mass during development (Reznick and Miles, 1989). Superfetation is the simultaneous presence of two or more broods at different stages of development in the same female (Turner, 1940; Scrimshaw, 1944; Wourms, 1981). Matrotrophy and superfetation are the derived conditions (Wourms, 1981), with the latter possibly evolving four or more times independently in the family (Reznick and Miles, 1989). Superfeting species are almost exclusively matrotrophic, whereas nonsuperfeters are exclusively lecithotrophic (Reznick and Miles, 1989).

It was once thought that all but one species of poeciliid (*Tomeurus gracilis*) were livebearers (Rosen and Bailey, 1963). Parenti (1981) included the egg-laying *Fluviphylax* and the aplocheilichthyines in the family, however, and downgraded the Poeciliidae to subfamily status (Poeciliinae). All references to poeciliids herein refer to the fishes of Parenti and Rauchenberger's (1989) Poeciliinae, in which a new tribe (the Scolichthyini) was added to Parenti's subfamily, along with a few internal modifications.

Species names (synonyms) follow Rosen and Bailey (1963).

Review of previous classifications.—The first description of poeciliid development was by Duvernoy (1844) for *Poecilia vivipara* (Bailey, 1933). This initial depiction is followed in the literature by a number of classifications, each designed for a single or only a few species and each differing in the amount of detail in stage descriptions, duration of development between stages, and portion of developmental sequence encompassed. Although the following list is most likely incomplete, brief synopses are presented for many previous developmental classifications. Table 1 aligns the developmental stages of several of these classifications with the stages proposed herein.

Some authors approached poeciliid development from an embryological perspective. Ryder (1885), Kuntz (1914), and Medlen (1952) each described different developmental series for the embryos of *Gambusia affinis*. Hopper (1943) described the early development of *Xiphophorus maculatus* from growth of oocytes to gastrula formation and noted the interbrood interval of individual females. Hopper also referred to Oppenheimer's (1937) stages of *F. heteroclitus* throughout his account. Tavolga and Rugh (1947) described the embryology of *X. maculatus* in 25 preparturient stages based on

internal and external morphological characters. Tavolga (1949) included a discussion of the effects of hybridization of *X. maculatus* and *X. helleri* on embryonic growth and described 26 stages in even greater detail than his previous work.

Several authors condensed earlier developmental series into broader stages; Table 2 outlines the condensation of two such series. Schoenherr (1977) separated propagules of *Poeciliopsis occidentalis* into five categories, the last three of which were condensed from Tavolga and Rugh (1947). Reznick (1981) consolidated the 25 stages of Tavolga and Rugh (1947) into six stages for *G. affinis*. Milton and Arthington (1983) modified the classifications of Tavolga (1949) and Reznick (1981) for staging embryos of *G. holbrooki*, *X. helleri*, and *X. maculatus*.

Other authors grouped propagules more or less arbitrarily. Turner (1938) defined the following ovary stages for *Brachyrhaphis episcopi*: stage 0—no embryos present; stage 5—embryos ready for birth; stages 1–4—intermediate stages. Hubbs (1971) used two different classifications in categorizing development of *G. affinis* and *G. heterochir*; the first was used to determine fecundity, the second in the examination of egg nutrients.

Most prior classifications staged propagules on the basis of external morphology; the following were presented for lecithotrophic species. Bailey (1933) arranged *X. helleri* females from earliest to latest stages of gestation and assigned "percentage positions" of development so that the fifth fish carried propagules that were 10% developed, the tenth, 20%, etc. Bailey also included a description of characters "of practical use in determining the age of the material." Self (1937) staged *G. affinis* embryos mainly by the number of somites present and included a description of the morphological characters in each stage. In a later paper on the sex cycle of *G. affinis*, Self (1940) placed females into one of six categories, the first indicating immature females (no eggs present) and the last those giving birth. Stearns (1978) described five stages of embryonic development in *Neoheterandria tridentiger* and later (Stearns, 1983) used these same stages in classifying the development of *G. affinis*. Stearns (1983) stated that the last four stages corresponded to those of Chambolle et al. (1970) as follows: stage 2—1–17; stage 3—18–24; stage 4—25–32; stage 5—33–35. Monaco et al. (1983) delineated five developmental stages for *Poecilia formosa* and its related sexual species, *P. mexicana* and *P. latipinna*, based on "major features of embryogenesis," and presented a table comparing their stages with those

TABLE 2. COMPARISON OF CLASSIFICATIONS THAT HAVE CONDENSED DEVELOPMENTAL SERIES OF TAVOLGA AND RUGH (1947) OR TAVOLGA (1949).

Condensed stage*	Initial developmental stage			
	Tavolga and Rugh		Tavolga	
	a	b	c	d
1	—	1–6	1–12	5–9
2	—	7–12	13–16	10
3	0–4	13–17	17–21	14
4	5–19	18–20	22–24	18
5	20–25	21–24	25–26	26
6	—	24–25	—	—

* (a) Schoenherr, 1977; (b) Reznick, 1981; (c) Milton and Arthington, 1983; (d) Monaco et al., 1983.

of Oppenheimer (1937), Armstrong and Child (1965), and Tavolga (1949). Meffe (1985) described six categories of development in *G. marshi*.

Developmental classifications of matrotrophic species have generally been restricted to *Heterandria formosa*. Scrimshaw (1944) used ovisac diameter as an indicator of developmental stage and claimed that *H. formosa* carries up to eight broods in the ovary simultaneously. Scrimshaw (1945) later ranked embryo stages of several poeciliids (both lecithotrophes and matrotrophes) by age by assuming that the time between stages was equal in all cases; fertilization was represented at the beginning of the time scale and parturition at the end. Fraser and Renton (1946) described the development of *H. formosa* propagules as a continuous progression, without delineating stages.

Finally, many authors have modified either a previously condensed classification or one based on gross morphology. Travis et al. (1987) used a slightly condensed version of Reznick's (1981) classification in their assessment of superfetation and clutch overlap in *H. formosa*: stages 1–4 were the same, but stage 5 combined Reznick's last two stages. Brown-Peterson and Peterson (1990) modified Meffe's (1985) classification for staging *G. affinis* propagules by the addition of five stages of early ovarian development. Reznick et al. (1992) used only the first five of Reznick's (1981) stages in categorizing development in *Poecilia picta*.

METHODS

The propagules of 46 species, representing 16 genera and six tribes, were examined for the presence of common ontogenetic characteristics that could be used to construct a standardized classification of poeciliid development. Pregnant females ($n = 3–70$ per species) were

dissected, their ovaries removed, and propagules examined for distinguishing traits. All stages of the classification were observed in the majority of species, although occasionally not enough females of a given species were available or some females were not in sufficient reproductive condition. More than one developmental stage observed in a single specimen was considered evidence of the presence of those stages in that species (see the discussion of protracted fertilization below).

RESULTS

The following developmental stages were delineated to categorize poeciliid development. Figure 1 illustrates the characteristics defined in each stage, with the obvious exception of color, for a superfetating matrotrophe (*Heterandria formosa*, left) and a nonsuperfetating lecithotrophe (*Gambusia affinis*, right). Drawings are freehand sketches by the author of actual propagules examined under magnification; individual propagules were not necessarily from the same females but were chosen because they accurately represented the characteristics outlined in the classification.

Stage 1: immature ovum: ovum small, opaque white in color, distributed throughout ovary, and often packed within masses of yolking ova and/or developing embryos.

Stage 2: early-yolked ovum: ovum in the process of yolking, opaque yellow-orange in color, but not full-sized; oil droplets, if present, unevenly distributed.

Stage 3: mature ovum: ovum fully yolked, translucent golden yellow in color (orange to reddish orange in some preserved specimens); oil droplets evenly dispersed over yolk surface.

Stage 4: blastodisc embryo: ovum recently fertilized; embryo appears as small white cap on yolk surface measuring about one-fifth (lecithotrophes) to one-half (matrotrophes) yolk diameter; oil droplets coalesced under blastodisc at animal pole.

Stage 5: embryonic shield/primitive streak embryo: blastodisc spread to form embryonic shield which nearly or completely covers one-half of yolk in lecithotrophes but may be hard to distinguish in matrotrophes; primitive streak appears as thin white line in center of shield with length about one-half yolk diameter (lecithotrophes), or as crescent-shaped tissue nearly circumscribing yolk (matrotrophes).

Stage 6: optic cup embryo: optic cups and otic vesicles present; little or no eye pigmentation; yolk portal system present in lecithotrophes.

Stage 7: early-eyed/limb bud embryo: eyes

pigmented but not complete; head greatly enlarged compared to trunk; caudal and pectoral fin buds present; dorsal pigmentation initiated in most species.

Stage 8: middle-eyed embryo: eyes complete but not full sized; head and trunk proportionate; little dorsal and possibly some lateral pigmentation; dorsal- and anal-fin buds present; caudal-fin rays forming; operculae forming but inconspicuous; snout buried in yolk up to eyes or above in lecithotrophes.

Stage 9: late-eyed embryo: eyes enlarged, but not full sized; moderate dorsal pigmentation; pigment present along lateral line in those species with such pigmentation; tail may be flexed over head or around tip of snout; pectoral-fin rays present; yolk sac still relatively large in lecithotrophes but may be completely absorbed in matrotrophes.

Stage 10: very late-eyed embryo: eyes full sized; operculae conspicuous and may be pigmented; dorsal- and anal-fin rays present; embryo much more elongate; yolk sac, if present, small and irregular; distinct "neck-strap" of receding extra-embryonic membranes present in some species.

Stage 11: mature embryo: yolk sac mostly or completely absorbed; "neck-strap" absent; pectoral fins elongate; scales present; embryo resembles small adult.

DISCUSSION

Problems with previous classifications.—This paper represents the first attempt at providing a standardized classification of poeciliid development for life-history studies. Previous classifications were not designed for this purpose and are lacking in this respect. The main reasons for this are as follows.

First, most poeciliid studies have been conducted on lecithotrophic, nonsuperfetating species, and developmental classifications have been similarly restricted. Species in the tribes Gambusiini and Poeciliini (i.e., *G. affinis* and *Poecilia reticulata*, respectively) are the most widely studied poeciliids. These species have large eggs and early embryos with easily observable ontogenetic characteristics. Species that exhibit matrotrophy have much smaller ova and the characteristics of early development are not as readily apparent. Also, Scrimshaw (1944) and Turner (1937) reported that female *H. formosa* carry up to eight or nine simultaneous broods, respectively, in different stages of development. Because the presence of eight or nine superfetating broods logically necessitates eight or nine distinctly different embryo stages, a classifica-

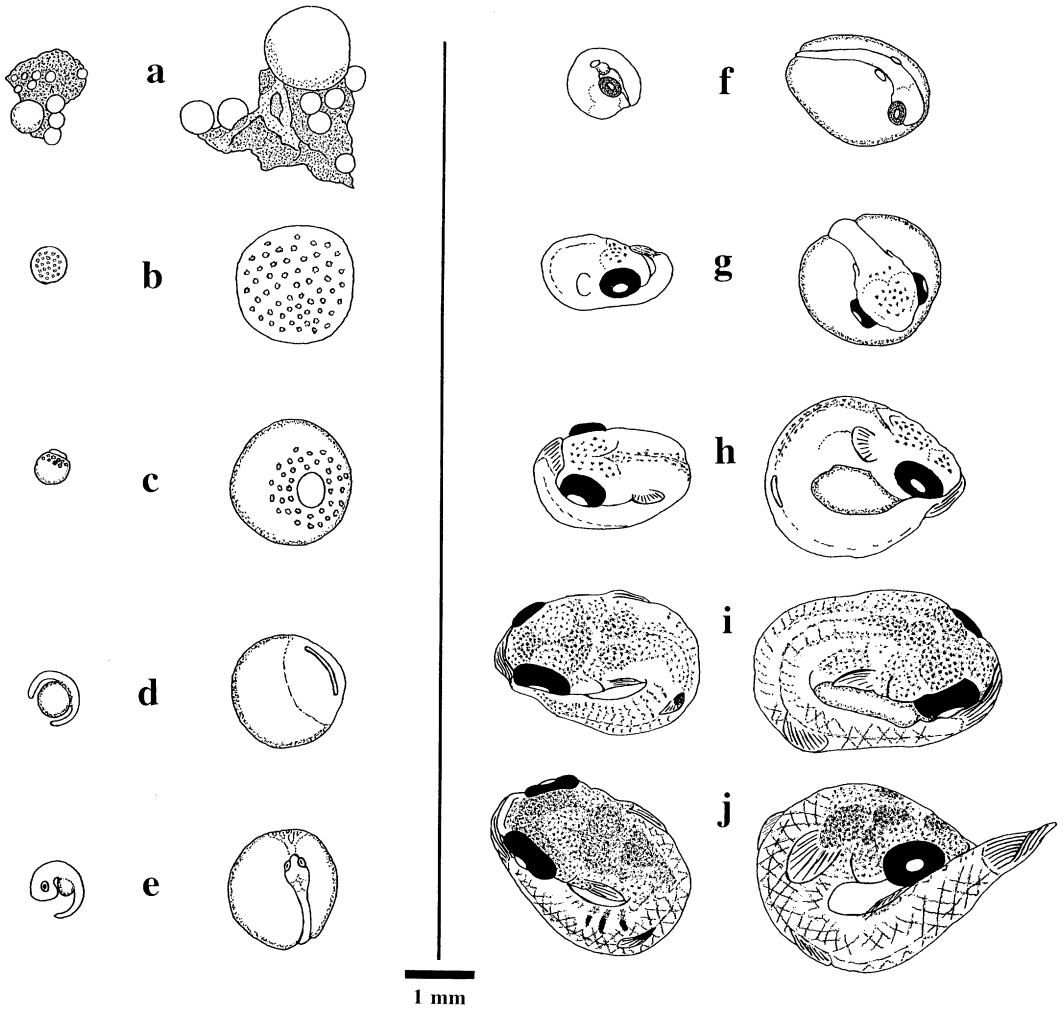


Fig. 1. Developmental stages of the proposed classification (*Heterandria formosa* on the left in each column, *Gambusia affinis* on the right): (a) Small ova are immature (stage 1), large are early-yolked (stage 2), stippling represents connective tissue; (b) mature ova (stage 3); (c) blastodisc embryos (stage 4); (d) embryonic shield/primitive streak embryos (stage 5); (e) optic cup embryos (stage 6); (f) early-eyed/limb bud embryos (stage 7); (g) middle-eyed embryos (stage 8); (h) late-eyed embryos (stage 9); (i) very late-eyed embryos (stage 10); (j) mature embryos (stage 11).

tion system containing only four or five would underestimate the extent of superfetation in such species.

Some workers have used the classifications of Reznick (1981) or Meffe (1985), both of which were designed for lecithotrophic, nonsuperfating species, in categorizing superfating embryos. A good example is Travis et al. (1987), who used a slightly condensed version (four instead of five embryo stages) of Reznick's (1981) classification to determine the extent of superfetation in *H. formosa*. The authors noted that this classification might not be appropriate for *H. formosa* in the following statement: "If fe-

males keep embryos at finer divisions of development than our five categories, we will underestimate the degree of superfetation" (Travis et al., 1987).

Although Meffe (1985) used morphology to delineate gross developmental stages, some ambiguity arises from his omission of certain important developmental features. For example, the second category is ambiguous because mature ova are not distinguished from fertilized eggs. Also, the initiation of eye development is overlooked, creating a gap in the classification between the stages corresponding to "primitive streak present, but eyes not yet distinguishable"

and "eyes present, but not full sized." Meffe's classification contained only four embryo stages and, thus, is also not applicable to extreme superfetating species.

Second, classifications in the literature have not always been developed for life-history studies. The most obvious examples are developmental series. Workers interested in life history have simplified such series, grouped embryos arbitrarily, or described embryo stages based on gross morphology. The fact remains, however, that none of the previous classifications were meant to be applied either to species other than those examined or to other types of studies.

At least two potential problems exist which may cause confusion or result in inaccurate assessment of developmental stage, regardless of which classification is used. One is protracted fertilization, which is a common phenomenon in lecithotrophes with large broods. In this situation, ova are fertilized over a period of time (sometimes days) and, thus, the embryos of a single brood may occur in two or more consecutive stages of development. It is likely that such cases represent variation around a mean developmental stage and that all embryos in the brood will be born together (Thibault and Schultz, 1978; D. Reznick, pers. comm.); "stragglers" may even be born with small amounts of yolk remaining.

Another potential problem is the presence of regressing embryos which often look like, and can be mistaken for, embryos in an earlier stage of development than the rest of the brood (D. Reznick, pers. comm.). When regressing embryos are present in the ovary, the younger-appearing brood will likely contain far fewer embryos than the more advanced brood. Also, when regressing embryos are compared with normal embryos of the same apparent developmental stage from another female, substantial differences should be apparent. D. Reznick (pers. comm.) suggests that only when such lateral comparisons are made does the abnormal nature of regressing embryos become clear. One way to determine whether embryos are regressing in a lecithotrophic species is to compare dry weights of the "early" and late embryos: if the early embryos are normal, they are likely to be heavier; if they are regressing, they are likely to be lighter (D. Reznick, pers. comm.).

Proposed classification.—Bailey's (1933) concept of eight embryo stages constitutes the foundation of the proposed classification. Many of Bailey's defining characters were found to be common to all species examined in this study and were incorporated into the stage descriptions.

Some of Meffe's (1985) terminology was incorporated into stage titles and character descriptions. The "neck-strap" characteristic of stages 10 and 11 was taken from Tivolga and Rugh (1947).

Most of the distinguishing characteristics are straightforward and need no further clarification; for others, additional explanation is warranted. For example, the relative size of the eyes during development is an important character. Although this feature may initially seem ambiguous, simultaneous examination of embryos from different eyed stages should allow the examiner to recognize subtle differences. Also, because of the small size of ova in matrotrophes, the characteristics of early development may be difficult to distinguish. For such species (i.e., *H. formosa*), superfetating broods can be accurately separated by size alone (Scrimshaw, 1944; pers. obs.); this can then be followed by closer inspection to elucidate less obvious character differences. The examiner is advised to pay special attention to groups of ova, within which early embryos are often hidden. Additionally, one characteristic is often not enough to distinguish among stages; only when a number of traits are observed collectively can this determination be made. Finally, workers are urged to use any other characteristic(s), perhaps not given in the above classification, exhibited by a species to identify a particular developmental stage.

This study revealed two independent lines of evidence that support the presence of eight gross embryo stages in poeciliids. First, *H. formosa*, a species which exhibits extreme superfetation and matrotrophy, consistently bears up to eight distinct groups of embryos (= broods), differing radically in size as well as morphological traits, in the ovary simultaneously (Scrimshaw, 1944; pers. obs.). Nonsuperfetating lecithotrophes possess the same sets of characteristics, in the same order, in embryos that appear to be in the same stages of development. Thus, species with very different developmental modes seem to be constrained by a similar developmental sequence. Second, superfetating species tend to have broods that are equally spaced in development and intervals between broods that suggest the presence of eight stages (Table 3). For example, species with a mean number of around two simultaneous broods have a separation of about four developmental stages between broods, whereas those with an average of four broods have a separation of about two stages between broods.

Concluding remarks.—The proposed classification of poeciliid development was found to be applicable to approximately 25% of all known

TABLE 3. MEAN AND RANGE OF SUPERFETATING BROODS AND MEAN BROOD INTERVAL FOR SEVERAL POECILIID SPECIES. Females not carrying embryos were excluded from analyses; those carrying only a single brood were excluded from the calculation of mean brood interval. Data in last two columns are presented as $\bar{x} \pm SD$.

Species	n*	Superfetrating broods		
		Range	Mean number	Mean interval
<i>Poeciliopsis occidentalis</i>	16/11	1-3	1.75 \pm 0.58	3.75 \pm 1.29
<i>P. fasciata</i>	5/4	1-2	1.80 \pm 0.45	4.50 \pm 1.29
<i>P. infans</i>	5/4	1-2	1.80 \pm 0.45	3.50 \pm 0.58
<i>P. viriosa</i>	7/6	1-2	1.88 \pm 0.35	3.33 \pm 1.03
<i>P. gracilis</i>	4/4	2	2	3.75 \pm 0.50
<i>P. turrubarensis</i>	4/4	2	2	3.25 \pm 0.50
<i>P. elongatus</i>	19/19	2-4	3.00 \pm 0.33	2.11 \pm 1.03
<i>P. prolifica</i>	4/4	2-5	3.75 \pm 1.26	1.91 \pm 0.83
<i>Heterandria formosa</i>	4/4	8	8	1

* Left of slash = number of females used in calculating mean number of broods; right of slash = number used in calculating mean brood interval.

species and, thus, appears to be generally applicable to the family (with the possible exception of the egg-laying *Tomeurus*, which was not examined). Although there is some variation between lecithotrophes and matrotrophes, and in the relative and absolute size of propagules and/or the timing and extent of pigmentation, defining characteristics were observed in those stages identified within each species. In addition, no obvious collections of characters suggested the presence of more than eight gross embryo stages. Therefore, even though poeciliids exhibit a variety of developmental modes, it appears that they are constrained by a similar developmental sequence that can be categorized in a standard manner.

MATERIAL EXAMINED

Specimens were obtained from the Mississippi State University Ichthyological Collection (MSU), the Tulane University Museum of Natural History (TU), the University of Michigan Museum of Zoology (UMMZ), and the University of New Orleans Vertebrate Collection (UNOVC). Institutional abbreviations TU and UMMZ are as given by Leviton et al. (1985); because MSU and UNOVC were not listed by Leviton et al., these abbreviations were provided by the respective curators. The organization of taxa follows the phylogeny of Parenti and Rauchenberger (1989). The number of females examined and the stages not observed in each lot follow the catalog number in parentheses. For example, in the case of *Alfaro cultratus*, three fish were examined and stages 3-6 and 10 were not observed in these three specimens.

Tribe Poeciliini: *Alfaro cultratus* UMMZ 190360 (3/3-6,10); *A. huberi* UMMZ 173245 (5/4,7,8), UMMZ 190575 (5/4-7); *Poecilia formosa* TU 96133 (3/5,6,8-10), TU 97464 (4/6-8); *P. latipinna* MSU 1269 (6); *P. reticulata* TU 30815 (8); *P. sphenops* TU 47287 (5/2,3,11); *Priapella compressa* UMMZ 210816 (4/7,8,10); *P. intermedia* TU 94110 (5/4-6), UMMZ 178535 (5/3,7,8); *Xiphophorus helleri* TU 94348 (5/7-9), UMMZ 197075 (12/5-7); *X. pygmaeus* TU 38998 (7); *X. variatus* TU 5581 (2/2-9), UMMZ 194929 (8).

Tribe Cnesterodontini: *Phalloceros caudimaculatus* UMMZ 215266 (5/9,10); *Cnesterodon* sp. (undescribed species) UMMZ 207748 (20/8,11).

Tribe Scolichthyini: *Scolichthys tota* UMMZ 187949 (15/7).

Tribe Gambusiini: *Brachyrhaphis olomina* TU 24840 (20); *B. parismina* TU 24910 (6); *B. rhaphidophora* TU 25094 (6/10), TU 25149 (10); *Gambusia affinis* UNOVC 9108 (45), UNOVC 9128 (25); *G. amistadensis* TU 73679 (4/5,6,11); *G. atrora* TU 38986 (12); *G. aurota* TU 38976 (7), TU 39028 (5); *G. geiseri* TU 4744 (30/11); *G. holbrooki* UNOVC 1284 (7/7,11), UNOVC 5716 (15/11); *G. marshi* TU 43878 (31); *G. nobilis*

TU 97050 (7/11), UNOVC 3884 (4/2-6); *G. panuco* TU 43612 (8); *G. senilis* TU 95880 (3/2-6), TU 95887 (9); *G. vittata* TU 38984 (7/11), TU 84845 (6/4,7-10); *G. yucatanana* TU 44351 (6); *Belonesox belizanus* TU 44347 (15).

Tribe Girardinini: *Carlhubbisia hidderi* UMMZ 144204 (11); *C. stuarti* UMMZ 197257 (8).

Tribe Heterandriini: *Priapichthys annectens* TU 25091 (5/6,7), TU 25254 (2/4,5,8-10); *Neoheterandria umbratilis* TU 24212 (9); *Heterandria bimaculata* TU 39109 (11/5-7), UMMZ 186370 (7/10); *H. formosa* MSU 828 (4); *H. jonesi* TU 38566 (5); *Poeciliopsis elongatus* TU 25098 (16/11), TU 25174 (4/5,7,11); *P. fasciata* TU 39058 (5); *P. gracilis* TU 39046 (4); *P. infans* TU 30735 (5); *P. occidentalis* TU 85546 (3/4-7), UMMZ 211408 (15/8); *P. prolifica* TU 94091 (4/3); *P. turrubarensis* TU 24949 (4); *P. viriosa* TU 30771 (7); *Phallichthys amates* TU 25255 (6).

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