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SEXUAL DIMORPHISM OF SHELL SHAPE AND GROWTH OF *VILLOSA VILLOSA* (WRIGHT) AND *ELLIPTIO ICTERINA* (CONRAD) (BIVALVIA: UNIONIDAE)

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ABSTRACT

Shell shape and growth of two unionacean species, *Villosa villosa* and *Elliptio icterina*, are analyzed with univariate and multivariate techniques. The relationship of shape variables to size variables is examined. Under the lognormal assumption, parametric tests of these allometric relationships are valid. Variables describing the ventro-posterior region of the shell are shown to be the best of those tested for discriminating between the sexes of both species regardless of statistical method. Neither species exhibits size sexual dimorphism. Shape sexual dimorphism of *V. villosa* is constant during adult growth, but the more subtle dimorphism of *E. icterina* changes as adults continue to grow.

INTRODUCTION

Shell shape and growth of bivalved molluscs has been extensively examined, particularly with regard to burrowing habits and to the effects of environmental factors (Ansell, Parulekar & Allen, 1978; Brown, Seed & O'Connor, 1976; Eager, 1978; Eager, Stone & Dickson, 1984; Hickman, 1979; Morton, 1976a; Seed, 1980a, b; Stanley, 1970). Considerably less attention has been given to the relationship of sex to shell shape and growth. Sexual dimorphism in bivalves is considered to be rare because the reproductive habits of most of these animals are unspecialized: gametes are spawned into the surrounding medium, in which fertilization and development occur (Sastry, 1979).

Shell sexual dimorphism in marine bivalves has been reported only among those species exhibiting larviparity, a specialized reproductive habit. Species in which dwarf males occur (*i.e.*, that display size dimorphism) include members of the Montacutidae (Chanley & Chanley, 1970; Deroux, 1960; Jenner & McCrary, 1968), the Galeommatidae (Morton, 1976b, 1981), and the Teredinidae (Turner & Yakovlev, 1983). Shape dimorphism occurs in some species of the Carditidae (Jones, 1963) and the Astartidae (Saleuddin, 1965) and is considered by Heaslip (1969) to be a direct consequence of larviparity.

Sexual dimorphism in the Unionacea was first reported by Kirtland (1834) in 8 species of the Lampsilini (Unionidae) and in *Plethobasus cyphyus* (Rafinesque) (Unionidae: Pleurobemini). He described the shells of females as possessing truncated posterior margins and inflated ventro-posterior regions. This shape, Kirtland (1834) stated, is necessary for the functioning of the ovaries and marsupial demibranchs, which lie in the ventro-posterior portion of the female. Males, which do not require space for the brooding of developing larvae, have shells that are less inflated and are more acute at the posterior margins.

The authors of other studies (Agrawal, 1974; Ball, 1922; Chamberlain, 1930; Grier, 1920; Hamai, 1938; Simpson, 1897; Sterki, 1895, 1903; Thomas, 1974) disagree as to which unionaceans exhibit sexual dimorphism and its systematic significance. All unionacean females brood developing larvae within the marsupial demibranchs; hence all species may exhibit dimorphism as was proposed by Kirtland (1834). However, sexual dimorphism is currently considered to occur only in the tribe Lampsilini and one species of the tribe Amblemini, *Tritogonia verrucosa* (Rafinesque) (Unionidae) (Burch, 1975; Davis & Fuller, 1981; Heard & Guckert, 1970). The objective of the present study is to compare a lampsiline species to a non-lampsiline species in order to identify a method by which the occurrence and nature of sexual differences in shell shape and growth can be explored, particularly in those species not presently thought to exhibit such differences.

MATERIALS AND METHODS

Specimens and Variables

Villosa villosa (Wright) (Lampsilini) and *Elliptio icterina* (Conrad) (Pleurobemini) were selected as examples of species having obvious and either cryptic or no shell sexual dimorphism, respectively. Thirty sexually mature males and 30 sexually mature females of each species were collected from a still-water site in Lake Talquin, Leon County, Florida. We assumed that the use of specimens from a single site would minimize ecophenotypic variation. The sex of each animal was ascertained by histologic examination of the gonad for the presence of gametes and/or of the marsupial demibranchs for the presence of larvae. None of the animals was infected with tissue-dwelling metazoan parasites.

Many authors have described shell shape and growth in terms of length and height. We used a larger array of variables in order to discover whether there are more precise means of describing shape. The length (L) and height (H) of each right valve were measured with Vernier calipers (Figure 1A). Each right valve was traced onto polar coordinate paper and the umbo-perimeter distances at 20° intervals (M at 10°, . . . , M at 150°) were measured (Figure 1B). The maximum umbo-perimeter distance (MUPD) and the angle at which it occurred were also measured (Figure 1B). All linear measurements were recorded to the nearest millimeter and transformed to $\log_{10}$. Three sets of variables were tested: 1) a set of size variables (log L, H, M at 10°, . . . , M at 150°, MUPD);

2) a set of shape variables of the form log x − log y, where x = L and y = H, M at 10°, . . . , M at 150°, MUPD; and 3) a set of shape variables of the form log x − log y, where x = MUPD and y = L, H, M at 10°, . . . , M at 150° (Table 1).

Statistical Methods

Under the lognormal assumption, differences among shape variables (log transformations of proportions) can be tested with parametric statistical tests (James & McCulloch, 1985; Mosimann, 1970; Mosimann & James, 1979). Sexual differences between the means of each of the 31 size and shape variables were tested with Student's t test (Brown & Hollander, 1977) using the family error rate. The chi-squared statistic was employed to determine the significance of the relationship between sex and angle at which the MUPD occurred (Brown & Hollander, 1977). Stepwise discriminant function analysis was performed separately on each of the 2 sets of shape variables (Table 1). Analyses of these functions revealed which variables within each set contributed to discrimination between the sexes and which did not (Tabachnick & Fidell, 1983). Shape-on-size regressions were performed using the least-squares method (Sokal & Rohlf, 1981). A modified Student's t test was used to test for sexual differences between regression line slopes and intercepts (Draper & Smith, 1966). The regression line slopes were tested against the standard of one, using the modified Student's t test to determine whether growth was isometric (slope = 1), positively allometric (slope > 1), or negatively allometric (slope < 1) (Huxley & Teissier, 1936).
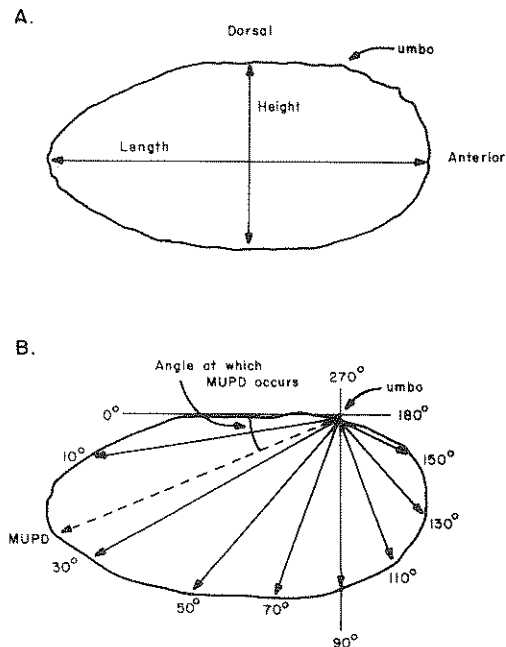
RESULTS

Regardless of species and sex, the variances associated with the MUPD (*V. villosa* males: 0.93, females: 0.67; *E. icterina* males: 0.25, females: 0.23) are lower than those associated with length (*V. villosa* males: 1.37, females: 0.92; *E. icterina* males: 0.33, females: 0.36).

In our sample, there is no statistical difference between the means of the sexes for any size variable of *V. villosa* or *E. icterina* (Table 2). However, there are sexual differences between the means of 5 shape variables of *V. villosa* (Table 3A). The means of females for log L − log H, log L − log M at 50°, log MUPD − log H, log MUPD − log M at 30°, and log MUPD − log M at 50° are significantly lower than those of males. These differences indicate that relative to length and to the MUPD the shells of females are higher and farther extended in the ventro-posterior direction than are shells of males. There are no sexual differences between shape variable means for *E. icterina*.

The relationship between sex and the angle

Fig. 1. Measurements taken on the right valve of each specimen.

Table 1. List of variables.

Size Variables	Shape Variables Based on Length	Shape Variables Based on Maximum Umbo-Perimeter Distance
log L	log L — log H	log MUPD — log L
log H	log L — log M at 10°	log MUPD — log H
log M at 10°	log L — log M at 30°	log MUPD — log M at 10°
log M at 30°	log L — log M at 50°	log MUPD — log M at 30°
log M at 50°	log L — log M at 70°	log MUPD — log M at 50°
log M at 70°	log L — log M at 90°	log MUPD — log M at 70°
log M at 90°	log L — log M at 110°	log MUPD — log M at 90°
log M at 110°	log L — log M at 130°	log MUPD — log M at 110°
log M at 130°	log L — log M at 150°	log MUPD — log M at 130°
log M at 150°	log L — log MUPD	log MUPD — log M at 150°
log MUPD		

at which the MUPD occurs is highly significant for *V. villosa* (Table 3B). The difference between the mean angles, 31.3° in females and 24.8° in males, again indicates the dimorphism of the ventro-posterior area of the shell. There is no significant sexual difference in the angle at which the MUPD occurs in *E. icterina*.

The 2 stepwise discriminant function analyses, one of shape variables based on log L and the other of shape variables based on log MUPD (see Table 1), distinguish equally between the sexes of *V. villosa*. The distance statistics, F and Rao's V, are identical, as are the Wilk's lambdas, which measure the amount of discriminating power within each variable set (Table 4). Although there are 10 variables available to each analysis, only 7 are required for each to classify 100% of the individuals correctly as to sex (Figure 2). The other 3 variables were

not included, as they contribute no additional discriminating information.

The 2 discriminant function analyses of the *E. icterina* data are not the same. The analysis of shape variables based on log L has a higher Wilk's Lambda and a lower Rao's V than that of shape variables based on log MUPD (Table 4). The former includes 5 variables to classify 67% of the individuals correctly, and the latter, 6 variables to classify 70% correctly (Figure 3). The variables containing the greatest amount of discriminating information, for both species, are those describing the ventro-posterior region of the shell (M at 50° and M at 70°).

Regressions of shape on size show a distinct difference between the species for every shape variable. The regression lines of male and female *V. villosa* are parallel, whereas those for *E. icterina* are tangential to each other (Figure

Table 2. Means and standard errors of measurements (raw size variables). M = Measurement; MUPD = maximum umbo-perimeter distance. All measurements in centimeters. T-tests showed no significant differences between sexes.

	Villosa villosa				*Elliptio icterina*			
	Males N = 30		Females N = 30		Males N = 30		Females N = 30	
	mean	S.E.	mean	S.E.	mean	S.E.	mean	S.E.
Length	5.51	0.21	5.13	0.18	7.04	0.11	7.02	0.11
Height	2.77	0.10	2.73	0.09	3.38	0.06	3.32	0.06
M at 10°	3.38	0.15	3.30	0.14	5.17	0.10	5.06	0.09
M at 30°	4.51	0.17	4.29	0.15	5.50	0.07	5.54	0.08
M at 50°	3.80	0.14	3.84	0.13	4.38	0.06	4.37	0.07
M at 70°	3.02	0.11	2.92	0.10	3.71	0.06	3.64	0.07
M at 90°	2.60	0.09	2.41	0.08	3.30	0.05	3.25	0.06
M at 110°	2.35	0.08	2.18	0.08	2.98	0.06	2.92	0.06
M at 130°	2.05	0.08	1.97	0.07	2.43	0.05	2.43	0.06
M at 150°	1.48	0.06	1.44	0.06	1.44	0.05	1.45	0.04
MUPD	4.65	0.18	4.31	0.15	5.99	0.09	5.97	0.09

Table 3. Univariate analyses of sexual differences in shape.

A. Means and standard errors of those shape variables exhibiting significant differences (t-test).

Villosa villosa

	Males		Females		
Variable	Mean	Standard Error	Mean	Standard Error	Significance*
log L − log H	0.297	0.003	0.273	0.003	$p < 0.01$
log L − log M at 50°	0.161	0.003	0.127	0.002	$p < 0.01$
log MUPD − log H	0.224	0.003	0.197	0.003	$p < 0.01$
log MUPD − log M at 30°	0.013	0.001	0.002	0.001	$p < 0.01$
log MUPD − log M at 50°	0.087	0.003	0.050	0.002	$p < 0.01$

Elliptio icterina
  no significant differences

B. Angle at which maximum umbo-perimeter distance occurs (χ^2).
Villosa villosa
Males' mean = 24.8° Females' mean = 31.3° $\chi = 43.5$ d.f. = 17 $p < 0.01$
Elliptio icterina
Males' mean = 20.2° Females' mean = 20.9° $\chi^2 = 11.9$ d.f. = 8 $p > 0.10$

* Significance of multiple comparisons using the family error rate.

Table 4. Results of separate stepwise discriminant function analyses for shape differences between the sexes.

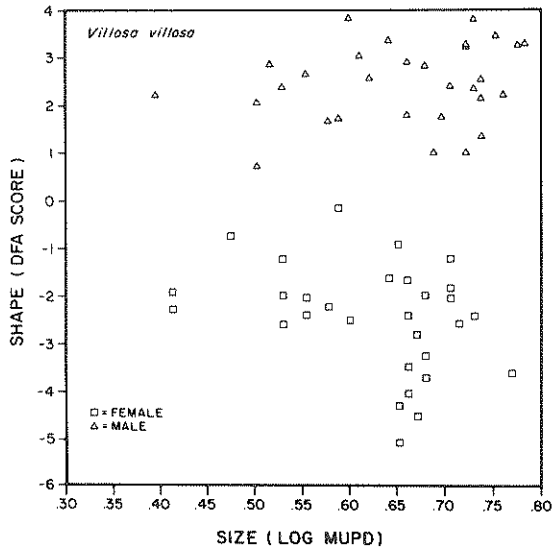| Discriminant Function Analysis	*Villosa villosa*	*Elliptio icterina*
Of shape variables based on log length		
Wilk's lambda	0.14	0.76
Group centroids	Males: 2.4 Females: −2.4	Males: 0.6 Females: −0.6
Correctly classified	100%	67%
Rao's V	349.9 $p < 0.01$	18.5 $p < 0.01$
F statistics	44.87 & 52 d.f. $p < 0.01$	3.45 & 54 d.f. $p < 0.01$
Variables in order of entry into function	log length − log M at 50°	log length − log M at 70°
	log length − log M at 10°	log length − log M at 50°
	log length − log MUPD	log length − log M at 130°
	log length − log M at 90°	log length − log M at 30°
	log length − log height	log length − log M at 150°
	log length − log M at 110°	
	log length − log M at 30°	
Of shape variables based on log MUPD		
Wilk's lambda	0.14	0.75
Group centroids	Males: 2.4 Females: −2.4	Males: −0.6 Females: 0.6
Correctly classified	100%	70%
Rao's V	349.9 $p < 0.01$	19.8 $p < 0.01$
F statistics	44.87 & 52 d.f. $p < 0.01$	3.45 & 54 d.f. $p = 0.01$
Variables in order of entry into function	log MUPD − log M at 50°	log MUPD − log M at 70°
	log MUPD − log M at 10°	log MUPD − log M at 50°
	log MUPD − log M at 90°	log MUPD − log M at 130°
	log MUPD − log height	log MUPD − log M at 30°
	log MUPD − log length	log MUPD − log M at 150°
	log MUPD − log M at 110°	log MUPD − log M at 10°
	log MUPD − log M at 30°	

Fig. 2. *Villosa villosa*. Plot of size (log maximum umbo-perimeter distance) against shape (discriminant score from analysis of shape variables based on maximum umbo-perimeter distance).

4). Shell shapes of male and female *E. icterina* converge at a length of 7.9 cm (log length: 0.89), but diverge as length increases beyond this point (Figure 4C).

The slopes of shape-on-size regression lines (Figures 4A & B) for male and female *V. villosa*

are not significantly different (Table 5). In both sexes, growth along all axes is negatively allometric relative to length and the MUPD (Figure 5A & B). There are differences (Table 5) between the sexes of *E. icterina* in the slopes of the regressions describing the ventro-posterior
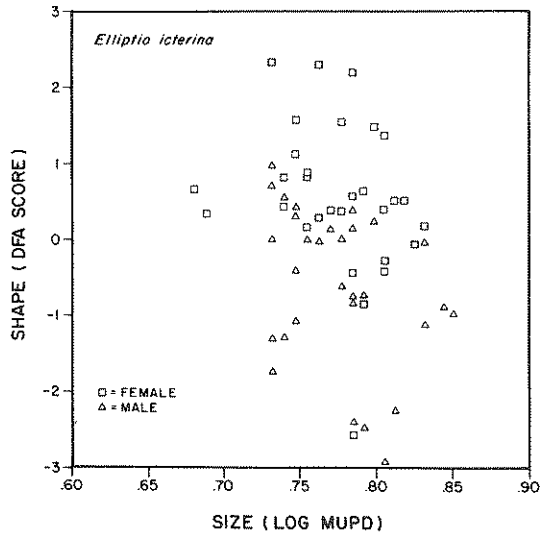

Fig. 3. *Elliptio icterina*. Plot of size (log maximum umbo-perimeter distance) against shape (discriminant score from analysis of shape variables based on maximum umbo-perimeter distance).
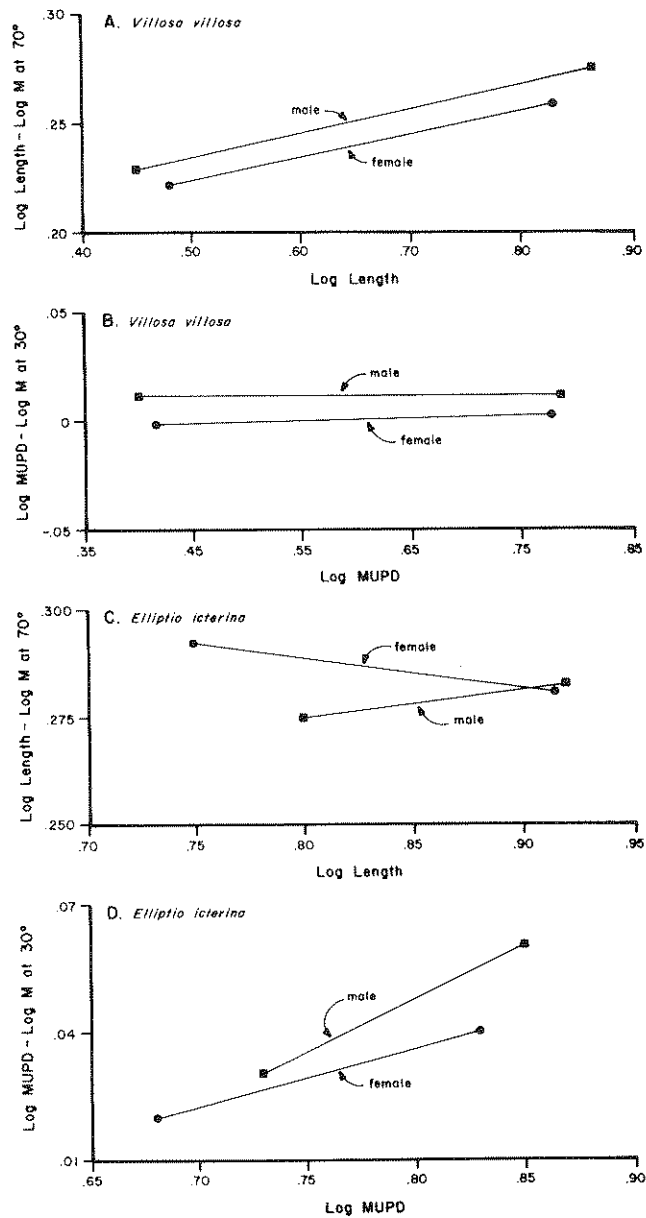
Fig. 4. Examples of shape-on-size regressions of *Villosa villosa* and *Elliptio icterina*. MUPD = maximum umbo-perimeter distance. A. Males: $Y = 0.18 + 0.10X$; Females: $Y = 0.17 + 0.10X$. B. Males: $Y = 0.01 + 0.01X$; Females: $Y = -0.01 + 0.01X$. C. Males: $Y = 0.22 + 0.07X$; Females: $Y = 0.34 - 0.07X$. D. Males: $Y = -0.13 + 0.21X$; Females: $Y = -0.03 + 0.08X$.

area: $\log L - \log M$ at 70° on $\log L$, $\log$ MUPD $- \log M$ at 30° on $\log$ MUPD, $\log$ MUPD $- \log M$ at 50° on $\log$ MUPD, and $\log$ MUPD $- \log M$ at 70° on $\log$ MUPD (Figure 4C & D).

Growth in females is negatively allometric relative to length and the MUPD along all axes except the 150° axis, along which growth is isometric relative to the MUPD (Figure 5C). In

Table 5. Significant sexual differences in slopes and intercepts of shape on size regressions.

	Slopes			Intercepts		
	Males	Females	Significance*	Males	Females	Significance*
Villosa villosa						
log MUPD − log M at 30° on log MUPD	no significant difference			0.01	−0.01	p < 0.01
Elliptio icterina						
log L − log M at 70° on log L	no significant difference			0.07	−0.07	p < 0.05
log L − log M at 130° on log L	0.44	0.67	p < 0.01	no significant difference		
log MUPD − log M at 30° on log MUPD	−0.13	−0.03	p < 0.01	0.21	0.08	p < 0.01
log MUPD − log M at 50° on log MUPD	−0.02	0.12	p < 0.05	0.20	0.02	p < 0.05
log MUPD − log M at 70° on log MUPD	0.10	0.28	p < 0.05	0.13	−0.08	p < 0.05

* Significance of muiltiple comparisons using the family error rate.

males, isometric growth occurs along the 130° and 150° axes relative to length and along the 150° axis relative to the MUPD. Growth along all other axes is negatively allometric relative to both size variables (Figure 5D).

The regression line intercepts of male and female *V. villosa* are not significantly different except for that of the log MUPD − log M at 30° on log MUPD regression (Table 4). The *E.*

icterina regression line intercepts that differ on the basis of sex are those related to the ventro-posterior region (log MUPD − log M at 30° on log MUPD, log MUPD − log M at 50° on log MUPD, and log MUPD − log M at 70° on log MUPD) and one related to the ventro-anterior region (log L − log M at 130° on log L) (Table 4). In spite of the fact that there is allometric shape change in *E. icterina* regression analysis,

A. ♀ *Villosa villosa*   B. ♂ *Villosa villosa*

1 cm

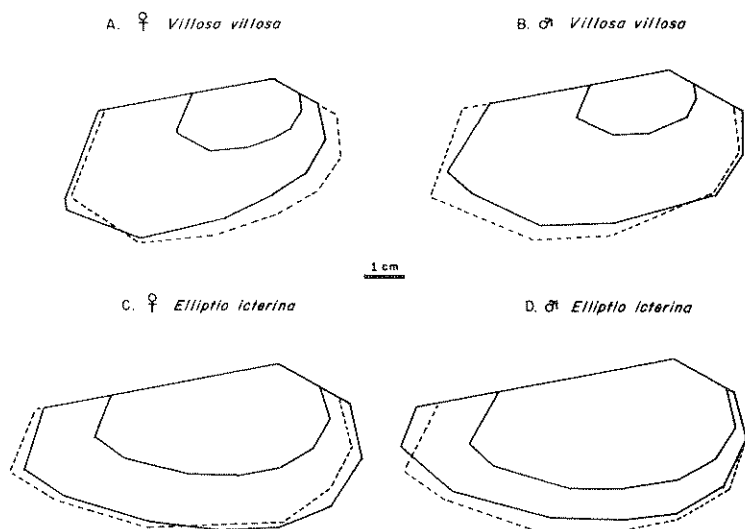C. ♀ *Elliptio icterina*   D. ♂ *Elliptio icterina*

Fig. 5. Shell growth of *Villosa villosa* and *Elliptio icterina*. Solid lines represent smallest and largest values for each measurement. Dashed lines represent extrapolated shell shape as if smallest had grown isometrically to same length as largest.

(*e.g.*, Figures 4C & D) could be employed to estimate the sex of individuals from new samples without use of invasive methods.

DISCUSSION

Neither species exhibits size sexual dimorphism (Table 2), but shape variables can be used to determine sex in *Villosa villosa* (Table 3). For *Elliptio icterina*, tests of these variables individually do not distinguish well between the sexes; however, simple plots of shape on size (Fig. 4C & D) reveal a subtle pattern of sexual dimorphism that varies with shell length.

The variables commonly used, length and height, are insufficient to describe the complex pattern of shape change and sexual dimorphism. For *V. villosa* and *E. icterina*, descriptors of the ventro-posterior region of the shell emerge as the most useful variables by which to distinguish sex regardless of the statistical method employed.

Allometric growth occurs in *V. villosa* and *E. icterina* of both sexes. In the former, shell shape changes from subelliptical to elliptical and, in the latter, from narrowly elliptical to broadly elliptical (Fig. 5). Ontogenetic changes in shell shape occur in most bivalves examined to date (Seed, 1980a). According to Seed (1980a), gradual changes, such as those exhibited by *V. villosa* and *E. icterina*, seem to be associated more with the maintenance of the surface-to-volume ratios within physiological limits than with changes in the envronment or in burrowing habit. However, shell shape of unionaceans is highly plastic (Eager, 1978; Tevesz & Carter, 1980) and has repeatedly been shown to be influenced by substrate type and hydrodynamic variables (Agrell, 1949; Ball, 1922; Eager, 1948; Grier & Mueller, 1926; Hinch, Bailey & Green, 1986; Horn & Porter, 1981; Ortmann, 1920). That *V. villosa* and *E. icterina* exhibit the elliptical shape typical of unionaceans inhabiting still water and burrowing into firm substrates (Eager, 1978) may be a reflection more of their habitat than of their systematic relationship.

Sexual dimorphism of shell shape, but not of allometric shell growth pattern, occurs in *V. villosa*. For *E. icterina* it is the allometric growth pattern, not a specific shape, that distinguishes males from females. This interspecific difference may be the result of differences in the age at which sexual maturity occurs. Although all individuals sampled were sexually mature as indicated by the presence of gametes in the gonads and/or larvae in the marsupial demibranchs,

there is no method by which the first reproductive cycle can be distinguished from subsequent cycles. The *V. villosa* individuals may have reached sexual maturity, hence adult shell shape, several years previously. The *E. icterina* individuals may have been undergoing their first reproductive cycle and may still have been in the process of differentiating toward adult shell shape. The age at which unionaceans attain sexual maturity is reported to be 1–9 years and varies greatly, even among congeners (Coker, Shira, Clark & Howard, 1922; Heard, 1975; Sterki, 1903).

The presence of sexual differences in shell shape and growth, particularly in the ventro-posterior region of the shell, reflects the requirement of females for an enlarged volume into which the gravid marsupial demibranchs may expand (Heaslip, 1969; Kirtland, 1834). The greater elaboration of the ventro-posterior region of *V. villosa* females relative to *E. icterina* females (Fig. 5A & C) may be related to differences in demibranch utilization. *V. villosa* exhibits the heterogenous condition in which only the posterior portions of the outer 2 demibranchs are marsupial, but *E. icterina* displays the homogenous condition, in which the entire length of each of the outer 2 demibranchs are marsupial (Heard & Guckert, 1970). The gravid portions of *V. villosa* demibranches enlarge ventrally, whereas those of *E. icterina* enlarge laterally (Ortmann, 1912). Unionaceans exhibit 8 different marsupial conditions (Heard & Guckert, 1970), but the relationships among marsupial condition, marsupial volume, and shell shape have yet to be explored quantitatively.

Although the discovery of shell sexual dimorphism in *E. icterina* was expected on the basis of functional morphology (Heaslip, 1969), recent authorities do not consider species belonging to the Pleurobemini, of which *E. icterina* is one, to exhibit shell sexual dimorphism (Burch, 1975; Heard & Guckert, 1970). There is, however, evidence that sexual dimorphism is of broader distribution. Kirtland (1834), as discussed previously, described the sexual dimorphism of *Plethobasus cyphus*. Sterki (1895) and Simpson (1897) observed that shell sexual dimorphism occurs with certain other conchological and anatomical character states. These character states were the criteria by which they divided the Unionacea into 2 groups: (1) the true unios, which exhibit no shell sexual dimorphism, have drab shell coloration, display the homogenous condition, and include species presently placed in the Amblemini and Pleurobemini, and (2) the *Lampsilis* group, which

displays conspicuous shell sexual dimorphism, have brightly colored shells, exhibit the heterogenous condition, and are presently placed in the Lampsilini. Sterki (1903) later reported sexual differences in the shell shapes of species presently included in the subfamilies Amblemimae and Anodontinae (Unionidae). The shells of female *Lamellidens marginalis* (Lamarck) (Pleurobemini) are broader and more convex than those of conspecific males (Thomas, 1974).

The first quantitative study of unionacean shell sexual dimorphism was performed by Grier (1920), whose results were to consistent with those of Sterki (1895) and Simpson (1897) but did support those of Sterki (1903). Grier (1920) found differences between the means of 7 shape variables of males and females belonging to the Amblemini, Anodontinae, Lampsilini, and Pleurobemini, including *Elliptio dilatata* (Rafinesque). Ball (1922) compared the obesities (= length/width) of species belonging to the Amblemini, Pleurobemini, and Lampsilini. The only sexual differences he found were within the Lampsilini. Neither Grier (1920) nor Ball (1922) determined the statistical significance of the differences they found.

Sexual dimorphism of growth has been examined in 3 unionacean species. Female *Lampsilis anodontoides* (Rafinesque) (Lampsilini) grow more rapidly than do conspecific males at certain ages (Chamberlain, 1930). Hamai (1938) found that growth at various points of the shell margins of *Inversidens japonenis* (Lea) (Amblemini) is allometric relative to length and that there are significant sexual differences in this growth pattern. Results remarkably identical to those of Hamai (1938) were reported by Agrawal (1974) for *Parreysia wynegungaensis* (Muller) (Amblemini).

The present study provides a method of size and shape analysis that can be used to reveal subtle forms of sexual dimorphism (*e.g.*, in *Elliptio icterina*) that are not detected by standard univariate or multivariate analyses. Furthermore, our results along with those discussed above indicate that sexual dimorphism may be more common among unionaceans than is currently thought. The presence/absence of sexual dimorphism has been used in unionacean systematics (*e.g.*, Simpson, 1897; Sterki, 1895) even though no negative character should be used to define taxa (Eldredge & Cracraft, 1980). Our results show (1) that the presence of sexual dimorphism cannot be considered a reliable character for unionacean systematics until size and shape analyses are performed for other populations/species and (2) that, unless sexual differences are demonstrated to be statistically non-significant, any study of shell growth must control for such differences.

SUMMARY

Sexually mature specimens of *Villosa villosa* and *Elliptio icterina* were collected from the same locality. Eleven linear measurements and the angle at which the maximum umbo-perimeter distance occurs were taken on each specimen, transformed to $\log_{10}$, and combined into shape variables of the form $\log x - \log y$.

T-test results show that there are no sexual differences in size for either species in the samples examined. *Villosa villosa* exhibits significant sexual differences on 5 of 20 univariate shape variables. No such differences are shown by *E. icterina*. The angle at which the maximum umbo-perimeter distance occurs is significantly different between males and females of *V. villosa*, but not of *E. icterina*. All specimens of *V. villosa* were correctly classified as to sex by discriminant function analyses of shape variables, whereas a maximum of 70% of the *E. icterina* individuals were correctly classified. Regressions of shape on size show that shape change of both species is negatively allometric relative to length and to maximum umbo-perimeter distance along most axes. There are no sexual differences in the way in which shape changes during growth in *V. villosa*, but there are significant differences between the shapes of male and female *E. icterina* during growth.

Analysis of shape, either univariate or multivariate, is sufficient to identify the sex of *V. villosa* individuals; however, size and shape must be analyzed to distinguish male from female *E. icterina*. Variables describing the ventro-posterior shell region are superior to those commonly used (length and height) to detect sexual differences in shape and growth. The similarity in shape of the two species may be the result of adaptation to their habitat and is not necessarily of systematic significance. The type of sexual dimorphism exhibited by *E. icterina* may be more common among unionaceans than is currently acknowledged.

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