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EFFECTS OF NONNORMALITY ON STUDIES OF MORPHOLOGICAL VARIATION
OF A RHABDOMESINE BRYOZOAN, *STREBLOTRYPA* (*STREBLASOPORA*) *PRISCA*
(GABB AND HORN)

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Abstract.—Documentation of morphological variability associated with spatial distribution (i.e., geography) is important for microevolutionary studies. In a study of geographical variation, the morphological variability of forty-six specimens (colony fragments) of *Streblotrypa* was documented from eight localities of the Winzeler Shale (Stephanian, Midcontinent, USA), along a 300-km-long transect. Multivariate analysis of 28 morphometric characters demonstrated the presence of a single species of *Streblotrypa* in the study material.

Evaluation of this large, morphometric data set demonstrated that a sample size of 5 observations per colony fragment is optimal for this type of study and that effects of violating assumptions of normality and homoscedasticity are present but do not affect overall conclusions with these data. Consequences of violating these assumptions are important, however, when strict probability cut-offs are employed.

Streblotrypa ulrichi and *S. striatopora* are recognized as astogenetic variants and designated as junior synonyms of *S. (Streblasopora) prisca*. The spelling of the type species of the genus is corrected to *Streblotrypa nicklesi*, and a neotype is designated.

INTRODUCTION

Failure to account for ecophenotypic and geographical variation can result in an erroneous interpretation of perceived evolutionary rates (Cuffey and Pachut, 1990; Hageman, 1992b). A large morphometric data set was collected from *Streblotrypa (Streblasopora) prisca* (Rhabdomesina, Cryptostomata) in order to test for ecophenotypic and geographical variation (Hageman, 1992b). The purposes of this paper are to provide a revised systematic description of *S. (Streblasopora) prisca*, to evaluate the quality of the morphometric data set collected for this species, and to discuss characteristics and limitations of morphometric data typically collected from bryozoans.

MATERIALS AND METHODS

Specimens (colony fragments) of *Streblotrypa* were collected from four stratigraphic horizons from Virgilian (Stephanian) sites in eastern Kansas of the Midcontinent of North America (Fig. 1). Data are summarized in Table 1, and locality information is listed in the Appendix. More than 200 colony fragments were collected from the base of the Winzeler Shale from eight localities that span a 300-km-long transect from south-central to northeastern Kansas (Fig. 1, localities 76, 151, 42, 15, 22, 25, 26, 27). Five colony fragments were studied from each locality (eleven from locality 25), and seven observations were measured from each colony fragment for each of 28 characters. Ten

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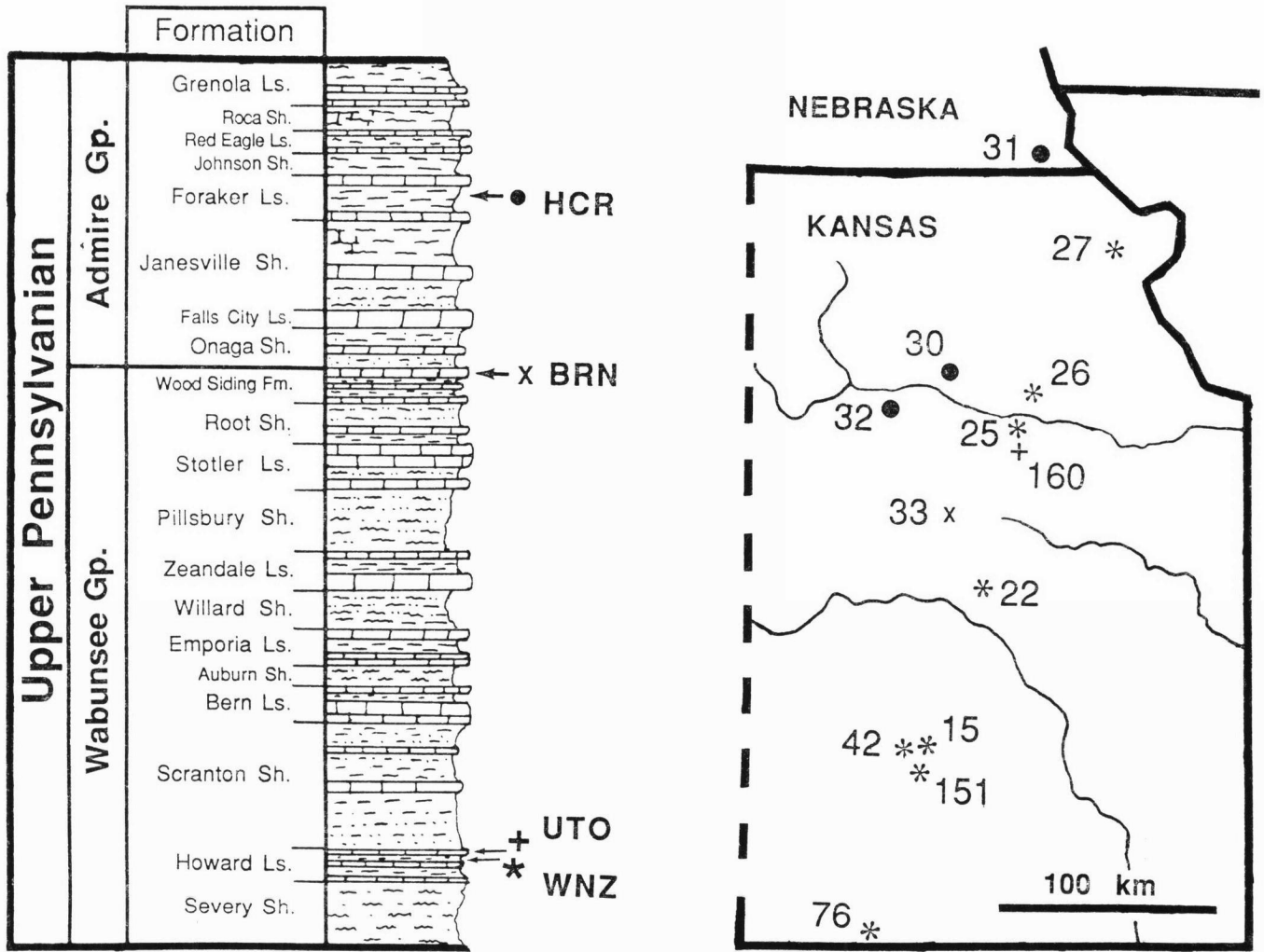


Fig. 1. Stratigraphic and geographical distribution of the streblotrypid localities listed in the Appendix: * WNZ, Winzeler Shale; + UTO, Utopia Limestone Member of the Howard Limestone; x BRN, Brownsville Limestone Member of the Wood Siding Formation; • HCR, Hughes Creek Shale Member of the Foraker Limestone.

colony fragments were studied from an exposure of the next unit above the Winzeler Shale, the Utopia Limestone Member of the Howard Limestone (Fig. 1, locality 160). Five colony fragments were studied from one locality of the Brownsville Limestone Member of the Wood Siding Formation (Fig. 1, locality 33) and from three localities of the Hughes Creek Shale of the Foraker Limestone (Fig. 1, localities 30, 31, 32). The Foraker Limestone is here recognized as uppermost Pennsylvanian, based on redefinition of the Pennsylvanian-Permian boundary in Kansas (Baars *et al.*, 1990). Five observations were measured from each colony fragment for 28 characters.

The term *population* is used here to represent a time-averaged assemblage of conspecific colony fragments collected from a single lithologic unit (member) from a single geographic locality. The degree of time averaging varies between rock units studied; it is minimal in the Winzeler (specimens consistently found in a 15-cm-thick, little disturbed section) and more significant in the Hughes Creek

(specimens variously distributed through 10 meters of minimally disturbed section).

Specimens were washed and sieved from bulk shale samples, cleaned using the paint thinner technique of Harris and Sweet (1989), and washed in an ultrasonic bath with detergent. Exterior features were photo-documented using alizarin red and ammonium chloride to enhance contrast.

Twenty-eight characters were measured (Table 2, Fig. 2) using a video digitizing system attached to a stereo microscope driven by *Bioscan Optimas™* image-analysis software. Computer programs were written in *Bioscan Optimas™* macro language to collect data for linear measurements, angle measurements, area measurements, and point counts. Modified versions of each of these programs were incorporated into larger programs adapted for customized collection of data (e.g., a user is prompted through all characters typically measured from a single, digitized image of longitudinal autozoocidal chambers). Calibrated data were

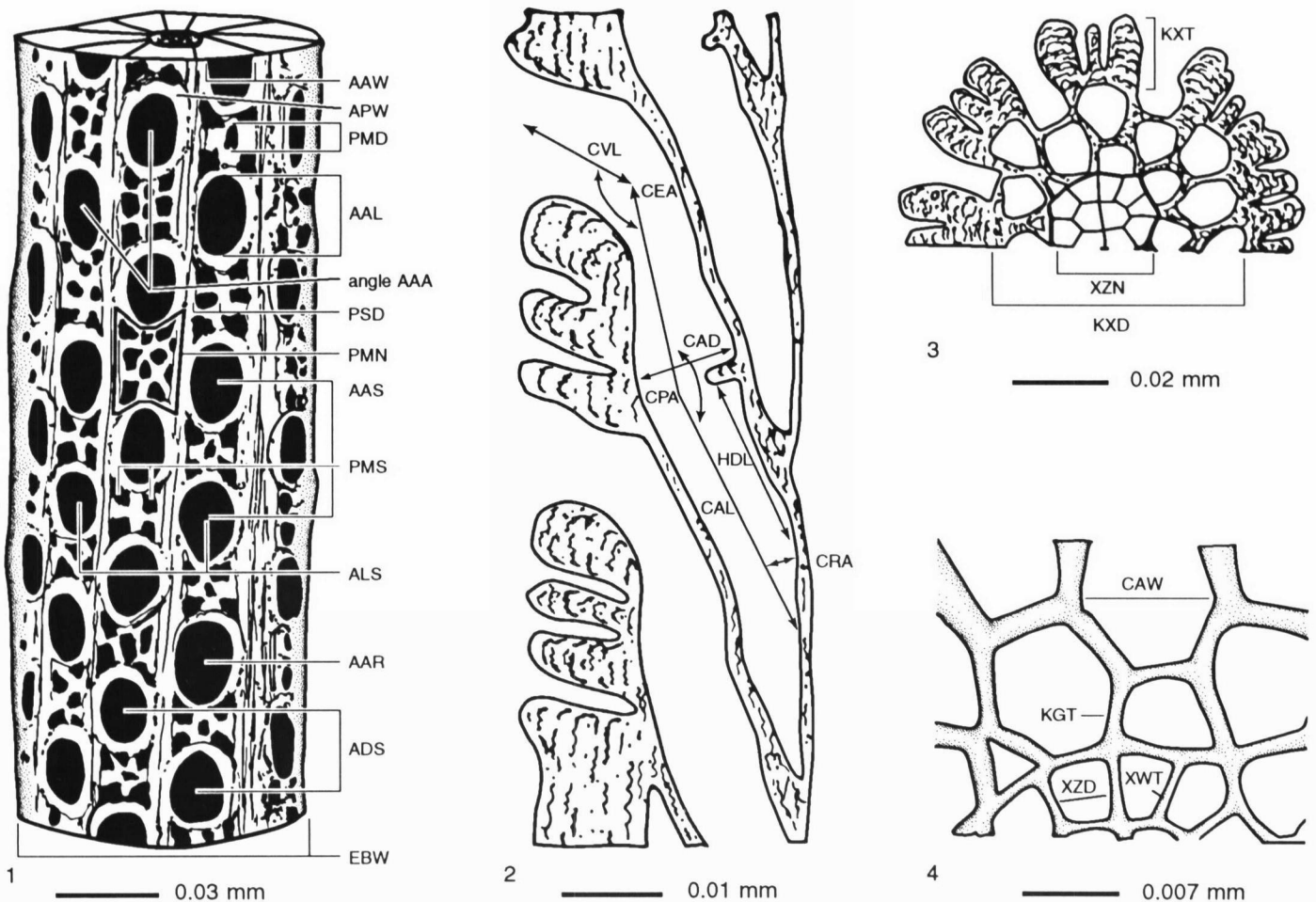


Fig. 2. Morphometric characters measured from *Streblotrypa prisca* (see Table 2 for explanation of characters and their abbreviations); 1, exterior, $\times 50$; 2, longitudinal section, $\times 130$; 3, transverse section, $\times 70$; 4, transverse section, $\times 200$.

transferred directly to *Microsoft Excel*TM spread sheets via *Dynamic Data Exchange*TM.

After exterior features had been measured, specimens were embedded in epoxy, and acetate peels were prepared

Table 1. Summary of *Streblotrypa* data sets; 28 characters measured for each composite zooid (CZ). Winzeler data set consists of localities 15, 22, 26, 27, 42, 76, and 151; Topeka data set consists of localities 25 and 160; and Upper data set consists of localities 30, 31, 32, and 33.

Data Set	# Localities	# Colony Fragments per Locality	# Composite Zooids per Fragment	#CZs
Winzeler	7	5	7	245
Topeka	2	10–11	5	105
Upper	4	5	5	100
Total	13	76	—	450

from oriented transverse, tangential, and longitudinal sections using standard methods (Boardman and Utgaard, 1964; Nye *et al.*, 1972).

Chamber orientation.—A problem encountered with measuring data from longitudinal sections of bryozoans is maintaining consistent orientation and depth between chambers. Usually, a series of sections through a chamber is required to assure proper orientation for each measurement. In order to optimize selection of chamber orientation and avoid duplication of measurements, this procedure was documented with laser prints of digitized serial sections (Fig. 3).

Composite zooids.—All characters cannot be measured from a single zoecium because the preparation technique is destructive (e.g., chamber length and chamber width require two separate sections). In this study, a composite zooid (CZ) is the operational unit in numerical analyses rather than a true zooid or a colony. For example, a single CZ in this study consists of the observed values for 28 characters represented by a complete suite of longitudinal characters measured from a single chamber plus a com-

Table 2. Morphometric characters measured from *Streblotrypa prisca* and their abbreviations (see Fig. 2).

Exterior Characters	
EBW	Branch Width (not measured at branch bifurcation, can be measured in transverse section but exterior preferred)
Apertural Characters	
AAL	Aperture Length (measured proximodistally)
AAW	Aperture Width (measured perpendicular to aperture length)
AAS	Aperture Spacing Along Branch (distance between aperture centers along branch)
ALS	Lateral Aperture Spacing (distance between aperture centers across branch)
ADS	Diagonal Aperture Spacing (distance between diagonal aperture centers)
APW	Peristome Width (measured at distal end of aperture)
AAR	Apertural Area (including inclined vestibule as needed)
AAA	Aperture Adjacent Angle (acute angle taken from proximodistal trace adjacent to lateral aperture)
Autozooeical Chamber Characters	
CAL	Autozooeical Chamber Length (maximum length measured down the middle of the chamber from the interior wall to the flexure of the vestibule, measured in longitudinal section)
CVL	Vestibule Length (measured down the middle of the vestibule from the flexure to the exterior)
CAD	Autozooeical Chamber Depth (measured perpendicular to chamber length in the longitudinal section)
CRA	Chamber Reverse Wall Budding Angle (angle of emplacement measured in longitudinal section)
CPA	Autozooeical Chamber Angle (angle measured at flexure in the middle of the maximum chamber length)
CEA	Autozooeical Exozonal Angle (angle measured between the chamber length and vestibule)
CAW	Autozooeical Chamber Width (measured across branch at endozone-exozone boundary in transverse section)
CAR	Autozooeical Chamber Area (measured in longitudinal section)
Zoarial Skeletal Characters	
KGT	Endozone Wall Thickness (transverse section)
KXD	Diameter of Endozone (transverse section)
KXT	Thickness of Exozone (transverse section)
Polymorph Characters	
PMD	Maximum Diameter of Polymorphs
PSD	Minimum Diameter of Polymorphs
PMS	Spacing of Polymorphs
PMN	Number of Polymorphs (in a rhombic field)
Axial Zooecia	
XZN	Number of zooecia across axial bundle (transverse section)
XZD	Axial Zooecia Diameter (transverse section)
XWT	Thickness of axial zooeical wall (transverse section)
Hemisepta	
HDL	Distance on Distal Wall (length from reverse-wall-budding-site to placement of hemisepta on proximal wall)

plete suite of transverse characters measured from a different chamber plus a complete suite of exterior characters measured from a third chamber. A composite zooid represents a single zooid, but is compiled from the observations (measurements) of three different zooids. CZs are also composites in the sense that such extrazooecial characters as branch width, which do not belong to any single zooid, are included.

In the operational sense of multivariate numerical methods, a composite zooid (CZ) is the equivalent of a single specimen of a noncolonial organism.

Numerical methods and curation of specimens.—Subsets of these data were used in various aspects of this and earlier (Hageman, 1992b) studies. A series of numerical tests was performed to evaluate morphological variability of *Streblotrypa* within and between colonies, populations, morphological variants, lithology and environments, and times of occurrence (Hageman, 1992b). Cluster analyses were performed with *NTSYS-pc* (1.60), discriminant and canonical variates analysis with *SAS* (5.18), descriptive and distribution-free statistics with *Statview II* (1.03), and normal scores test with macros written in *Microsoft Excel* (Hageman, 1992a). See Neff and Marcus (1980) and Hageman (1992a, 1992b) for review of methods. Materials studied are housed in the following museums: United States National Museum (USNM), Academy of Natural Sciences of Philadelphia (ANSP), Department of Geology, University of Illinois (UI), Illinois State Geological Survey (ISGS), University of Kansas Museum of Invertebrate Paleontology (KUMIP).

Species distinctions.—This study employs a single morphological group of rhabdomesine cryptostome Bryozoa. Members of the genus *Streblotrypa* form a group distinct from other related genera, based on placement of metapores and orientation of axial zooecia. All morphs of *Streblotrypa* present in the study area were employed in these analyses, but taxonomic distinctions were not made *a priori*. Seven CZs (composite zooids) measured from each colony fragment were treated individually in cluster analysis. Composite zooids tended to cluster into small groups corresponding to the colony fragments from which they were measured, indicating some vague factors controlling morphogenesis in these bryozoans (Hageman and Blake, 1992). End members of two exterior morphotypes (robust and striated) are apparent in casual observation and were established *a priori* (Figs. 4, 1 and 4, 3). Composite zooids did not, however, form coherent clusters corresponding either to these morphotypes or to their geographical distribution. Failure of CZs to form coherent clusters, other than with the fragment of the colony from which they were measured, suggests that all fragments are from a conspecific group (Cheetham, 1986; Budd, 1990).

The interpretation of a single *Streblotrypa* species in this material is supported by recognition of the end members of the morphological gradient (striated and robust) as astogenetic variants found growing from a single colony

fragment (Figs. 4, 9 and 4, 10). Visual inspection of more than 200 colony fragments also revealed many intermediate forms.

All specimens of *Streblotrypa* in this study are therefore regarded as belonging to a single species. The two morphs originally described as separate species, *Streblotrypa ulrichi* and *S. striatopora*, are here recognized as astogenetic variants of *Streblotrypa prisca* (Gabb and Horn, 1862).

SYSTEMATIC PALEONTOLOGY

Phylum BRYOZOA Ehrenberg, 1831

Class STENOLAEMATA Borg, 1926

Order CRYPTOSTOMATA Vine, 1884

Suborder RHABDOMESINA Astrova and Morozova,
1956

Family HYPHASMOPORIDAE Vine, 1886

Genus STREBLOTRYPA Ulrich in Vine, 1885, p. 391

Type species.—*Streblotrypa nicklesi* Ulrich in Vine, 1885, p. 391.

Description.—Same as Blake (1983, p. 590).

Remarks.—The taxonomy of *Streblotrypa* is checked with nomenclatorial problems. It is affirmed here that *Streblotrypa nicklesi* Ulrich (in Vine, 1885) be recognized as the type species, but in accordance with Article 32c (ii) of the 1985 edition of the *International Code of Zoological Nomenclature* (ICZN), it is proposed that the spelling of the trivial name be corrected from *nicklisi* to *nicklesi*. Because both specimens originally described and illustrated by Vine (1885) are lost, specimen USNM 114392 is here designated as the neotype. The following chronology of nomenclatural events justifies these actions.

1884: Ulrich proposed the genus *Streblotrypa* in a manuscript and designated *S. nicklesi* as the type species in honor of John M. Nickles, who first collected specimens in abundance from the Chester Group near Kaskaskia, Illinois, and presented them to Ulrich (Vine, 1885; Ulrich, 1888).

1885: J. M. Nickles sent specimens of *S. nicklesi* from Kaskaskia, Illinois, to G. R. Vine in England in 1883. Vine recognized a similar specimen in the Carboniferous of Yorkshire, England. He did not want to introduce a new name, so he used the name in Ulrich's 1884 manuscript, but misspelled it *Streblotrypa nicklisi*. Vine's brief description, which validated the generic name *Streblotrypa* Ulrich (in Vine, 1885), was based on a combination of Kaskaskia material and single Yorkshire specimen (Duncan, 1949). Vine (1885, pl. 21, figs. 4 and 5) illustrated one Kaskaskia specimen and the Yorkshire specimen.

1888: Ulrich published descriptions of eight new species of *Streblotrypa* (Ulrich, 1888), but did not include *S. nicklesi*. In a footnote (p. 84), however, he remarked that

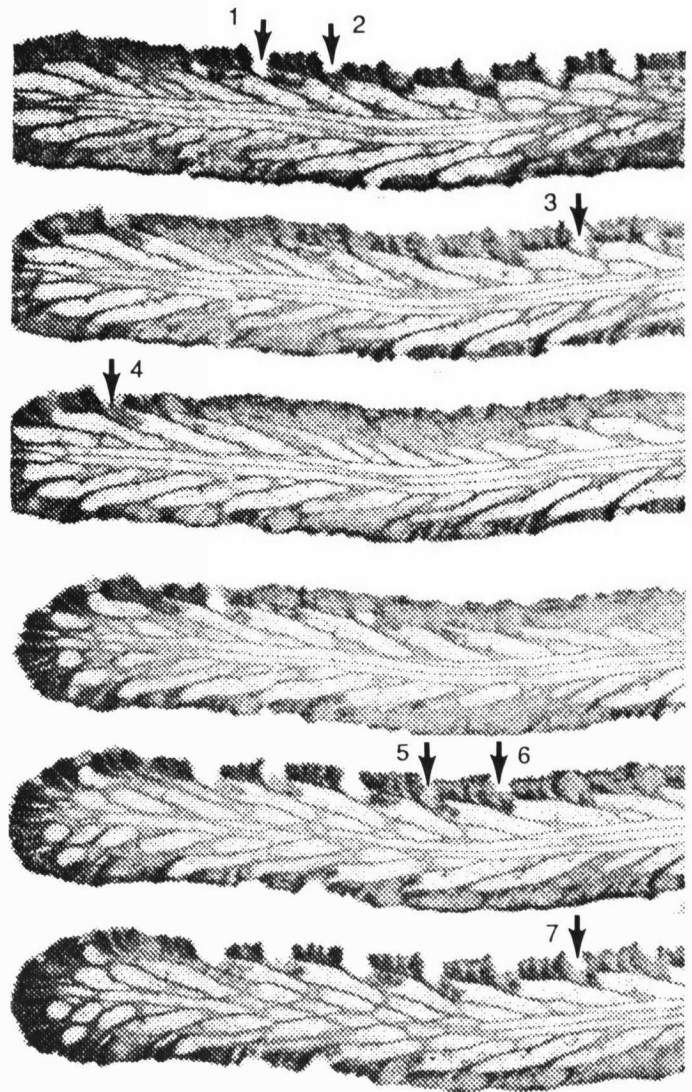


Fig. 3. Six longitudinal serial sections through a single streblotrypoid colony (UI X-7055). Arrows indicate zooids from which longitudinal characters were measured for this specimen. This type of map helps to ensure that the best available zooids are measured and that measurements are not repeated.

S. nicklesi is the type species for the genus per his 1884 manuscript and Vine (1885).

1890: Vine (1890) stated that his Yorkshire specimen of *S. nicklesi* (1885) was missing and presumed lost. The location of the figured Kaskaskia specimen and other Kaskaskia material used by Vine is also unknown (Duncan, 1949).

1890: Ulrich (1890), described five species of *Streblotrypa*, including *S. nicklesi* (p. 667–668), and acknowledged it as the type species for the genus (p. 403). Ulrich did not designate a type specimen but considered figured specimens (pl. 71, fig. 9) to be syntypes.

1949: Duncan (1949) noted that with the loss of Vine's specimens, *S. nicklesi* did not have any type specimens and proposed that the suite of Nickles's topotypes, cataloged as

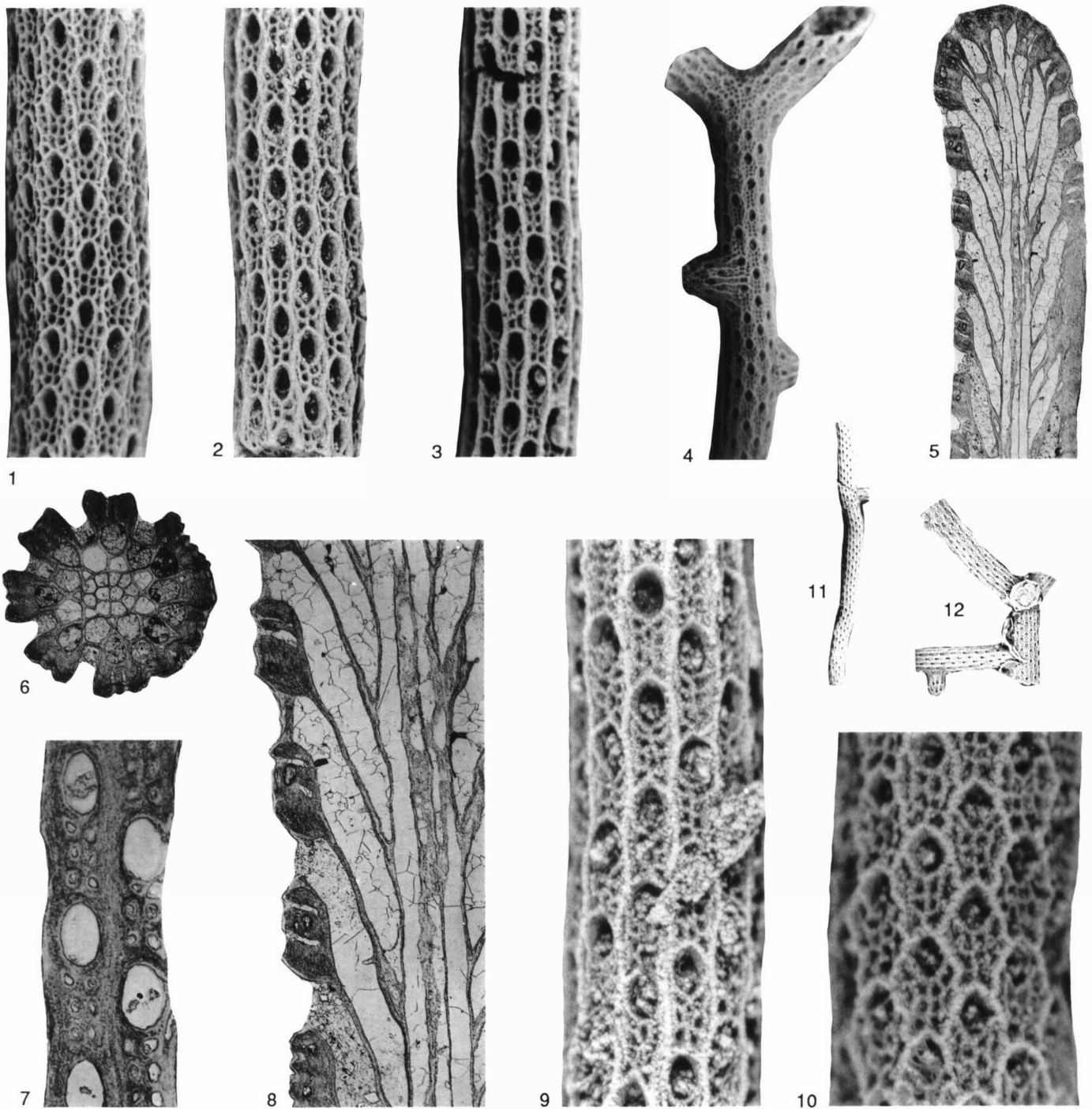


Fig. 4. *Streblotrypa prisca*. 1, astogenetically mature morph, UI X-7072, $\times 25$; 2, astogenetically intermediate morph, UI X-7098, $\times 25$; 3, astogenetically young morph, UI X-7057, $\times 25$; 4, specimen illustrating Y bifurcation and secondary branching at right angles, UI X-7086, $\times 10$; 5, longitudinal section through growing tip, UI X-7084, $\times 25$; 6, transverse section, UI X-7084, $\times 30$; 7, shallow tangential section illustrating metapores, UI X-7084, $\times 70$; 8, longitudinal section, UI X-7084, $\times 70$; 9–10, single colony of *Streblotrypa prisca* expressing two morphs, UI X-7092, $\times 40$; 9, intermediate morph with thin walls and longitudinal ridges; 10, robust, mature morph with increased number of metapores; 11–12, examples of branching patterns expressed in *S. prisca*; 11, lectotype, ANSP 31271, $\times 3$; 12, UI X-7094, $\times 4$.

USNM 43311, be designated as types and that Vine's erroneous spelling of *nicklisi* be corrected to *nicklesi* as intended by Ulrich (1884, 1888, 1890).

1983: In the rhabdomesine chapter of the revised edition of the *Treatise on Invertebrate Paleontology*, Blake (1983) noted that Duncan's (1949) suggestion of replacing Vine's

type specimen with a suite of fossils does not fulfill ICZN rules but stated, "Nevertheless, the concept of *S. nicklisi* has been generally based on North American specimens illustrated here." Blake (1983, figs. 293, 2a–e and 294, 2a–c) illustrated specimens from the syntype suite USNM 43311. Blake (1983) did not designate a neotype but retained Vine's (1885) spelling of *nicklisi*.

This paper: Because Vine (1885, p. 391) stated that the species was named in honor of Mr. Nickles, the spelling of the trivial name is here corrected from *S. nicklisi* to *S. nicklesi*, in accordance with ICZN [Art. 32c (ii)].

ICZN Recommendation 75A states that preference should be given to topotypic material during selection of a neotype. Because *Streblotrypa nicklesi* was originally described from Kaskaskia material in Ulrich's unpublished manuscript and the name was validated in Vine (1885) using a combination of Kaskaskia specimens and a single Yorkshire specimen (now lost), a neotype from the Kaskaskia material is designated here. Specimen USNM 114392, figured in Ulrich's original description of the species (1890, pl. 71, fig. 9a) and included as a syntype by Duncan, is designated neotype for *Streblotrypa nicklesi*. This specimen was originally designated as a syntype by Ulrich and numbered USNM 43311.

Other important specimens of this species include eight paralectotypes Ulrich (1890), seven of which were originally designated USNM 43311 and are now designated USNM 465280 (Ulrich, 1890, pl. 71, fig. 9' bottom specimen), USNM 465281, USNM 240786, USNM 465282 = 43311-1*, USNM 248242 = 43311-2*, USNM 465283 = 43311-3*, USNM 2407088 = 43311-4 (* designates specimens now represented by thin sections and peels); and one specimen housed in the Illinois State Geological Survey ISGS, (ISM) 2821-10 (Ulrich, 1890, pl. 71, fig. 9' top specimen). Additional important material labeled as *S. nicklesi* by Ulrich includes four from Nickles's original locality designated ISGS (ISM) 4445-2. Approximately fifty unnumbered specimens collected from the original locality by J. M. Nickles are housed at the USNM and labeled as locality #40 = Ch2. In Mr. Nickles's locality journal (housed at USNM), the original locality of all specimens named in this section is described as "small exposures of Chester Gr. strata in banks of two ravines one-half mile south of ferry to Kaskaskia—at that time across Okaw River (39,40)."

Subgenus STREBLASCOPORA Bassler, 1952, p. 385

Type species.—*Streblotrypa fasciculata* Bassler, 1929, p. 66.

Description.—Species of *Streblotrypa* with more or less clearly defined bundle of axial zoecia and more than ten axial zoecia at any level in the branch.

Remarks.—Bassler (1929) originally separated *Streblascopora* from *Streblotrypa* based on presence of axial zoecial bundles. Blake (1983) noted that many intermediates exist between the well-defined end members of *Streblotrypa* and *Streblascopora* and therefore reduced *Streblascopora* to subgeneric status.

Table 3. Summary of morphometric characters for *Streblotrypa prisca*; n = 230 observations of each character. Abbreviations described in Table 2 and illustrated in Figure 2.

Character	Mean	Standard Deviation	Coefficient of Variation	Observed Range
1. EBW	0.8736	0.0971	11.11	0.6615–1.1340
2. AAL	0.1945	0.0190	9.75	0.1485–0.2452
3. AAW	0.1193	0.0171	14.32	0.0876–0.1733
4. AAS	0.4249	0.0443	10.44	0.3064–0.5749
5. ALS	0.3488	0.0437	12.53	0.2651–0.4796
6. ADS	0.2758	0.0317	11.48	0.2106–0.3972
7. APW	0.0315	0.0073	23.16	0.0179–0.0587
8. AAR	0.0176	0.0035	19.71	0.0105–0.0308
9. AAA	38.59	5.75	14.91	18.16–52.20
10. CAL	0.6581	0.0600	9.11	0.4582–0.8336
11. CVL	0.1035	0.0456	44.08	0.0233–0.2421
12. CAD	0.1107	0.0113	10.16	0.0859–0.1408
13. CRA	22.02	3.25	14.76	11.62–30.65
14. CPA	172.37	4.40	2.56	159.72–186.21
15. CEA	125.65	7.03	5.59	108.88–150.29
16. CAW	0.0972	0.0107	10.98	0.0678–0.1294
17. CAR	0.0803	0.0110	13.66	0.0551–0.1116
18. KGT	0.0154	0.0041	26.72	0.0077–0.0273
19. KXD	0.5596	0.0770	13.76	0.2176–0.7564
20. KXT	0.1134	0.0461	40.67	0.0174–0.2518
21. PMD	0.0368	0.0136	37.07	0.0152–0.0844
22. PSD	0.0231	0.0104	44.98	0.0065–0.0590
23. PMS	0.0729	0.0137	18.80	0.0406–0.1274
24. PMN	8.91	3.10	34.82	4–19
25. XZN	3.4783	0.6654	19.13	2–6
26. XZD	0.0519	0.0110	21.25	0.0295–0.0865
27. XWT	0.0081	0.0022	26.62	0.0032–0.0159
28. HDL	0.2249	0.0453	18.49	0.1265–0.3953

STREBLOTRYPA (STREBLASCOPORA) PRISCA (Gabb and Horn, 1862)

Figures 4.1–4.12

Cavea prisca Gabb and Horn, 1862, p. 175–176, pl. 21, fig. 67.

Streblotrypa ulrichi Rogers, 1900, p. 3–4, pl. 1, figs. 3–3a.

Streblotrypa striatopora Rogers, 1900, p. 4, pl. 4, fig. 1.

not *Streblotrypa prisca* Condra, 1903, p. 103, pl. 20, figs. 3–8.

Description.—Branch diameter 0.7 to 1.0 mm, constant between branch bifurcations. Branching at right angles common, with smaller branch resulting from exozonal budding. Longitudinal ridges well developed in early astogeny (*sensu* Pachut *et al.*, 1991) to absent in late astogeny, yielding well-defined fields proximal to apertures in early astogeny. Generally six metapores in early astogeny arising in exozone in two parallel rows in rhombic fields proximal to apertures, increasing in number

later in astogeny to as many as 15 per aperture. Well-defined bundle of axial zooecia varying from two to six zooecia across axial section, but most commonly with one or two central zooecia surrounded by one layer of axial zooecia, six to eight total. Autozooecial sections polygonal in transverse section. Zooecial divergence from axial region approximately 20 degrees. Autozooecial length approximately 1.72 mm, depth 0.11 mm, width 0.09 mm. Short hemisepta well developed to absent (consistent within colony) on distal wall, opposite to bend in proximal wall; diaphragms absent. Exozone width 0.09 to 0.13 mm (relatively consistent for colony), endozone diameter 0.55 mm. Stylets, paurostylets, and acanthostyles absent. Summary statistics for morphometric characters are listed in Table 3.

Remarks.—This species was originally assigned to the cheilostomes (Gabb and Horn, 1862). The authors expressed doubt that the specimens from Fort Belknap, Texas, were Cenozoic and suspected (correctly) that they were Carboniferous. Four syntypes were designated by Gabb and Horn (1862), and specimen ANSP 31271 (Gabb and Horn, 1862, pl. 21, fig. 67) is here designated as the lectotype. Three specimens ANSP 77550 are designated as paralectotypes. Acetate peels of tangential, transverse, and longitudinal sections were taken from one specimen of ANSP 77550 for this study.

Rogers (1900) described two species, *S. ulrichi* and *S. striatopora*. *Streblotrypa ulrichi* is a junior synonym of *S. prisca* (Gabb and Horn) (see Condra, 1903). An examination of over two hundred specimens makes it apparent that *S. striatopora* is also a synonym of *S. prisca* (Gabb and Horn). Although its exterior is distinctive (Fig. 4,1), it is simply a more mature expression of the colony, having a thicker exozone, an increased number of metapores, and a weakening of linear ridges. This is apparent in Figures 4,9 and 4,10, which show two fragments at different stages of maturity from the same colony.

Blake (1983) stated that hemisepta are rare or absent in members of the subgenus *Streblascopora*, but hemisepta are common in this species, which is otherwise clearly a *Streblascopora*. Condra's (1903, pl. 20, fig. 7) illustration of *S. prisca* does not clearly show an axial zooecial bundle and may represent an undescribed form. *Streblotrypa prisca* and *S. striatopora* were described by Ceretti (1962), but the material is poorly preserved, and illustrations are not adequate to establish an identification.

Material studied includes Gabb and Horn's (1862) *Streblotrypa prisca* lectotype, the three paralectotypes from the Academy of Natural Sciences of Philadelphia, and more than 200 specimens collected from the Late Pennsylvanian of Kansas, 76 of which were sectioned and repositated at the University of Illinois and University of Kansas. Rogers's (1900) specimens from the University of Kansas and Condra's (1903) specimen from the Nebraska Geological Survey are missing. All specimens of *Streblotrypa nicklesi* listed above were also studied, as well as Ulrich's (1890) syntypes of *S. subspinosa*, ISGS (ISM) 4457; *S. major*, ISGS

(ISM) 4452; *S. radialis*, ISGS (ISM) 4456; and *S. distincta*, ISGS (ISM) 4485.

EVALUATION OF DATA

Morphometric data sets such as those used in this study provide an opportunity to test how the distribution and other properties of the data affect results of quantitative analyses and influence scientific conclusions. The Winzeler data set was tested in order to determine if sample size is adequate to represent the population in question and whether fewer observations could approximate the population in an adequate manner.

Quantity versus quality of data.—A series of discriminant analyses were performed in order to determine if composite zooids (CZs) could be allocated to the colony fragment from which they were measured. Initially, an analysis was performed using all the data; then the procedure was repeated with the last (seventh) composite zooid from each colony fragment omitted from the analysis. Next, the sixth and seventh composite zooid from each colony fragment were omitted from the analysis; and finally the fifth, sixth, and seventh were omitted. Another series of discriminant analyses omitted the first composite zooid from each colony fragment; then first and second; and finally first, second, and third.

Results can be compared by looking at the *allocation efficiency ratio* of each analysis. The *allocation efficiency ratio* is obtained by taking the total number of composite zooids correctly assigned to their *a priori* group (here the known colony fragment) divided by the total number of composite zooids. This number can be converted to an *allocation efficiency rate* by multiplying by 100.

When composite zooids were allocated to colony fragments, group sample size did not affect results (Table 4). When, however, the same procedure is repeated in an

Table 4. Number of composite zooids in sequence of their measurement and *allocation efficiency ratios* of a series of discriminant analyses allocating CZs to colony fragments and to morphs. All misclassified CZs in analyses using First 6 and All 7 are from the same colony fragments.

CZ Ranks	Allocation of CZs to Colony Fragments		Allocation of CZs to Morphs	
	Count	Percentage	Count	Percentage
First 3	107/107	100%	107/107	100%
First 4	140/140	100%	140/140	100%
First 5	175/175	100%	172/175	98.3%
First 6	209/210	99.5%	205/210	97.6%
All 7	244/245	99.6%	239/245	97.6%
Last 6	210/210	100%	207/210	98.6%
Last 5	175/175	100%	170/175	97.1%
Last 4	140/140	100%	135/140	96.4%
Last 3	107/107	100%	102/105	97.1%

Table 5. Group sample sizes of streblotrypid data and allocation efficiency ratios for discriminant analysis with allocation of composite zooids to colony fragments and allocation of composite zooids to morphs.

Colony Fragments per Locality	Allocation of CZs to Colony Fragments		Allocation of CZs to Morphs	
3	147/147	100%	147/147	100%
4	196/196	100%	193/196	98.5%
5	244/245	99.6%	239/245	97.6%

attempt to allocate composite zooids to morphs (robust vs. striated), two trends are apparent (Table 4). Observations measured first are of better value in distinguishing between morphologies than later ones. Second, as sample size increases, the allocation efficiency ratio drops. Both of these factors can be accounted for by the quality of the data, especially those from longitudinal sections.

Adequate longitudinal sections of autozoecial chambers are often difficult to obtain, especially for smaller fragments. The best-oriented chambers are generally measured first. It can be more difficult to obtain an adequate chamber for the seventh observation than it is to measure the first four chambers combined (Fig. 3). In this instance, the need to collect good data requires that the assumption that individual observations are chosen randomly (inherent in many statistical tests) be violated. This phenomenon is not a function of the diligence of the worker collecting the data. Because colony branches (fragments) are rarely straight beyond a short distance, a very large number of parallel sections cut through even a large colony fragment would yield only a small number of properly oriented chambers. The scale of branch irregularities is far too small to allow for compensation during sectioning.

The sample size of five observations per colony fragment was chosen to achieve a balance between adequate representation of population distribution and quality of data collected. It is noteworthy that Cheetham (1986) arrived at the same number through different criteria, using five observations per specimen in a study of cheilostome bryozoans.

Small group sample sizes can artificially increase allocation efficiency ratios for discriminant analyses, as illustrated by results from a series of analyses where the overall number of composite zooids was decreased in each analysis by using fewer colony fragments (Table 5). This trend is also apparent in analyses where the number of composite zooids is decreased (Table 4). This pattern, however, is not great enough to alter conclusions here, which are very robust.

Of greater concern is the fact that in the discriminant analysis package available in SAS 5.18, a single-calibration matrix is calculated for the entire data set. Values of a test

observation are included in the calibration matrix, and the test is therefore weighted toward the unknown's original group, resulting in an inflated allocation efficiency ratio. Although the procedure uses a lot of computer time, it is more desirable to jackknife the data set (cross-validate), calculating new calibration matrices for each test composite zooid, excluding the test CZ each time. This procedure was performed on the Topeka subset of the data (localities 25 and 160) in order to test the magnitude of inflated allocation efficiencies. One CZ was randomly selected from each colony fragment, resulting in 84 CZs in a calibration data set and 21 CZs in a test data set. Discriminant analysis was performed, and the randomization procedure was repeated by selecting a new test set from the original calibration set and then returning the old test set to the calibration pool. This was repeated five times. Results show that the average allocation efficiency, 88.6 percent, is indeed less than the 100 percent obtained without jackknifing (Table 6). An allocation rate of 88.6 percent still, however, provides a strong case for individual CZs being assigned to the colony fragment from which they were measured.

Nonnormality and heteroscedasticity.—Most parametric statistical tests assume that data have a normal (Gaussian) distribution. Deviations from normality can affect results of tests, causing errors in interpretation; see Hageman (1992a) for review.

The UNIVARIATE procedure from SAS (5.18) uses the Kolmogorov-Smirnov D statistic to test the goodness of fit with a normally distributed population (see Zar, 1984, p. 53–58). Table 7 summarizes results of this test for 28 morphometric characters of *Streblotrypa prisca* (230 observations of 46 colony fragments) from the Winzeler Shale. Superscripts designate subsets of the data: a = all Winzeler specimens ($n = 230$), i = astogenetically immature colony fragments ($n = 168$), m = astogenetically mature colony fragments ($n = 77$). In Table 7, superscripts to the left of the character abbreviation indicate that the subset of the data for that character is normally distributed at a probability of $p > 0.05$; and superscripts to the right of the character abbreviation indicate that the subset of the data

Table 6. Allocation efficiency ratios from five discriminant analyses using cross validation (84 calibration CZs and 21 test CZs) of the Topeka subset (Table 1) of the streblotrypid data.

Allocation of Calibration CZs to Colony Fragments	Allocation of Test CZs to Colony Fragments
84/84 = 100%	19/21 = 90.5%
84/84 = 100%	20/21 = 95.2%
84/84 = 100%	18/21 = 85.7%
84/84 = 100%	17/21 = 81.0%
84/84 = 100%	19/21 = 90.5%
	mean 88.6%

that resulted in changes that crossed critical probability thresholds (e.g., $p < 0.05$), were generally very close to the probability limit to begin with. It is also clear from Table 8 that some characters are more affected than others.

Canonical variates analysis, employed frequently in this study and by Hageman (1992b), is generally robust to deviations from assumptions of multivariate normality and homoscedasticity (Nie *et al.*, 1975). To the author's knowledge, there are no multivariate equivalents of normal-scores tests. Ghent (1974) proposed a method of testing effects of nonnormality and heteroscedasticity of univariate tests by substituting normal order deviates (rankits) for the original data and then performing the standard parametric test (Ghent, 1974; Hageman, 1992a). This is not a true normal scores test but does indicate the relative magnitude of effects when they are present. This method is extended to multivariate methods here.

Measurements of 28 characters of *S. prisca* ($n = 245$ CZs) were converted to rankits for all Winzeler data (except locality 25), using methods described in Hageman (1992a). Discriminant analysis was performed on the rankit data. When composite zooids were allocated to colony fragments, the original data and the equivalent rankit data resulted in an allocation efficiency ratio of 245:245 (100 percent). When composite zooids were allocated to localities from which they were measured, the original data had an allocation efficiency ratio of 203:245 (83.0 percent), and the equivalent rankit data 197:245 (80.4 percent). In this instance, the effect of multivariate nonnormality and heteroscedasticity is to increase slightly the allocation efficiency ratio. If the results were near a critical threshold for making a decision, this difference may have required further evaluation. In this instance, however, the trend of allocation of composite zooids to localities remains relatively high, and conclusions are unchanged.

SUMMARY

1. Twenty-eight morphological characters of *Streblotrypa* were measured from 13 Upper Pennsylvanian localities for a study of ecophenotypic and geographical variation.

2. Multivariate analyses demonstrated that multiple morphs present are astogenetic variants of a single species. As a result, *Streblotrypa ulrichi* and *S. striatopora* are designated as junior synonyms of *S. (Streblascopora) prisca*.

3. The spelling of the type species of the genus is corrected to *Streblotrypa nicklesi*, and a neotype is designated.

4. Difficulties encountered in obtaining adequately oriented longitudinal sections result in a limited number of acceptable measurements of each specimen. Five observations per specimen (colony fragment) were determined as the optimal number for this type of morphometric study.

5. Cross-validation (jackknife) procedures in discriminant analysis yield a lower (and more representative) allocation efficiency ratio than standard procedures. Results in both instances, however, demonstrate a high tendency

for allocation of composite zooids to the colony fragments from which they were measured.

6. Many of the 28 morphometric characters are nonnormally distributed, but characters measured from mature forms have a greater tendency for normality than immature forms.

7. In a comparison of equivalent parametric and non-parametric tests, 12 type-I errors and 16 type-II errors can be attributed to effects of violating assumptions of normality and homoscedasticity (an error rate of 4.8 percent). No standard presently exists for an acceptable error rate.

8. An error rate of 19.2 percent with respect to marginally significant characters raises serious concern about employing strict *ad hoc* probability limits for conclusions.

9. Substitution of normal order deviates (rankits) for original data revealed small effects from multivariate nonnormality (± 2.6 percent). This again should raise concerns about employing strict *ad hoc* probability limits for conclusions.

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APPENDIX

LOCALITY DESCRIPTIONS FOR *STREBLOTRYPA*

- SJH-0015 Tonovay, SE NW SE 33-25S-11E, Tonovay-7.5' quad, Greenwood Co., Kansas. Cut on US-54 one mile SW of Bachelor Creek. UI-loc. Z-3012. Winzeler Shale.
- SJH-0022 Arvonja Strip-mine, SW SW 21-19S-14E, Lebo-7.5' quad, Osage Co., Kansas. Abandoned strip mine one mile north, two miles west of Lebo. UI-loc. Z-3013. Winzeler Shale.
- SJH-0025 Topeka, NW NW 24-12S-15E, Wakarusa 7.5' quad, Shawnee Co., Kansas. Cut on the north side of westbound off-ramp of I-470. UI-loc. Z-3014. Winzeler Shale.
- SJH-0026 Meriden, SW SW NE 23-10S-16E, Meriden-7.5' quad, Shawnee Co., Kansas. Cut on east side of gravel road 1.5 miles west, 1.5 miles south of Meriden. UI-loc. Z-3015. Winzeler Shale.
- SJH-0027 Severence Creek, SE SE NE 35-3S-19E, Bendena

- 7.5' quad, Doniphan Co., Kansas. Creek bank in stream, 0.7 miles south of Severence on west side of K-120. UI-loc. Z-3016. Winzeler Shale.
- SJH-0030 St. Marys, NW NW 35-9S-12E, St. Marys 7.5' quad, Pottawatomie Co., Kansas. Stream ditch two miles north, one-half mile east of St. Marys. KU-loc. N13B1. Hughes Creek Shale.
- SJH-0031 Salem, S SE SW 4-1N-15E, Salem 7.5' quad, Richardson Co., Nebraska. Hillside one mile west of south side of Salem. KU-loc. N15B2. Hughes Creek Shale.
- SJH-0032 Wabunsee, SW SW 12-11S-9E, Alma 7.5' quad, Wabunsee Co., Kansas. Road cut and stream ditch. KU-loc. 6716. Hughes Creek Shale.
- SJH-0033 Admire, SW SW NW 21-16S-12E, Admire 7.5' quad, Lyon Co., Kansas. Stream bank in Hundred and Forty-two Mile Creek. KU-loc. 2175. Bachelor Creek Limestone.
- SJH-0042 Eureka, SE SE NW 6-26S-11E, Eureka 7.5' quad, Greenwood Co., Kansas. Cut at the west junction of K-99 and US-54, two miles east of Eureka. UI-loc. Z-3017. Winzeler Shale.
- SJH-0076 Grant Creek, NW NW SW 3-34S-9E, Cedarvale East 7.5' quad, Chautauqua Co., Kansas. Cut on the north side of US-169, 0.1 miles west of Grant Creek. UI-loc. Z-3018. Winzeler Shale.
- SJH-0151 Otter Creek 99, SE SE NE 25-27S-9E, Piedmont NE 7.5' quad, Greenwood Co., Kansas. Cut on K-99, 0.8 miles south of Otter Creek. UI-loc. Z-3019. Winzeler Shale.
- SJH-0160 93rd & Morrill, SW SW SW 24-13S-15E, Wakarusa-7.5' quad, Shawnee Co., Kansas. Cut on county road at intersection of 93rd SW and Morrill, 0.1 miles west of AT&SF railroad. UI-loc. Z-3020. Utopia Limestone.

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