Standard Nomenclature and Metrics of Plane Shapes for Use in Gregarine Taxonomy

RICHARD E. CLOPTON

Department of Natural Science, Peru State College, Peru, Nebraska 68421, U.S.A. (e-mail: rclopton@oakmail.peru.edu)

ABSTRACT: Current practice in gregarine (Apicomplexa: Eugregarinorida) taxonomy does not include a standard nomenclature and metric set for plane shapes even though most taxonomic works within the group depend on shapebased descriptions. The lack of a uniform shape nomenclature and metric set has produced considerable confusion in gregarine systematics: descriptions of species often are not directly comparable even among congeneric taxa. As a step toward unifying taxonomic practice within Eugregarinorida, a standard nomenclature and metric set for 278 plane shapes in 23 shape series is delineated.

KEY WORDS: taxonomy, Apicomplexa, Eugregarinorida, Gregarine, shape, nomenclature.

Robust taxonomic description is the foundation of any biological study. Taxonomic studies of Eugregarinida usually depend on shape analysis and are often made difficult because there is neither an established set of morphometric landmarks for quantitative analysis nor a uniform shape nomenclature for categorical analysis. The lack of a uniform shape nomenclature and metric set has produced considerable confusion in gregarine systematics: descriptions of species often are not directly comparable even among congeneric taxa. Geometric morphometric analysis has undergone a revolution over the last decade, but multivariate techniques based on outline and landmark analysis have not been applied to gregarine systems. Thus, simple lengthwidth ratios and absolute size metrics remain the only morphometric landmarks for quantitative analysis. A uniform shape nomenclature for categorical analysis of gregarine form is possible and will significantly increase the comparative power and precision of gregarine taxonomy. Concomitant adoption of a standard metric set for standardized plane shapes in taxonomy is a first step toward meaningful landmark analysis within Eugregarinida.

METHODOLOGY

Herein, I propose both a standardized nomenclature and a metric set for plane shapes used in gregarine taxonomy. This nomenclature system is based on one proposed by the Committee for Descriptive Biological Terminology of the International Association for Plant Taxonomy (SA system) (Anonymous, 1962). Based on existing botanical systems, the SA system was innovative in its recognition that a single typological shape could be extended to form a shape series by warping the shape in a Cartesian plane according to predefined axial ratios. Thus, the SA system provided mechanisms for establishing both a quantitative categorical system for recognizing deviations from typological shape and a semistandard nomenclature for each member of a shape series. Designed for use in botanical taxonomy, the SA system is not readily applicable in zoological or protistan systems because it is limited to plane shapes without reentrant margins or distortions of the main axis. Thus, it is limited to 9 shape series, many of which are not encountered in zoology or protistology. However, I have used successfully a modified and expanded version of the SA system in eugregarine systematics for more than a decade (e.g., Clopton et al., 1993, 2004; Clopton, 1996, 1999, 2000, 2004; Kula and Clopton, 1999; Clopton and Nolte, 2002). My extended uniform nomenclature and metric system for plane shapes is presented in this study.

Axial ratios for warping typological shapes are consistent with those proposed by the Systematics Association Committee for Descriptive Biological Terminology (Anonymous, 1962). Typological shape names and derivations attempt to reconcile notions of shape terminology from established sources (Torre-Bueno, 1937; Harris and Harris, 1994; Hickey and King, 2000) with their use in a standard protistological benchmark reference (Kudo, 1946).

SHAPE NOMENCLATURE AND METRICS

The shape nomenclature system is divided into 23 shape series, each containing a typological base shape and up to 12 morphs produced by warping the typological shape using a standardized series of axial ratios (Tables 1–4). Equilateral shapes (1:1 length–width ratio) are denoted by a midline "x" in each







Table 3. Uniform nomenclature for vertically symmetrical plane shapes with reentrant margins.



table. Table 1 includes shape series without reentrant margins that are symmetrical along both vertical and horizontal axes. In these series the greatest lengths and widths always coincide with the vertical and horizontal axes of plane symmetry. Table 2 includes shape series without reentrant margins that are symmetrical along the vertical axis and asymmetrical along the horizontal axis. In these series the greatest length coincides with the vertical axis of plane symmetry, but the greatest width is displaced from the midpoint of the vertical axis of symmetry. Table 3 includes shape series with reentrant margins. The lomentiform series (series 15) is symmetrical along both the vertical and horizontal axes. The remaining series in Table 3 are symmetrical along the vertical axis and asymmetrical along the horizontal axis. For all series in Table 3, the greatest length coincides with the vertical axis of plane symmetry, but the greatest width is displaced from the midpoint of the vertical axis of symmetry. Table 4 includes shape series that are concavoconvex in nature. This table includes 3 typological series (series 18–20) that are symmetrical along the vertical axis and 3 derived asymmetrical series (series 21-23). In Tables 1-4, typological base shapes in each series are denoted by left cross-hatching. The system retains several specific terms (quadrate, orbicular, and quadratorhombiform) that apply to equilateral shapes with a 1:1 length-width ratio (denoted by right cross-hatching), even though they are part of a larger shape series. In general, the standard term for each shape is derived by combining the descriptors at the base of each vertical column (corresponding to a length-width ratio) with the name of the series given along the left margin. Length-width ratio columns are lettered, and individual shapes are numbered to facilitate their direct reference in the discussion below.

Series 1: Oblong (Table 1) This is essentially a rectangular series, but biological forms usually possess rounded corners rather than the 4 sharp right angles of a true rectangle or square. "Lorate" also has been used to describe this form in the botanical literature. Shape 7 (Table 1) is an equilateral shape for which the term quadrate is retained.

Metrics for the oblong series (Fig. 1) are as follows: length (L), distance along vertical axis of symmetry; and width (W), distance along horizontal axis of symmetry.

Series 2: Dolioform (Table 1) The dolioform series departs from the oblong series with the distinct symmetrical curvature of the lateral margins (Table 1). "Dolioform" refers to a "barrel shape," but "dolioform," "oblong," and "navicular" have been used interchangeably in the gregarine literature to describe shapes belonging to series 1–5 of the system described in this study. This mixed usage has been particularly problematic among taxa within *Gregarina*. Columns A and H of series 2 are not included because their shapes are nearly indistinguishable from columns A and H of series 1, respectively.

Metrics for the dolioform series (Fig. 2) are as follows: length (L), distance along vertical axis of symmetry; width (W), distance along horizontal axis of symmetry; and width of terminus (WTe), distance between apices along terminal margin.

Series 3: Elliptoid (Table 1) The elliptoid series departs from the dolioform series with the distinct symmetrical curvature of the terminal margins. This series includes the equilateral circle (shape 32, Table 1) for which the term orbicular is retained. The term oval has been used for some members of the elliptoid series but cannot be recommended because its use also encompasses some members of the dolioform (series 2, Table 1) series and ovoid series (series 7, Table 2). The elliptoid series gives rise to series 7–10 (Table 2) as the greatest horizontal axis of the typological shape moves away from the midpoint of the vertical axis of plane symmetry.

Metrics for the elliptoid series (Fig. 3) are as follows: length (L), distance along vertical axis of symmetry; and width (W), distance along horizontal axis of symmetry.

Series 4: Fusiform (Table 1) The typological base shape of the fusiform series represents the intersection of 2 circles, producing a shape that is similar to the ellipse (series 3C, Table 1) but with sharply pointed terminalia. The fusiform series departs from the dolioform series with the acuminate symmetrical curvature of the terminalia. Although distinctly different shapes, "fusiform" has been used interchangeably with "dolioform" and "navicular" in the gregarine literature. Column H of series 4 is not included because its shape is nearly indistinguishable from column H of series 3.

Metrics for the fusiform series (Fig. 4) are as follows: length (L), distance along vertical axis of symmetry; and width (W), distance along horizontal axis of symmetry.

Series 5: Rhomboid (Table 1) The series includes forms commonly referred to as diamond shaped. The equilateral shape (shape 56, Table 1) is technically not a rhombus but rather a quadrate form rotated 45°; nonetheless, it is a logical member of the series for which the term quadratorhombiform is retained. Columns A and H of series 5 are not included because their shapes are nearly indistinguishable from columns A and H of series 3, respectively. Metrics for the rhomboid series (Fig. 5) are as follows: length (L), distance along vertical axis of symmetry; and width (W), distance along horizontal axis of symmetry.

Rhomboid forms are plane shapes and not recommended for describing gregarine oocysts. Oocysts that appear rhomboid in lateral view are usually either bipyramidic (e.g., *Calyxocephalus* [see Clopton 2004]; *Nubenocephalus* [see Clopton et al. 1993]) or prismatic (e.g., *Prismatospora* [see Ellis 1914] 3dimensional forms. Bipyramidic forms are composed of 2 pyramids joined at their bases. In contrast, prismatic forms are composed of 2 terminal pyramids whose bases are joined along each edge by regular oblong facets. Descriptions of bipyramidic and prismatic oocysts should indicate the number of sides comprising each pyramid (inferred from equatorial cross sections of the oocyst) as well as the presence and form of any intercalating facet.

Series 6: Hesperidiform (Table 1) The typological base shape of the series has been called lemon shaped, but extensions of the series, particularly those in columns A and B, have been referred to as spindle shaped and fusiform (Table 1). Column H of series 6 is not included because its shape is nearly indistinguishable from column H of series 3.

Metrics for the hesperidiform series (Fig. 6) are as follows: length (L), distance along vertical axis of symmetry; width (W), distance along horizontal axis of symmetry; length of terminal knob (LTk), distance from terminus to base of terminal knob constriction; and width of terminal knob (WTk), horizontal distance from margin to margin at the proximal base of the terminal knob constriction.

Series 7 and 8: Ovoid and obovoid (Table 2) The ovoid and obovoid series are modifications of the elliptoid series in which the greatest horizontal axis is placed at one third of the distance along the vertical axis of symmetry from the posterior and anterior termina, respectively (Table 2). (In the elliptoid series, the greatest horizontal axis is placed at the midpoint of the vertical axis of symmetry.) As with the series presented in Table 1, the typological base shapes of the ovoid and obovoid series fall in column C, and the column descriptors (base of series 8, Table 2) are the same as those used in Table 1. Columns A and H are not included because their shapes are nearly indistinguishable from shapes established by other series.

Metrics for the ovoid and obovoid series (Figs. 7, 8) are as follows: length (L), distance along vertical axis of symmetry; equatorial width (WE), distance along horizontal axis at midpoint of vertical axis of symmetry; maximum width (WM), distance along horizontal axis at point of greatest width; anterior distance to maximum width (LAM), distance from anterior terminus to horizontal axis of greatest width; and posterior distance to maximum width (LPM), distance from posterior terminus to horizontal axis of greatest width;

Series 9 and 10: Deltoid and obdeltoid (Table 2) The deltoid and obdeltoid series are modifications of the elliptoid series in which the greatest horizontal axis is placed at one fourth of the distance along the vertical axis of symmetry from the posterior and anterior termina, respectively (Table 2). Additional series could be derived by varying the placement of the greatest horizontal axis, but series 3 (Table 1) and series 7–10 (Table 2) provide a broad range of shapes and, if necessary, could be combined (e.g., ovodeltoid) to create additional intermediate series as needed. The typological base shape of the deltoid and obdeltoid series are equilateral; thus, the column descriptors (base of series 12, Table 2) are expanded to accommodate the range of shapes in these series. Several additional terms are commonly used in gregarine taxonomy and are retained for members of the deltoid and obdeltoid series: "ensiform" for shape 96 (Table 2), "gladiate" for shape 97 (Table 2), and "spatulate" for shapes 110 and 111 (Table 2).

Figures 1–23. Standard metrics of plane shapes for use in gregarine taxonomy. Individual metrics are indicated using the typological base shape of each shape series. 1. Oblong series. 2. Dolioform series. 3. Elliptoid series. 4. Fusiform series. 5. Rhomboid series. 6. Hesperidiform series. 7. Ovoid series. 8. Obovoid series. 9. Deltoid series. 10. Obdeltoid series. 11. Trullate series. 12. Obtrullate series. 13. Pyriform series. 14. Panduriform series. 15. Lomentiform series. 16. Obpanduriform series. 17. Obpyriform series. 18. Falciform series. 19. Luniform series. 20. Crescentic series. 21. Semifalciform series. 22. Semiluniform series. 23. Semicrescentic series. Con, concavity; Cur, curvature; Cvx, convexity; L, length; LAC, anterior distance to constriction; LAM, anterior distance to maximum width of secondary hemisphere; LPC, posterior distance to constriction; LPM, posterior distance to maximum width of primary hemisphere; LPM2, posterior distance to maximum width of secondary hemisphere; LPM2, width; WC, constriction width; WM1, maximum width of terminal knob; W, width; WC, maximum width in primary hemisphere; WM2, maximum width in primary







←Crv+

-w



Metrics for the deltoid and obdeltoid series (Figs. 9, 10) are as follows: length (L), distance along vertical axis of symmetry; equatorial width (WE), distance along horizontal axis at midpoint of vertical axis of symmetry; maximum width (WM), distance along horizontal axis at point of greatest width; anterior distance to maximum width (LAM), distance from anterior terminus to horizontal axis of greatest width; and posterior distance to maximum width (LPM), distance from posterior terminus to horizontal axis of greatest width.

Series 11 and 12: Trullate and obtrullate (Table 2) These are essentially triangular series with rounded apices. As with series 9 and 10 (Table 2), the typological base shape of the trullate and obtrullate series are equilateral and the column descriptors (base of series 12, Table 2) are expanded to accommodate the range of shapes in these series.

Metrics for the trullate and obtrullate series (Figs. 11, 12) are as follows: length (L), distance along vertical axis of symmetry; and width (W), distance along typological base.

Series 13 and 17: Pyriform and obpyriform (Table 3) All the shapes in Table 3 are derived from elliptoid forms with the addition of a distinct constriction. The pyriform and obpyriform series (Table 3) are horizontally constricted in the terminal one third of the vertical axis of symmetry with reentrant postconstriction margins. Series 13 is constricted in the anterior one third of the vertical axis of symmetry, whereas series 17 is constricted in the posterior one third of the vertical axis of symmetry. Although literally "pear shaped," "pyriform" has also been used to identify "flame-like" shapes with acuminate anterior margins rather than the rounded margins illustrated in Table 3. Rather than distinguish another typological base shape and series, "flame-like" shapes should be described as pyriform or obpyriform with acuminate, aristate, or cuspidate anterior or posterior apices, as appropriate.

Metrics for the pyriform and obpyriform series (Figs. 13, 17) are as follows: length (L), distance along vertical axis of symmetry; equatorial width (WE), distance along horizontal axis at midpoint of vertical axis of symmetry; maximum width (WM), distance along horizontal axis at point of greatest width; constriction width (WC), distance along horizontal axis at point of greatest width; constriction (LAC), distance from anterior distance to constriction (LPC), distance from posterior terminus to horizontal axis of greatest constriction; posterior distance to constriction (LPC), distance from posterior terminus to horizontal axis of greatest constriction; anterior distance to maximum width (LAM), distance

from anterior terminus to horizontal axis of greatest width; and posterior distance to maximum width (LPM), distance from posterior terminus to horizontal axis of greatest width.

Series 14 and 16: Panduriform and obpanduriform (*Table 3*) The panduriform and obpanduriform series (Table 3) are horizontally constricted in the terminal one third of the vertical axis of symmetry with reemergent postconstriction margins. Series 14 is constricted in the anterior one third of the vertical axis of symmetry, whereas series 16 is constricted in the posterior one third of the vertical axis of symmetry.

Metrics for the panduriform and obpanduriform series (Figs. 14, 16) are as follows: length (L), distance along vertical axis of symmetry; equatorial width (WE), distance along horizontal axis at midpoint of vertical axis of symmetry; maximum width in primary hemisphere (WM1), distance along horizontal axis at point of greatest width of primary (largest) hemisphere; maximum width in secondary hemisphere (WM2), distance along horizontal axis at point of greatest width of secondary hemisphere; constriction width (WC), distance along horizontal axis at point of greatest constriction; anterior distance to constriction (LAC), distance from anterior terminus to horizontal axis of greatest constriction; posterior distance to constriction (LPC), distance from posterior terminus to horizontal axis of greatest constriction; anterior distance to maximum width of primary hemisphere (LAM1), distance from anterior terminus to horizontal axis of greatest width of primary hemisphere; posterior distance to maximum width of primary hemisphere (LPM1), distance from posterior terminus to horizontal axis of greatest width of primary hemisphere; anterior distance to maximum width of secondary hemisphere (LAM2), distance from anterior terminus to horizontal axis of greatest width of secondary hemisphere; and posterior distance to maximum width of secondary hemisphere (LPM2), distance from posterior terminus to horizontal axis of greatest width of secondary hemisphere.

Series 15: Lomentiform (Table 3) Shapes in the lomentiform series (Table 3) are horizontally constricted at the midpoint of the vertical axis of symmetry with reemergent postconstriction margins. Of all the shapes considered in this study, the lomentiform series is associated with the widest variety of synonyms in the gregarine literature, including "biscuit shaped," "lozenge shaped," "cookie shaped," and "dumbbell shaped."

Metrics for the lomentiform series (Fig. 15) are as

follows: length (L), distance along vertical axis of symmetry; equatorial width (WE), distance along horizontal axis of symmetry at midpoint of vertical axis of symmetry; maximum width in anterior hemisphere (WM1), distance along horizontal axis of symmetry at point of greatest width of anterior hemisphere; maximum width in posterior hemisphere (WM2), distance along horizontal axis of symmetry at point of greatest width of posterior hemisphere; constriction width (WC), distance along horizontal axis of symmetry at point of greatest constriction; anterior distance to constriction (LAC), distance from anterior terminus to horizontal axis of greatest constriction; posterior distance to constriction (LPC), distance from posterior terminus to horizontal axis of greatest constriction; anterior distance to maximum width of anterior hemisphere (LAM1), distance from anterior terminus to horizontal axis of greatest width of anterior hemisphere; posterior distance to maximum width of anterior hemisphere (LPM1), distance from posterior terminus to horizontal axis of greatest width of anterior hemisphere; anterior distance to maximum width of posterior hemisphere (LAM2), distance from anterior terminus to horizontal axis of greatest width of posterior hemisphere; and posterior distance to maximum width of posterior hemisphere (LPM2), distance from posterior terminus to horizontal axis of greatest width of posterior hemisphere.

Series 18-23: Falciform, luniform, crescentic, semifalciform, semiluniform, and semicrescentic (Table 4) Falciform, luniform, and crescentic shapes are encountered primarily among the oocysts of Menosporinae, but they logically give rise to series 21-23, which are of broader use in describing gregarine hook shapes (Table 4). Series 18-23 are all derivations of the fusiform series created by warping the figure to bring the terminal ends together and form a convexoconcave shape. Falciform, luniform, and crescentic typological base shapes differ primarily in the eccentricity of the concavoconvex shape. Semifalciform, semiluniform, and semicrescentic typological base shapes are derived by splitting the parent base shapes along their line of symmetry. The typological base shapes of series 18-23 have a length-width ratio of 5:6 (column E, Table 4). This displacement of the typological base shape relative to Table 1 is accommodated by an alteration of column descriptors (base of series 23, Table 4) consistent with those used in Table 2.

Metrics for the falciform, luniform, crescentic, semifalciform, semiluniform, and semicrescentic series (Figs. 18–23) are as follows: length (L), distance along greatest absolute vertical axis; width (W), distance along greatest absolute horizontal axis; curvature(Cur), distance from "tip-to-tip" along basal horizontal axis; convexity (Cvx), distance along the vertical axis of symmetry; and concavity (Con), distance from interior concave margin to basal horizontal axis along the vertical axis of symmetry.

CONCLUDING REMARKS

The shape nomenclature and metrics described in this study can be used to describe gregarine forms both categorically and quantitatively. In general, a gregarine form is broken into components and described in posteriad sequence from the anterior end, beginning with the epimerite and followed by the diamerite, protomerite, and deutomerite, as appropriate. Each component is assigned a standard shape or shape range accompanied by appropriate morphometric data and marginal irregularities. The metrics delineated in this study provide data suitable for landmark, multivariate, or geometric shape analysis in subsequent taxonomic or systematic studies. Although developed primarily for use in gregarine taxonomy, the system described could be adopted and used effectively in a broader protistological or helminthological context.

ACKNOWLEDGMENTS

I gratefully acknowledge Associate Editor Dennis J. Richardson for taking full editorial responsibility of the manuscript, thus allowing me to support the Helminthological Society of Washington through publication in *Comparative Parasitology*. This material is based in part on work supported by the National Science Foundation under Grant No. 9705179. Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author and do not necessarily reflect the views of the National Science Foundation.

LITERATURE CITED

- Anonymous. 1962. Report of the Systematics Association Committee for Descriptive Biological Terminology, II and IIa. Terminology of simple symmetrical plane shapes (Charts 1, 1a). Taxon 11:145–155, 245– 247.
- Clopton, R. E. 1996. Leidyana migrator n. sp. (Apicomplexa: Leidyanidae) from the Madagascar hissing cockroach, Gromphadorhina portentosa (Insecta: Blattodea). Invertebrate Biology 114:271–278.
- Clopton, R. E. 1999. Revision of the genus Xiphocephalus and description of Xiphocephalus ellisi n. sp. (Apicomplexa: Eugregarinida: Stylocephalidae) from Eleodes opacus (Coleoptera: Tenebrionidae) in the

western Nebraska Sandhills. Journal of Parasitology 85:84-89.

- Clopton, R. E. 2000. Stylocephalus occidentalis n. sp. (Apicomplexa: Eugregarinida: Stylocephalidae) from Trimytis pruinosa (Coleoptera: Tenebrionidae) in the Nebraska Sandhills. Journal of Parasitology 86:560– 565.
- Clopton, R. E. 2004. Calyxocephalus karyopera g. nov., sp. nov. (Eugregarinorida: Actinocephalidae: Actinocephalinae) from the ebony jewelwing damselfly Calopteryx maculata (Zygoptera: Calopterygidae) in southeast Nebraska: implications for mechanical prey-vector stabilization of exogenous gregarine development. Comparative Parasitology 71:141–153.
- Clopton, R. E., T. J. Cook, and J. L. Cook. 2004. Naiadocystis phykoterion n. gen., n. sp. (Apicomplexa: Eugregarinida: Hirmocystidae) from the Mexican Pygmy Grasshopper Paratettix mexicanus (Orthoptera: Tetrigidae) in the Texas Big Thicket with recognition of three previously described species of Naiadocystis. Journal of Parasitology 90:301–307.
- Clopton, R. E., and C. M. Nolte. 2002. Clitellocephalus americanus n. gen., n. sp. (Apicomplexa: Eugregarinida: Gregarinidae) from Cratacanthus dubius (Coleoptera: Carabidae: Harpalinae) in the Nebraska Sandhills and Clitellocephalus ophoni n. comb. (Apicomplexa: Eugregarinida: Gregarinidae) from Ophonus pubescens (Coleoptera: Carabidae: Harpali-

nae) in Sète, France. Journal of Parasitology 88:750-757.

- Clopton, R. E., T. J. Percival, and J. Janovy Jr. 1993. Nubenocephalus nebraskensis n. gen., n. sp. (Apicomplexa: Actinocephalidae) from adults of Argia bipunctulata (Odonata: Zygoptera). Journal of Parasitology 79:533–537.
- **de la Torre-Bueno, J. R.** 1937. A Glossary of Entomology: Smith's "An Explanation of Terms Used in Entomology" Completely Revised and Rewritten. Brooklyn Entomological Society, Brooklyn, New York. ix plates + 336 pp.
- Ellis, M. M. 1914. An acanthosporid gregarine from North American dragonfly nymphs. Transactions of the American Microscopical Society 33:215–222.
- Harris, J. G., and M. W. Harris. 1994. Plant Identification Terminology: An Illustrated Glossary. Spring Lake Publishing, Payson, Utah. 198 pp.
- Hickey, M., and C. King. 2000. The Cambridge Illustrated Glossary of Botanical Terms. Press Syndicate of the University of Cambridge, Cambridge, U.K. 208 pp.
- Kudo, R. R. 1946. Protozoology, 3rd ed. Charles C. Thomas, Springfield, Illinois. 778 pp.
- Kula, R. R., and R. E. Clopton. 1999. Amoebogregarina nigra n. gen., n. comb. (Apicomplexa: Gregarinidae) from adult Melanoplus differentialis (Orthoptera: Acrididae) in southeastern Nebraska. Journal of Parasitology 85:321–325.