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Two types of uncini in *Polycirrus* (Polychaeta: Terebellidae: Polycirrinae) revealed using geometric morphometrics

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Abstract

Geometric morphometric methods were used to investigate shape variation in the neuropodial chaetae (uncini) of the polychaete genus *Polycirrus* (Terebellidae: Polycirrinae). Illustrations of 82 uncini from 47 specimens/taxa (one to three uncini per specimen/taxon) were digitized and 10 landmarks, representing putatively homologous points, were identified on the outline of each uncinus. Two distinct types of uncini were identified and described graphically using a Principal Component technique (Relative Warps Analysis) and non-metric ordination (multi-dimensional scaling). Type 1 uncini with a short occipitium and flat base and Type 2 with a long occipitium and arched base represent states of a new character available for future phylogenetic studies of the group. The shape of the uncini alone subdivided the genus into two groups, one containing 14 taxa and another with 33 taxa. The type of uncini correlated well with the presence of long pinnate notochaetae and the last occurrence of notopodia, enabling further subdivision of the genus into four provisional groups; a key is provided to distinguish the groups. The landmarks identified on the surface of *Polycirrus* uncini are considered homologous with those on the uncini of other Terebellidae and therefore landmark-based geometric morphometrics could be applied to investigate shape changes in other uncini-bearing Terebellidae.

Keywords: Geometric morphometrics, multi-dimensional scaling, Polychaeta, Polycirrinae, *Polycirrus*, Terebellidae, uncini

Introduction

Polycirrus Grube is one of the most species-rich terebellid genera with about 65 species worldwide. Species occur from the intertidal to depths exceeding 1500 m, often in soft sediments, but may also be found on reefs associated with algae, sessile invertebrates, dead shells, and coral. *Polycirrus* species have reduced parapodia bearing finely sculptured bristles in the dorsal position (notochaetae) and hook-like uncini in the ventral position

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(neurochaetae). The uncini are thought to be homologous with uncini/hooks in other groups of polychaetes (Bartolomaeus 1995; Meyer and Bartolomaeus 1996) now collectively referred to as Canalipalpata, which includes most of the tube-dwelling polychaetes; their likely function is to anchor the worm and prevent it from being dislodged from its tube (Woodin and Merz 1987; Merz and Woodin 2000). However, *Polycirrus* are unusual in that they do not live in obvious tubes, although they may construct a temporary mucous sheath (Holthe 1986a; C. J. Glasby, personal observation); this may explain the extremely small size of the uncini of *Polycirrus* which have been reduced through redundancy. The small uncini and the lack of other features often associated with Terebellidae (branchiae, cephalic lobes) makes *Polycirrus* species difficult to identify.

Polycirrus has had a complicated and somewhat confused taxonomic history. Since its original circumscription by Grube (1850), 10 other genera have been proposed to encompass the same or similar concepts, including *Anisocirrus* Gravier, *Aphlebina* Quatrefages, *Apneuma* Quatrefages, *Cyaxares* Kinberg, *Dejoces* Kinberg, *Ereutho* Malmgren, *Leucariste* Malmgren, *Litancyra* Hutchings, *Torquea* Leidy, and *Pseudoampharete* Hartmann-Schröder. All of these genera are now considered junior synonyms of *Polycirrus* (Hessle 1917; Holthe 1986a; Hutchings and Glasby 1986), although in the opinion of Hessle (1917), *Anisocirrus* represented by *Anisocirrus decipiens* Gravier was separable and he retained it as valid genus. However, only *Pseudoampharete*—represented by a single species, *P. tentaculata*—has been shown by cladistic analysis to actually share a phylogenetic history (sister-group relationship) with other *Polycirrus* species (Glasby et al. 2004).

In a notable attempt to subdivide the genus into smaller ‘natural’ subunits, Caullery (1915) erected three subgenera (*Polycirrus*, *Ereutho*, and *Leucariste*), based primarily on the segment on which the uncini first appear in relation to the distribution of segments bearing notochaetae. Thus, species of *Ereutho* have uncini starting on segments after the last notochaetigerous segment whereas species of *Polycirrus* and *Leucariste* have uncini starting on segments prior to the last notochaetigerous segment; in *Polycirrus* uncini start on chaetigerous segments 7–10 (=segments 8–12, assuming the first notochaetiger may occur on body segment 2 or 3) and in *Leucariste* uncini appear on chaetigerous segment 13 (=segment 14 or 15). Despite the apparent utility of the classification, Caullery’s taxonomic schema has not been adopted because a few species, including those identified herein and *Polycirrus twisti*, could not be allocated into this classification (Potts 1928). Further, and most importantly, his schema was based on only two characters, and without phylogenetic support for the sub-groupings most taxonomists have been reluctant to adopt them. Nevertheless, in order to provide an historical context and evaluate further his taxonomy we have applied Caullery’s subgeneric names to the *Polycirrus* species considered in this study (Table I).

Before a phylogenetic analysis of the group can take place, however, it is necessary to identify a sufficient number of good cladistic characters, i.e. characters that are independent, not linked by development or selection. An early attempt at a cladistic analysis of the Polycirrinae including *Polycirrus* was uninformative in terms of identifying relationships within the genus primarily because of insufficient numbers of characters in relation to numbers of species (Hutchings and Glasby 1991). The present study attempts to redress this situation by re-assessing characters associated with the form and position of chaetae. Characters selected include the shape of the uncini, the presence/absence of pinnate notochaetae, the first and last occurrence of notopodia, and the first occurrence of neuropodia. These characters were chosen because they have been used in previous

Table I. *Polycirrus* taxa included in the study, subgenus classification after Caullery (1915), and source of illustrations of uncini (literature or specimen illustrated by C. J. Glasby and P. A. Hutchings, unpublished).

| Uncinus number ^a | Species/subspecies | Subgenus | Illustration source |
|-----------------------------|---|-------------------|--|
| 1 | <i>P. albicans</i> (Malmgren, 1866) | <i>Leucariste</i> | Type? SSM 6738, No. 7726 |
| 2 | <i>P. antarctica</i> (Willey, 1902) | <i>Ereutho</i> | Willey (1902, Figure 6) |
| 3–4 | <i>P. aquila</i> Caullery, 1944 | <i>Ereutho</i> | Holotype ZMA Vpol 1532 |
| 5–7 | <i>P. arenivorus</i> Caullery, 1915 | <i>Leucariste</i> | MHNH? Type unreg. |
| 8–9 | <i>P. aurantiacus</i> Grube, 1860 | <i>Polycirrus</i> | Syntypes ZMB Q4999 |
| 10 | <i>P. bicrinalis</i> Hutchings and Glasby, 1986 | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 6e) |
| 11–12 | <i>P. boholensis</i> Grube, 1878 | <i>Ereutho</i> | Holotype ZMB 10654 |
| 13–15 | <i>P. broomensis</i> Hartmann-Schröder, 1979 | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 7c) |
| 16–18 | <i>P. californicus</i> Moore, 1909 | <i>Polycirrus</i> | Holotype CAS 005272 |
| 19–20 | <i>P. carolinensis</i> Day, 1973 | <i>Polycirrus</i> | Holotype USNM 43122 |
| 21–22 | <i>P. chilensis</i> Schmarda, 1861 | <i>Polycirrus</i> | Holotype SSM 571 |
| 23 | <i>P. clavatus</i> (Kinberg, 1867) | <i>Polycirrus</i> | Type? SSM 993 |
| 24 | <i>P. coccineus</i> Grube, 1870 | <i>Ereutho</i> | Holotype ZMB 529 |
| 25 | <i>P. disjunctus</i> Hutchings and Glasby, 1986 | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 7j) |
| 26 | <i>P. dodeka</i> Hutchings, 1990 | <i>Ereutho</i> | Hutchings (1990, Figure 1c) |
| 27–29 | <i>P. eximia dubius</i> Day, 1973 | <i>Polycirrus</i> | Holotype USNM 43130 |
| 30 | <i>P. glaucus</i> Hutchings, 1993 | <i>Ereutho</i> | Hutchings (1993, Figure 1c) |
| 31 | <i>P. haematodes</i> (Claparède, 1864) | <i>Leucariste</i> | Non-type BMNH ZK 1921.5.1.4119 |
| 32–33 | <i>P. hamiltoni</i> Benham, 1921 | <i>Polycirrus</i> | Syntype OM W611 |
| 34–35 | <i>P. hesslei</i> Monroe, 1930 | <i>Ereutho</i> | Syntype BMNH ZK1930.10.8. 2911–15 |
| 36 | <i>P. insignis</i> Gravier, 1907 | <i>Ereutho</i> | Hartman (1966, Plate 35, Figure 10) |
| 37 | <i>P. kerguelensis</i> McIntosh, 1885 | <i>Ereutho</i> | Holotype BMNH 1885.12.1.372 |
| 38 | <i>Ereutho kergeulensis</i> McIntosh, 1885 | <i>Ereutho</i> | McIntosh (1885, Figure 21) |
| 39–41 | <i>P. latidens</i> Eliason, 1962 | <i>Ereutho</i> | Holotype UUZM 196a |
| 42–43 | <i>P. luminosus</i> Verrill, 1900 | <i>Polycirrus</i> | Non-type YPM 1311 from type locality |
| 44–45 | <i>P. medius</i> Hesse, 1917 | <i>Leucariste</i> | Type? UUZM nv 183a |
| 46 | <i>P. medusa</i> Grube, 1850 | <i>Ereutho</i> | Holthe (1986b, Figure 71d) |
| 47–48 | <i>P. multisetigerous</i> Hartmann-Schröder, 1962 | <i>Polycirrus</i> | Holotype HZM P15172 |
| 49 | <i>P. multus</i> Hutchings, 1990 | <i>Leucariste</i> | Hutchings (1990, Figure 2c) |
| 50 | <i>P. nephrosus</i> Hutchings and Glasby, 1986 | <i>Leucariste</i> | Hutchings and Glasby (1986, Figure 8e) |

Table I. (Continued.)

| Uncinus number ^a | Species/subspecies | Subgenus | Illustration source |
|-----------------------------|---|-------------------|--|
| 51–53 | <i>P. nervosus</i> Marenzeller, 1884 | <i>Leucariste</i> | Syntype? MMW 1794 |
| 54–55 | <i>P. norvegicus</i> Wollebaek, 1912 | <i>Polycirrus</i> | Type ZMO C3205 |
| 56 | <i>P. octoseta</i> (Hutchings, 1977) | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 8j) |
| 57 | <i>P. parvus</i> Hutchings and Glasby, 1986 | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 9d) |
| 58 | <i>P. paucidens</i> Hutchings and Glasby, 1986 | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 9k) |
| 59–60 | <i>P. perplexus</i> Moore, 1923 | <i>Polycirrus</i> | Holotype USNM 17366 |
| 61–62 | <i>P. phosphoreus</i> Verrill, 1880 | <i>Polycirrus</i> | Type USNM 9275 |
| 63–64 | <i>P. plumosus</i> (Wollebaek, 1912) | <i>Ereutho</i> | Holthe (1986b, Figure 73d) |
| 65 | <i>P. porcata</i> Knox and Cameron, 1971 | <i>Polycirrus</i> | Hutchings and Glasby (1986, Figure 10b) |
| 66–68 | <i>P. pumilis</i> Hartmann-Schröder, 1990 | <i>Polycirrus</i> | Hartmann-Schröder (1990, Figure 43) |
| 69–71 | <i>P. purpureus</i> Schmarda, 1861 | <i>Leucariste</i> | Type NMW 1795 |
| 72 | <i>P. quadratus</i> Hutchings, 1990 | <i>Ereutho</i> | Hutchings (1990, Figure 3c) |
| 73 | <i>P. rosea</i> Hutchings and Murray, 1984 | <i>Polycirrus</i> | Hutchings and Murray (1984, Figure 25.5) |
| 74–76 | <i>P. swakopianus</i> Augener, 1918 | <i>Polycirrus</i> | Type HZM V8802 |
| 77–78 | <i>P. tesselatus</i> Hutchings and Glasby, 1986 | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 10k) |
| 79–80 | <i>P. twisti</i> Potts, 1928 | Unplaced | Potts (1928, Figure 212) |
| 81–82 | <i>P. variabilis</i> Hutchings and Glasby, 1986 | <i>Ereutho</i> | Hutchings and Glasby (1986, Figure 11e, g) |

^aUncinus number corresponds to numbers in Figure 2. Institutional abbreviations: AM, Australian Museum, Sydney; BMNH, The Natural History Museum, London; CAS, California Academy of Sciences, San Francisco; HZM, Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg; MNHN, Muséum National d'Histoire Naturelle, Paris; NMW, Naturhistorisches Museum Wien, Vienna; OM, Otago Museum, Dunedin; SSM, Naturhistoriska Riksmuseet, Stockholm; USNM, National Museum of Natural History, Washington DC; UUZM, Uppsala Universitets Zoologiska Museum, Uppsala; YPM, Peabody Museum of Natural History, Yale University, New Haven; ZMA, Zoölogisch Museum, Instituut voor Taxonomische Zoölogie, Universiteit van Amsterdam, Amsterdam; ZMB, Zoologisches Museum, Universität Humboldt, Berlin (now Museum für Naturkunde, Institut für Systematische Zoologie); ZMO, Zoologisk Museum, Universitetet i Oslo, Oslo.

taxonomic studies in both keys and classifications, and some at least appear to exhibit a degree of correlation among species (Hutchings and Glasby 1986; C. J. Glasby, personal observation).

We use the method of geometric morphometrics (Bookstein 1991) to explore shape variation in *Polycirrus uncini* and to identify and characterize the different types of uncini in a rigorous, repeatable way. Geometric morphometrics is preferred over traditional morphometrics for several reasons. It can better correct for the effect of size of an individual or structure, results can be more easily interpreted in an evolutionary context because shape change is based on an analysis of homologous points, and it enables graphical representations of shape differences whereas traditional techniques reduce forms to a set of numbers (Rohlf and Marcus 1993; Adams et al. 2004). In addition to quantifying the shape variation of the uncini of *Polycirrus* using landmark-based geometric morphometrics, we also investigate whether, and to what extent, the shape of uncini is correlated with other characters associated with the form and position of both noto- and neurochaetae. In this way we hope to discover new suites of characters available for future phylogenetic studies of the group. In addition, an interim phenetic sub-division of the genus based on characters identified here will facilitate identification of members of the group in lieu of a phylogenetic classification.

Materials and methods

Polychaete material

Forty-seven species/subspecies of *Polycirrus* from all over the world were used in the analysis. For each taxon, one to three uncini were examined from neuropodia of the mid-body (posterior thorax to the mid-abdomen) from a single individual specimen, usually the type (Table I). Variation in the shape of uncini within a specimen was accounted for in 26 species but for the remainder only a single uncinus was used (Table I). Eighteen nominal species of *Polycirrus* were excluded from the study, either because type material could not be located or because type illustrations in the literature were unavailable or thought to be inaccurate (see Appendix).

Data scoring and acquisition

Illustrations of uncini were obtained mainly from Hutchings and Glasby (1986) and a revision of *Polycirrus* types currently in preparation by C. J. Glasby and P. A. Hutchings. For a few species, illustrations of uncini were taken from other literature (Table I). Illustrations were digitized at 635 dpi and the images scaled and reorientated in CorelDRAW™ 7. Digitized landmark coordinates—for a definition see next section—were placed on the images, and transformed into x , y coordinates using OPTIMAS™ 6.0 (data matrix available at <http://www.nt.gov.au/nreta/museums/magnt/collectionsresearch/naturalsciences/annelids.html>). Terminology associated with the different regions of the uncini follows Holthe (1986a) as it provides sufficient detail to enable an effective description of shape changes.

Data for other chaetal characters used in this study—the first appearance of notopodia and neuropodia and the last occurrence of notopodia—were obtained from the literature (e.g. Caullery 1915; Holthe 1986a, 1986b; Hutchings and Glasby 1986) (Table II). *Polycirrus* exhibit a range of different types of notochaetae including smooth, hirsute, and

Table II. Distribution of selected character states in relation to uncinus type for *Polycirrus* species. Species arranged alphabetically according to the provisional groups identified in the key.

| Provisional taxonomic group | Species | Shape of uncini | Pinnate notochaetae in posterior fascicle | Pinnate notochaetae in anterior fascicle | First notopodial segment | Last notopodial segment | First neuropodial segment |
|-----------------------------|--------------------------|-----------------|---|--|--------------------------|-------------------------|---------------------------|
| 1A | <i>albicans</i> | Type 1 | A | A | 3 | 18 | 16 |
| 1A | <i>antarcticus</i> | Type 1 | A | A | 3 | 11 | 16 |
| 1A | <i>bicrinalis</i> | Type 1 | A | P | 3 | 14–16 | 17–20 |
| 1A | <i>broomensis</i> | Type 1 | A | P | 2 | 12 | 14 |
| 1A | <i>dodeka</i> | Type 1 | A | A | 2 | 12 | 14 |
| 1A | <i>haematodes</i> | Type 1 | A | A | 2 | 16 | 11 |
| 1A | <i>hesslei</i> | Type 1 | A | A | 2 | 13 | 15 |
| 1A | <i>insignis</i> | Type 1 | A | A | 3 | 11 | 14–15 |
| 1A | <i>kerguelensis</i> | Type 1 | A | A | 3 | 11 | 14 |
| 1A | (E.) <i>kerguelensis</i> | Type 1 | A | A | 2 | 13 | 6 |
| 1A | <i>latidens</i> | Type 1 | A | A | 3 | 12 | 14 |
| 1A | <i>medusa</i> | Type 1 | A | A | 3 | 10–13 | 13–16 |
| 1A | <i>nephrosus</i> | Type 1 | A | A | U | ~18 | ~14 |
| 1A | <i>norvegicus</i> | Type 1 | A | A | 3 | 16 | 10–15 (?) |
| 1A | <i>plumosus</i> | Type 1 | A | P | 2 | 17–19 | 18–20 |
| 1A | <i>rosea</i> | Type 1 | A | A | 2 | 10 | 10–11 |
| 1A | <i>variabilis</i> | Type 1 | A | A | 3 | 10–17 | 15–19 |
| 1B | <i>arenivorus</i> | Type 1 | A | A | 2 | 29 | 12 |
| 1B | <i>aurantiacus</i> | Type 1 | A | A | 3 | 46 | 14 |
| 1B | <i>californicus</i> | Type 1 | A | A | 3 | 28 | 7 |
| 1B | <i>carolinensis</i> | Type 1 | A | P | 2 | 29 | 8 |
| 1B | <i>chilensis</i> | Type 1 | A | P | 2 | 35–37 | 8 |
| 1B | <i>eximia dubius</i> | Type 1 | A | A | 2 | 31 | 10 |
| 1B | <i>hamiltoni</i> | Type 1 | A | P | 3 | 30–34 | 8 |
| 1B | <i>luminosus</i> | Type 1 | A | A | 3 | 25 | 10 |
| 1B | <i>multisetigerous</i> | Type 1 | A | P | 2 | 48 | 8 |
| 1B | <i>multus</i> | Type 1 | A | A | 2 | 30 | 14 |
| 1B | <i>nervosus</i> | Type 1 | A | A | 3 | 42 | 15 |
| 1B | <i>perplexus</i> | Type 1 | A | A | 3 | 42 | 10 |
| 1B | <i>phosphoreus</i> | Type 1 | A | A | 2 | 24 | 10 |
| 1B | <i>purpureus</i> | Type 1 | A | A | 3 | 82–84 | 14 |
| 1B | <i>swakopiamus</i> | Type 1 | A | A | 2 | 26 | 7 |
| 1B | <i>tesselatus</i> | Type 1 | A | A | 3 | 10–16 | 10–16 (?) |
| 2A | <i>aquila</i> | Type 2 | P | P | 3 | 16 | 17 |
| 2A | <i>boholensis</i> | Type 2 | P | A | 2 | 10–12 | 14 |
| 2A | <i>clavatus</i> | Type 2 | P | P | U | 14+ | 4–5 |
| 2A | <i>coccineus</i> | Type 2 | P | P | 2 | ~20 | 20 |
| 2A | <i>disjunctus</i> | Type 2 | P | A | 3 | 10–11 | 10–14 (?) |
| 2A | <i>glaucus</i> | Type 2 | P | P | 3 | 11 | 14 |
| 2A | <i>medius</i> | Type 2 | P | P | 2 | 17 | 15 |
| 2A | <i>pumilis</i> | Type 2 | P | U | 3 | 10–11 | 7 |
| 2A | <i>twisti</i> | Type 2 | P | A | 3 | 10 | ? |
| 2B | <i>octoseta</i> | Type 2 | A | A | 3 | 8 | 10 |
| 2B | <i>parvus</i> | Type 2 | A | A | 3 | 9–13 | 14 |
| 2B | <i>paucidens</i> | Type 2 | A | A | 3 | 7–9 | 14 |
| 2B | <i>porcata</i> | Type 2 | A | A | 3 | 12 | 6 |
| 2B | <i>quadratus</i> | Type 2 | A | A | 2 | 12 | 14 |

Type 1 uncini, short neck and flat base; Type 2 uncini, long neck and arched base; P, present; A, absent; U, unknown; ?, uncertain.

pinnate types; the pinnate types are the most characteristic as they are found only in *Polycirrus* and their putative sister-group *Lysilla* (Glasby et al. 2004). Thus the presence or absence of pinnate notochaetae was considered an important character to include in the study. Pinnate notochaetae appear to be present in the genus in two different lengths—relatively long pinnates in the posterior fascicle (or row) of the notopodia and shorter pinnates in the anterior fascicle; in small specimens the two fascicles per se are difficult to distinguish but the two different length chaetae are evident. Pinnate-type notochaetae, as observed in light microscopy, have also been referred to in the taxonomic literature as spinose or corn-eared chaetae; they appear to comprise overlapping spiral palisades in three-dimensional scanning electron micrographs (Hutchings and Glasby 1986, Figure 4b).

Landmark selection

Landmarks are discrete points on the outline of a biological structure that can be recognized as the same (homologous) among different taxa. Ten landmarks were identified on digitized images of the uncini for each specimen in order to capture information about the positions of: (1) attachment points of tendons or muscles (Bookstein Type I Landmark); (2) points of sharpest curvature (Type II); and (3) extreme points, or points taken as farthest from other points (Type III). Using Bookstein's categories two landmarks were classified Type I (apex of anterior process, apex of posterior process), five were classified as Type II (junction between rostrum and capitulum, apex of primary capitulum, apex of rostrum, junction between rostrum and upper subrostrum, junction between occipitum and posterior process), one was Type I or II (subrostral process), and two were Type II or III (junction between base and posterior process, mid-occipitum) (Figure 1a–c). No landmarks above the primary capitulum were identified because many *Polycirrus* species lack secondary rows of teeth. These 10 landmarks probably represent the minimum set of homologous points on all uncini-bearing Terebellidae; indeed terebellids with teeth above the primary capitulum will have more landmarks.

Reference configuration

The Reference form selected—the average shape of the uncini of all specimens (Figure 1d)—was chosen as it minimizes the average distortion of distances between specimens and ensures that Euclidean distances in the tangent space are accurate approximations of the distances in shape space (Bookstein 1996; Rohlf 1998; Zelditch et al. 2004). Shapes of all uncini were aligned to the shape of the ‘reference’ uncinus using generalized orthogonal least-squares Procrustes superimposition; the alignment step and calculation of the reference configuration is built into the Thin-Plate Spline programs (see below). Procrustes analysis takes the digital raw data and turns it into coordinate data including non-affine (=non-uniform) shape components and affine (=uniform) shape components; shape changes related to location, orientation, and size were normalized. The non-affine shape components are the partial warps (below). See Bookstein (1991, 1996) for further details.

Morphometric and statistical analyses

Relative Warps Analysis (RWA; Bookstein 1991) was used to describe the shape variation between uncini. As the components of variance extracted by RWA were unweighted, as

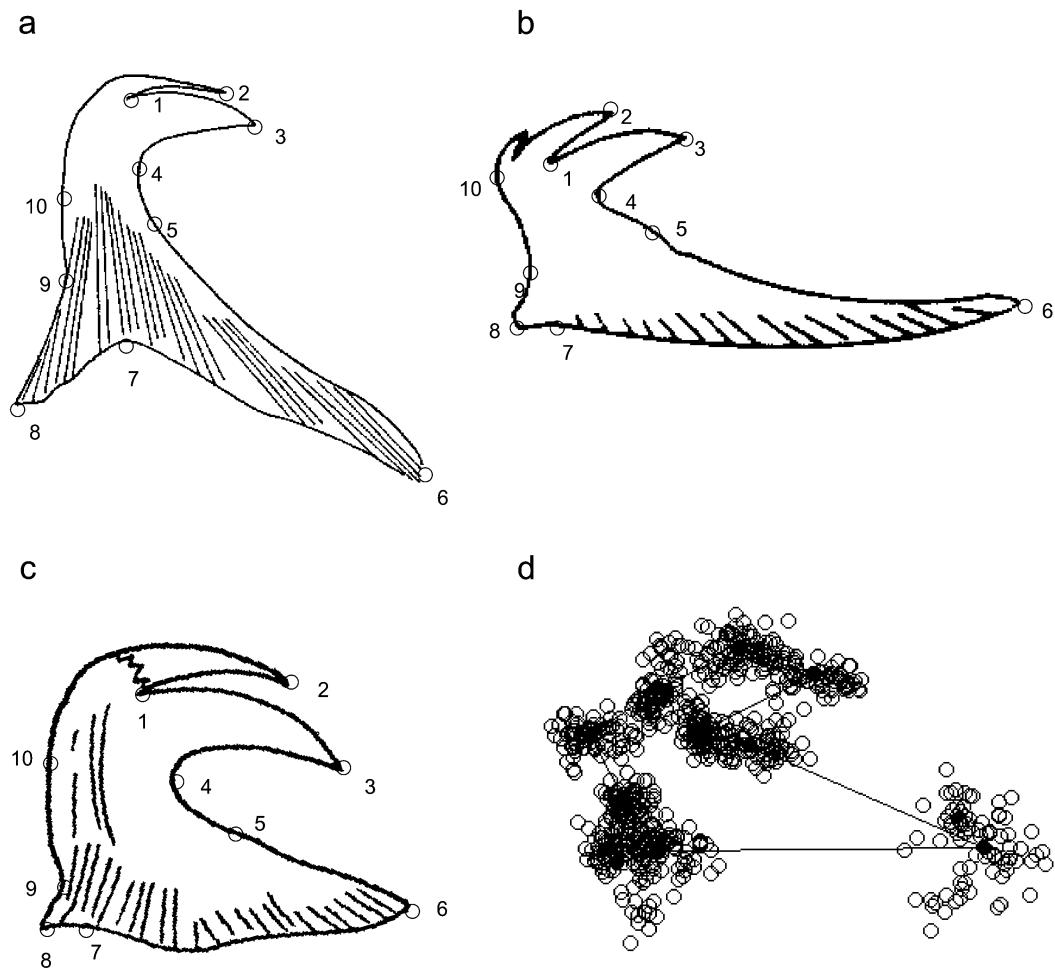


Figure 1. Range of variation in shape of uncini in *Polycirrus* (a) uncini of *P. medius* showing landmarks; (b) uncini of *P. variabilis* showing landmarks; (c) uncini of *P. clavatus* showing landmarks; (d) reference, or average configuration, uncinus showing landmarks for all specimens. 1, junction between rostrum and capitulum; 2, apex of primary capitulum; 3, apex of rostrum; 4, junction between rostrum and upper subrostrum; 5, subrostral process; 6, apex of anterior process; 7, junction between base and posterior process; 8, apex of posterior process; 9, junction between occipitum and posterior process; 10, mid-occipitum.

recommended by Rohlf (1993), the analysis is equivalent to a Principal Component Analysis (PCA). The analysis describes shape changes as the deformation of landmarks from the reference configuration (Figure 1d). The deformation can be thought of as placing a thin metal plate over the outline of an uncinus, constrained at the landmark coordinates, but otherwise free to adopt the form that minimizes the bending energy. Eigenvalues describing these bending energies are converted to eigenvectors called principal warps. Partial warp vectors were derived by projecting each uncinus on to the principal warps to determine landmark displacement in the x , y plane. An RWA of the partial warp scores generated the relative warps (=principal components), which are eigenvectors that summarize the variation among the uncini in as few dimensions as possible.

All analyses were done using the Thin-Plate Spline suite of programs written by F. James Rohlf (<http://life.bio.sunysb.edu/morph/>). TPSRELW 1.16 was used to compute the relative warps. The two relative warps most influential in explaining the variation in shape were plotted in a bivariate plot, and potential groups within *Polycirrus* identified. In order to account for all possible components of shape variation, including components that are possibly biologically meaningful, we analyzed the partial warp scores by multivariate statistics, as recommended by Rohlf et al. (1996); however, unlike these authors we use the iterative non-metric multi-dimensional scaling (nMDS) algorithm to construct an ordination of the samples (Clarke 1993). Using this technique, all components of variation are considered equally and three-dimensional plots can be rotated in order to best visualize the structure of the underlying data matrix and so identify natural groupings of samples. Further, an nMDS ordination is far better at accurately representing dissimilarities among samples than is a PCA projection. The partial warp scores and uniform shape component for each specimen (available at <http://www.nt.gov.au/nreta/museums/magn/collections-research/naturalsciences/annelids.html>), were used to create a matrix of Euclidean distances between each pair of samples (specimens). The nMDS algorithm (PRIMER software package, Plymouth Marine Laboratory, UK) was repeated 20 times using the rank orders of inter-sample distances contained in the distance matrix. This produced natural groupings of the samples which were displayed using a three-dimensional nMDS ordination.

Results

Evaluation of Caullery's schema

Polycirrus species assigned to Caullery's (1915) subgeneric groups, including 26 species described after Caullery's study, are listed in Table I. This revealed further problems with his classification and slight changes had to be made to his subgeneric diagnoses in order to accommodate some species. Thus, the concept of *Ereutho* was broadened slightly to include species having neuropodia starting on or after the last notopodial segment, *Polycirrus* was broadened to include species having neuropodial uncini starting from segments 4 to 12, and *Leucariste* was modified to include species having uncini appearing on segments 13–16. Despite these changes *Polycirrus twisti* still could not be placed *a priori* into any of Caullery's subgenera (also noted by Potts 1928), because uncini do not start until segment 23. This unusual neurochaetal position does not necessarily mean that *P. twisti* does not belong with other *Polycirrus*, rather it points to the inadequacy of a classification system that is based essentially on only two characters. Further, two of Caullery's initial species assignments were found to be erroneous based on a re-examination of type material (C. J. Glasby and P. A. Hutchings, unpublished data); as emended both *P. (Leucariste) californicus* and *P. (Ereutho) clavatus* are reassigned to the subgenus *Polycirrus*.

Morphometric analysis of uncini

RWA yielded 14 relative warps and two (x, y) uniform shape components, that is, a total 16 shape variables (Table III). The first two relative warps accounted for about 74% of total shape variation. A bivariate plot of relative warp 1 against relative warp 2 shows that the uncini of most specimens can be allocated into one of two groups: Group 1 with 33 species and Group 2 with 14 species (Figure 2). Four uncini representing *P. clavatus* (uncinus 23;

Table III. Shape variables and relative warp (RW) scores summarizing total variation among the uncini, and percentage of total variance explained for each variable.

| Shape variable | RW score | % of total variance |
|----------------|----------|---------------------|
| 1 | 1.48597 | 50.81 |
| 2 | 1.00484 | 23.23 |
| 3 | 0.53872 | 6.68 |
| 4 | 0.41951 | 4.05 |
| 5 | 0.36442 | 3.06 |
| 6 | 0.34485 | 2.74 |
| 7 | 0.29440 | 1.99 |
| 8 | 0.28285 | 1.84 |
| 9 | 0.25778 | 1.53 |
| 10 | 0.20595 | 0.98 |
| 11 | 0.20171 | 0.94 |
| 12 | 0.17061 | 0.67 |
| 13 | 0.16359 | 0.62 |
| 14 | 0.12899 | 0.38 |
| 15 | 0.11716 | 0.32 |
| 16 | 0.08873 | 0.18 |

Figure 1c) and *P. pumilis* (uncini 66–68), appear to have equivocal group membership on the basis of the shape of the uncinius. This may be because the bivariate plot does not account for 26% of the shape variance, including the third largest relative warp, which explains ~7% of the variance (Table III); the common rule of thumb is to interpret any

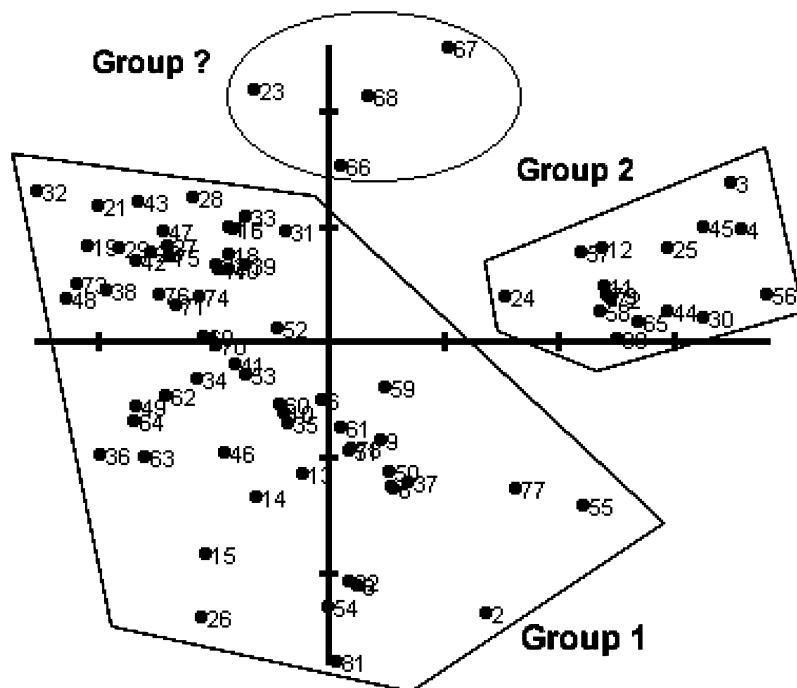


Figure 2. Ordination plot from RWA analysis; relative warp 1 against relative warp 2 showing partitioning of uncini into two groups (1, 2) and an uncertain group (?) containing uncini of *P. clavatus* (23) and *P. pumilis* (66–68). See Table I for species corresponding to numbered uncini.

component that represents more than 5% of the variance (Zelditch et al. 2004, p 168). The nMDS plot of all 16 components of shape variation showed that the ‘equivocal’ uncini clearly belong to Group 2 (Figure 3). Further, like other members of Group 2, *P. pumilis* and *P. clavatus* possess long pinnate notochaetae, which are absent in members of Group 1 (see below). We therefore assign both species as belonging to Group 2, but suggest that the uncini of *P. pumilis* at least need to be re-examined as the digitized images were based on literature illustrations rather than a re-examination of type material.

The largest amount of variation in shape is explained by relative warp 1 (51%), which represents compression or expansion in the horizontal plane of the uncini, resulting in the constriction of the mid-part of the uncinius and in the formation of the deeply arched base exhibited by taxa of Group 2 (Figure 4b, f); Group 1 taxa show the opposite—a stretching in the mid-part of the uncinius resulting in a flat base (Figure 4a, e). Relative warp 2 (23% of total shape variation) represents primarily vertical compression or elongation of uncini; Group 1 taxa display shortening of the occipitum and posterior process causing an upward tilting of the rostrum (Figure 4c, e), and taxa in Group 2 display lengthening of the occipitum, prolongation of the posterior process, and downward tilting of the rostrum (Figure 4d, f). Thin-Plate Spline displays of an uncinius from each group show the net effect of the two most influential relative warps on the form of the uncini; the short occipitum/flat base type (Figure 4e) and the long occipitum/arched base type (Figure 4f) are hereafter referred to as Type 1 and Type 2 uncini, respectively. Relative warp 3 (7% of variation) and the remaining warps appear also to be important contributors to shape variation; however, it is not possible to describe how these components specifically affect the shape of the

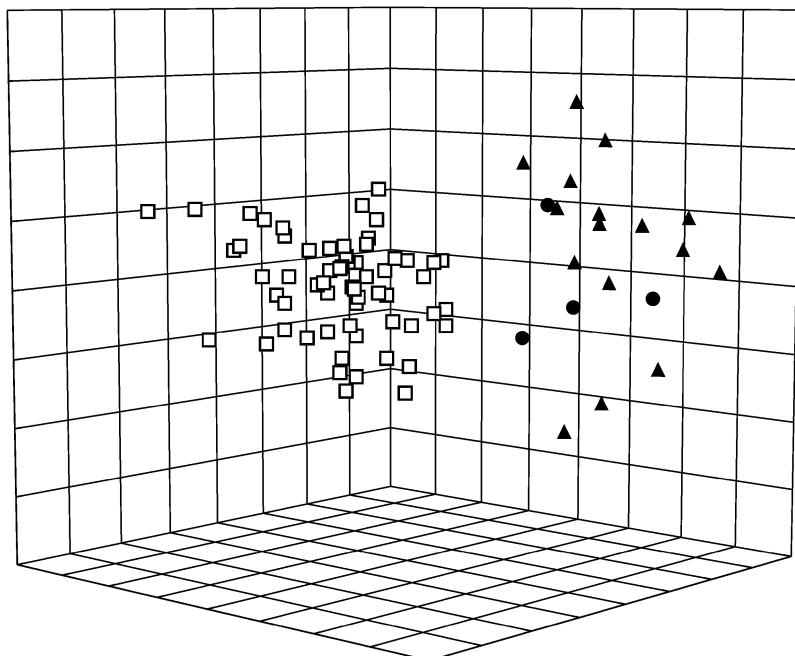
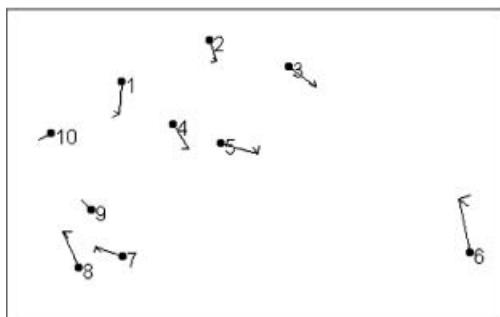


Figure 3. Three-dimensional nMDS ordination depicting the Euclidean distances among samples based on 16 shape measurements of uncini (using partial warp scores). Stress=0.06, indicating a very accurate representation of the data in the distance matrix (Clarke 1993). (□) Uncini contained in Group 1 of Figure 2; (▲) uncini contained in Group 2 of Figure 2, including uncini 23 and 66–68 (denoted by •) which had equivocal status.

GROUP 1

a

GROUP 2

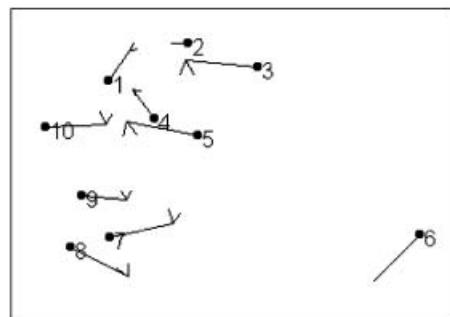
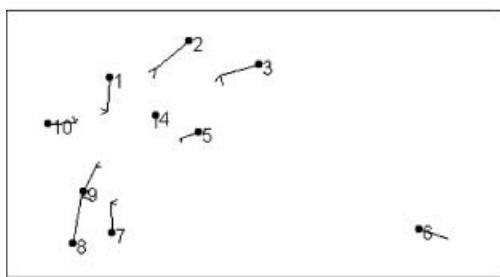
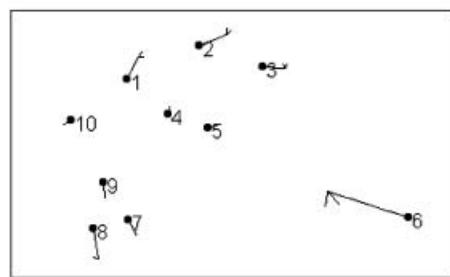
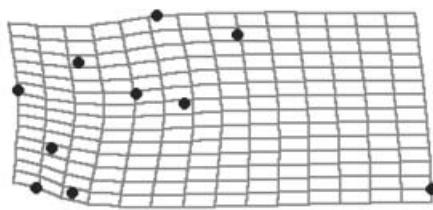
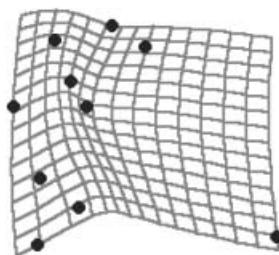
b**c****d****e****f**

Figure 4. (a-d) Eigenvectors associated with a hypothetical 'average' uncinus: (a) Group 1 uncinus for relative warp 1; (b) Group 2 uncinus for relative warp 1; (c) Group 1 uncinus for relative warp 2; (d) Group 2 uncinus for relative warp 2. (e-f) Thin-Plate Spline displays: (e) Group 1 uncinus (*P. medusa*); (f) Group 2 uncinus (*P. disjunctus*).

uncinus. Nor is it possible to attribute any biologically meaningful explanation for any shape component other than a possible anchoring hypothesis discussed later.

Shape of uncinii and other chaetal characters

Uncini shape shows some concordance with other chaetal characters not analysed morphometrically or statistically. The following relationship between the shape of the

uncini and the presence/absence of long pinnate notochaetae and last occurrence of notopodia was found (Table II): species having Type 2 uncini typically have long pinnate notochaetae, except for *octoseta*, *parvus*, *paucidens*, *porcata*, and *quadratus* which lack long pinnate notochaetae. Species having Type 2 uncini always have fewer notochaetigers (last occurrence of notopodia on segment 20 or before) than those species with Type 1 uncini. Species with Type 1 uncini always lack long pinnate notochaetae and may have either the fewer number or the larger number of notochaetigers. This inter-relationship among chaetal characters enables us to distinguish four provisional groups of *Polycirrus*, which can be identified in the following key:

Key to provisional groups within *Polycirrus*

Further, we found weak concordance between the shape of the uncini and the first occurrence of neurochaetae, the latter being the character considered by Caullery (1915) to be important to subdivide the genus. Thin-Plate Spline visualizations of the uncini show that taxa having first occurrence of uncini from segments 13 to 20—corresponding to Caullery’s subgenera *Leucariste* and *Ereutho*—tend to be found as a rule in species having Type 2 uncini (Figure 5a) and that taxa having first occurrence of uncini from segments 4 to 12—corresponding to Caullery’s subgenus *Polycirrus*—tend to be found in species having Type 1 uncini (Figure 5b); however, the correlation is clearly not strong, since there are some species with Type 2 uncini that have an early first occurrence of neurochaetae (*P.*

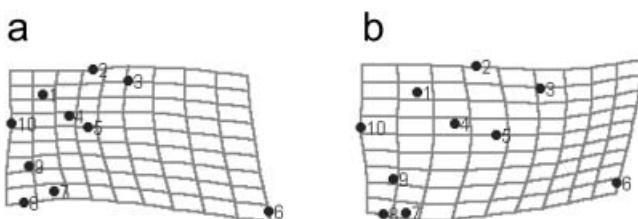


Figure 5. Thin-Plate Spline displays of uncini for (a) hypothetical ‘average’ uncinus in a species having neurochaetae first occurring from segments 13 to 20; (b) hypothetical ‘average’ uncinus in a species having neurochaetae first occurring from segments 4 to 12.

clavatus, *P. octoseta*, *P. porcata*, *P. pumilis*), and many species with Type 1 uncini that have a late first occurrence of uncini (Table II).

Discussion

Variation in the shape of uncini within and among individuals

In Thelepodinae and other Terebellidae, the shape of the uncini varies within an individual, both within a neuropodial row of a segment and between segments along the body (Hutchings and Glasby 1987; C. J. Glasby, personal observation). The extent of this variability has not been widely appreciated, although polychaete taxonomists have long known that uncini of the first one or few segments of Terebellidae can differ markedly from those more posteriorly. According to Caullery (1915), members of the subgenus *Polycirrus* show dimorphic uncini as follows: uncini on the mid- and posterior body (chaetiger 13 and thereafter) are attached by fine filaments ("soies tendineuses"), whereas those prior to chaetiger 13 lack the filaments. However, this type of variation would not be detected in the present analysis since the filaments, which extend proximally from the anterior and posterior processes (Figure 1), are not associated with any landmarks defined here. The absence of filaments attaching the uncini to the body musculature could not be confirmed for Caullery's subgenus *Polycirrus* as a whole; indeed the southern Australian species *Polycirrus* (*P.*) *porcata* appears to have a filament associated with uncini of both the anterior and posterior body, contrary to Caullery's observation (Hutchings and Glasby 1986, Figure 10a, b; filaments are referred to as tendons). The presence or absence of filaments is an area worthy of further investigation because they possibly have a role in attaching the uncini to underlying muscles and thereby facilitating changes in orientation.

Dimorphism of uncini is apparently present within individuals in some species of the subgenus *Polycirrus*, but it appears to involve only the uncini of the first few uncinigerous segments. For example, both *Polycirrus* (*P.*) *porcata* and *Polycirrus* (*P.*) *clavatus* show differences in size and elongation of the occipitium and in the form of the base between anterior-most and posterior uncini. However, since the uncini of these anterior-most thoracic chaetigers were not used in the present study, this observed dimorphism will not have affected our results. The occurrence and extent of dimorphic uncini within a *Polycirrus* species also needs to be investigated further before the feature can be used to diagnose subgroups within *Polycirrus*.

Individuals of species in the genus *Polycirrus* may also display a slight size difference between anterior-body and posterior-body uncini, but in terms of overall shape they appear to be similar and should not be regarded as dimorphic (in any case the effect of size is corrected for in geometric morphometric studies). The inclusion of up to three uncini per individual, along different parts of the body, enabled some account to be made for variability along the body within individuals. By contrast, variation in the shape of the uncini among individuals (i.e. within a population) was not accounted for since the study was based primarily on the type specimen of each species. There is limited evidence in other subfamilies of Terebellidae, however, that the amount of variation in the shape of the uncini among individuals of a population is not significantly different from that within an individual (Hutchings and Glasby 1987).

Variation in the shape of uncini within and among species

The results of this study clearly distinguish two groups of species within *Polycirrus* on the basis of the shape of the uncini. Even species having uncini apparently intermediate in

shape, e.g. *P. clavatus* (Figure 1c), could, on the basis of the three-dimensional nMDS ordination using information on all available shape variables, be placed unequivocally into one of two groups. That is, interpretation of group membership was improved by incorporating the residual 26% of shape variation not explained by the first two principal components. This confirms the importance in considering any principal component that explains more than 5% of the shape variance (Zelditch et al. 2004).

Chaetal characters, correlation, and cladistic variables

This study has identified a new character for *Polycirrus* systematics, shape of uncini, with two states: a short occipitum and flat base (Type 1), and a long occipitum and concave base (Type 2). All currently known species can be assigned one of these two states. The shape of the uncini appears to show a strong correlation with other characters traditionally regarded as important in the systematics of the group, particularly the presence/absence of long pinnate notochaetae and the position of the last notopodial segment. This correlation does not mean that the correlated characters are manifestations of the same genetic system, hence are not independent. Possibly, it indicates a functional complex of characters (i.e. linkage) since the form of the chaetae (uncini and notochaetae) and their position along the body are presumably involved closely with movement and anchoring. If these characters are linked by selection then their use in a cladistic analysis should be done with caution to avoid the possibility that they are incorrectly counted as separate synapomorphies.

Terebellids and other tubicolous polychaetes having uncini or hook-like neurochaetae use these structures to resist removal of the worm from their tubes (Woodin and Merz 1987; Merz and Woodin 2000). However, since *Polycirrus* species lack such a permanent tube, their uncini are presumably freed from the evolutionary constraints imposed by anchoring, which might involve having a large rostrum, strong attachment points (posterior and anterior processes), and optimizing orientation on the body. Given these requirements, then it is clear that the Type 1 uncinius, with its short occipitum and flat base (which is most common among members of the genus), may be less effective as an anchor. In addition, the relative size of Type 1 uncini is smaller than that of Type 2, a further indication of their lesser anchoring potential. These two different types of uncini therefore point to differences in the behaviour, and possibly also habitat, among the two groups of *Polycirrus* species, which would be an interesting topic for further study.

Both the present informal classification scheme and that of Caullery are essentially phenetic constructs; the advantage of the present one is that all currently described species can be unequivocally allocated to one of the four groups. However, despite the robustness of these groupings, we do not propose formal amendments to the classification of *Polycirrus*. Ideally, classifications should reflect phylogeny so that all taxa are monophyletic. Without resort to a phylogenetic analysis utilizing a full range of characters, we cannot know whether the four groups identified here are monophyletic.

Whether partial warps or other geomorphometric variables can be used as potential phylogenetic characters has been hotly debated; see Forey (2002) for summary of differing opinions. Forey (2002) concludes that “there is no inherent reason why they [morphometric variables] should not be used but there remain problems and agreed criteria by which such variables are to be coded”. These are essentially the same issues that have beset the use of any quantitative data in phylogenetic analysis. Until methodological advances enable the use of quantitative data, including geomorphometric variables, phylogenetic analysis of species-rich morphologically homogeneous taxa like *Polycirrus* will remain problematical.

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Appendix. *Polycirrus* taxa excluded from the study

- Polycirrus arcticus* Sars, 1864
- Polycirrus caliendrum* Claparède, 1868
- Polycirrus corallicola* Verrill, 1900
- Polycirrus decipiens* (Gravier, 1905)
- Polycirrus denticulatus* Saint-Joseph, 1894
- Polycirrus elisabethae* McIntosh, 1915
- Polycirrus eous* Annenkova, 1924
- Polycirrus eximius* (Leidy, 1855)
- Polycirrus jubatus* Bobretzky in Annenkova, 1924
- Polycirrus leocene* (Quatrefages, 1865)
- Polycirrus mexicanus* (Rioja, 1947)
- Polycirrus pallidus* (Claparède, 1864)
- Polycirrus pellucidus* (Quatrefages, 1865)
- Polycirrus pennulifera* Verrill, 1900
- Polycirrus smitti* (Malmgren, 1866)
- Polycirrus tentaculata* (Hartmann-Schröder, 1960)
- Polycirrus tenuisetis* Langerhans, 1880
- Polycirrus triglandula* Langerhans, 1880