Hopkins and Lidgard
Fossil species lineages and their defining traits—taxonomic "usefulness" and evolutionary modes

Appendix B. Justification for coding assignments, arranged in alphabetical order**.**

*AICc results from Hunt 2007
#taxonomic importance coded by SL; all others by MJH.

Acuticryphops acuticeps **from France**
Data from Cronier et al 2004

Cronier and Feist (2000) note that the number of eye lenses is quite variable within samples that otherwise show no variation within traits. Other closely related species (the genus *Acuticryphops* is monospecific) are characterized by similarly low numbers of eye lenses (though species of *Weyerites* are distinguished by number of eye lenses among other traits). Because the authors lump specimens despite the high variation in this characters, this character is considered "not useful" for classification within *Acuticryphops*.

#Afrobolivina afra **from west Africa**
Data from Campbell and Reyment 1978

Campbell and Reyment (1978) state on p. 348 that metric variables were "selected for analysis as it was thought they might be useful for exposing possible differences due to polymorphism in the foraminiferal life cycle." They do not present criteria for distinguishing *A. afra* from related species. Reyment (1959) erected both the genus and the species. In the latter paper, the generic diagnosis includes among the "peculiarities": "roughly cylindrical with the greatest breadth in or around the middle, or sides slightly convex with the greatest breadth near the top of the test." (p. 19). The species diagnosis (p. 21) includes these characteristics: "Test roughly cylindrical, site of greatest inflation in the middle or in the last third of the length of megalosphcric individuals and usually across the last two chambers of microspheric individuals." The species description (p 23) notes, " The following details were measured: Number of chambers (C), length of the test (L), breadth of the test (B), the maximum thickness of the test (T), distance of maximum breadth from top of last chamber (E), the diameter of the proloculus (P). The following indices were calculated from these figures and expressed together with them in Table I, L/B, B/T." Thus, the length, breadth, and thickness of the test all appear to be implicated as taxonomically important components of ratios (shape). Also in Reyment (1959), *Afrobolivina afra* is distinguished from *A. bantu* in obtaining a larger size, in having a convex instead of concave sides, and in having a different type of reticulated ornament. Because of this, the length of the test is considered to be useful for classification. This does not necessarily indicate that all other length measurements are useful in classification. For example, the ratio of length to width in *A. afra* ranges between 2 and 5, whereas this same ratio ranges between 1.4 and 1.7 for *A. bantu*. Thus these two differ in absolute length much more than they do in absolute width.

Amorphognathus tvaerensis **from Europe**
Data in Djik 1990

Bergstrom (1971) states that *Amorphognathus tvaerensis* may be distinguished from its descendent *A. superbus* by the appearance of several elements, but particularly the presence of an extra postero-lateral process on the dextral amorphognathiform element of the former. Djik

(1994) uses both the number of denticles on the ne element as well as the relative length of the branches of the posterior process on the sp element (= amorphognathiform element) in the diagnoses of *A. tvaerensis* and *A. superbus*. Thus both traits are considered useful for classification.

Amydrotaxis praejohnsoni
Data from Murphy and Springer (1989)

Murphy and Springer (1989) distinguish this species from *A. druceana* in having a smaller number of large denticles rather than a large number of poorly developed denticles. For this reason, the number of denticles across the blade (D) as well as in the anterior part of the blade (Dm) are considered useful traits for classification. *A. praejohnsoni* and *A. johnsoni* are also distinguished by the lateral profile of the narrow platform lobe (sloping in the former, shouldered in the latter) (Klapper and Murphy 1980, Murphy and Springer 1989); none of the traits capture this part of the tooth. The profile of the narrow platform lobe in upper view is also important for classification but does not necessarily influence the length and width of the element at this point (Lip or W, respectively). No mention has been made regarding the length and width of the outer platform process, at least within the genus (Lop, Wop). Thus these four traits are apparently not useful for classification.

Mawson (1986) illustrates both *A. preaejohnsoni* (her *A. johnsoni* alpha morph) and *A. johnsoni* (her *A. johnsoni* beta morph), showing how the denticle expression varies between the two species and suggesting that the relative height of the anterior denticle (Hb) and the relative height of the cusp opposite the basal cavity (Hbc) covaries with denticle expression. Thus these two characters are considered useful for classification.

Amyzon aggregatum from British Columbia
Data from Barton and Wilson 1999

Wilson (1977) first described *Amyzon aggregatum*. The primary characters that distinguish it from other *Amyzon* species are the number of dorsal fin rays, the length of the dorsal fin and the body depth to length ratio. Meristic characters such as number of vertebrae, number of precaudal and caudal vertebrae, number of anal, pectoral, and pelvic fin rays have different ranges in different species but the ranges overlap—thus the mean number might be significantly different but the trait itself could not be used to assign any particular specimen to a species unless the value of the trait happened to be at an extreme. In addition, many meristic traits are believed to be adaptive and have both an ecophenotypic component as well as a genetic component to their expression, suggesting that they are not as useful for classification (Barton and Wilson 1999). While the number of dorsal fin rays is considered useful for classification, there is variation in its expression within samples.

Anadara staminea from the Maryland Miocene.
Data from Kelley, 1983

Kelley (1983, p. 583) stated that she retained the taxonomy of Glenn (1904) and Martin (1904), as revised by Schoonover (1941), Vokes (1957) and Ward and Blackwelder (1975).

The species has a long synonymy. In 1992, Ward split previously classified specimens of *Anadara staminea* between *Dallarca elevata* and *D. elnia* (with most belonging to the former), neither of which include *Arca staminea* of Say, 1832. The material described as *A. staminea* by Schoonover 1941 was divided between these two species (Ward, 1992, p. 58-59),

so we suspect that that Kelley measured a mix of specimens from what are now considered two species.

Species within *Anadara* have traditionally been distinguished by the outline of the valve (Vokes, 1957). In addition, the primary difference between the younger *D. elevata* and the older *D. elnia* is the shape of the shell margin ('rectangular' vs. 'rounded', respectively [Ward, 1992]). This distinction directly affects the ratio between the dorso-ventral shell height (trait 'H') and the antero-posterior shell length. The ratio between the shell length and the length (trait 'LCA') and height of cardinal area parallel to hinge line (trait 'HCA'), appears to be correlated with the overall valve shape (for example, compare '*Anadara staminea*" and *Anadara arata*, Vokes 1957).

In contrast the ratio between the antero-posterior shell length and (1) the length of anterior adductor muscle scar (trait 'LAA'), and (2) the distance to dorsal margin from base of anterior adductor, measured perpendicular to hinge line (trait 'DDM') and (3) distance from beak to anterior margin of shell (trait 'DBAM') are not necessarily correlated with shell outline. In addition, the overall convexity (trait 'CON' or trait 'W') of the valve is not mentioned in species descriptions (e.g., Vokes 1957, Ward 1992). Finally, the number and nature of grooves on the ribs are mentioned as important for species-level distinction but not the number of ribs themselves (trait 'NR'). None of these traits are considered useful for classification.

Arvicola terrestris from central and western Europe
Data from Heinrich 1987 and van Klofschoten 1990 (redrafted in Lister 1993)

Van Klofschoten (1990) succinctly states that "Almost all fossil species have been defined on dental characters, thickness of the enamel of one or more molars, morphology of m1 and M3, and size of the molars (m1 in particular). All these characters have also been used to demonstrate evolution in *Arvicola*." (p. 45). For example, Heinrich (1987) discriminated between *Arvicola cantiana* and *A. terrestis* by the enamel index (SDQ): the former had SDQ values greater than 100, the latter had SDQ values lower than 100. Van Klofschoten (1990) synonymized all species of *Arvicola* (including *A. cantiana*) into *Arvicola terrestris* based on comparison of the range of variation in dental characters (particularly SDQ) in modern populations to fossil samples. Thus, while this character has been useful in the past, it appears to be out of favor in more recent taxonomic schemes, including among the authors who recorded the trend analyzed here.

In part, this is because the two modern European species of *Arvicola* are distinguished by karyotype and by the shape of the nasal bones but are almost identical in molar morphology; in addition, the SDQ values for m1 and M3 overlap (van Klofschoten, 1990) and the range of variation expressed by modern *A. terrestris* is similar to that expressed by all but the very oldest samples. Of the two modern species, *A. sapidus* M1 molars are slightly larger than the largest belonging to *A. terrestris*.

Prior to comparison with variation and trait usefulness in modern populations, this sequence was considered to be a "lineage". Now that it appears that SDQ is not useful for classification in the modern, the sequence is considered a species and the trait is not longer useful. The size of M1 appears to still be useful in that it separates fossil and modern populations of *A. terrestris* from modern populations of *A. sapidus* (Spain).

**Asterocyclina sp.* from Israel
Data from Fermont 1982

Ten species of *Asterocyclina* have been described, usually on the basis of size, or size-dependent parameters, and outer morphology (Fermont, 1982). The outer diameter (B) is thus considered useful for classification. The relative thickness [A], however, appears to be controlled by depth and may not be useful for classification. Traits that Fermont (1982) uses in the taxonomic section of his monograph for distinguishing *A. taramellii* and *A. stella* from one another and other species include degree of enclosure and size of embryon (including the diameter [D1] and height [H1] of the protoconch and the diameter and height of the deuteroconch). Thus these traits are considered useful for classification. Because the number of periembryonic chambers (N2) is size-dependent, it is considered useful for classification. The height of the periembryonic chambers [HC] is more variable than other traits (Fermont, 1982) but correlation charts show that it separates the two species, as does the degree to which the protoconch is enclosed by the deuteroconch [R]; therefore these two traits are considered useful for classification.

#*Belemnella obtusa-sumensis-cimbrica* from NW Europe
Data from Schulz 1979 [in German]

[title transl.: A study of the morphometry and statistical variation of the belemnite *Belemnella* of the Lower Maastrichtian of NW-Europe and its bearing on phylogeny] Schulz notes in the abstract (p 4) that "The most important characteristics for the distinction of the different species are the ontogenetical development of the length of the rostrum solidum (Ls) in relation to the dorsoventral diameter at the protoconch (Dp) and the shape of the guard in ventral and lateral aspect (A V, AL), which can be defined quantitatively by means of a combination of three different guard diameter measurements." The author seeks to find characteristic morphometric values [growth-related traits] that are independent [or less dependent] on sample size. Thus he devised a number of length:length ratios, some of them complex, which do not readily correlate with size alone (p. 29): "I have also checked the extent to which very small and very large specimens of 'populations' addressed in the relevant feature of 'population mean' differ." He uses a growth-curve "fitted" expression for LSN, the standardized length of the rostrum. He groups stratigraphically limited "layer group populations" of individuals for comparative analyses.

In reference to grouping significant clusters, he writes on p. 33, "I have largely avoided performing complex statistical procedure. Distance grouping analysis would indeed be helpful in some cases, but the available material is not large enough, since for only relatively few copies of a layer group fauna all characteristics could be measured. The advantage of the simultaneous analysis of many features would have been offset by the significant reduction in sample size. In essence, I have confined myself in the variational statistical analysis on the creation of scatter plots and distribution curves and the calculation of "population" averages for the various features. In each case the 95% confidence interval of the mean value was calculated…Differences between 'population' mean values are referred to as 'significant' if they do not overlap their 95% confidence intervals…"

For classification of species, he notes (p. 34), "If there is a continuous series of large populations of a complete profile, any boundary between two types is arbitrary, since the differences between two consecutive populations in general are at best on the subspecies level." And on p. 35, "Each successive species within the main development in the series (subgenera) of *Belemnella* I have taken if possible according to the [definition based on the holotype]. Most species show significant phylogenetic change over their stratigraphic range." With these caveats stated, the author DOES utilize traits to outline an evolutionary, phylogenetic map with dotted species boundaries using measured traits in Fig 33, plotted as a relationship between traits Lsn and AV. In his discussion of the map, he notes that phylogenetic changes in other characteristics are discussed in later sections.

The "usefulness" of these measured traits is interpreted by us, based on a long series of figures (#38-53), many of which depict species in phylogenetic sequence and respective trait-value distributions at each level of the sequence. Further, the author's species determinations in a later section make extensive, explicit use of these trait values.

Schulz's traits:

Lsn   standardized length of rostrum (= Ls + WQs*(Dpn-Dp))   length-length ratio (sort-of)
WQs   growth rate (=(Ls2-Ls1)/(Dp2-Dp1))   length-length ratio
AV   ventral aspect (=(Bs-Bc)/Bp)*100)   length-length ratio
AL   lateral aspect (=(Ds-Dc)/Dp)*100)   length-length ratio
Avc   ventral aspect of rostrum solidum [=(Bp-Bc)/Bp*100]   length-length ratio
ALC   lateral aspect of rostrum solidum [=(Dp-Dc)/Dp*100]   length-length ratio
Avs   ventral aspect of rostrum cavum [=(Bs-Bp)/Bp*100]   length-length ratio
Als   lateral aspect of rostrum cavum [=(Ds-Dp)/Dp*100]   length-length ratio
Qc   cross-sectional ratio at rostrum cavum [=Bc/Dc]   length-length ratio
Qp   cross-sectional ratio at protoconch [=Bp/Dp]   length-length ratio
Qs   cross-sectional ratio at rostrum solidum [=Bs/Ds]   length-length ratio
WA   alveolar angle angle
SW   Schatsky distance   length
AS   Schlitzboden amplitude   length
WS   Schlitzboden angle   angle
WSm   Schlitzboden angle M angle
WS1   Schlitzboden angle 1 angle
WS2   Schlitzboden angle 2 angle

*Belemnitella mucronata from Norfolk
Data from Christensen 2000

Christensen (1995) notes that the relationship between the length from the apex to the protoconch (LAP) and the dorso-ventral diameter at the protoconch (DVDP) is isometric; this ratio is called the Birkelund Index and used in classification. Overall size (LAP) is also important for species discrimination. Adult specimens of small species and adolescent specimens of large and very large species are difficult to tell from one another based on shape of the guard or vascular markings; rather discrimination is based on internal characteristics, including the Schatzky distance (= distance between protoconch and bottom of ventral fissure) and the alveolar angle (SD and AA, respectively). The fissure angle (FA) is a feature of the internal morphology, so it is considered useful for classification. However, the maximum lateral diameter (MLD) and lateral diameter at the protoconch (LDP) are not considered to be useful because they are related to shape of the guard, which is generally not diagnostic.

Biscutum constans from France
Data from Bornemann and Mutterlose 2006

Bornemann and Mutterlose (2006) consider mostly whether subspecies of *Biscutum* should be lumped together (which they conclude they should). However, Mattioli et al (2004) distinguish other *Biscutum* species from one another based on the size of both the coccolith and the size of the central opening as well as the ratio of the two lengths. They also state that while there is some variation, ellipticity of the coccolith is not useful for disciminating between cogenerics. The length:width ratio of the central area is not mentioned; therefore it is considered "not used" in classification.

*_Bradleya sp_., deep sea ostracod
Data from Brown and Hunt unpublished

Steineck and Yozzo (1988) mention size only to say that two species of _Bradleya_ are similar in size. Generally size is considered to be a plastic trait, influenced by water depth/temperature in species of ostracod (Reyment 1963, p. 26). Therefore size is considered not useful for classification in this genus. Ornamentation, such as the absence or presence of the posterior bridge complex, distribution of pores, and expression of ridges, is of primary importance for discriminating species of ostracods. Of the _Bradleya_ species described by Steineck and Yozzo (1988), all are of elongate form. However, Benson (1972) notes that some _Bradleya_ species are easily distinguished by shape form. For example, _B. normani_ has a robust, subquadrate form while _B. diction_ has an elongate, delicate form with little gradation (i.e., intermediates) between the two. Thus the length/width is considered useful for classification.

*_Buntonia beninensis_, _Buntonia bopaensis_, _Trachylebris teiskotensis_, _Cytherella sylvesterbradleyi_, _Ovocytheridea pulchra_ from Nigeria
Data from Reyment 1963

Size variation in ostracods is strongly influenced by environmental factors (Reyment, 1963, p. 26) and is thus not considered useful for classification. Thus all three length measurements tested for these species are considered "not useful". However, it should be noted that strong sexual dimorphism is apparent in discriminant functions derived from analysis of the pooled covariance matrix for _Buntonia beninensis_. Length of the valve is important for distinguishing sex in _Trachylebris teistotensis_, although it is secondary to shape and ornament for species level distinctions. In _Cytherella sylvesterbradleyi_, height and length of the valve is used for determining growth stage, but again is secondary to shape and ornament for species level distinctions. For the former two, it appears that Hunt (2007) tested the trend for either males or females; for the latter two, it appears that data for only one growth stage was tested.

Calcidiscus leptoporus from multiple deep sea cores
Data from Knappertsbusch 2000

Knappersbusch (2000) cites multiple authors that have used both the diameter of the distal shield and the number of elements per cycle to distinguish different morphotypes of _C. leptoporus_ as well as distinguish between _C. leptoporus_ and the morphologically similar _C. macintyrei_ (see also Knappertsbusch et al. 1997). Thus both traits are considered useful for taxonomy.

*_Cantius sp_. from Wyoming
Data from Clyde and Gingerich 1994

In his diagnosis of _Cantius torresi_ (one of the chronospecies included in the tested trend), Gingerich (1986) distinguishes _C. torresi_ from _C. ralstoni_, _C. eppsi_ and other _Cantius_ species in being smaller (presumably based on the log area of the molars), in having relatively square upper molars, and having shorter, broader lower premolars and molars. Thus all length measurements and length to width ratios are considered useful for classification.

While the height and distinctness of cusps and notches on the tooth are often described, we have seen no descriptions that mention the relative cusp position in designation of congenerics. However, the relative cusp position appears to be more important for higher-

level taxonomy. For example, Gingerich and Haskin (1981) mention a "broader and shallower talonid basin" in *Copelemur* and "*Pelycodus*" from Wyoming compared to *Pelycodus* s.s. from New Mexico (p. 334). The talonid basin includes the hypoconid and the entoconid, and so a change in the shape of this region of the tooth is likely to result in changes in the relative cusp positions. For this reason, the x- and y-coordinates of the position of the entoconid, metaconid, and paraconid are all considered "not useful" for species level classification in this genus.

This is supported by discussion (or lack thereof) in Godinot (1998) and Gazin (1952). Godinot (1998) suggests that convergence in dental characters may be common and synonymizes "*C. consortus*" and "*C. limosus*", previously potentially distinguished by the presence and placement of the paraconid on M/2-3. Gazin (1952) also noted that the paraconids on these teeth was highly variable. Gazin (1952) states that the paraconid is "strong" on M1, but that, in general, the molar teeth in "*C. limosus*" are not particularly distinctive. Nowhere does either author suggest that relative position of cusps on M1 to be useful for classification, and both imply that the relative position of cusps on other teeth comprises intraspecific variation.

Chesapecten nefrens, pectenid (bivalve) from Maryland Miocene
Data from Kelley, 1983

C. nefrens differs from *C. covepointensis* and *C. santamaria* in having:
- Narrower, unflattened ribs
- Larger gapes between disk flanks
- Larger gapes along ventral commissure
- Coarser, nonuniform scabrous lirae [=ornamentation on plicae]
- Larger byssal notch
- Larger auricles

C. nefrens differs from *C. coccymelus* by:
- Larger size
- Lack of concave spines
- Subequal auricle size

Diagnosis also includes a statement about relative convexity of right valve (Ward and Blackwelder, 1975, Ward, 1992).

Based on these descriptions, the number of ribs on the auricle (trait 'NAR') appears unimportant for classification, but the length of the anterior and posterior auricles relative to the antero-posterior shell length (traits 'LAAU' and "LPAU', respectively), as well as the convexity of the valve (trait 'CON") and the width of the left valve perpendicular to the plane of the commissure relative to the length (trait 'W') are important.

While not stated in the diagnosis for *C. nefrens*, other species of this genus are discriminated based on the size of the hinge area (summarized by the length of resilifer, trait 'LRES'), the number or range in number of ribs (trait 'NR', also referred to as plicae), and the roundness of the disk outline (capture by trait 'H').

Chiasmolithus from the North Atlantic and from Antarctica
Data from Bralower and Parrow 1996

The data for the *Chiasmolithus* lineage includes specimens of *C. bidens* and unclassified forms. The shape and ultrastructure of the central cross are important for classification of species (Bralower and Parrow, 1996), and so the mean axes ratio, the mean junction ratio, the area of the holes and the ratio of the area of small to large holes are all considered either useful for classification (the former two) or correlated with changes in the shape of the central axis (the latter two). The ratio of length to width of the overall coccolith does not appear to be important. However some species of *Chaismolithus*, including *C. danicus*, differ in the size of the central area and width of the shield (van Heck and Perch-Nielsen 1987, van Heck and Prins 1987) and is included in earlier descriptions of *C. bidens* as a diagnostic character (Hay and Mohler 1967). Bralower and Parrow (1996) do not mention size of the coccolith or size of parts of the shield to be important for (current) classification within the genus but do note that they are useful for classification between *Sullivania* (formerly considered *Chiasmolithus*) and *Chiasmolithus*.

#*Contusotruncana sp*. from both North and South Atlantic
Data from Kucera and Malmgren 1998

Contusotruncana is a valid genus of Foraminifera, apparently revised by Korchagin (1982) with the genotype *Pulvinulina arca var. contusa* Cushman, 1926. [We have not obtained the reference (in Russian or English?). A synonym is apparently *Rosita* Caron, González-Donoso, Robaszynski & Wonders, 1984]

The authors assert that the genus "represents a single phylogenetic lineage (chronocline) with one evolutionary transition involving gradual development of highly conical *Contusotruncana contusa* from its flat ancestor *C. fornicata*. These two species represent arbitrary segments of a single phylogenetic branch (Pessagno 1967; Masters 1977; Caron 1985)." They do not list characters that form the basis for species determination of *C. fornicata* and *C. contusa*, but focus instead on documenting trend[s] in morphology between the two. No phylogenetic analysis is offered. They state on p. 50, "Partly due to the great morphological variability within this genus, partly due to the common practice to describe "extreme morphologies" as new taxa, a large number of species and subspecies referable to the genus *Contusotruncana* have been described in the literature...It has been concluded that these mutually intergrading forms can be found together in a normal paleopopulation (Masters 1977); quantitative morphological studies have failed to recognize more than one discrete morphotype of the genus in one time interval (Pessagno 1967; Kucera and Malmgren 1996)." Thus the 'usefulness' of different measured characters for the purpose of classification is extremely difficult to interpret in the context of this paper. They appear to maintain only two end-member species, and state on p. 50, (1) that the ecological relevance of morphological changes can be assessed from variations in the abundance of the evolving species and (2) that the true nature of any evolutionary pattern cannot be properly established without knowing its geographical structure." We infer from this and other statements that those traits which show consistent temporal trends in multiple locations are most relevant in classification (with respect to this chronocline and its end-members); traits which vary geographically in the same temporal interval are less relevant. We infer only conicity (y- coordinate of third landmark relative to baseline of 2 other landmarks) to represent 'useful' classifying characters in this paper.

[The following papers were noted but not examined by us:

Caron, M. 1985. Cretaceous planktic foraminifera. Pp. 17-86 in H. M. Bolli, J. B. Saunders, and K. Perch-Nielsen, eds. Plank-ton stratigraphy. Cambridge University Press, Cambridge.

Masters, B. A. 1977. Mesozoic planktonic foraminifera. Pp. 301- 731 in A. T. S. Ramsay, ed. Oceanic micropaleontology, Vol. 1. Academic Press, London.

Pessagno, E. A., Jr. 1967. Upper Cretaceous planktonic fora-minifera from the western Gulf Coastal Plain. Paleontographica Americana 5:245-445.]

Cosomys primus from Idaho
Data from Lich 1990

Lich (1990) used the size of M1 to distinguish *Cosomys* from *Ophiomys*. Since then (?) *Cosomys* and *Ophiomys* were recombined with *Mimomys*, so that what previously might have been considered genus-level characters are now considered sub-genus or species-level characters. In the case of the length and width of M1, both are used to distinguish between *Mimomys panacaensis* and *M. (Cosomys) primus* (Mou 1997) (*M. (Ophiomys) mcknighti* is similar in size to *M. panaceaenis* and thus could still be distinguished from *M. (Cosomys) primus* based on size). Features of the posterior loop/lobe may be useful for classification, but the width of the posterior loop/lobe is not mentioned in Mou (1997), nor is it included in the biometry of *Mimomys* in Chaline and Laurin (1986).

Cruciplacolithus tenuis from North Atlantic
Data from Bralower and Parrow, 1996

While size is historically important for species discrimination in this genus (van Heck and Prins, 1987), Bralower and Parrow (1996) distinguish this species in the samples they measured based on the presence of "feet" at the ends of the cross in distal view. Therefore, size is not considered important for classification. While not explicitly described for this species, the angle of the arms of the cross to one another is important for distinguishing *Cruciplacolithus edwardsii* from *Sullvania asymmetrica*, therefore, for the purposes of this study, characteristics that are affected by changes in the shape of the central cross (here the area of holes) are considered to be useful for classification. All other characteristics are considered to be not useful.

Cruciplacolithus primus from two sections in Europe
Data from Romein 1979

While size has been used by other workers to discriminate between species of this genus (van Heck and Prins, 1987), Romein (1979) does not appear to have relied on it for species discrimination. In the case of *C. primus*, he explicitly expands the size range to include new specimens that share characteristics of the cross-structure (p. 101). Thus it is considered not useful for species-level classification.

Cryptopecten vesiculosos, pectinid (bivalve) of the Japanese Islands
Data from Hayami 1984

Cryptopecten vesiculosus has two subspecies. While *C. vesiculosus vesiculosus* has a larger range of radial ribs (13-18), the range in number of ribs in *C. vesiculosus makiyami* overlaps with the range of the former (15-18) so it cannot necessarily be used to identify individual specimens. However, *C. vesiculosus makiyami* is found only in one fossil population included in the sequence (Kg1) and both the average number of radial ribs and the overall size are used to defined the population as a 'geographical (or ecological) subspecies' (Hayami, 1984, p. 110). In addition, both average number of radial ribs and shell size are used to distinguish species oF *Cryptopecten* from one another.

"Hi" is the shell height to the first growth ring, and is considered to be a proxy for growth rate. It appears to correlate to some extent with mean maximum body size but has very high intrapopulational variation and is not used as criteria in systematic descriptions.

Cycladophora sakaii-davisiana from northwest Pacific
Data from Motoyama 1997

Cycladophora sakaii has a large thorax with an external spongy layer (Motoyama 1996, 1997). The presence of the spongy later in *C. sakaii* appears to be independent of thorax size (Motoyama 1997) and thus is a feature that distinguishes this species from others lacking the spongy layer (including *C. davisiana*). Characters distinguishing this species from *Cycladophora spongothorax* (also with a spongy layer) include lacking "steps" in the profile of the thorax and in having larger thoracic pores and shorter apical horns (Motoyama 1996). *C. pliocentrica* is distinguished from *C. sakaii* by having a prominent knot on the surface of the test and "roughness" of the outer surface whereas *C. sakaii* is smooth. *Cycladophora davisiana* may be separated from *Cycladophora cornutoides* by the thorax width to length ratio (but not either length). Nonetheless, thorax size is a distinguishing feature between *C. davisiana* and *C. biocornis*.

Based on this assessment, the length of the apical horn (AHL), the width of the thorax (TXW), the length of the thorax (TXL), the pore diameter (PD), and the development of the spongy layer (SPL) are considered useful for classification as the species level. Pore number (PN) is related to other measurements [PN = TXW*pi/(PD + BW)], and while TXW and PD are both useful for classification, no mention is made that either the bar width (BW) or PN are distinguishing characteristics.

Motoyama (1997) notes that C. davisiana and C. sakaii are similar in having small cephalis (CPW), implying that this feature discriminates between other closely related species. Length and width of abdomen (ABL, ABW) are often measured as part of the species description but not used to distinguish between species.

Cytheridea from Rhone Basin, southeastern France
Data from Reyment et al 1977

Reyment et al. (1977) state that marginal spines are ignored in descriptions of species, and that ornamentation and valve outline are of more importance for classification. In general, both anterior and posterior spines occur in variable number within species. Thus they are considered to be "not useful". This opinion is supported by reports of high variability in test shape in extant echinoids and cases of correlation with environmental conditions.

Cythereis longaeva longaeva, *C. perturbatrix*, and *Mosaeleberis sp*. from Bohemia
Data from Pokorny 1966

Pokorny (1966) notes that most workers do not consider size to be taxonomically useful for ostracods, but that there are some that maintain that it could be useful for taxonomy and that species with large size ranges are probably lumped taxonomically or ontogenetically. Pokorny does not express his own opinion, however, and classification usefulness remains equivocal.

Discoaster multiradiatus from sections in Europe
Data from Romein 1979

Size ranges are listed under species diagnoses in *Discoaster*. However size ranges show considerable overlap amongst cogenerics and size itself is not mentioned in diagnoses or

comparisons between species (Romein 1979). Therefore size is considered "not used" in species discrimination.

Discocyclina sp. from Israel
Data from Fermont 1982

30 species of *Discocyclina* have been described. The shape of the embryon and the number of periembryonic chambers is highly variable. The degree of enclosure (R) and number of periembryonic chambers (n2) are size-dependent. *D. varians s.s.*, *D. augustae*, and *D. douvillei* are distinguished by thickness of the test (though despite any morphological break) and the size of the embyron is correlated with thickness. Therefore the diameter (D1) and height (H1) of the protoconch is considered useful for classification. Despite the potential for the size of the embryon to be depth-dependent in *D. varians* (Fermont, 1982), traits that correlate with size, such as the degree of enclosure (R), thickness, and size itself are used to distinguish between this species and *D. augustae*. While the size of periembryonic chambers (Hc) has been used historically for species grouping in the Discocyclinidae, it is highly sensitive to depth and highly variable and Fermont (1982) questions previous taxonomy that relied on this trait.

Brolsma (1973) described species of *Discocyclina* and *Asterocyclina* from France, (Fermont [1982] used the same trait measurements). Brolsma considered the presence or absence of pustules, definition of umbo, and size to be useful for discriminating between *D. augustae* and *D. archiaci*. In addition, these two species and *Asterocyclina stellata* can be distinguished from one another using external features, but differences in size and arrangement of the protoconch, deuteroconch, and auxiliary chambers also exist. The traits that appeared to be most useful include the number of periembryonic chambers on the deuteroconch and the degree of enclosure (which he calls "embracing"). Brolsma (1973) reports measurements for the size of the periembryonic chambers (Hc) and this size measurement is notably different between the two *Discocylina* species under examination. However, there is no further discussion of this trait, perhaps because it is redundant to other size measures, or because it is just seen as less reliable (perhaps because of high variability). Thus Fermont (1982) and Brolsma (1973) are generally consistent in their results.

Discoides subucula from the United Kingdom
Data from Smith and Paul 1985

Smith and Paul (1985) recognize a gradual change in test shape in *Discoides subucula* that correlates with the type of sediment being deposited; they interpret this as ecophenotypic variation and note that other "more important" characters remain static during the sequence. *Discoides subucula* differs from the stratigraphically younger *D. infera* in the arrangement of the military tubercles and the relative size of the peristome (smaller in *D. infera*). Thus, the height to diameter ratio is considered not useful for classification while the peristome to test diameter ratio is considered to be useful.

Equus aff. ferus from Alaska
Data from Guthrie 2003

Guthrie (2003) notes that the metacarpals is used for distinguishing between species but does not mention specifically if the length is one of the defining characteristics. He cites Eisenmann and Karchoud (1982, Bull. Mus. Natl. Hist. Nat. Paris. Ser. 4, p. 75) but we were not able to obtain this reference. Taxonomic utility assignment remains equivocal.

*_Equus germanicus_ from France
Data from Forsten 1990

Forsten (1990) states that "nothing indicates taxonomic change, such as clear shifts in size and/or discrete morphological traits", suggesting that size of teeth is important for classification.

*_Eucrassatella turgidula_, crassatellid from Maryland Miocene
Data from Kelley, 1983
Currently _Marvacrassatella turgidela_

Vokes 1957 states that specimens of _Eucrassatella_ can be separated based on the outline of the valves, primarily the roundness of the ventral margin and the dorsal slope. More dorsal slope results in narrower, or more 'elongate' anterior or posterior ends, particularly the latter in _E. marylandica_ (p. 14). This variation is expressed in the distance from the beak to the anterior margin (trait 'DBAM') and the dorso-ventral shell height (trait 'H') relative to the antero-posterior shell length. The relative shell height measured at anteriormost point of posterior adductor (trait 'LPA'), the relative distance to the posterior margin from anterior-most point of posterior adductor (trait 'DPM'), the shell height measured at anteriormost point of posterior adductor (trait 'SHPA'), the width of hinge plate measured from the beak to the point of maximum curvature of the hinge plate (trait 'TL') and the distance from beak to point of maximum extent of the umbonal ribs, measured along the umbonal ridge (trait 'DRB') are all likely to be correlated with variation in the outline of the valve. Thus all of the above characters are considered to be useful for classification.

In addition, Ward 1992 states that some species are flatter than others (_M. melina_, p. 88), implying that the convexity of the valve (trait 'CON') and the relative width of the valve perpendicular to the commissure (trait 'W') are important for classification.

In contrast, the length of posterior adductor muscle scar (trait 'LPA') does not appear to have any bearing on classification. Because the relative distance to posterior margin from anterior-most point of posterior adductor (trait 'DPM') is not mentioned and is not necessarily correlated with shell outline, it is considered not useful for classification.

Eucyrtidium calvertense-matuyami from the North Pacific
Data from Kellogg 1976

Hays (1970) described the difference between _Eucyrtidium calvertense_ and _E. matuyami_ as primarily a difference of size. Hays also stated that while any number of parameters would demonstrate the size difference, the best is the maximum width of the test, almost invariably equivalent to the width of the fourth segment (and used by Hays to document the evolution of _E. matuyami_ from _E. calvertense_).

*_Gasterosteus doryssus_ from Nevada
Data from Bell et al 1985, Bell et al 2006

Modern species of stickleback (Gasterosteidae) are similar in overall morphology but distinguishable based on the presence of cusps on pelvic spines, presence, number and orientation of dorsal spines, size and number and arrangement of lateral plates. Morphs within the threespine stickleback (_Gasterosteus aculeatus_) differ based on number and arrangement of lateral plates (Mattern 2007, Wootton 1984). _Gasterosteus doryssus_ is a low plated form.

Some Pliocene specimens have a reduced pelvic girdle, few or no lateral plates, and few dorsal spines; these were originally referred to as *G. apodus* but are now considered to be variants within *G. doryssus* based on comparison to variation in these traits in modern populations of *G. aculeatus* (Bell 1994, Wootton 1976). Bell (1994) states that *G. doryssus* may be separated from the *G. aculeatus* species complex because of the extreme armour (plate) reduction in specimens, but that these species are similar in dorsal spine number and pelvic condition.

In 2007, there were only two recognized extant species of *Gasterosteus*. *Gasterosteus wheatlandi* is distinguishable from other threespined sticklebacks by its nuptial coloration, low number of lateral plates (5-11) on anterior portion of the body, and lack of a caudal peduncle keel and posttemporal and supracliethra bones. This species is also sexually dimorphic for lateral plates, vertebrae number, overall length, second dorsal spine length, gill rakers, and anal fin ray number. Where analyzed, this species is smaller than *G. aculeatus* in sympatry (Mattern 2007).

G. aculeatus shows so much intraspecific variation that 40 different species have been proposed. Most of the taxonomic splitting was based on the extent of lateral plating. The presence of a keeled caudal peduncle appears to be associated with the extent of lateral plating. Populations are often divergent in standard meristic characters (e.g., number of lateral plates, number of gill rakers, number of vertebrae, orbit diameter, body depth, body width, dorsal and pelvic spine lengths, pubic-plate length, peduncular depth, Ross 1973), and standard length may be used to standardize these trait values (Ross 1973).

Based on these descriptions, it appears that standard length (SL), number of dorsal spines (DS), pelvic condition (PG) and predorsal pterygiophore number (PDP), dorsal fin ray number (DFR) and anal fin ray number (AFR) are not useful for classification within the genus *Gasterosteus*, though some, particularly size, pelvic condition and dorsal fin ray number, are important at the genus level within the family.

Globorotalia conoidea-inflata; Globorotalia tumida; Globorotalia crassiformis; Globorotalia tosaensis; Globorotalia truncatulinoides
Data from Malmren and Kennett 1981, Malmgren et al 1983; Lazarus et al 1995, Renaud and Schmidt 2003, Lohmann and Malmgren 1983

While Spencer-Cervato and Theirstein (1997) state that *G. crassiformis* is the ancestor to *G. tosaensis*, which is the ancestor to *G. truncatulinoides*. This is not controversial except that it should be clear that these three species co-occur (see also, Lazarus et al 1995), so this is not an anagenetic trend and each species is considered separately.

Among these three species, the presence of more than four chambers in the final whorl characterizes *G. tosaensis* (Lazarus et al 1995; Spencer-Cervato and Theirstein 1997). *G. truncatulinoides* differs from *G. tosaensis* by having a complete keel (Lazarus et al 1995). *G. truncatulinoides* and *G. tosaensis* differ from *G. crassiformis* by being more conical in side view (rather than globular) though the degree of conicity is known to vary with latitude (Lohmann and Malmgren 1983; Lazarus et al 1995; Spencer-Cervato and Thierstein 1997; Renaud and Schmidt 2003). Box area ratio and radius ratio in side view, while being untraditional characters (according to Lazarus et al 1995), quantitatively capture the difference in shape described by qualitative descriptions of conicity/sphericity (a "traditional" character), and is thus considered to be useful for classification. The environmental variation within *G. truncatulinoides* does not encompass the globular shape of *G. crassiformis* (compare Figure 8, Lazarus et al 1995 with Figure 1, Renaud and Schmidt 2003). All three species have named subspecies (see, for example, Rögl, 1974).

Radius ratio in top view quantitatively captures the difference between species with a protruding final chamber and those that are rectangular. This appears to covary with the

arrangement of final chambers as either evolute, or involute, respectively, but does not necessarily covary with the number of final chambers (for example, *G. crassaformis* is involute with four final chambers, *G. truncatulinoides* is evolute with five final chambers, but *G. crassaconica* is evolute with four final chambers, Hornibrook 1981). Nonetheless, because both evolute and involute species occur in the genus, radius ratio in top view is assumed to be useful for classification.

Size is not considered important for classification by Lazarus et al (1995). In contrast, Malmgren et al (1983) used test size to distinguish between *G. tumida* and its ancestor *G. plesiotumida* (along with relative size of carina and test wall thickness). Thus this trait is considered useful for the studies done by Malmgren and colleagues. Banner and Blow (1960) remark on the apparent tendency for overall test size to increase during phylogeny, citing *G. tumida* as such an end-member. Peripheral roundness ("roundness") is simply a length measure though it changes within *Globorotalia* independently of size (Malmgren and Kennett 1981). Wei (1994) states that peripheral roundness (a length measure) shows the most allometric variation and is the best univariate variable—in conjunction with size—to differentiate *G. inflata* and *G. puncticulata*. Although this suggests that it is really the ratio of roundness to size that is useful, Wei (1994) demonstrates that roundness is a particularly strong discriminator compared to other variables. Likewise, he also demonstrates that length and height of aperture are often particularly strong discriminators. And while it is often the shape of the aperature (sometimes measured as the ratio of length to width, Malmgren and Kennett, 1981) that is useful for classification (Lazarus et al. 1995), Berger (1969) mentions their size as well as number and position as useful for species-level characters of planktic foraminifera as a whole. Aperture size varies between subtropical and subantarctic populations of *G. puncticulata* (Scott et al. 2007)

 Specimens do show shape change during growth but this is minimal for specimens larger than 0.25 mm (Lohmann and Malmgren 1983). All specimens selected for the studies included in this dataset were at least 0.25 mm (250 microns) in length (Lohmann and Malmgren 1983; Lazarus et al 1995) or at least 150 microns in length (Renaud and Schmidt 2003).

 The number of chambers in the final whorl is commonly used for species-level discrimination (e.g., Lazarus et al. 1995, Scott 1980). The conical angle (Malmgren and Kennett 1981) covaries with conicity, and is thus useful for classification. The conical angle may also be referred to as the G1 angle (Wei and Kennett 1988). The G2 angle is not mentioned as being useful for classification.

 Variation in test shape measured using outlines agrees with genetic differences in extant populations of *G. truncatulinoides*, although there is also an environmental component to this variation. Renaud and Schmidt (2003) measured trends in outline data for each core but later used the outline data to assign taxa to previously determined genetic species, stating the samples from particular cores were "mainly" composed of one species or the other. Because of this and the correlation between outline data and other useful traits (e.g., conicity), the PC scores of outline data are considered useful for classification.

Haplomylus speirianus-scottianus from Clarks Fork Basin
Data from Gingerich 1994

Size is important for separating co-generics. In particular, size (estimated from molar size) is the distinguishing characteristic between these two species. In the stratophenetic series, the species boundary is drawn arbitrarily (Gingerich, 1994).

Holmesina septentrionalis-floridanus from Florida

Data from Hulbert and Morgan 1993

Edmund (1987) described all *Holmesina* specimens from Florida as being of one unbranching lineage, but avoided assigning a boundary between the two end member species. Hulbert and Morgan (1993) discuss a few taxonomic interpretations, including one boundary which relies on morphological differences in dentition, post-cranial skeletal characters, and abrupt size differences and is historically favored. They favor this hypothesis over one that distinguishes between species solely by the rate of size increase. Body size is believed to be reflected in adequate samples of *types* of osteoderms, in part because shape and proportions of comparable osteoderms within *Holmesina* are similar among differently-sized individuals through time (Edmund, 1987). Thus osteoderm size (length and width) has been used for classification. While thickness is not mentioned in taxonomic descriptions, it appears to be correlated with size. All measurements are considered useful for taxonomy.

Homagnostus obesus from Sweden
Data from Lauridsen and Nielson 2005

According to the caption for text-fig. 4, "Measurements used for species identification and morphological changes…B, in *H. obesus* the maximum width of the axis (d) is compared with the length (a) of either the cephalon or pygidium". However, it is not clear in the the text itself how these measurements are related to the discrimination of *H. obesus* from other species. Allometric plots of width/length ratios of cephalon and pydidia are given in text-fig 5, but are not singled out as species level determinants in the text. A taxonomic reference not listed in the paper (Pratt 1992) indicates that the pygidial shape/elongation has been used as a diagnostic feature at the genus level, hence the pygidial ratio is considered by us as taxonomically useful, based on both the original paper (text-fig. 4 & 5) and the secondary reference. The cephalon ratio is more problematic. Pratt's discussion includes remarks about height levels of intraspecific variability in both the cephalon and the pygidium, as well. To remain consistent, we treat the cephalon ratio as also having taxonomic use (implicitly), due to its treatment in the original source (text-fig. 4 & 5).

Hyopsodus
Data from Gingerich 1974 and Bookstein et al. 1978

31 species have been described within the genus *Hyopsodus*, of which 12 were regarded as valid by Gazin (1968). Gazin (1968) notes that species are difficult to separate based on teeth and jaw characters with the exception of size. Gazin (1968) uses the range in variation of length of M1 to support the synonymy of *H. miticulus* and *H. mentalis* and he uses the range in variation of length of M2 to support synonymizing other species. Size is also historically important for classification (Gazin, 1952). Finally, Gingerich (1974) states that at a given stratigraphic level, size differences of molars alone distinguishes species, and Gingerich (1994) uses size differences to diagnose the species *H. pauxillus*.

Hyracotherium grangeri from Clarks Fork Basin
Data from Gingerich 1991

Gingerich (1991) describes several species of *Hyracotherium*, including *H. grangeri*. Additional collecting has obscured separation between species based on size of the M1, and the size and shape of other teeth are important for diagnosis, particularly where the holotype does not include M1. Nonetheless, size is always included in the diagnosis of a cogeneric and

discussions include how different species differ in size, particularly where in cases where other features are similar. Historically subspecies have also been separated based on size.

Icriodus steinachensis from Nevada
Data from Murphy and Cebecioglu 1984

Murphy and Cebecioglu (1984) state that the elongation index is useful in combination with other characters. Therefore it is considered useful for classification.

Inoceramus (Sphenoceramus) naumanni from the Cretaceous of Japan
Data from Tanabe 1973

The author examined biometrically numerous specimens of *I. naumanni*, noting the occurrence of other species of the genus that co-occur in the same strata. On p. 166, it is noted that *I. naumanni* is easily distinguishable from these other species "by the analysis of individual relative growth and the apical angle". Text-fig. 7 shows the relative distribution of shell heights (including the "concentric ring stage") for successive populations, by depth in one section; text-fig. 9 illustrates the morphometric measurements used in the study, including shell height overall and at the concentric ring stage. Numeric data of heights from the concentric ring stage (from combined sections(??)) are given in Table 2. "Individual relative growth" is not defined, but would appear to be contingent – at least in part – on shell height at known growth stages. We therefore consider this measure to be taxonomically useful.

**Lagurus curtatus* from Washington State
Data from Rensberger and Barnowsky, 1993

Both Carroll and Genoways (1980) and Rensberger and Barnowsky (1993) mention characters of M3 as diagonstic of this species, but neither mention M1. It is thus assumed that the length of M1 is not useful for within-genus classification.

#Lymnocardium conjungens lineage from Lake Pannon
Data from Geary et al 2010

On p 595, the authors state, "Phylogenetic analysis (Schneider and Magyar 1999) indicates that each lineage [*L. conjungens* and *L. diprosopum* analyzed by us] is a monophyletic unit and stratigraphic evidence (described below) supports their interpretation as anagenetic, species-level lineages." [We have not obtained the reference Schneider, J. A., and I. Magyar. 1999. Evolution of brackish- and freshwater cockles (Bivalvia: Cardiidae) in the central and eastern Paratethys. Geological Society of America Annual Meeting Abstracts with Programs 31(7):399.] Originally, various authors had assigned members of the whole assemblage to 6 species. The *L. conjungens* lineage is interpreted by the authors to include the "anagenetic" stratigraphic species series *L. conjungens* to *L. penslii* to *L. schmidti*. They note on p. 595 that, "These species are characterized by two anterior lateral teeth in the right valve, ribs that are triangular in cross-section and separated by intercostal spaces, and a posterior gape. Schneider and Magyar's (1999) cladistic analysis included 47 taxa (species of Lymnocardiinae plus outgroups; 29 characters, 155 character states). *Lymnocardium conjungens* and *L. penslii* are sister species in this analysis; *L. schmidti* was not included." The non-measured characters they note describe the lineage as a whole, but don't differentiate the 3 species. The authors instead used "morphometrics and eigenshape analysis to quantify variation and change" (p 597), particularly shell shape. Traces of the shell outline were used for eigenshape analysis and eigenshape2 is explicitly used to provide support for an anagenetic trend (Figure 6).

Likewise PC 2 and PC 4 show the most change through time and shell shape traits (length/height, relative beak height, "hinge curve" and anterior length/length all load on these two components. Thus all of the above are considered useful for classification. In contrast, PC1 and PC 3 show weak to no net change through time and angles that describe the beak rather than shell shape load on these two components; thus these are considered not useful for classification.

Lymnocardium diprosopum lineage from Lake Pannon
Data from Geary et al 2010

Phylogenetic analysis indicates that species in lineage are monophyletic, and include *L. subdiprosopum*, followed by *L. diprosopum*, and ending with *L. arpadense*. Species in this lineage differ in only three cladistic characteristics: development of a moderate lunule in *L. arpadense*, loss of posterior gap after *L. subdiprosopum*, and shell shape. Szónoky et al. (1999) assert that *L. arpadense* and *L. diprosopum* are undoubtedly closely related yet distinguishable species. *L. diprosopum* differs from *L. arpadense* in having a lower height/length ratio and lacking robust hinge teeth (Lennert et al. 1999); therefore length/height and anterior length/length are considered to be useful. Differences in size are also considered taxonomically useful on the basis that juveniles of the same size differ in number of ribs and hinge teeth (Szonoky et al., 1999); therefore length (Ln height) is considered to be useful. The two species are not known to occur together (Szonoky et al., 1999). In Geary et al. (2010), traditional morphometrics measurements (length measurements and length-length ratios) were chosen to represent overall shape as well as dentition. Traces of the shell outline were used for eigenshape analysis; therefore, all variables generated from this analysis were considered to be useful for classification. ABP is also correlated with the first two eigenshape axes. The angles ABP and ABS load onto the first PC, and because PC 1 is used to provide support for the anagenetic trend (Figure 9), they are considered useful for classification. Even though it shows weak change through time, variation in relative beak height is expected to influence overall shape and so was also considered useful for classification. PC III is also considered useful for classification because anterior length/length loads on it. However, there is nothing in the paper to suggest that PC II would be useful for classification: it is not used to describe differences between species and only angles describing the beak load on it (BPS, APS, and PAS). These are thus considered "not useful".

Mammuthus meridionalis-trogontherii-primigenius of North America
Data from Lister 1993

Maglio (1973) discusses the difficulty in species-level taxonomy of this genus: "All available evidence suggests that these taxa represent a series of more of less successional populations in which progressive evolutionary change in masticatory adaptations paralleled those of the European mammoth lineage…It is important to keep in mind that "species" which represent segments along a phyletic continuum are arbitrary units." (p. 61). Height of crowns (hypsodonty index), number of plates on M3, thickness of enamel and lamallar frequency are all used to synonymize previously described species, suggesting that despite these difficulties, these characteristics serve to distinguish "species" or at least morphs within a sequence. Maglio discusses *M. meridionalis* and M. *primigenius* (which he considers valid species) but not *M. trogontherii*.

Mandarina spp. of Japan
Data from Chiba 1996, 1998

Recent species of *Mandarina* are known to show ecotypes within species and species of the same ecotype are very similar to one another, despite some character displacement among sympatric ecotypes (Chiba 2004). In addition, size variation in land snails has both a genetic and plastic component (Goodfriend 1986). Thus recent species of *Mandarina* are distinguished primarily by genetic morphology (Chiba 2004). However, this information is not available for fossil species. In his 1996 study, Chiba focused on *M. chichijimana*, which has three subspecies that differ on the basis of allozyme variation and are each endemic to a different island of the Bonin Islands [however, it is unclear if some of these subspecies were elevated and included in the 2004 study].

Chiba (1989) states that classification based on juvenile shells matches well with that based on genitalia whereas adult shell characters are strongly influenced by environmental conditions—and suggests that they may be useful for identifying habitat occupation in fossil species. Only the height (PH) and the diameter (PW) of the protoconch are juvenile characters measured in this sequence; thus only these two characters are considered useful for classification.

Melanopsis impressa-M. fossilis lineage from Pannonian Basin
Data from Geary 1990

Shouldering and shell height are the two characters that best distinguish *M. impressa* from *M. fossilis*, so clearly this trait is useful for classification. Apical angle is useful for distinguishing *M. fossilis* and *M. vindobonensis*, so it is clearly useful for classification at the species level. However, it is not useful for distinguishing *M. fossilis* and *M. impressa*.

#*Metrarabdotos micropora-butlerae* from southern U.S.A.
Data from Cheetham 1968

Cheetham (1968) introduces the Taxonomy section, beginning on p. 33, stating, "The taxonomic procedure adopted for this study has consisted of: (1) grouping sampling units on significant morphologic resemblance, (2) projecting the similarity groups so obtained into a stratigraphic framework to infer their probable phylogenetic relationships, and (3) recognizing taxonomic clusters in the phylogenetic pattern. The taxa established on this basis are polythetic and, as far as interpretation of the data permits, monophyletic."
Binary characters used for phenetic analysis are given in table 6 (p 39) and "standard" quantitative metric characters are summarized in fig. 9 (p 24), and p 23: "In the present study eleven variates (Figure 9) were determined on selected, or in some cases on all available, zoarial fragments preserving the requisite morphologic features by rotating each one so that every zooecium or gonoeciimi observed had in turn its frontal surface perpendicular to the axis of the microscope. Measurements, including those of secondary orifice and avicularium, are thus of frontal projections." However, under "Phenetic comparison" (p. 34), he notes: "Slightly more than half the characters were susceptible of expression in two-state code; the others required codes running to as many as five states (Table 6). 1. Three methods of character weighting were employed. Those quantitative characters which the multivariate analysis suggested to be redundant were omitted. Thus the mean values of the first three principal components, zooecial size and shape and avicularian-oral "ratio," were used in place of the six original variates." These 6 variates are: Lz, Iz, ho, lo, Lav, and na. We take this to mean that these traits *contributed* to the clustering pattern and were represented in the codes given in Table 6; thus, they appear to be used in taxon determination.

Miniochoerus? forsythae-Miniochoerus chadronensis-affinis
Data from Prothero and Heaton 1996

Stevens and Stevens (1996) revised the taxonomy of this genus, and their taxonomy is used by Prothero and Heaton (1996) to assign species names to specimens. Stevens and Stevens (1996) state that *?M. forsythae* is a likely ancestor to *M. chadronensis*; that *M. chadronensis* gave rise to both *M. affinis* and *M. gracilis*, and that *?M. forsythae*, *M. chadronensis*, and *M. affinis* represent a chronocline in which the latter two species are distinguished based on stratigraphic placement, depth of preorbital fossae, and overall size (estimated from molar size). Therefore, this trait (average molar length) is considered useful for classification.

Miogypsina cf. bermudezi-complanata/formosensis from western India
Data from Drooger and Raju 1978a, b

Drooger and Raju (1978) refer to the lower part of the sequence as *Miogypsina cf. bermudezi*. In the upper part of sequence, specimens that would formerly be assigned to *M. complanata* alternate with specimens that would have been assigned to *M. formosensis* based on variation in the mean number of nepionic chambers (X). The authors hesitantly lump all specimens together into one group. Nonetheless, they continue to separate the *M. complanata/formosensis* complex from the underlying *M. cf. bermudezi* specimens as well as other cogenerics based on the number of nepionic chambers (X), the number of operculinid chambers (Y), and the diameter of the protoconch (I) (Drooger and Raju 1978a, b, Raju 1974)). Thus all three characters are considered useful for classification. There is a consistent positive correlation between X, Y, number of nepionic chambers up to and including the largest chamber in the spiral (Z), and angle between embryonic chambers relative to apical-frontal line (gamma) (Raju and Drooger 1978a, b), thus these latter two characters are also considered to be useful for classification.

All three species belong to the subgenus *Miogypsinoides*. There is no mention of the diameter of the deuteroconch (II) when describing cosubgenerics of *Miogypsinoides* (Raju 1974, Drooger and Raju 1978a, b). However, this trait is used to separate the subgenus *Miogypsinoides* from *Miogypsina s.s.* Thus this trait is also considered "useful" in classification.

The diameter of the embryonic-nepionic part of the test (P) is a variation on a trait that is expected to correlate with X (Drooger and Raju 1978a, b). However, within the sequence it shows a correlation with either I or X but rarely both. It was not used in earlier systematic descriptions of the Miogypsinidae (Raju 1974), thus its classification value is uncertain though likely "not useful" in the context of the current species concepts.

Miogypsina sp. of Italy
Data from Wildenborg 1991

Drooger (1963) stated that the arrangement of the nepionic part of the test has been used as the primary feature in species-level classification, including the 200 a/b scale (particularly in younger species of the genus, including *M. intermedia*, *M. cushmani*, and *M. mediterranea*) and the angle gamma. Thus both of these features are considered useful. There are differences in protoconch diameter between samples (see for example, fig. 14 in Drooger [1963]), and some increase of the mean protoconch diameter through phylogeny (e.g., fig. 15, Drooger [1963], where the 200a/b scale is used as a proxy for time), but it appears that this feature is not considered useful for classification, presumably because of the poor correlation between this length measure and some nepionic features, such as gamma, and the high

variation. Subsequent work has also shown environmental influence on embyron size (summarized in Wildenborg, 1991).

Monograptus subhercynicus-hercynicus from Nevada
Data from Springer and Murphy 1994

Springer and Murphy (1994) note that regardless of whether these two taxa were considered species or subspecies, they were subdivided based on secular width, and maintain this as the major distinguishing feature (but do discuss some qualitative differences) between them. Therefore this character is considered to be useful for classification.

**Monotis ochotica*, monotid (bivalve) from Japan
Data from Ando, 1987

High variation in this species has lead to the naming of numerous subspecies. Intra- and interspecies variation in *Monotis* is summarized in Figure 26 of Ando (1987). Number of radial plicae and elongation in the posterior part of the valve ((L-A)/B) are shown, and the relative size of the postumbonal length ((L-A)/A) as well as the ratio of L to H are reflected in changes in shell outline. This figure is not explicit, however, about which features are important for species-level distinction. However, based on the systematic section, the number of radial plicae and the expression of secondary plicae are most important for species-level distinction; the elongation of the posterior half of the valve and the overall outline of the valve appears to be of secondary importance.

In the case of the two subspecies, the author notes that these are explicitly chrono-species that each represent the end of one part of a gradual trend, and that the distinction is ultimately arbitrary (p. 85) although *M. ochotica ochotica* comprises most of the variation (and most of the variates previously described).

Morozovella velascoensis from the northwest Pacific
Data from Corfield and Granlund 1988

Corfield and Granlund (1988) select the outline of the describe morphological change in the sequence analyzed based on previous work where it was shown to contribute to species discriminating ability in foraminifera. In the systematic paleontology section, they use differences in the acute axial angel and development of muricae to distinguish among species. Since the former influences test shape, this trait is considered useful for classification.

Mosaeleberis sp. from Bohemia
Data from Pokorny 1966

See description for *Cythereis longaeva longaeva*

**Neogloboquadrina pachyderma* dextral/sinistral from the North Pacific
Data in Kucera and Kennett 2002

The dextral and sinistral forms of this species are analyzed separately because the two forms are genetically distinct (Kucera and Kennett 2002). *Neogloboquadrina pachyderma* differs from similar species on the basis of the perforation of the wall (reticulate rather than finely perforate), size and character of spines, character of aperature, and the shape of the keeled edge (Bandy, 1972, in which he refers to the species as *Globorotalia (Turborotalia)*

pachyderma; Collen and Vella 1973 assign the species to *Neogloboquadrina*). Collen and Vella (1973) distinguish *N. pachyderma* from *Neogloboquadrina dutertrei*, at least in part, by the number of chambers in the final whorl; otherwise they are almost entirely identical in surface details. In addition, Kucera and Kennett (2000) reidentify some *N. pachyderma* specimens as a distinct species (*Neogloboquadrina inglei*) based on size of test, rounded shape of axial periphery, and inflation of chambers. These features are captured by the shape indices (elongation ratio, compactness coefficient, circularity ratio, and box ratio) calculated by Kucera and Kennett (2002) and included in the principal components analysis.

Neogloboquadrina acostaensis from mid-Atlantic core
Data from Biolzi 1991

Biolzi (1991) states that characters that distinguish among this species and putative descendent species (*Neogloboquadrina humerosa* and *N. dutertrei*) include "size, chamber number, spiral height, and lobation (chamber overlap). Thus all measured characters are considered useful for classification.

Neopolygnathus communis-subplanus-purus from Poland
Data from Dzik 1997

According to the taxonomy of Dzik (1997), the relative position of the platform margin and its convexity and ornamentation are important for species-level classification. The elongation of the platform might correlated with platform position, as mentioned for some specimens of *Neopolygnathus subplanus*, but it is not mentioned as a distinguishing character between species. Therefore this character is considered to be not useful for classification.

Ogmodontomys sawrockensis-poaphagus from Kansas
Data from Marcolini and Martin 2008

Ogmodontomys species (and previously named subspecies) have been distinguished based on tooth length, width and height, degree of closure between alternating triangles and the development of dentine tracts on the labial side (Zakrzewski 1969). Of the 17 measurements made by Marcolini and Martin (2008)—all in occlusal view—V6 and V2 are measures of overall size, and V31, V33, V34, andV35, and conceivably V24 and V26, relate to the degree of closure between alternating triangles. These eight are considered useful for classification while all of the others are considered not used.

Olenus sp. from Sweden
Data from Lauridsen and Nielsen 2005

Lauridsen and Nielsen (2005) note that some species in this chonoseries differ from one another in having a broader pygidium but that between some species the transition is gradual and effectively arbitrary, leaving other discrete features as more appropriate for classification. Nonetheless, it seems clear that the width to length ratio has been used historically to separate this and other species in the lineage. Furthermore, the caption for text-fig. 4 reads: "Measurements used for species identification and morphological changes. A, in the pygidia of *O. gibbosus, O. truncatus, O. wahlenbergi, O. attenuatus and O. dentatus*, width (AA) is compared with length (CH). B…"

Ommartartus hughesi lineage from equatorial Pacific
Data in Kellogg 1980

This dataset comprises a lineage where the older end-member is *Cannartus pettersoni* and the younger end-member is *Ommartartus hughesi*. The primary difference between these two species is that the polar columns are subdivided into multiple polar caps in *O. hughesi*. Intermediate forms where only the proximal portions of the columns are divided are considered to be *C. pettersoni*. Since the presence of multiple polar caps is not known be correlated with the size (either in length, width, or area) of the cortical shell, these characters are all considered to be uninformative for classification.

Ommartartus tetrathalamus lineage from equatorial Pacific
Data in Kellogg 1980

This dataset comprises a mulitspecies lineage where the oldest end-member is *Cannartus prismaticus* and the youngest end-member is *Ommartartus tetrathalamus*. The primary difference between these species is the combination of presence of polar column, width of polar column if present, presence of polar caps, and developmental degree of polar caps, if present. Since these combinations of characters are not known be correlated with the size (either in length, width, or area) of the cortical shell, these characters are all considered to be uninformative for classification.

**Orbitoides sp* from France
Data from Drooger and DeKlerk 1985 and Baumfalk 1986

Drooger and DeKlerk (1985) note that previous work by Van Hinte resulted in a numerical classification based on Li + li, E, and P. Therefore all three are considered useful for classification. Further, Drooger and DeKlerk equate P with Y + 1. Because E/P is correlated with E, it is also considered useful for classification. The average thickness of the embryonic walls (T) and the sphericity of the embryon (LD) are not mentioned regarding classification.

mC is inversely related to E/P (Drooger and DeKlerk 1985); therefore it is considered useful for classification. Lo is likely correlated with Li + li; thus even though it apparently has not been relied on for classification, it considered useful. The principal components in the analysis by Baumfalk (1986) have the following loadings: "Vector I reflects overall embryon size and the related number of epi-embryonic chambers E. Vector II heavily weighs mC: specimens with high mC will score high on this axis, especially when E is low and the size of the embryon is relatively large. Vector III reflects the shape of the embryon (ratio between long axis and short axis variables)". Thus both PC1 and PC2 reflect variation in characters used for classification and are themselves considered useful. PC3, however, reflects a character that is not mentioned regarding classification and is considered not useful.

#Orbitolina lenticularis from France and Spain
Data from Hofker 1963

With respect to external characters used previously to determine *Orbitulina* species, the author says on p. 217, "Apparently none of these single characteristics can be successfully used for defining the species of *Orbitulina;* even combinations are unreliable and not typical in the sense of Schindewolf's definition. Only one part of the test remains to a large extent unaffected by ecologic conditions. This is the embryonic apparatus, which is formed in the protecting protoplasm or the microspheric generation. The present author noticed that in each sample studied, the variation in shape of the embryonic apparatus is limited and that the same forms are found in contemporaneous samples from geographically different localities.

Moreover, in the megalospheric embryonic apparatus a distinct evolution can he observed. Consequently, this apparatus can be best used as a taxonomic criterion in *Orbitulina*." We infer from the text on p. 217, which refers to the "apparatus (measured by the diameter of the deuteroconchs, chart IV)", that the charts used by us refer to analogous measures for different sites. On page 218, he refers to these subdivisions of the genus as "form groups". He considers the genus to consist of one single species, *O. lenticularis.*

Orbulina universa from the Mediterranean
Data from Spaak 1982

Spaak (1982) lists multiple studies which document that variation in diameter is related to water temperature. Orbulina universa are characterized by a spherical shell perforated by pores of two sizes (Hecht et al., 1976). Morphological features separating *Orbulina universa* from other forams (albeit from other genera, since *Orbulina* is currently monotypic, de Vargas et al 1999) include surface texture and apertures (Be et al 1973). Desai and Banner (1985) note that the only difference between earlier species of *Orbulina* and *O. universa* is thee thick wall. Considering this, as well as Spaak's use of test diameter in order to reconstruct water temperature supports the "not useful for classification assignment".

#Otoscaphites puerculus from Japan
Data from Tanabe 1977

Differences between *Otoscaphites puerculus* (formerly *Scaphites puerculus*) and *Scaphites planus* include: shell size, apertural shape, rate of involution, spiral length of phragmocone, number of septa, and complexity of adult sutures. Similarities include similarity of suture patterns [?], growth patterns of radius length, whorl height and breadth, umbilicus and ventral wall and septal thickness about 9pi stage. Characters that have been suggested to indicate sexual dimorphism include size differences, presence of umbilical swellings, and presence of simple aperatures vs small lappeted forms. Tanabe (1977) states that the "two species evolved in parallel, and cannot discount the possibility of sexual dimorphism. However, he could not find discontinuous variation in size differences or existence of umbilical swellings (the point in development where the latter varies from specimen to specimen). He made a variety of individual trait measurements, including ratios, showing insignificant differences in the ratio of radius length to rotational angle through juvenile growth stages (Fig. 5). Nepionic size also showed mostly insignificant differences. We interpret this to mean that these characters did NOT prove useful in classification. The author does note that adult stages sometimes showed significant differences (pp 386); this was not fully clarified for the traits we analyzed. Tanabe retained his nomenclature throughout the analysis, but declined to speculate on the existence of one versus two species in his conclusions.

Parkiella angulocamerata-globocamerata from DSDP 171
Data from Kucera and Widmark 2000

Kucera and Widmark (2000) explicitly chose to measure the chamber angle, the umbrella angle, and the shell globularity because they corresponded to diagnostic features used by Widmark and Kucera (1998) to distinguish between *Parkiella angulocamerata* and *P. globocamerata* (two end-member species). Thus all three are considered useful for classification.

The first eigenvector from the eigenanalysis of test outline describes the variation from oval shells with globular chambers to angular shells with chambers extended by distinct spines

(Kucera and Widmark 2000), features which were considered the most distinctive between the two end-members (Widmark and Kucera 1998). Thus this trait is considered useful for classification.

All variables but shell size contribute to the first PC and the Kucera and Widmark (2000) determine that the first PC is more efficient at discriminating between the two end members than any individual variable. Shell size alone contributed to the second PC, confirming the authors' impression that size did not vary much between samples or end-member species. Both holotypes are the same size within 0.01 mm (Widmark and Kucera, 1998). Thus all size measures ("log size", "size", "height", "PC2", "proloc-gen1", "proloc-gen2") are considered "not used" for classification. PC 1 is considered useful.

Pelycodus mckennai-trigonodus-abditus
Data from Bookstein et al 1978

Gingerich and Simons (1977) describes several species of *Pelycodus*. While characteristics other than teeth are important for diagnosis, size (inferred from the size of M1) separates species and is included in diagnoses and discussions of cogenerics, particularly in cases where other features are similar.

Planorbulinella rokae-astriki-caneae **from various sections of Crete and southern Italy**
Data from Drooger et al. 1979

The lineage *Planorbulinella rokae*, *P. astriki*, and *P. caneae* was divided by Freudenthal (1969) by the mean number of spiral chambers (trait Y) (Drooger et al., 1979). Y and the diameter of the embyron (d12) are negatively correlated with one another (Drooger et al., 1979) and these two traits as well as the sum of Y and the number of relapse chambers (Y + R) are used to distinguish between other cogenerics (Thomas 1977). Thus Y, d12, and Y + 1/2R are all considered useful for classification.
        The ratio of the diameter of the embyron (d12) was used by Thomas (1977) to distinguish between extant species *P. larvata* and *P. elatensis*. Thomas (1977) also notes the difference in both Y + R and R values between the two species.
        P is only partly correlated with d12 and Y (Drooger et a 1979) and Y – R is not necessary correlated with either. As these are not "classical" parameters anyway, they are considered "not used" in classification.

Pleuriocardia pauperculum **from western interior basin**
Data from Geary 1987

Subgenera within *Pleuriocardia* are distinguished by being ovate to subquadrate (Scott 1978), therefore length to axial length and height to axial length characters are considered to be important for species-level classification.

P. subcurtum from *P. pauperculum* may be distinguished by the ratio of posterior ribs to total ribs (Geary 1987). In addition, *P. subcurtum* is distinguished from *P. bisculptus* on the basis of the large size of the posterior ribs and the size of the area of the umbonal ridge in the latter (Geary 1987). These differences are likely reflected in the number of posterior ribs and the total number of ribs, thus all characters relating to ribbing are considered useful.

In addition, morphometric analyses support the systematics within this species—and canonical variates analysis based on size and ribbing characteristics—serve to distinguish

congenerics, and Geary (1987) states that these variables were selected on the basis of both their ability to describe interspecific variation as well as intraspecific variation.

Poseidonamicus major, *P. miocenicus*, and *P. riograndensis*, deep sea ostracods
Data from Hunt 2007 and Brown and Hunt unpublished

Overall outline ("quadrate" vs. "elongate") is among the characters used to discriminate species of *Poseidonamicus* (Benson 1972). Only centroid size is considered for *P. miocenicus* and *P. riograndiensis*. For reasons described for other ostracods, centroid size is considered not useful for classification. PC scores cannot be assigned.

Pseudocubus vema near Antarctica
Data from Kellogg 1975

Dumitrica (1973) describes specimens identified as *Pseudocubus cf. vema*, and remarks that this species is different from *P. obeliscus* by having a cephalic lattice shell and three-bladed spines. Hays (1965) named *Helotholus vema* and distinguished it from other members of the genus in having a small hemispherical cephalis and broad cylindrical thorax, but these are relative size descriptors not absolute size descriptors. The thoracic width reported for this species by Hays (1965) encompasses most but not all of the range measured by Kellogg (1975); notably, the first 8 samples that oscillate before the series first increases are outside the range originally reported. Thus the thoracic width is considered not used in classification. NOTE: By citing Hays (1965), Hays and Opdyke (1967), Keany and Kennett (1972) and Dumitrica (1973) as publications that describe the taxonomic affinities and ranges of *P. vema*, Kellogg (1975) implies that all of the specimens, including Opdyke and Hay's *Helotholus vema*, and Dumitrica's *Pseudocubus cf. vema* all belong to the same species, even though some of the cited authors are themselves not sure of the extent to which each described sample corresponds (see for example, Dumitrica, p. 836). Keany and Kellogg (1972) use "*Pseudocubus vema*" but may not be the workers that rename it; Hays and Opdyke (1967) still use "*Helotholus vema*".

Pterospathodus eopennatus-amorphognathoides from Estonia
Data from Jones 2009

The sequence describes size and shape of the P1 element [=Pa elements in traditional morphology-based notation [Jones 2009]) from a stratophenetic series of *Pterospathodus*. Jones (2009) chose to analyze this element because it had previously been described as having undergone substantial morphological change. *Pterospathodus amorphognathoides angulatus* differs from *Pterospathodus eopennatus* by having a longer blade (Mannik, 1998), corresponding to the length of the element in lateral view; thus this character is considered to be useful for classification. The height of the base is often used to distinguish between morphs within a species but is not clearly used to distinguish between species; thus the length/width ratio is not considered to be useful. The length of the lateral process is not mentioned in species-level descriptions (Männik 1998). Finally, Jones (2009) notes that species in this sequence are diagnosed using elements other than the Pa element and that there is considerable range of variation in the Pa element (as also indicated by the number of P1 morphs described by Mannik [1998]).

Because variation in diagnostic features affect outlines, traits extracted from multivariate analyses of outlines are considered useful for classification.

Pygomalus ovalis-analis - Collyrites elliptica - Cardiopelta bicordata from France

Data from Thierry 1974

Thierry 1974 considers the sequence of *Pygomalus ovalis-analis* to *Collyrites elliptica* to be an typical anagenetic trend where some of the measured characters (I/L, G, e/L) show relative little variation and the others (bt/L, pp/H, ps/L) show rapid change.

Features that change during the upper Callovian (with the appearance of Cardiopelta bicordata) include "…appearance of a depression at the level of the anterior ambulacral area, the progressive prominence of the plastron, the narrowing of the test towards the back, and the descent of periproct along the posterior ambulacral area ambulacral…". The shift in the periproct would influence pp/H, and narrowing could influence e/L. pp/H would also be influenced by whether the bivium is attached to periproct, a feature used to distinguish between *Pygomalus analis* and *Collyrites elliptica* (Thierry 1974). Other features used to distinguish between *Pygomalus* species include the test height, how "streamlined" the test is between the bivium and trivium, and truncation of the rear of the test (Thierry 1974). The relative postion of the peristome would be affected by the truncation of the rear and any ratios using the height would be influenced. Based on these observations, pp/H, e/L and ps/L are considered useful for taxonomy. The usefulness of the other traits is less clear except for the following: At the boundary between the Middle Callovian (in which *Collyrites elliptica* is found) and the upper Callovian (in which *Cardiopelta bicordata* is found), Thierry (1974) notes that "a second discontinuity appears, here tight enough sampling permits [supports] the idea that an important modification appears in *all* the characters. This discontinuity may have taxonomic value." (p. 393, emphasis added). Thus implies that while each might contain taxonomic information, they have not all been used for classification before. This is supported by the abstract which says that *some* characters *may* have taxonomic utility. The remaining three traits (I/L, G, and bt/L) are considered to be not useful.

#*Spaniomys sp*. from Argentina
Data from Anderson et al 1995

Anderson et al. examine two lineages, the marsupial *Acdestis oweni,* from the Pinturas and Santa Cruz formations, and the octodontoid rodent genus *Spaniomys,* from the Santa Cruz Formation. The *Acdestis* sequence has insufficient sample sizes. The authors combined smaller and larger specimens of *Spaniomys* from below and above a tuff, respectively, into one lineage, stating, "We believe that each lineage represents an essentially unbroken series of evolving conspecific populations, subject to biological events that may have occurred throughout this period of time and especially at the time of deposition of tuff unit 8." These had previously been assigned by Ameghino (1887) to the chronospecies *S. modestus* and the larger *S. riparius*. [We have not been able to obtain the reference: Ameghino, F. 1887. Enumeracion sistematica de las especies de mamiferos fosiles coleccionados por Carlos Ameghino en los terranos eocenos de la Patagonia austral y depositados en el Museo de La Plata. Boletin Museo de La Plata 1:1-26. Whether tooth dimensions play a role in separating species is not known] No other information is given in the source paper. Patterson & Pasqual (1968, p. 3) clarify classificatory role of "tooth structure" rather than "variable" dimensions in the genus *Spaniomys* and its relatives. The sequences analyzed are specifically the length and width of the first molar, not tooth structure.

**Spermophilus townsendii* from Washington State
Data from Rensberger and Barnosky 1993

Spermophilius townsendii is distinguished in part from *S. columbianus* and *S. richardonii* by having shorter lower and upper M3 and from *S. washingtoni* by having longer lower M3

relative to its width, and is considered useful in classification (Barnosky 1985, Rensberger and Barnosky 1993). In the latter comparison, M3 overlaps in width, thus it does not appear to be useful for classification. P4 in *S. townsendii* lack a prominent anterior cingulum but no mention is made of relative size of this tooth compared to other species, so it is considered not useful for classification.

Stephanomys donnezani-thaleri lineage
Data from Renaud et al 1996

S. donnezani and *S. thaleri* are reported to be different in size and size comparisons are made between species in taxonomic descriptions (e.g., Bachelet and Ruiz 1990). However, size is not mentioned in the diagnosis for *S. calvetti* Bachelet and Ruiz 1990; rather the nature of stephanodonty, presence and expression of spurs, and the shape of cingulum and cusps are all characters that are used to designate this species. Nevertheless, size appears to be useful for distinguishing among at least some of the species in the genus, including those analyzed here.

Stephanodiscus yellowstonensis from Wyoming
Data from Theriot et al 2006

Theriot et al (2006) state that the most useful character for distinguishing *Stephanodiscus yellowstonensis* from *S. niagarae* is the spine count, so this character is considered useful for classification. Number of costae and cell diameter are known to correlate with spine count (Theriot, written communication, 2012) and have both been used with spine count in discriminant analyses to distinguish between species (e.g., Theriot 1992, Theriot and Stoermer 1984). Thus these two characters are also considered useful for classification.

Stewartia anodonta, lucinid (bivalve) from Maryland Miocene
Data from Kelley, 1983

From Bretsky (1976): "The similarity between shell interiors of *L. (L.) pensylvanica* [sic], *L. (S.) anodonta*, and *L. (S.) floridana* is striking…externally there is less resemblance, because the dorsal areas of *Stewartia* are not conspicuous…[*L. (S.) floridana*] has more distinct dorsal areas and a better-defined, wider, and deeper lunule than *L. (S.) anadonta*, and lacks secondary thickening of the shell interior." (p. 256-257).

Since 1976, *Stewartia* has been elevated to genus status but *S. anadonta* does not appear to have been redescribed (Ward, 1992).

In general, it appears that features of the dorsal margin (the expression of the beak and the lunule) as well as the thickness of the shell are the most important species-level characteristics in this genus. The valves, at least between *S. anadonta* and *S. floridana*, are similar in outline and relative dimensions (see ranges for each in Bretsky 1976). Thus none of the measured traits in Kelley 1983, particularly those related to muscle scars, are considered for classification purposes.

Striatojaponocapsa plicarum-synconexa-conexa from Japan
Data from Hatakeda et al 2007

Hatakeda et al (2007) state that the "four *Striatojaponocapsa* species discussed in this study had been classified, without quantitative evidence, based on the presence of longitudinal plicae, the arrangement pattern of pore frames, this size and shape of the overall test, and

basal structure". They go onto say that "typical specimens were easily identified by those characters, but atypical morphotypes could not be assigned to a species". Therefore, maximum width (MW), total height (TH), and ratio of total height to maximum width (HW), the number of longitudinal plicae are all considered useful for classification. While Hatekeda et al include other measures of the test in order to capture "variation in size and shape", the height of the abdomen (HA), the width and height of the cephalo-thorax (WCT and HCT, respectively) and the ratio of the width of the cephalo-thorax to the maximum width (CM) are not discussed as distinguishing characters in species-level descriptions (notably O'Dogherty et al [2005]). Therefore these latter four characters are considered not useful for classification.

There has been debate in the literature about whether *S. plicarum* and *S. synconexa* constitute different species. Originally they were distinguished by the size of the basal appendage and presence or absence of a circular depression (*S. plicarum* = large basal appendage, no circular depression; *S. synconexa* = small basal appendage, circular depression), but with many intermediate forms. It appears that Hatakeda et al. (2007) have assigned many intermediate forms (in terms of basal appendage size) to *S. plicarum* (fig. 3) based on the absence of depressions in these forms. Thus basal appendage is considered historically useful for classification but currently less useful than other characters. In addition, two morphotypes of *S. plicarum* were described by Baumgartner (1984): one with a more slender spindle shape (see Baumgartner 1984, pl. 10, fig. 6) and one with a stouter spindle shape (see Baumgartner 1984, pl. 10, fig. 7; reassigned by O'Dogherty et al 2005). While the latter specimen has been reassigned to *S. synconexa* (O'Dogherty et al 2005), it is unclear whether all shape of abdomen coincides with presence or absence of the circular depression. As such this difference may or may not be captured by the ratio of total height to maximum width.

Stricklandia lens-laevis from Norway
Data from Baarli 1986

Williams (1951) separated subspecies of *S. lens* on the basis of ornamentation and cardinalia morphology. The earliest subspecies (*S. lens prima* and *S. lens lens*) have similar cardinalia but differ based on ornamentation (the former is smooth, the latter shows faint plicae). Younger subspecies also exhibit plicae but the cardinalia is more robust overall and the inner plates are progressively larger relative to the outer plates. In addition, Cocks (1978) elevated *S. lens ultima* to species-level (= *S. laevis*) based on the exceptionally reduced outer plates. The relative size of inner and outer plates is captured by the a/b trait measured by Baarli (1986) and is thus considered to be useful for classification. Williams (1951) also notes that the position of the inner plates relative to the outer plates may be used to distinguish subspecies; this characteristic is likely captured by (or at least correlated with) the c/b trait measured by Baarli (1986). Thus this trait is also considered useful for classification as is the ratio of their sum relative to length b.

The remaining traits all relate to the distance between inner plates (d), outer plates (e) and distance to point where outer plates meet the hingeline (f). Even though f is a measure of the size of the outer plates, the ratio of f/b does not appear to vary with size of outer plates (if outer plates are large, so are both; if small, so are both; ratio between the two stays the same). Therefore d/b, e/b, and f/b are considered "not used" for classification.

Teilhardina lineage
Data from Rose and Bown 1986, Bown and Rose 1987

Primary differences between congenerics include relative breadth of teeth, the height of the crown of various teeth, and the presence, location, and size of metaconids or paraconids on p3

(Bown and Rose 1987). Because relative breadth is important, the M1 L/B is considered useful for classification. While size of teeth is used at the generic level (Bown and Rose 1987), it does not appear to be useful for distinguishing species within genera. Thus the M1 LxW and M2 LxW traits are considered "not useful".

Tetonius-Pseudotetonius lineage from Wyoming
Data from Rose and Bown 1986, Bown and Rose 1987

Most of the traits used to describe the difference between species in these genera belong to premolars (Bown and Rose 1987). Molar size is not mentioned and so M1 LxW and M2 Lxw are considered "not useful".

Turritella plebia, turritelid (gastropod) of Maryland Miocene
Data from Kelley, 1983

According to Vokes, 1957, species are distinguished primarily by shell size, convexity of the sides of the whorls, and the spiral sculpture, particularly the expression of ribbing; Ward (1992) adds to this list the spiral angle. Because most of the traits included for *Turritella* were not standardized by another length measure, these are all 'size measures' and are thus all relevant, if indirectly so, to classification. The number of ribs (striae) on whorl five (trait 'NR5') may be related to their expression, but in general appears not to b used for classification.

Triarthrus beckii from Appalachia
Data from Kim et al 2009

Kim et al (2009) state that the difference between *Triarthrus beckii* and *T. eatoni* is the size and backwards extension of the eye. This is captured by the landmarks selected by the authors, but they choose to use cross validation within a CVA to confirm previous assignments. The PCA axes are not explicitly used to discriminate species in this study. However, because the authors provided us with the superimposed landmark coordinates, we were able to run a PCA. The first principal component is dominated by a backwards shift of the eyes but without lengthening, thus this PC captures one of the morphological features that is useful for discriminating between species but the variation described is different. PC 4 and 5 both show changes in the eye size and position that might be coincident with that describing the difference between species, but other parts of the cranidium shift as well and the overall amount of variation described by these two axes is small (6-7%). Thus the PC axes are considered not used for classification, nor coincident/correlative with characters that are used. Size is not mentioned by Kim et al (2009) or in the revision of Ordovician olenid trilobites referenced by Kim et al (Ludvigsen and Tuffnell 1983).

Viverravus acutus from Wyoming
Data from Polly 2002

Polly (1997) originally defined species based on phylogenetic analysis of clusters of specimens that were morphologically discrete within each interval. The clusters (OTUs) were recognized based on the ratio of length to width of M1. Species boundaries were placed at cladogenetic events such that ancestor-descendent series (that might be considered by other workers to represent chronoclines) were considered to be single species. Ultimately, species were defined by size differences, estimated from molar area. Thus this trait is considered useful for classification.

***Watznauria barnesiae, Watznaueria communis* and *W. aff communis* from France**
Data from Bornemann and Mutterlose 2006; Tiraboschi and Erba 2010

Watnaueria species are distinguished from one another based on the length of the central area (Tiraboschi and Erba 2010). Some cogenerics are discriminated from one another based on size and ellipticity of the coccolith (Mattioli 1996). Thus the length and length:width ratio of the coccolith are also considered useful for classification. It is likely the usefulness of the length of the central area is considered in the context of the length of the coccolith; thus this is likely useful as well. No mention is made of the length:width ratio of the central area; therefore this is considered "not used" in classification.

***Wurmiella wurmi* from Nevada**
Data from Roopnarine et al 2005

Roopnarine et al (2005) describe the aspect of margin shape that each SVD axis represents: the first axis describes the overall arch or concavity of the platform; the second axis describes the concavity of the margin anterior relative to the posterior margin; the third describes the relative position of the cavity and the shape and concavity of the margin posterior to the cavity. Because taxonomic descriptions distinguish *Wurmiella wurmi* from other *Wurmiella* species in part on the basis of lower profile shape (*W. wurmi* has a biconvex lower profile, *W. tuma* has a straight or angular one, *W. n. sp.* has an uniformly arched one) (Murphy et al. 2004, Roopnarine et al. 2005), SVD 1 and 2 are considered useful for taxonomy (or at least reflect aspects of overall lower margin shape). The relative position of the cavity and shape of posterior margin alone are not used for taxonomic discrimination, and so SVD 3 is considered "not useful".

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