

APICAL DEVELOPMENT IN TURRITELLID  
CLASSIFICATION WITH A DESCRIPTION  
OF *CRISTISPIRA PUGETENSIS*  
GEN. ET SP. NOV.

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ABSTRACT. The nature of primary spiral ribs on apical whorls of *Turritella* (*s.l.*) is utilized for subdivision of the genus. However, variation causes some doubt as to the actual value of this criterion. Recognized variation is of two kinds: (1) 'variation' within a stock or group arising from improper grouping of species due to inadequate descriptive notation, and (2) actual variation displayed by various specimens of single species. Inadequate application of the terms 'unicarinate', 'mesocostate', 'unicostate', 'bicarinate', 'bicostate', &c. has confused efforts to arrange six Gulf Coast Eocene taxa in homogeneous groups. Notational systems proposed by Marwick (1957*a, b*) and Kotaka (1959) permit uniform description of apical developmental characters, and provide a firm base for taxonomic differentiation. The six taxa discussed belong to three separate apical types.

Some species are constant in apical development, while others show considerable variation. A given spiral rib may appear at various distances from the apex, but always seems to appear in a constant order relative to other spiral ribs. As long as this sequential order of appearance remains constant, Kotaka's notation allows continued use of apical ontogenetic features for taxonomy. This constancy of sequential appearance of primary spirals is not yet demonstrated for all apically variable turritellids; further investigation is needed to confirm apical developmental characters as reliable tools for all turritellids.

A new turritellid from the Eocene of Washington, *Cristispira pugetensis* gen. et sp. nov., illustrating orderly apical variation, is described and represents a new stock seemingly unrelated to presently known species from the north Pacific.

RECENTLY, a new turritellid was collected from the Raging River Formation (Eocene) of Washington by James D. Vine of the U.S. Geological Survey. The specimens were submitted to me by F. Stearns MacNeil for study and description. The material consists of approximately eighty external moulds which have been studied by means of latex casts.

The fossils are from a locality in the centre of the NE.  $\frac{1}{4}$  of the SW.  $\frac{1}{4}$  of section 15, Township 23 North, Range 7 East, Willamette Survey, in the Tiger Mountain-Taylor Mountain upland area, King County, Washington, U.S. Geological Survey locality M-648 (see USGS 7 $\frac{1}{2}$ -minute Hobart Quadrangle, 1953). The fossil locality is about 1,600 feet below the top of the Raging River Formation, and currently stands as the stratigraphically lowest recorded fossil occurrence in that formation. The subjacent sedimentary rocks of the Raging River Formation are approximately 1,000 feet thick but no fossil material is known from them. Vine (1962*a*, pp. 7-11) named the Raging River Formation and discussed its stratigraphic relationships and age. Lists of marine fossils identified by F. Stearns MacNeil and Welden W. Rau were included. *Turritella* n. sp. aff. *T. yabei* Kotaka of MacNeil's checklist is the *Cristispira pugetensis* gen. et sp. nov. of this paper. MacNeil concluded that the Raging River Formation is of middle Eocene to early late Eocene (late Ulatisian to early Narizian) age.

In view of the present trend towards subdivision of the genus *Turritella* Lamarck, it seems advisable to present at least a limited discussion of turritellid classification in connection with the description of the new genus. It is hoped that this discussion will emphasize the value of taxonomic subdivision of turritellids to palaeontologists.

The types and figured specimens of *Cristispira* are deposited in the U.S. National Museum. The hypotypes of *Turritella temblorensis* Wiedey and *Turritella arenicola* (Conrad) are in the Museum of Paleontology, University of California, Berkeley.

#### TURRITELLID CLASSIFICATION

*Familial subdivision.* The generic assignment of turritellas has been, and remains, difficult. Systematists have attempted to subdivide the inclusive genus *Turritella* (*sensu lato*) with varying degrees of success, and several investigators have closely examined the morphologic criteria used to subdivide the family. Notable have been the works of Palmer (1937), Bowles (1939), Merriam (1941), Palmer *in* Harris and Palmer (1947), Marwick (1957*a, b*), and Kotaka (1959). Each of these papers contains a history of previous efforts, so it is not repeated here. Merriam (1941, p. 35) has clearly stated the need for subdividing *Turritella* Lamarck. He states (*loc. cit.*):

The major desideratum with regard to the establishment of a universal classification of Turritellidae is information concerning the apical development of those subdivisions, mostly European and austral, to which taxonomic designation has already been given. Figures, descriptions, and available material are not satisfactory for this purpose.

It appears evident that if there is justification for subdivision of Lamarck's genus—and there undoubtedly is—a large number of units of at least subgeneric standing must ultimately be erected and adequately defined. In this manner alone can the classification be placed on a basis of actual genetic relationship.

There is still much to be done before the existing taxonomic units are thoroughly understood and described, but studies such as those of Marwick (1957*a*) have laid a firm foundation for further elaboration of turritellid classification.

Collectively these previously mentioned workers have given increasingly careful attention to the shape of the growth-line on the whorl sides and base, to the nature of the ontogeny of the primary spirals, to the type of protoconch, and to the details of the aperture. Such studies have shown an amazing diversity within the Turritellidae. One of the most significant advances has been the recognition of various groups or stocks of turritellids which have evolved along quite different lines. These groups are restricted in their zoogeographic distribution. Seemingly, no world-wide classification based on simple growth-line similarities (e.g. Guillaume's *Groupes*) can adequately express phylogenetic relationships. Convergences in adult appearance are rather common even though apical developmental characters may be quite divergent.

The morphologic criteria previously enumerated form the best basis for classification yet proposed, but some difficulties are still apparent, and the absolute significance of each of these characters in classification of all turritellids has not yet been demonstrated. Perhaps the most useful character has been the apical ontogeny. Many recognized groups, such as Merriam's stocks, have been found to be amazingly consistent in their ontogenetic development. This constancy seems to indicate that the youthful development is a valuable criterion which may be applied to turritellid classification.

*Notation of apical whorls.* The terminology applied to the apical whorls of gastropods is far from standardized. Cox (1955, pp. 195–8) and Cox *in* Moore *et al.* (1960, pp. I 111–14) has reviewed these terms and pointed out some of the limitations in their usage. The early whorls which immediately follow the protoconch in turritellids have been

variously referred to as the 'nuclear whorls', the 'nepionic whorls', and the 'neanic whorls'. Table 1 summarizes several authors' usages of the terminology applied to the protoconch and early portion of the teleoconch as used herein. For several reasons none of the terms enumerated above is satisfactory. 'Nuclear whorls' neither agrees with Dall's (1890-8) usage of 'nucleus' nor with Cox's (1955 and 1960) use of the same term. In addition, as Cox (1955, pp. 196-7) has pointed out, 'nucleus' is not an appropriate term for a series of whorls. The terms 'nepionic' and 'neanic' are equally objectionable as applications of life-cycle terminology to the hard parts of an organism, the precise

TABLE 1. Comparison of terminology applied to apical whorls of gastropods

Dall (1890-1898)	Palmer (1937, 1947)	Merriam (1941)	Cox (1955, 1960)	Marwick (1957a, b)	Kotaka (1959)	This Paper
Protoconch = earliest caplike shell	Nucleus	Protoconch	Protoconch (nucleus = point of origin)	Nucleus = semi-globular initial part	Protoconch (nucleus = point of origin)	Protoconch (nucleus = point of origin)
				Protoconch		
	Nepionic whorls (first 3 or 4) or post-nuclear whorls		Early part of teleoconch	Neanic whorls	Neanic whorls	Early part of teleoconch

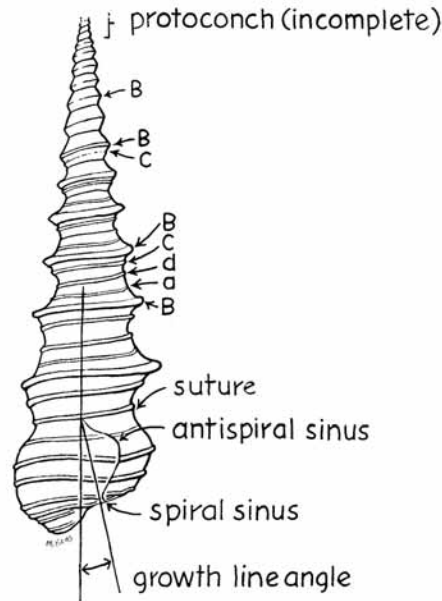
life history of which is unknown. Usage of 'nepionic' depends on correlation of the protoconch with the embryonic stage, an assumption that is clearly not warranted. If modern usage of 'embryo' is to be followed, the embryonic stage must be that part of the ontogeny before the animal becomes self-supporting. While some turritellids (e.g. *Gazameda gunnii* (Reeve) and others) have been shown to be ovoviviparous, developing the protoconch and the early whorls of the teleoconch within the embryo, other species (e.g. *T. communis* Risso) seem to be oviparous, though remaining only a short time in the plankton (Merriam 1941, pp. 12-13). The usage of 'neanic whorls' for the early part of the teleoconch implies that the protoconch represents the 'nepionic' stage. This implication would clearly not be true for ovoviviparous turritellids. Cox (1955, p. 195) has also pointed out that ornamentation may appear before the termination of the planktonic larval stage in many gastropods. For this reason, the implication that the protoconch and the 'nepionic' stage are correlative may also be incorrect for oviparous species; this latter usage would be correct only when the protoconch is terminated at the end of the planktonic larval stage. The usage of 'neanic whorls' also contradicts the usual application of this term in cephalopod literature where most authors have followed Hyatt. It seems clear that unless the life cycle of the gastropod in question is understood, there is no firm basis for application of these life-

cycle terms to the hard parts of gastropods. It is best to use the definition of 'protoconch' given by Cox (1955, p. 197) and to apply the term 'teleoconch' to the remainder of the shell, wholly avoiding the life-cycle terms. The protoconch and the early whorls in which the principal developmental stages are observed may be referred to collectively as the 'apical whorls', though it must be remembered that spiral rib development often continues throughout life in the Turritellidae.

Palmer (1937), Merriam (1941), Bowles (1939), and Palmer *in* Harris and Palmer (1947) have grouped species into unicarinate, mesocostate, unicostate, bicarinate, bicostate, cingulate, tricarinate, tricostate, and multicostate groups or stocks. Palmer *in* Harris and Palmer (1947, p. 280) has pointed out that her terms 'bicarinate', &c. have priority over Bowles's and Merriam's 'bicostate', &c., and that the former terms are more appropriate (see p. 670). Finlay (1930), Ida (1952), Marwick (1957*a, b*), and Kotaka (1959) have described these same relationships using several systems of notation with capital or capital and lower-case letters and numerals (see Marwick 1957*a*, p. 148; 1957*b*, pp. 12-14; and Kotaka 1959, p. 59). These latter systems describe the actual ontogeny more precisely, thus providing a more accurate basis for comparison.

The notation of Kotaka is here used to designate the major elements of the spiral sculpture (see text-fig. 1). B is the medial primary, D the peribasal one involved with the anterior suture; A is the first to appear adapical to B, and C is the first to appear abapical to B (between B and D). The conventions used by Kotaka (*loc. cit.*) and Marwick (*loc. cit.*) for secondary and tertiary spirals are not used in the present study because of their limited significance for generic differentiation, although they may be used advantageously in specific diagnoses. When the primaries are weakly developed, they are noted by a lower-case

letter (e.g. b) instead of the capital. Numerical subscripts indicate order of appearance (e.g. B<sub>1</sub> indicates primary B appears first). D has been included in the formula when present, but no numerical subscript is given due to the difficulty in determining its point of origination. It should be capitalized when it forms a prominent element of the ornamentation visible on the whorl side, and designated by the lower-case d when it simply forms the angulation between the whorl base and side, remaining level or nearly level with the suture. In the present study 'unicarinate', 'mesocostate', 'bicarinate', 'unicostate', 'bicostate', &c. are used only to delimit the condition of the earliest



TEXT-FIG. 1. Diagrammatic representation of *Cristispira pugetensis* gen. et sp. nov. showing notational usage. The formula is  $a_3 B_1 C_2 d$ . The antispiral and spiral sinuses of the growth-line are indicated on the body whorl. The suture is immediately abapical to d.

post-protococonch whorls. Weak primaries are not neglected (e.g. a species with  $a_1 B_1 c_1$  is considered tricostrate, not unicostrate or mesocostate). These terms should not be applied to whorls other than those showing the first ornamental stage.

*Notation and progressive ontogenetic change.* Palmer (1937, pp. 188–9) and Palmer in Harris and Palmer (1947, pp. 280–1) has classified her Gulf Coast Eocene species according to the sculpture of (1) the ‘nepionic’ whorls (first 3 or 4) and (2) the first ‘post-nepionic’ whorls, with each of these stages furnishing a basis for subdivision into unicarinate, bicarinate, and tricarinate species groups. As a consequence, the same species may be considered unicarinate on the basis of the ‘nepionic’ whorls, or bicarinate on the basis of the first ‘postnepionic’ whorls. This classification was an early attempt to provide a framework which describes the normal ontogenetic change in turritellids, and yet one which could accommodate certain unusual ontogenetic reversals (see discussion of *T. arenicola danvillensis*). This progressive change during ontogeny has been emphasized by Palmer (1947, p. 279):

Fragments taken from different parts in the length of the shell, unless fitted into the total pattern [of ontogeny], may seem to belong to different species. The change of ornamentation in the ontogeny of gastropods is universal but such a process is particularly accelerated and profusely developed in the Turritellidae.

She also states (op. cit., p. 280)

The factor of change enumerated in the first paragraph of this discussion [see above] is not accounted for in the Bowles–Merriam grouping. A species may be unicarinate on the nepionic or postnepionic whorls, becoming bicarinate and later multicarinate on the mature whorls. . . . There is no rigidity in their carination over the entire length of their shell. Therefore a qualifying statement must accompany any outline as to what part of the shell the ‘type carination’ may occur.

From this data, one may easily visualize the results of tachygenesis and bradygenesis. A unicostrate form might be ‘accelerated’ in ontogenetic development to the point of being apically tricostrate, or a tricostrate form might be ‘retarded’ to a unicostrate condition.

This progressive ontogenetic change may take three forms: (1) simple addition of spiral ribs, (2) changes in relative strength of ribs, either weakening or strengthening, and (3) loss of ribs present in earlier stages. All three features may occur independently of gerontism.

*Inconsistent notation and variation.* While the recognition of the basic type carination has proved useful in arranging many species, difficulties have been encountered with others. This difficulty stems from two major causes: (1) inadequate or inconsistent application of the terms ‘unicarinate’, ‘mesocostate’, ‘unicostrate’, ‘bicarinate’, ‘bicostrate’, &c., and (2) actual apical variation. For example, Palmer has not considered weak primaries in her assignment of the terms ‘unicarinate’, &c. (i.e. ‘unicarinate’ may signify only one primary present, or one primary which is stronger than its adjacent cohorts). Bowles and Merriam generally have followed the practice of recognizing in their terminology all primaries present. This difference between Palmer’s scheme and that of Merriam and of Bowles results from a difference in emphasis. Palmer has emphasized the enlarged ribs and applied the term ‘carinate’, while Merriam and Bowles have emphasized all the ribs and have applied the term ‘costate’ (‘carinae’ referring to strong keeled ribs and ‘costae’ referring to any rib). Therefore a form with  $a_1 B_1 c_1$  might be considered uni-

carinate in Palmer's scheme and tricostrate in Merriam's and Bowles's schemes (Palmer, personal communication, 6 April 1964). Where these terms are used, care should be taken to apply the proper termination, though usage of Kotaka's notation is less apt to result in confusion. As a result of the differing emphasis of these schemes, and of the inconsistent application of these terms by various investigators, a variety of apical developmental types may bear a single descriptive term. In addition, different primary ribs may appear first in separate unicarinate or unicostate genera [e.g. *Acutospira* with  $C_1$  (unicostate) and *Cristispira* with  $B_1$  (mesocostate)]. Note that mesocostate implies the  $B_1$  condition; unicostate means a single primary (A, B, or C) appears first; unicarinate means a single primary rib which is keeled (A, B, or C) appears first, but may or may not be the only rib present. Merriam and Bowles have partially accounted for this problem by recognizing a 'cingulate' division for those species which have  $A_1 C_1$ , although the  $B_1 C_1$  and  $A_1 B_1$  conditions would both receive a 'bicostrate' designation. This lack of precision in definition and usage of the terms 'unicarinate', 'mesocostate', 'unicostate', 'bicarinate', 'bicostrate', &c. and the resultant improper grouping of species creates the impression that there is apical variation in otherwise consistent stocks. While the costate or carinate terms are useful in classification, they do not provide a sufficiently refined basis for comparison of species. Because of its greater precision and simplicity, the notational system of Kotaka should be more generally adopted as a tool in turritellid classification.

An example of the utility of this notation is provided by consideration of six Gulf Coast taxa; all have been wholly or partially referred to as 'unicarinate' or 'unicostate' at some stage during their life cycle and therefore warrant comparison to *Cristispira pugetensis*. Three separate apical developmental types may be recognized among these species; one, *T. arenicola* (Conrad), illustrates actual variation in the apical characters of different individuals. It is hoped that this view will explain some anomalies in classification based on apical development. The features of these six taxa are summarized in the following discussion (note the inadequacy of simple 'carinate' and 'costate' classification).

*Turritella alveata* Conrad 1855

*Development.* Data are from Palmer in Harris and Palmer (1947, pp. 288-90, pl. 36, figs. 7-12). The earliest post-protoconch whorls show  $a_1 B_1 c_1$  with  $a_1$  very fine and much weaker than  $C_1$  at first, shortly progressing to  $a_1 B_1 C_1$ , and finally to  $A_1 B_1 C_1 d$ .  $c_1$  is stronger than  $a_1$  initially. The protoconch consists of one to one and a half whorls.

*Remarks.* Palmer has considered this species apically unicarinate (op. cit., p. 281): 'Obscure unicarinate stage, followed by a short bicarinate stage, succeeded by a tricarinate stage.' The weak primaries, a and c, are neglected in the 'nepionic' whorl designation. Bowles's (1939, p. 271) tricostrate diagnosis of the form is in agreement with the classification adopted here. The apical development apparently remains constant. *T. creola* and *T. alveata* appear to be closely allied species.

*Turritella creola* Palmer in Harris and Palmer 1947

*Development.* Data are from Palmer in Harris and Palmer (1947, p. 286, pl. 35, figs. 2, 4, 5, 11). The development is  $a_1 B_1 c_1$ , i.e. the species is truly tricostrate initially, soon

showing a stronger C, or  $a_1 B_1 C_1 d$ .  $c_1$  is much stronger than the very weak  $a_1$  initially. The protoconch consists of one whorl.

*Remarks.* Palmer (loc. cit.) has classified this species as a unicarinate-bicarinate form, these statements applying to the  $a_1 B_1 C_1$  stage and the  $a_1 B_1 C_1$  stage respectively. The species should be considered tricostate. Palmer (ibid.) states:

This species [*T. creola*] may be differentiated from *T. arenicola* in that the bicarinate feature has been formed as a definite character by the stage of the fifth whorl and the unicarinate phase is shortened and limited to the first four postnuclear whorls. In this respect *T. creola* seems to be more of a derivative of *T. dutexata* and allies of the lower Claiborne, than directly related to *T. arenicola*.

She states again (op. cit., p. 287):

*T. creola* is apparently the Jackson representative of the *T. dutexata* stock of the lower Claiborne.

While tachygenic development of *T. dutexata* ( $a_2 B_1 C_1 d$ ) or *T. arenicola* ( $a_3 B_1 c_2 d$ ) could develop a species such as *T. creola*, the latter is better classified along with those species included in Bowles's 'tricostate group' (Bowles 1939, pp. 270-1). Application of the terms 'carinate' and 'costate' therefore seems to have obscured the relationships of this species.

*T. creola* has not been cited for apical variability.

#### *Turritella apita* de Gregorio 1890

*Development.* Data taken from Palmer (1937, pl. 24, figs. 1, 3, 7, 10). The development is  $a_2 B_1 C_1 d$ , soon becoming  $a_2 B_1 c_1 d$ . In other words, the species is actually bicostate apically;  $a_2$  is always weak, and  $C_1$  (never as strong as  $B_1$ ) becomes reduced in strength relative to  $B_1$ . The latter spiral remains strong and gives the whorls an angulate appearance. The protoconch consists of about two whorls.

*Remarks.* Bowles (1939, p. 275) has classed *T. apita* as a unicastate species, although his illustration (pl. 31, fig. 4) does not show the earliest whorls. The text implies an  $a_3 B_1 c_2$  development. Palmer in Harris and Palmer (1947, p. 285, no fig.) classes *T. apita* as a bi-unicarinate species (referring to the 'nepionic' and first 'postnepionic' whorls respectively). She states (loc. cit.):

It and *T. arenicola danvillensis* are the only two Turritellas [*sic*] of the Claiborne-Jackson Eocene which belong in such a group [bi-unicarinate]. *T. apita* passes into the unicarinate stage and retains it throughout life, while in *T. arenicola*, the unicarinate stage is a transitional phase, developing five and more spiral ribs, depending on the locality of its occurrence.

The discrepancies in assignment seem to be the result of inadequate material and insufficiently precise terminology. The treatment of Palmer in Harris and Palmer ignores the adult  $a_2 c_1$  and utilizes only the young  $B_1 C_1$  and the adult  $B_1$  characters.

#### *Turritella arenicola danvillensis* Stenzel and Turner 1940

*Development.* Data taken from Stenzel and Turner (1942, card 58), and K. V. W. Palmer (personal communication).  $B_1 C_1$  appear on the third whorl. By the seventh or eighth whorl  $C_1$  weakens (but does not disappear) and the species is 'unicarinate' though still 'biscostate' at this stage;  $C_1$  strengthens on the ninth or tenth whorl;  $a_2$  then appears along with several other secondaries on the posterior slope.  $d$  angulates the whorl at the

suture. The protoconch consists of about two whorls (see Palmer *in* Harris and Palmer 1947, pl. 34, fig. 4).

*Remarks.* Palmer *in* Harris and Palmer (1947, pp. 284–5, pl. 34, figs. 1, 4, 5; pl. 35, fig. 1) reports examination of over one thousand fragments with abundant apical material from the type locality at Danville Landing, Louisiana. She mentions no disagreement with Stenzel and Turner's description of the apical ontogeny. Dr. Palmer has informed me (personal communication, 6 April 1964) that the double carination of the third whorl is sharp, after which the lower rib weakens until the whorls are 'unicarinate', and that the lower rib then increases in size until the whorls again become 'bicarinate'. However,  $C_1$  does not actually disappear. The species should be considered apically bicarinate, but such a simple statement seems to be insufficient for evaluation of its relationships. *T. apita* and *T. arenicola danvillensis* are both classified as bicarinate–unicarinate by Palmer; on *T. arenicola danvillensis*  $C_1$  is weakened temporarily on the early whorls, while it is weakened throughout adult whorls in *T. apita*. This seems to be evidence of close relationship, differing in degree rather than in kind. *T. arenicola danvillensis* could be sufficiently bradygenic to show an ancestral bicarinate condition, followed by a descendent unicarinate stage with a 'normal'  $a_3 B_1 C_2 d$  development.

It is interesting to note that the apical development of *T. arenicola danvillensis* is different from that of *T. arenicola*. *T. arenicola* is apically unicostate, but some specimens (Pl. 92, fig. 10) very closely approach the bicostate condition; such convergence may very well attest to the close relationship of the two taxa. However, it seems likely that *T. arenicola danvillensis* should be given independent specific and generic rank. Even if the two species are closely related, attainment of the unicostate condition in *T. arenicola* could form a convenient arbitrary boundary for discrimination of separate generic entities. Careful study of the apical stages from various demes of *T. arenicola* and *T. arenicola danvillensis*, coupled with a similar analysis of their stratigraphic relationships, should aid in the interpretation of the phyletic relationships and the dependent taxonomy.

*T. arenicola danvillensis* apparently is consistent in its early development, for Palmer records no individual variation in her study of the abundant specimens from Danville Landing.

*Turritella arenicola* (Conrad) 1865

*Development.* Data taken from Bowles (1939, pp. 275–6, pl. 31, figs. 5–7). The development is  $a_3 B_1 C_2 d$  plus several more secondaries posteriorly. One or both secondaries posterior to  $a_3$  seem to appear concurrently with it. This is a truly unicarinate and mesocostate species. B is slightly anterior of the whorl midline apically, later migrating to a more central position on the adult whorls. The protoconch consists of about two whorls (figured for comparison on Pl. 92, fig. 10).

*Remarks.* Palmer (1937, pp. 197–8), Bowles (*loc. cit.*) and Palmer *in* Harris and Palmer (1947, pp. 281–3) have concurred in classifying *T. arenicola* as a unicarinate or unicostate species. However, Bowles has remarked on the individual variation seen on the apical whorls. He states (*op. cit.*, p. 276):

There is a certain amount of individual variation in the persistence of the unicarinate sculpture on the apical whorls. On some specimens the second prominent revolving rib appears as early as the third



whorl, while in others it is still absent on the eighth or ninth whorls. It invariably does appear, however, and it always appears anterior to the original carination.

$c_2$  appears as a fine thread almost immediately after  $B_1$  on the specimen figured for comparison. The point of initiation of a given spiral element (number of whorls from the protoconch) is quite variable in other species as well (e.g. *Cristispira pugetensis*), even in specimens from a single locality. Bowles does not clearly specify whether variants are common among specimens from a single locality or if the variation is more commonly between individuals from separate localities. However, the order of rib appearance, and therefore the notation used here, remains constant in *T. arenicola* and in all other variable species with which the writer is acquainted.

Bowles (1939, p. 276) notes the close resemblance of *T. arenicola* (Conrad) to *T. dutexata* Harris, which seems to be a bicostate ( $a_2 B_1 C_1 d$ ) form. Palmer (1937, p. 199) classifies *T. dutexata* as tricarinate–bicarinate. Her illustration of an incomplete specimen (pl. 26, fig. 1) shows a tricarinate (tricostate) individual, which remains so, but the specimen of fig. 4 on the same plate is clearly bicarinate (bicostate). Harris originally described the species as bicarinate to the very apex, mentioning no tricarinate stage. If *T. dutexata* or its relatives are ancestral to the *T. arenicola* group, we might think of the  $a_3$  and  $c_2$  of *T. arenicola* as having been retarded in their point of insertion (bradygenesis).

#### *Turritella arenicola branneri* Harris 1894

*Development.* Data from Palmer in Harris and Palmer (1947, pl. 34, figs. 2, 3, 6, 7). The primary spirals develop in the order  $a_3 B_1 c_2 d$ , plus several other secondaries posteriorly. This is a truly uncarinate and mesocostate subspecies. The protoconch consists of about two whorls.

*Remarks.* Palmer (1937, p. 197, pl. 23, figs. 1, 2) and Palmer in Harris and Palmer (loc. cit.) has considered *T. arenicola branneri* uncarinate. Bowles (1939, p. 275) considers it a junior synonym of *T. arenicola* (Conrad), and Palmer (1947, p. 282) considers that it has been synonymized with good reason. Nevertheless, she lists it separately 'to tabulate the characters of extreme forms so that such may be used as criteria for judging other variations and the value of named units.' *T. arenicola branneri* seems properly considered as a junior synonym.

*T. arenicola branneri* has not been specifically cited for apical variation.

#### Summary

Careful study of these species suggests that the apical variation previously implied is in part real and in part the result of inadequate terminology. *T. alveata* Conrad and *T. creola* Palmer in Harris and Palmer are better considered as members of Bowles's 'tricostate group'. *T. apita* de Gregorio and *T. arenicola danvillensis* Stenzel and Turner seem to be related and should either be placed in a group by themselves (bicarinate–uncarinate group of Palmer) or in Bowles's 'bicostate group'. *T. arenicola* (Conrad) and *T. arenicola branneri* Harris belong to Bowles's 'unicostate group'. Thus constituted, three separate groups are recognized, each group apparently warranting taxonomic recognition. Formal designation of these taxa should await review and inclusion of other Gulf Coast species.

While these six taxa have not been classified as members of a single group, all have had the term 'unicarinate' or 'unicostate' applied to some part of their ontogenetic cycle. Classification of these six species in one group would necessitate inconsistent application of the criteria used to designate the class; i.e. the variation in such a group would be unnatural and in part the result of insufficiently refined descriptive notation for the comparison of apical stages. This 'variation' actually constitutes valid differences which we may recognize in taxonomy.

Among these six taxa, only *T. arenicola* (Conrad) has been specifically cited for its individual apical variation. As I have previously emphasized, the various spirals appear at different distances from the protoconch in different individuals of the species, but the order of appearance remains constant. *Cristispira pugetensis* also is markedly variable in this same fashion, but again the sequential order of spiral rib appearance remains constant. Instances in which the sequential order of insertion of the primary spirals is reversed in individual variants are unknown to the writer; such cases would create considerable difficulty for the uniform application of the sequential order of apical spirals to taxonomy, but in their absence such criteria seem to be of considerable value.

Variable species may not be well adapted with respect to their apical shell characters, hence showing a wider phenotypic expression in the absence of direct selection pressure. Constant species may be more thoroughly adapted with a lesser range of phenotypic expression. Conversely, environmental influences may be more important than genetic factors in producing apical variation. Studies on living turritellids should be undertaken in order to evaluate these factors. Variation between separate demes (stratigraphic and geographic separation) of the same species should also be investigated. If comparisons show the position of primary rib appearance to differ consistently between separate demes, we may find tachygenesis and bradygenesis to be significant mechanisms of evolution in the Turritellidae. Interpretation of such processes may provide a usable tool in reconstructing the broad outlines of phyletic history.

The diversity of the many Gulf Coast turritellid species does not militate against use of apical ontogeny as a taxonomic key, but presents various examples of rather rapid diversification (radiation). In all likelihood, taxonomy based on these apical characters as well as growth-line characteristics, &c., would closely approach a true phyletic classification. Instances will be found in which arbitrary 'cut-offs' will be necessary, but this is a natural result of well-documented phyletic relationships being expressed in taxonomy.

It is impossible in this brief study to give a thorough review of all cases which may have bearing on the validity of using apical ontogeny in classification. The six taxa discussed have been chosen for examination because of their bearing on the new material from the Washington Eocene and because they illustrate the applicability of more refined notation in comparing apical stages of turritellids.

#### SYSTEMATIC DESCRIPTION

Phylum MOLLUSCA  
 Class GASTROPODA  
 Subclass PROSOBRANCHIA  
 Order CAENOGASTROPODA

Family TURRITELLIDAE Woodward 1851  
 Subfamily TURRITELLINAE Woodward 1851  
 Genus CRISTISPIRA gen. nov.

*Type species.* Here designated *Cristispira pugetensis* sp. nov.

*Diagnosis.* Shell turritelliform; protoconch of three or four (?) smooth whorls; primary spirals appearing in order  $a_3 B_1 C_2 d$ ; adult growth-line with double sinus, deepest part of antispiral sinus usually above whorl midline and substantially embayed; spiral sinus shallower and broader with deepest part of embayment on d or slightly above; growth-line angle variable, ranging from about  $15^\circ$  to  $25^\circ$ ; base of whorl with prominent revolving spirals; aperture subovate with heavy parietal wash.

*Name.* Latin *crista*, f. = crest; *spira*, f. = coil, twist.

*Discussion.* The very slightly effuse basal and columellar lips and the subovate aperture of *Cristispira* are vaguely reminiscent of *Mesalia* and other genera assigned to the Pareorinae Finlay and Marwick 1937. However, the concave basal growth-line and lack of a ridge on the adapical columellar lip show that it is a member of the Turritellinae (see Marwick 1957a, p. 164, under 'Zaria').

*Cristispira pugetensis* sp. nov.

Plate 92, figs. 1-9, 12-14

1962a *Turritella* n. sp. aff. *T. yabei* Kotaka, MacNeil in Vine, p. 9.

*Description.* Shell of medium size; maximum observed length 56 mm.; maximum observed diameter 16 mm. Pleural angle averages about  $19^\circ$ , ranges from about  $15^\circ$  to  $30^\circ$ ; apical angle usually about same as pleural angle, but on some specimens much wider than pleural angle. Spire profile normally conical to concave conical, but specimens with wider apical angle obconical adapically. Primary spirals develop in order  $a_3 B_1 C_2 d$ ; d forms angulation between side and base exactly at suture nearly throughout ontogeny, only rarely becoming raised on whorl side adjacent to anterior suture. Protoconch of about three or four (?) sharply convex smooth whorls (multispiral); about

EXPLANATION OF PLATE 92

- Figs. 1-9, 12-14. *Cristispira pugetensis* gen. et sp. nov. USGS locality M-648, Raging River Formation, Washington. Rubber casts. USNM Cat. No. 132. Fig. 3, holotype; remainder, paratypes. 1, specimen with  $B_1 d$  alone ( $\times 1.7$ ), 648626. 2, specimen with  $B_1 d$  alone ( $\times 1.6$ ), 648627. 3, specimen with  $a_3 B_1 C_2 d$  ( $\times 1.7$ ), 648628, holotype. 4, specimen with  $B_1 C_2 d$  ( $\times 1.7$ ), 648629. 5, specimen with  $a_3 B_1 C_2 d$  ( $\times 1.5$ ), 648630. 6, specimen with  $B_1 C_2 d$  showing slightly effuse columellar lip and parietal wash ( $\times 1.6$ ), same as fig. 14, 648631. 7, specimen with  $B_1 d$  alone showing protoconch partially decorticated ( $\times 2.6$ ), 648632. 8, specimen with  $B_1 C_2 d$  ( $\times 1.7$ ), 648633. 9, specimen with  $B_1 C_2 d$  ( $\times 1.7$ ), 648636. 12, specimen with  $B_1 C_2 d$  ( $\times 1.7$ ), 648634. 13, gerontic whorl showing heavy growth-lines ( $\times 2$ ), 648635. 14, same as fig. 6, showing parietal wash ( $\times 1.3$ ), 648631.
- Figs. 10, 11. *Turritella arenicola* (Conrad). UCMP locality A-1043, Jackson Group, Louisiana. 10, specimen with  $a_3 B_1 C_2 d$  plus posterior secondary; accelerated specimen with  $c_2$  as a fine thread almost immediately after  $B_1$  ( $\times 9.3$ ), UCMP 36491. 11, specimen showing growth-line ( $\times 1.9$ ), UCMP 36492.
- Fig. 15. *Turritella temblorensis* Wiedey. UCMP locality B-7853, Topanga Formation, California. Specimen showing double sinused growth-line with ?  $a_3 B_1 C_2 d$  ( $\times 0.95$ ), UCMP 36493.

fifth whorl a strong medial angulation ( $B_1$ ) appears, increasing in strength and angulating whorls throughout ontogeny until last one or two, when it may decrease in strength slightly with onset of gerontism; normally with five or six unicarinate apical whorls before appearance of  $C_2$  on lower third of whorl, though point of insertion of  $C_2$  is quite variable,  $C_2$  failing to appear at all on some smaller specimens;  $C_2$  variable in strength from coarse thread to slightly subordinate to  $B_1$ ;  $a_3$  even more variable, making its appearance in only about one-third of specimens, apparently never earlier than in young adult whorls;  $a_3$  variable from coarse thread, when discernible, to weak primary, but always subordinate to  $B_1$  and  $C_2$ . Whorl profile variable with diverse development of primaries, from strongly angulate medially on specimens with no  $a_3$  or  $C_2$  to 'pagoda-form' on specimens with strong, subequal  $B_1$  and  $C_2$  with no  $a_3$ , subrounded with slight medial angulation on specimens with  $a_3$   $B_1$   $C_2$  d all developed. Well-preserved specimens with many fine spiral threads. Body whorls of occasional large specimens with gerontic features such as slight obsolescence of primaries, heavy strengthening of growth-lines, and a slight tendency toward looser clasping of preceding whorl causing d to be weakly exposed and suture more deeply impressed. Suture normally moderately impressed and clearly discernible. Base flattened and ornamented with four or five coarse secondary spirals. Aperture subovate with heavy parietal wash; basal and columellar lips very slightly effuse, continuing to parietal wash; peristome incomplete. Growth-line moderately variable; antispiral sinus moderately deep with deepest part of embayment usually between  $a_3$  and  $B_1$ ; growth-line usually spirally convex just below posterior suture; spiral sinus shallower and broader than antispiral sinus with maximum at d or slightly above; growth-line with broad shallow antispiral concavity on base; growth-line angle moderate and variable, ranging between  $15^\circ$  and  $25^\circ$ .

*Name.* The species name refers to the Puget Sound region and Puget Lowlands of western Washington.

*Holotype.* USNM 648628. *Paratypes,* USNM 648626-7, 648629-35. All material is from U.S. Geological Survey locality M-648.

*Discussion.* Only three primary spiral developmental combinations occur:  $B_1$  d,  $B_1$   $C_2$  d, or  $a_3$   $B_1$   $C_2$  d (i.e.  $a_3$   $B_1$  d or  $a_3$   $C_2$  d are never found in this species) in spite of the variation in point of insertion of  $a_3$  and  $C_2$ . Specimens lacking  $C_2$  invariably lack  $a_3$ , although  $C_2$  may be present without  $a_3$ .  $a_3$  is therefore always retarded first, and  $C_2$  next; the primary spirals are both inserted and retarded in an orderly manner. This sequential order of rib appearance has also been described in *T. arenicola* (Conrad) (Bowles 1939, p. 276, also quoted on page 673 of this paper). A fundamental order of this nature seems to be usual in turritellids; the apical ontogeny may be variously retarded or accelerated, but the sequence of spiral appearance in different groups remains constant and is therefore a useful criterion in classification.

MacNeil *in* Vine (1962a) has classified *C. pugetensis* as '*Turritella* n. sp. aff. *T. yabei* Kotaka' and Kotaka has included *T. yabei* under *Acutospira*. In 1959 Kotaka (pp. 101-2) proposed *Acutospira* as a new subgenus of *Colpospira* Donald 1900, and referred three Japanese Tertiary species to it. The type species, *A. okadai* Nagao 1928, develops the primaries in the order  $A_2$   $b_3$   $C_1$  d, with  $C_1$  appearing just slightly before  $A_2$ . Therefore the apical ontogeny differs markedly from that of *Cristispira*. The type species of *Colpospira* Donald is multicostate apically with a deep antispiral sinus and a very shallow or negative growth-line angle (see Marwick 1957a, pp. 151-3). The growth-line of

*Acutospira* Kotaka is similar, but in view of the differences in apical development, the subgeneric relationship of *Acutospira* to *Colpospira* seems questionable.

*A. tashiroi* Kotaka has a growth-line with a strongly negative angle; apparently it is tricostate, but the apical development is not known. Adult whorls have a very heavily developed A. *A. yabei* Kotaka seems to be bicostate, developing B and C at about the same point apically with A appearing later (d also present). This differs considerably from the development of typical *Acutospira*. The growth-line is sharply and deeply embayed and the deepest part lies on A; the growth-line angle is very small or negative. In general appearance 'A.' *yabei* resembles *C. pugetensis*, but the latter has a prolonged early development of B. In *Cristispira*, the maximum depth of the growth-line is usually between  $a_3$  and  $B_1$  and the growth-line angle is wider, never becoming negative.

MacNeil (1964, pp. B-2, 3, pl. 1, figs. 5-8, 12-18) has described a bicostate turritellid, *Turritella kotakai*, with a strong B on the adult whorls, from the Miyara Formation (middle or late Eocene) of Ishigaki-shima, Ryūkyū Islands. This new species seems to be related to 'A.' *yabei* Kotaka. Its apical development is  $B_1 C_1 d$  with no A appearing.

While some of the early Tertiary Japanese turritellids are similar in gross aspect to *C. pugetensis*, the refined generic concepts used here preclude congeneric assignment.

*C. pugetensis* seems to have no definite relatives among described species from the Pacific Coast Tertiary. Various subspecies assigned to the *T. variata* and *T. diversilineata* branches of the *T. uvasana* stock of Merriam (1941) are similar in general appearance and have the coarsely ornamented whorl base, but they are bicostate on the apical whorls. Among other Pacific Coast species, those referable to the *T. broderipiana* stock of Merriam (1941) are unicostate, but these have a broad, shallow growth-line with a single sinus. This latter group seems to be referable to *Archimediella* (*Toruloidella*) Sacco 1895 (see Marwick 1957a, pp. 159-60).

One species, *T. temblorensis* Wiedey, from the Californian Miocene, warrants comparison. It is apparently a unicostate form which may develop the primary spirals in the order  $a_3 B_1 C_2 d$  as in *Cristispira*, but the very earliest apical whorls are not known. Merriam has considered the growth-line to be single sinused (1941, p. 116), but better material from the Topanga Formation shows it to be double sinused and concave on the base (see Pl. 92, fig. 15). Loel and Corey (1932, p. 265) have called attention to the similarity in appearance of *T. temblorensis* and *Zaria duplicata* (Linnaeus), but the latter bears the characteristic convex basal growth-line of the Pareorinae, while the former belongs to the Turritellinae. As Merriam has suggested (op. cit., p. 117), the similarity is one of homeomorphy. In general appearance *T. temblorensis* is very similar to *Cristispira*. The whorl base bears the coarse revolving ribs, the growth-line angle is about the same, and a small parietal wash seems to be present. However, the growth-line has a much broader and shallower antispinal sinus with its deepest part falling near B. The segment of the growth-line above the maximum flexure is spirally concave rather than convex as in *Cristispira*. C apparently develops very soon after B and follows after several whorls, along with a secondary just below the posterior suture (concurrently?). A unicostate stage does not seem to be prolonged as in *C. pugetensis*. In spite of the several similarities between these two species, I am inclined to judge the difference in growth-line as of supraspecific importance. Discovery of more complete apical material of *T. temblorensis* and stratigraphically and geographically intermediate forms may further elucidate their relationship.

The developmental patterns of several Gulf Coast Eocene species have been reviewed in the preceding pages. *T. apita* de Gregorio differs from *Cristispira* in its apical development ( $a_2 B_1 C_1$  becoming  $a_2 B_1 c_1 d$ ) although the adult shell is reminiscent of some variants of the Washington species. *T. arenicola danvillensis* Stenzel and Turner also differs markedly in the early development ( $B_1 C_1$  with  $C_1$  weakening for a few whorls, then strengthening and followed by  $a_2$ ) and has more evenly convex and regularly ornamented adult whorls. *T. creola* Palmer and *T. alveata* Conrad are apically tricostrate ( $a_1 B_1 c_1 d$ ) and therefore not closely related.

*T. arenicola* (Conrad) and *T. arenicola branneri* Harris are the only Gulf Coast taxa which warrant careful comparison with *C. pugetensis*. Apically their development is  $a_3 B_1 c_2 d$ ;  $a_3$  and a secondary just posterior to it seem to appear concurrently. The protoconch consists of about two whorls and a parietal wash is present. The growth-lines have their maximum flexure near the midline of the whorl above  $B_1$  and below  $a_3$ . The antispiral sinus is deeply embayed, though not so sharply as in *Cristispira*. The growth-line, as in *Cristispira*, has a very slight spiral convexity just below the suture, and the growth-line angle measures about  $10^\circ$ . The base of the whorl bears revolving ribs of moderate strength (Palmer 1937, pl. 23, fig. 2) but the complete apertural details are not known.

Conrad originally assigned *T. arenicola* to *Mesalia*?, but this assignment seems to have been based on the rather shallow whorl height and broad pleural angle rather than apertural characteristics. *T. arenicola branneri* Harris differs from *T. arenicola* only in the number of secondaries on the adult whorls and in the pleural angle. Bowles (1939, p. 275) has properly considered it a junior synonym of *T. arenicola* (Conrad).

While *T. arenicola* (Conrad) and *T. arenicola branneri* Harris are similar to *Cristispira* in many aspects, I am somewhat hesitant to assign them to the latter genus. The Gulf Coast taxa have a much rounder whorl profile and more numerous revolving spirals, with one of the posterior secondaries appearing concurrently with  $a_3$ ; the basal spirals are not so well developed as in *Cristispira*. Perhaps the most significant difference is the more broadly rounded antispiral sinus with the narrower growth-line angle. As Marwick (1957a, pp. 156, 158) has emphasized in his discussions of *Kurosioia* Ida, *Maoricolpus* Finlay, and *Stiracolpus* Finlay, geographic and stratigraphic factors should not be ignored for purposes of classification. Convergences are quite common in the Turritellidae. Marwick (1957a, p. 158) states: 'Close agreements in outer lip characters and in primary spiral ontogeny are essential for generic grouping, and even then the possibility of convergences of distant stocks with simple characters must be considered.'

Unfortunately, the phyletic relationships of *Cristispira* remain obscure. No certain ancestor or congener is yet known from the Tertiary deposits of the Americas and the western Pacific. While *T. temblorensis* Wiedey and *T. arenicola* (Conrad) are similar morphologically, both differ in the details of the growth-line. Wide geographic or stratigraphic separation, or both, in the absence of intermediate forms, contributes additionally to the speculative nature of congeneric assignments. In all probability relatives of *Cristispira* will be found in as yet unknown north Pacific fossil faunas.

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ALLISON, *Turrillids*