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LATITUDINAL VARIATION IN SHELL GROWTH PATTERNS OF BIVALVE MOLLUSCS: IMPLICATIONS AND PROBLEMS

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Abstract

During the growth of the shell of the California surf clam *Tivela stultorum* (Mawe, 1823) and the subtidal bivalve *Callista chione* (Linnaeus, 1758) from the northern Adriatic Sea, a period of slower growth occurs annually. This period of growth is manifested by a macroscopic growth band or biocheck, consisting of relatively thin and closely spaced shell growth increments and a relatively thick band of fast growth: together they form an annual growth band. The number of growth increments in biochecks and bands of fast growth varies with age, latitude and water depths at which populations of the two taxa are living. Examples are: (i) there is a maximum of 307 daily growth increments in the annual growth bands of 3-year-old individuals of *C. chione* and only a maxmum of 210 daily shell growth increments present in 12-year-old individuals; (ii) there is an average of 82 daily growth increments in the fourth annual biocheck of shells of *T stultorum* from near 35° N latitude (eastern Pacific Ocean), while near 26°30′ N latitude there is an average of 111 daily growth increments in biochecks of the same age- and year-class. Latitudinal gradients in shell growth increments and patterns could be an aid in suggesting positions of geographic poles during the past; however, comparisons should be made between the same age-classes.

Comparing the same age-classes of Pliocene and Holocene individuals of *C. chione*, the average number of daily growth increments is greater in biochecks of Pliocene individuals (114 and 86, 1- and 4-year age-classes) than in biochecks of extant individuals (86 and 64, 2- and 4-year age-classes) from near 45° N latitude, northern Italy. Latitudinal gradients in shell growth of the extant *C. chione* must be documented, as they were for *T. stultorium* Preliminary studies suggest that ecological factors such as depth also influence shell growth. Thus, caution should be exercised when formulating palaeolatitudinal or palaeoclimatological interpretations.

Introduction

Shell growth responds to a number of environmental factors (Weymouth, 1923; Smith, 1928; Davenport, 1935; Pratt, 1953; Green, 1957; Barker, 1964; Lammens, 1967; Montfort, 1967; Clark, 1968; House and Farrow, 1968; Pannella and MacClintock, 1968; Kennedy *et al.*, 1969; Rhoads and Pannella, 1970; Farrow, 1971, 1972; Pannella, 1972), and the interpretation of shell growth increments and cyclic shell growth bands must be approached with caution. However, once shell growth diversity gradients can be determined in modern organisms, it may be possible to: (i) follow the development of these gradients through time and to suggest palaeolatitudes; (ii) note significant differences in shell growth patterns, which reflect broad-scale environmental changes, such as in marine palaeoclimate, through time and across time boundaries between geological epochs; (iii) delimit present-day and fossil molluscan provinces and (iv) apply diversity gradients in shell growth to structural geology problems such as displacements of shell growth diversity gradients measured in terms of hundreds of miles along major faults (Hall, 1960).

The purpose of this paper is to present incremental shell growth data relative to marine bivalve molluscs: *Callista chione* (Linnaeus, 1758) and *Tivela stultorum* (Mawe, 1823). Specimens of *Callista chione* studied were collected from the northern Adriatic Sea and from Pliocene and Pleistocene rocks of Italy. Specimens of *Tivela stultorum* were collected alive along the west coast of North America over a latitudinal range of approximately 9°. Analysis and interpretation

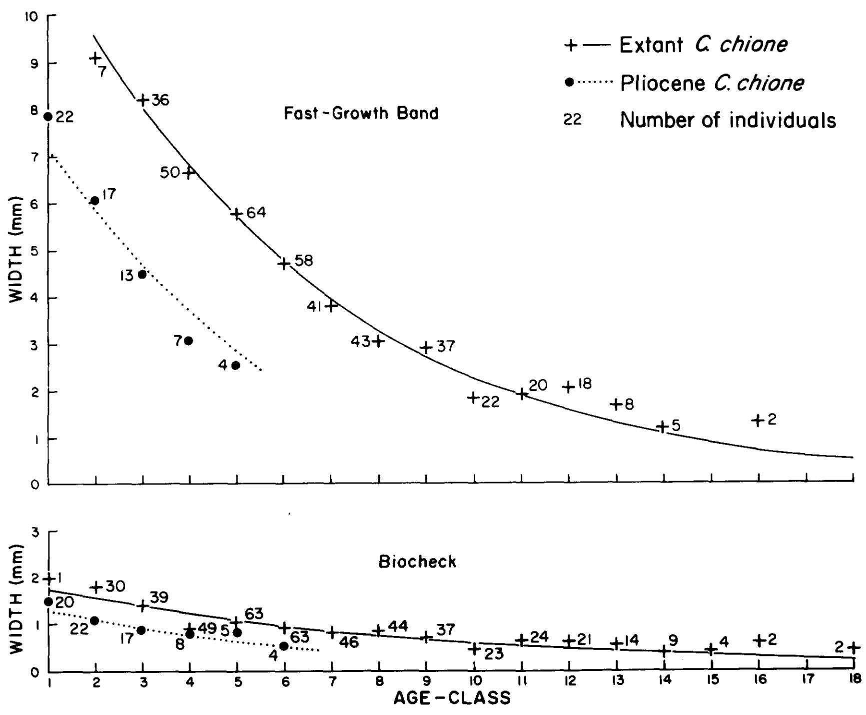

FIGURE 1. Growth (in mm) within bands of fast growth and biochecks of individuals of *Callista chione* from 1–18 years of age. The mean thickness of the growth band of a particular age-class within all year-classes studied is shown by a plus (+) for extant individuals and by a dot (·) for Pliocene individuals. The numbers refer to the number of individual bands measured. For example, the mean width of 30 second-year biochecks is 1·88. The data for the extant individuals are from Hall (1974)

of the incremental shell growth data from these taxa suggest that: (a) age must be considered when evaluating periodicity of growth increments; (b) there are latitudinal differences in growth patterns in shells of individuals from the same bathymetric zone, year- and age-class and (c) the direct or indirect affects of substrate and depth on shell growth are not sufficiently understood.

Growth increments

Extant Callista chione

An analysis of 474 bands of slow growth or biochecks and 414 bands of fast growth in 137 individuals of *Callista chione* (Linnaeus, 1758) from 5–10 m of

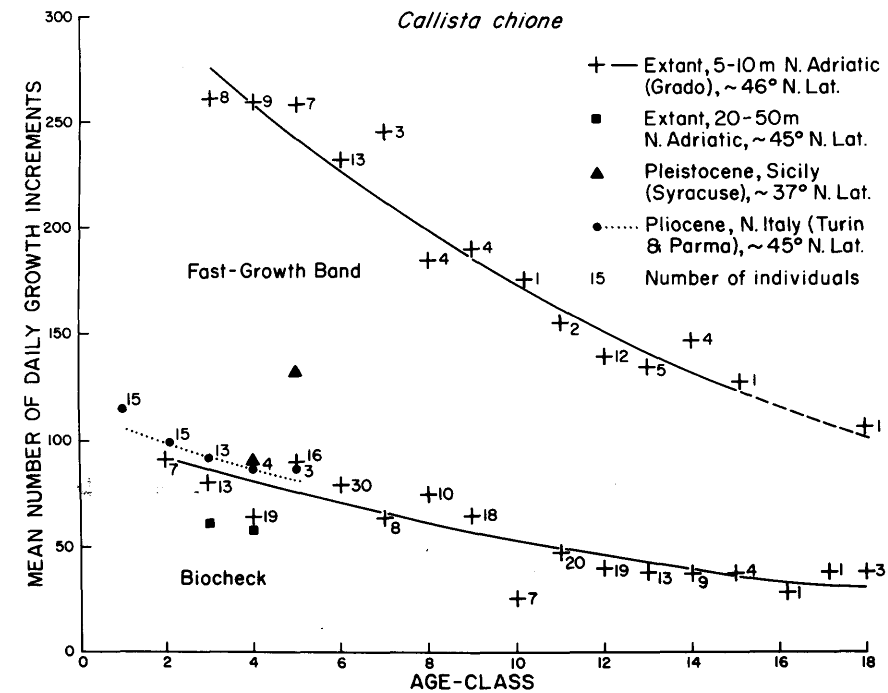

FIGURE 2. Number of shell growth increments in the band of fast growth and the biocheck plotted against the age-class of individuals of *Callista chione*. Example: the mean number of daily shell growth increments within seven 2-year-old biochecks is 88·8. The numbers beside these averages refer to the number of growth bands counted. The data for the curves for extant individuals collected from 5–10 m of water in the northern Adriatic Sea, near Grado, are from Hall (1974). Pliocene specimens were collected by P. G. Caretto near Turin and by C. A. Hall near Parma. Both Pliocene collections are from upper Pliocene rocks. The extant specimen from 20–50 m of water was collected by L. M. J. U. van Stratten in the northern Adriatic Sea, and the single specimen from the Pleistocene rocks of Sicily was collected by Italo Di Geronimo

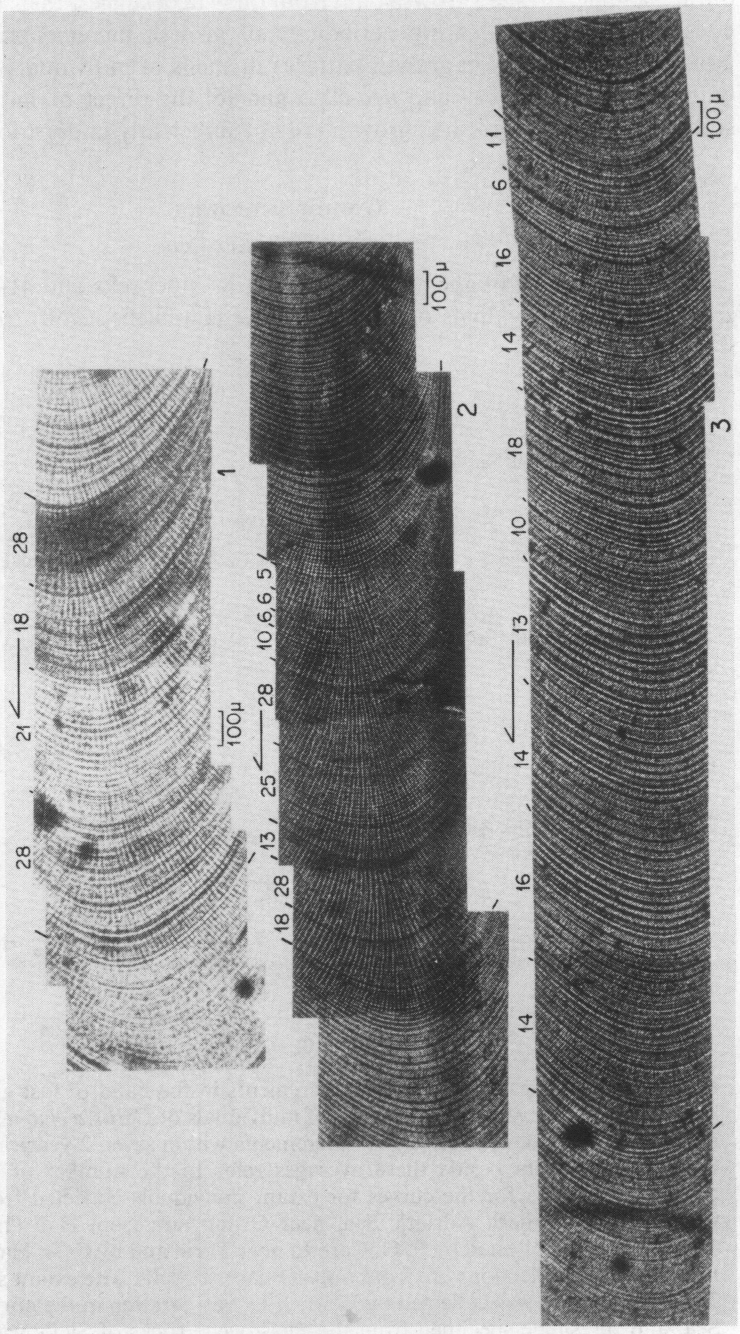
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FIGURE 3. Numbers refer to the number of daily growth increments in bundles of growth increments. There is no significance to bundles or groupings of growth increments, which are only provided for purposes of understanding what is being counted as a presumed daily shell growth increment. Arrows indicate direction of growth

1. *Callista chione* (Linnaeus, 1758). Collected live 23 February 1971, from 5–10 m of water off Grado, northern Adriatic Sea. UCLA hypotype No. 49035. Fifth annual biocheck of a 9-year-old individual. Approximately 90 daily shell growth increments are present in the biocheck.

2. *Callista chione* (Linnaeus, 1758). Collected live from silty sand, 0·8 km south of Badagnano (approximately 7 km southwest of Castell' Arquato, near 45° 51′ 00″ N latitude, northern Italy. Locality is between Piacenza and Parma in the Picacentine Hills of the Apennines of northern Italy. Piacenzian Stage, upper Pliocene rocks. UCLA hypotype No. 49036. Fifth annual biocheck in an 8-year-old individual. Approximately 139 daily shell growth increments are present in the biocheck.

3. *Callista chione* (Linnaeus, 1758). Collected from silty sand near Floridia (Syracuse), Sicily. Sicilian Stage, Pleistocene. UCLA hypotype No. 49037. Fifth annual biocheck of an 8- or 9-year-old individual. Approximately 132 distinct shell growth increments are present in the biocheck; not all are presumed to be daily

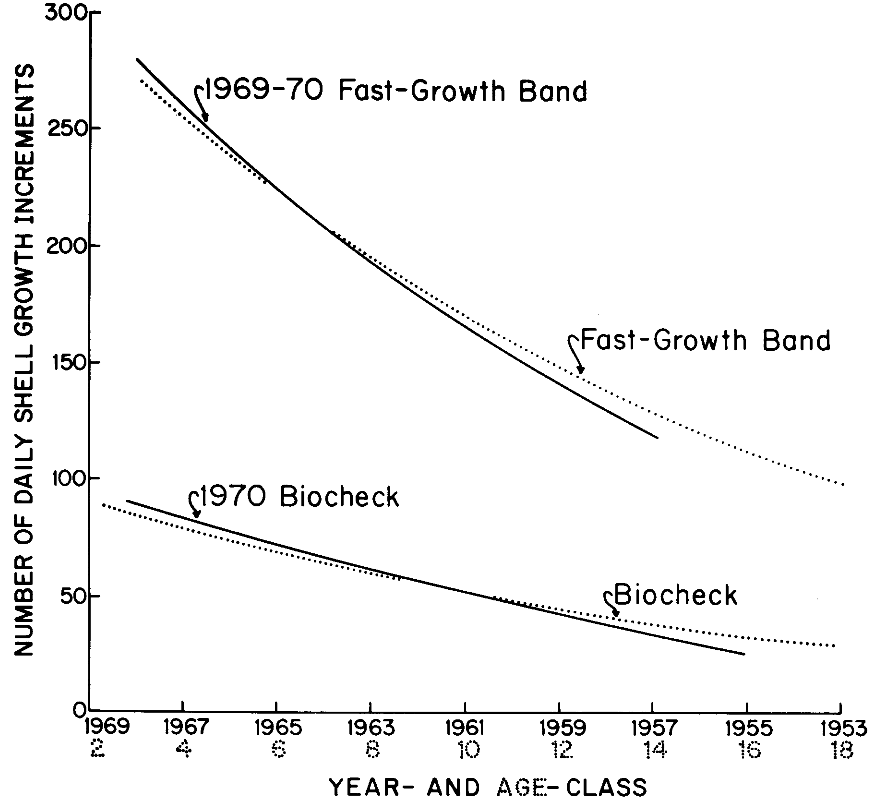

FIGURE 4. Average number of growth increments in the band of fast growth and the biocheck, *Callista chione*, deposited during 1969–1970 and 1970, respectively, plotted against the year-class (solid lines). The solid-line curves (1969–1970 and 1970) represent the average number of daily growth increments of a particular age-class within the same year-class. The other curves (dotted lines 'fast-growth band' and 'biocheck') show the average number of growth increments in the band of fast growth and the biocheck plotted against the age-class. The data from both curves are from Hall (1974) and illustrate that a study of shell growth increments in age-classes would not significantly differ from interpretations based on year-classes of fossil populations if year-classes could be determined in fossil populations

water in the northern Adriatic Sea (~45° N latitude) has been made (Hall, 1974). From this study of *C. chione*, it is known that a period of slower growth occurs annually and is manifested by a macroscopic, seasonal growth band or biocheck, 0·9–3·60 mm wide. The biocheck is not formed during the months when sea surface temperatures are at their lowest, nor is it formed during known periods of spawning. Based on limited evidence, the biocheck begins abruptly, follows the period of spawning, and precedes the onset of the coldest winter sea surface temperatures. The width of the band of fast growth is from 0·60–11·80 mm. The biocheck and fast-growth band form an annual growth band composed of 13–121 daily growth increments in the biocheck and 73–307 daily growth increments in the band of fast growth. Older individuals, i.e. from 4–18 years of age, do not deposit as great a thickness of shell nor as great a number of daily shell growth increments as do younger individuals (Figures 1 and 2). Note also in Figures 1, 2 and 3 that there are relative differences in shell growth and numbers of shell growth increments between Pliocene, Pleistocene and extant *C. chione*. There is close agreement between the number of daily growth increments in the biochecks of individuals of the same age-class from the same locality, collected at the same time of the year. There is also close agreement between the number of daily growth increments in biochecks of the same age-class but different year-classes of extant individuals (Figure 4).

The size of a specimen and the width of biochecks and fast-growth bands are smaller in a single sample of *C. chione* (supplied by L. M. J. U. van Stratten) from 20–50 m of water, than are the same features of an average specimen of the same age from 5–10 m of water. All specimens being compared in this case are from the northern Adriatic Sea. There are also fewer daily shell growth increments in the biochecks of the specimen from 20–50 m of water than there are in the average biochecks of the same age-classes collected in 5–10 m of water near Grado, at the head of the Adriatic Sea (Figure 2). From the paucity of material collected from relatively deep water, it is not possible definitively to suggest the direct or indirect influence of depth on shell growth. However, without knowledge of shell growth gradients related to bathymetry and substrate (Figure 5), analyses of the shell growth increments of fossil populations of *C. chione* are incomplete.

Extant Tivela stultorum

Some 115 biochecks and 74 bands of fast growth were counted in 100 individuals of *Tivela stultorum* (Mawe, 1823) collected along the coast of California and Baja California (~35° N latitude to ~26° 30′ N latitude) (Hall, 1974). Weymouth (1923) studied more than 2000 individuals of *T. stultorum* over a period of more than two years and conclusively documented the fact that a relatively narrow growth band appears annually. This narrow growth band is referred to here as the biocheck. The annual growth band, i.e. fast-growth band and a biocheck, commonly contains more than 300 growth increments, 5–200 μm thick. The more-than 300 growth increments in the biocheck and band of fast growth are assumed to be daily growth increments.

Growth in *T. stultorum* may exceed 20 mm per year in young clams and is less than 1 mm per year in older individuals. In this taxon 80% of the total length is reached by the end of the seventh or eighth year of growth, and some individuals reach an age of 50 or more years (Weymouth, 1932; Coe and Fitch, 1950; Fitch, 1965). Within shells of 12–23-year-old individuals of *T. stultorum* collected from Baja California, Mexico, and near Santa Monica, California, there is an average of 60 daily growth increments in the biocheck and less than

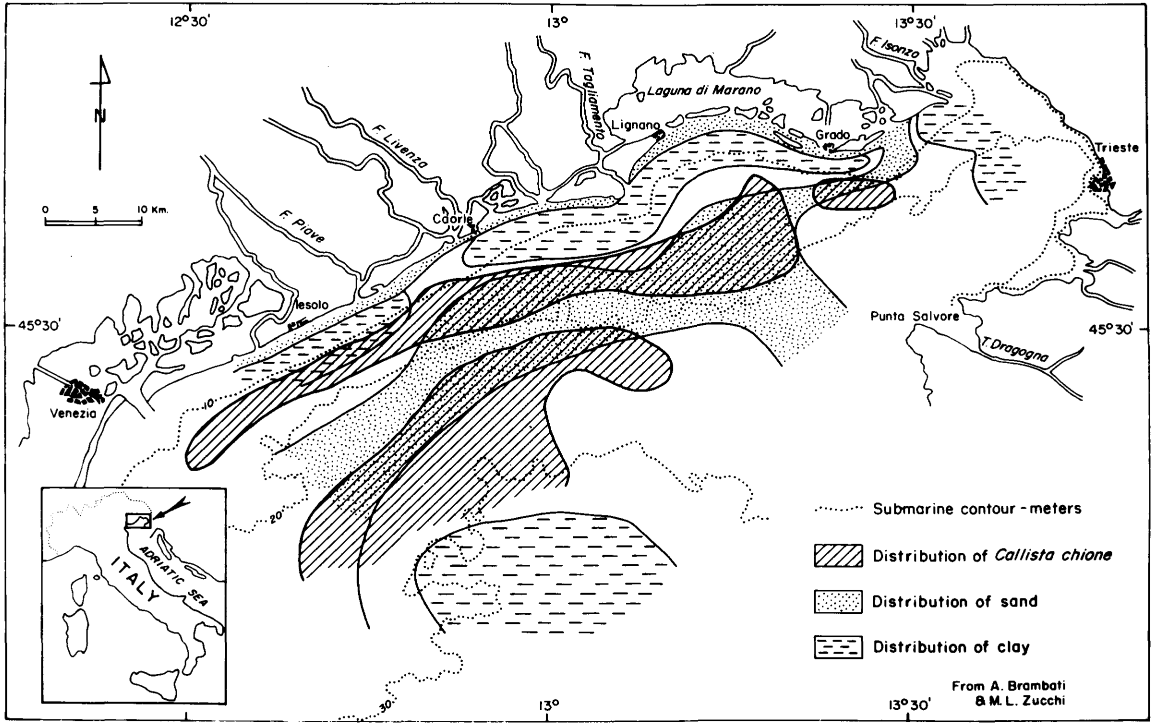

FIGURE 5. Distribution of *Callista chione* in the northern Adriatic Sea based on the work of Brambati and Zucchi (1969) and Brambati (written communication, 1970). The individuals of *C. chione* used by me for the study of this taxon from the northern Adriatic Sea (Hall, 1974) were living in sandy substrates. Brambati and van Stratten (written communication, 1970) show that *C. chione* also lives in silty sand, but rarely in clay. The relation of substrate to shell growth patterns in this taxon is not known, nor are the relationships between shell growth patterns and bathymetric gradients clear. Note that rock's termed 'clay' are called 'pelite' by Brambati. According to Brambati (written communication, 1974), these sediments have a grain size of less than 50 μm and include silty to sandy pelite facies. Unpatterned areas on the map are an intermediate facies between the argillaceous or mud facies and the sand. Reproduced from Brambati, A. and Zucchi, M. L. (1969), *Studi Trentini di Scienze Naturali*, Sez, A, **46**, 30–40 by permission of the Museo Tridentino di Scienze Naturali

200 daily growth increments in the fast-growth band; in some cases there are less than 100 (Hall, 1974). A maximum of 239 and a minimum of 164 daily growth increments were present in an annual band of growth in individuals older than 12 years. There is an absence of 126–201 or more daily growth increments in an annual band of growth in individuals of *T. stultorum* older than 4–6 years. In order to study the number of days in a year during the geological past, such as the study reported by Pannella *et al.* (1968), the application of suitable techniques to account for the trend of slowing growth is required.

Near the southern limit of the range of *T. stultorum* within individuals, for example, of the year-class of 1965, there is an average of 111 daily growth increments in the fourth-year biocheck, whereas near the northern limit of the range of this species, there is an average of 82 daily growth increments. Until more individuals of the same age- and year-class from different microhabitats of the same latitude and different latitudes are studied, there are reservations about the

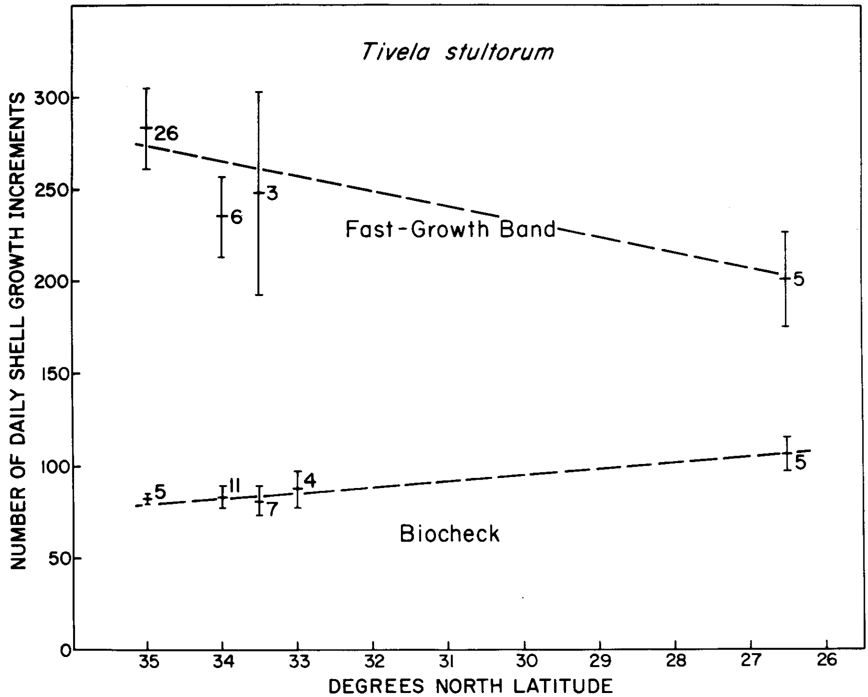

FIGURE 6. Number of daily shell growth increments per biocheck and bands of fast growth in the year-classes 1961 through 1968 and age-classes 1–8 of *Tivela stultorum* from the west coast of North America plotted against latitude. The numbers refer to the number of individual bands from which growth increment counts were made. Diagrammatic curves show increasing numbers of daily shell growth increments in biochecks with decreasing latitude and decreasing numbers of daily shell growth increments in fast-growth bands with decreasing latitude

acceptance of the observed relationship between latitude and the number of daily growth increments in the biocheck (Figure 6).

Fossil Callista chione

Pliocene specimens of *C. chione* have been collected from near the same latitude as that from which the living specimens of *C. chione* were taken. The Pliocene shells are from near Turin (Castelnuovo, Valle Andona, late Pliocene, collected by P. G. Caretto) and Parma (Castell'Arquato and Badagnano, late Pliocene, collected by C. A. Hall) in northern Italy. Based on 76 observations of 1–6-year-old individuals of *C. chione*, the width of the biocheck and band of fast growth is less than that of extant specimens from near the same latitude collected from 5–10 m of water (Figure 1). The average number of daily growth increments in 50 Pliocene individuals of *C. chione* is greater than in biochecks of extant individuals of the same age-classes. For example, there is an average of 114–86 daily shell growth increments in biochecks within 1–4-year-old Pliocene individuals versus averages of 88–64 growth increments in extant 2–4-year-old individuals collected during 1970 and 1971 (Hall, 1974; Figure 2). If there is a latitudinal gradient in the number of shell growth increments of *C. chione*, as there seems to be in *T. stultorum*, then it is possible that the greater number of shell growth increments in biochecks of Pliocene individuals from near 45° N latitude reflects warmer marine climate during the Pliocene than at that latitude today.

A single specimen of *C. chione* from Sicilian Pleistocene rocks (collected by Italo Di Geronimo near Syracuse, Sicily) has a significantly greater number of shell growth increments in its biochecks than biochecks of the same age-classes of extant specimens from the northern Adriatic and Pliocene specimens from northern Italy (Figure 2). Again, the sample size is inadequate, but the relatively large number of growth increments in the biocheck is provocative and should stimulate further investigation.

Summary

Measurement and growth-increment counts of *C. chione* (Hall, 1974) show unmistakably that, with increasing age, there are fewer growth increments in both the biocheck and the band of fast growth in the annual growth band. Clearly, age must be considered when trying to determine the number of days in a year based on shell counts of growth increments in molluscs.

Although not entirely conclusive, there seem to be more daily growth increments in biochecks of *Tivela stultorum* near the southern limit of its range than in biochecks of the same age-classes near the northern limit of its range. If true, *T. stultorum* and other taxa may provide a means for suggesting the positions of palaeolatitudes and palaeoclimate. For example, the relatively greater number of daily shell growth increments in biochecks of *C. chione* from Pliocene rocks near 45° N latitude in northern Italy, as compared with daily growth increments in biochecks of the same age-classes of extant individuals from the Adriatic Sea, may reflect warmer sea temperatures during the Pliocene than today. However, other factors, such as the effect of substrate, depth, etc., on shell growth in *C. chione* are not sufficiently well enough understood to accept such an interpretation based on shell growth alone.

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DISCUSSION

SCRUTTON: How do you define the boundaries of the biocheck? Biochecks look rather diffuse.

HALL: Biochecks can be distinctly recognized on the surface of the shell, and the growth patterns in thin section can be matched with the external pattern. Biochecks are distinguished by an abrupt change from widely spaced to narrow increments.

EVANS: If you have demonstrated fewer daily increments to be deposited by older animals, how could the increments indeed by daily?

HALL: In 1–4-year-old specimens. I could count nearly 365 daily lines by calling them daily. In older individuals, the animal may not have added increments every day.

CLARK: If there are fewer lines in older individuals, when does growth stop being invariably daily? Do you mean the clam follows a daily periodicity for only the first part of its life, then drifts?

HALL: No. There is probably an equilibrium between deposition and non-deposition which changes.

DOLMAN: Why should there be such an abrupt difference between the biocheck and the fast growth series? Could they be caused by storms?

HALL: I don't know.

CLARK: As far as the influence of spawning is concerned, it is important to note that not all species have a spawning check.

EVANS: And not all species have a winter slowdown.

BUDDEMEIER: Perhaps different environmental parameters in different habitats are important. In the corals I studied, temperature seems to control growth increment production. Once outside the normal temperature range, I can't be so certain. The limiting parameter shifts.

PANNELLA: We should also consider sexual differences: male and female bivalves have different spawning series.

HALL: We must also consider age differences. *Tivela* don't spawn in their first year.