

EVOLUTION IN THE RADIOLARIAN SPECIES - COMPLEX *PTEROCANIUM*

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ABSTRACT--A global taxonomic and biometric study of five lineages of the radiolarian genus *Pterocanium* during the last 6 million years shows: (1) phyletic change was gradual but occurred at variable rates; (2) a trend toward decreasing size in all lineages but with common reversals of trend; (3) the two speciation events that occurred during the interval were both gradual (~ 500,000 yrs); (4) of the two extinction events one was gradual, the other abrupt; (5) the extinctions eliminated the largest species and within species phyletic trends result in the elimination of larger morphotypes. (6) Hybridization between lineages is common, particularly in regions of strong upwelling.

Our data suggest that for many microfossil taxa, the homeostatic species concept may not be valid, nor is the peripheral isolate (allopatric) model of speciation. Hierarchical models of population structure and parapatric speciation theory appear to be fruitful concepts for future research.

INTRODUCTION

Deep-sea microfossil records provide an unusual opportunity to study and compare patterns of geographic variation to patterns of evolutionary change within lineages. We have studied geographic and temporal patterns of morphologic evolution in the genus *Pterocanium*, a common and diverse member of the Neogene radiolarian assemblage. The study integrates traditional taxonomic analysis and biometric data from globally distributed samples taken throughout the Plio-Pleistocene section (Table 1).

Five major species level lineages are recognized (Table 2). *P. trilobum* (Haeckel) is a polytypic group in which we recognize at least three (not formally described) subspecies. *P. grandiporus* Nigrini, while not examined in this study, is morphologically very similar to *P. trilobum* and may constitute a fourth subspecies. *P. praetextum* (Ehrenberg) is also polytypic, with two recognized variants - *P.p. praetextum* and *P.p. eucolpum*. The extinct lineages *P. audax* Riedel and *P. prismatium* Riedel, by contrast are more nearly monotypic, while *P. korotnevi* (Dogiel) represents a large group whose internal phyletic relationships are not yet clearly delineated.

Each *Pterocanium* lineage has a distinctive geographic distribution through time (Figure 1). *P. trilobum* and *P. praetextum* are common in both tropical and subtropical waters. The other taxa are less widely distributed. *P. prismatium* was entirely restricted to tropical environments, while *P. audax* was primarily a subtropical form. *P. korotnevi* is and has been common only in the subpolar regions.

Table 1: Cores Examined

Core	Lat.	Long.
DSDP 158	7°N	85°W
DSDP 278	57°S	160°E
DSDP 348	69°N	12°W
E14-8	60°S	160°W
RC8-80	48°S	163°W
RC12-66	3°N	148°W
RC12-335	6°N	71°E
RC12-431	44°N	168°W
RC14-22	11°S	75°E
V19-169	10°S	82°E
V19-171	7°S	81°E
V20-105	39°N	178°W
V21-145	34°N	165°E
V21-148	42°N	161°E
V29-40	10°S	78°E

PHYLOGENY

Examination of numerous samples (only a subset of which are shown in Figure 1) reveals a complex reticulate pattern of evolution in *Pterocanium* (Figure 2). Seven million years ago, three species of *Pterocanium* existed - one each in low, middle and high latitudes. Each species is distinctly different from the others over most of its geographic range, but in regions of intense upwelling intermediate forms between the species are occasionally seen. With the passage of 1 million years, the morphologies and abundances of these lineages change.

## RELATIVE ABUNDANCE OF *PTEROCANIUM* SPECIES IN LATE NEOGENE OCEANS

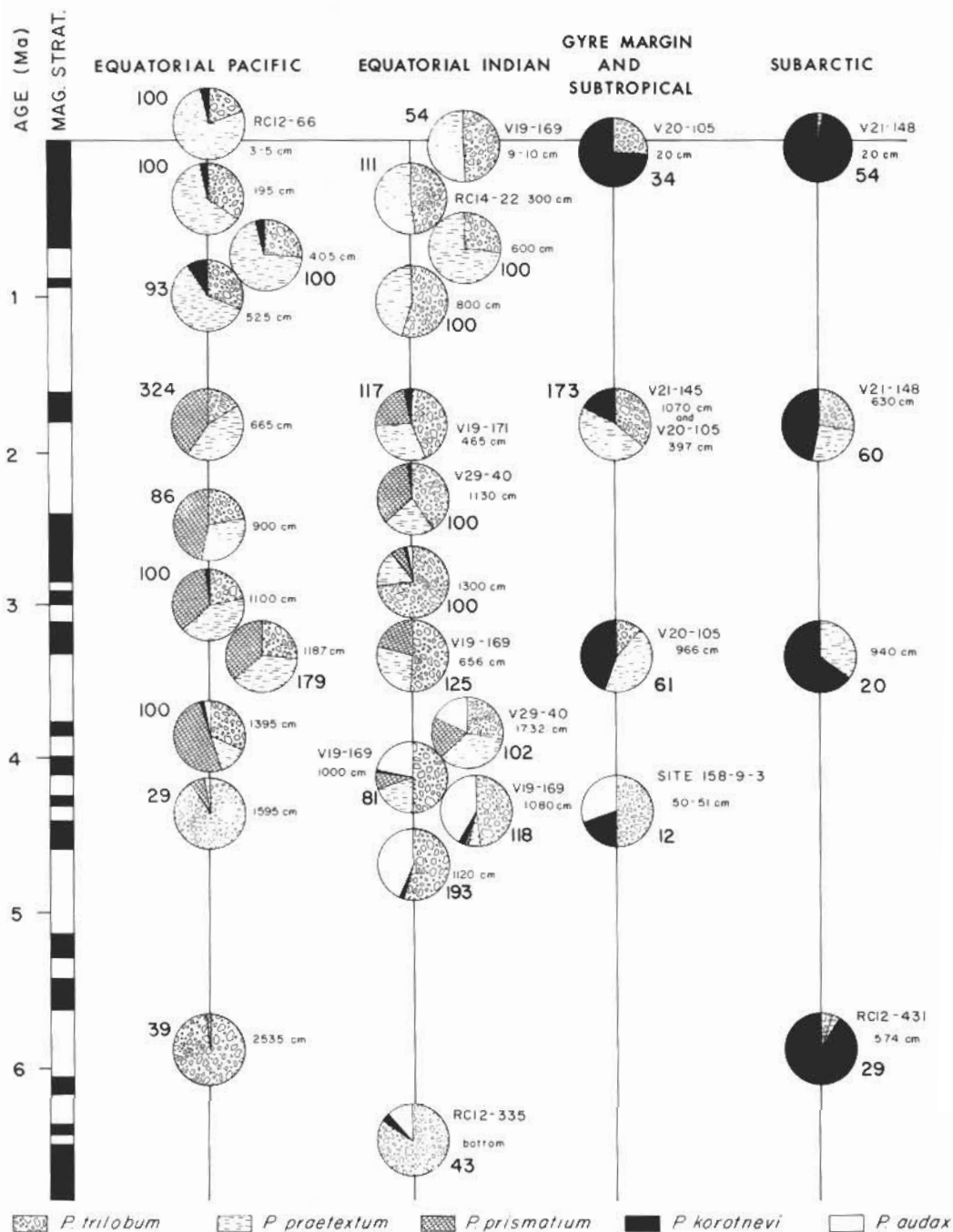


Figure 1 Relative abundances of species in biometrically analyzed populations of *Pterocanium*. Sample sizes shown in boldface.

Table 2: Taxonomic analysis of *Pterocanium*

Numbers on right give average state of characters listed on left. Extreme values indicated by a '0' or a '2', intermediate conditions by a '1'. Individual specimens typically deviate substantially from average state.

CHARACTER				TAXON DIAGNOSIS									
Name		End members of continuous variable character states (1 = intermediate)		trilobum group			grand-aporus		praetextum group		korot-nevi	prisma-tium	audax
		0	2	variant	a	b	c	prae-euol-textum	pum				
Apical Spine	length	long	short	0	1	1	0	1	1	2	1	0	
	thorns	prominent	absent	1	2	2	2	2	2	2	2	0	
Cephalis	size	large	small	0	1	0	0	2	2	2	0	0	
	shape	sphere	hemisphere	1	0	0	1	0	0	1	0	2	
Thorax	wall	flat	inflated	0	1	0	0	2	1	0	0	0	
	rib shape	1 tetrahedral	2 prismatic	4	1	1	4	1	1	3	2	4	
		3 hemispherical	4 recurved										
Thorax lattice	size	large	small	0	1	2	0	2	2	1	0	0	
Pores	shape & distr.	regular	irregular	0	2	1	0	1	1	0	1	0	
Bars	thickness	thin & smooth	thick & framed	1	1	0	1	1	1	2	0	2	
	width	narrow	wide	2	0	0	1	0	0	2	2	2	
Accessory Body Spines		prominent	absent	1	0	1	1	0	1	2	0	2	
	length	long	short	1	2	2	0	0	1	0	1	0	
	thickness	thin	thick	1	0	0	1	0	0	2	1	2	
Feet	shape	straight	curved	2	1	1	2	0	1	1	0	0	
	attachment	parallel	angled	NA	1	2	NA	0	0	1	0	2	
	base	porous	hyaline	1	1	0	1	0	1	2	1	2	
abdominal veil		prominent	absent	1	1	1	0	0	0	2	1	2	

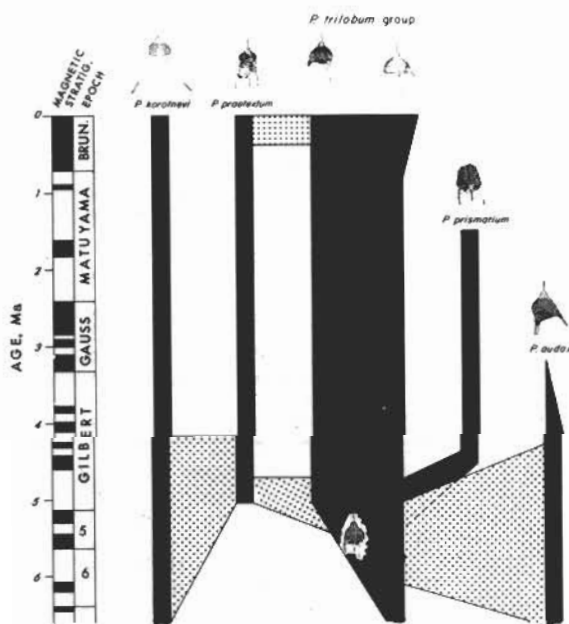


Figure 2 Diagram of lineage relationships in *Pterocanium*. Lightly shaded areas are regions of morphologic intergradation.

*P. audax*, *P. trilobum* and intermediate forms are still common in subtropical sediments. Changes in the morphology of *P. korotnevi* are seen which prefigure later evolutionary trends. By 4.5 Ma (Megannum), *P. audax* and *P. trilobum* have extended their range into subpolar waters. Typical *P. korotnevi* forms are common, but so are forms intermediate between *P. korotnevi* and *P. praetextum*. *P. praetextum* is already well established in the equatorial Indian Ocean, together with intermediates between *P. praetextum* and *P. trilobum*. A few early forms of *P. prismatium* are also seen, mostly in the equatorial Pacific. Thus, in the 1.5 million years between 6 Ma and 4.5 Ma, *P. praetextum* has evolved, although the presence of intermediate forms suggests that this event is not yet complete. At 3 Ma, individual lineages are well defined, and intermediates are rare. *P. prismatium* is a common member of the assemblage in equatorial regions, and *P. praetextum* has spread into the equatorial and subtropical Pacific. In the latter part of the Pliocene and in the early Pleistocene, *P. audax* and *P. prismatium* become extinct. Within the *P. praetextum* lineage, a shift from dominant *P.p. eucolpium* morphology to *P.p. praetextum* morphology is seen.

#### BIOMETRY

It is not yet possible to quantify the majority of the diagnostic characters given in Table 2. Thus, biometric data only partially document the morpho-

# EVOLUTION OF THORAX WIDTH IN *PTEROCANIUM* LINEAGES (in $\mu\text{m}$ )

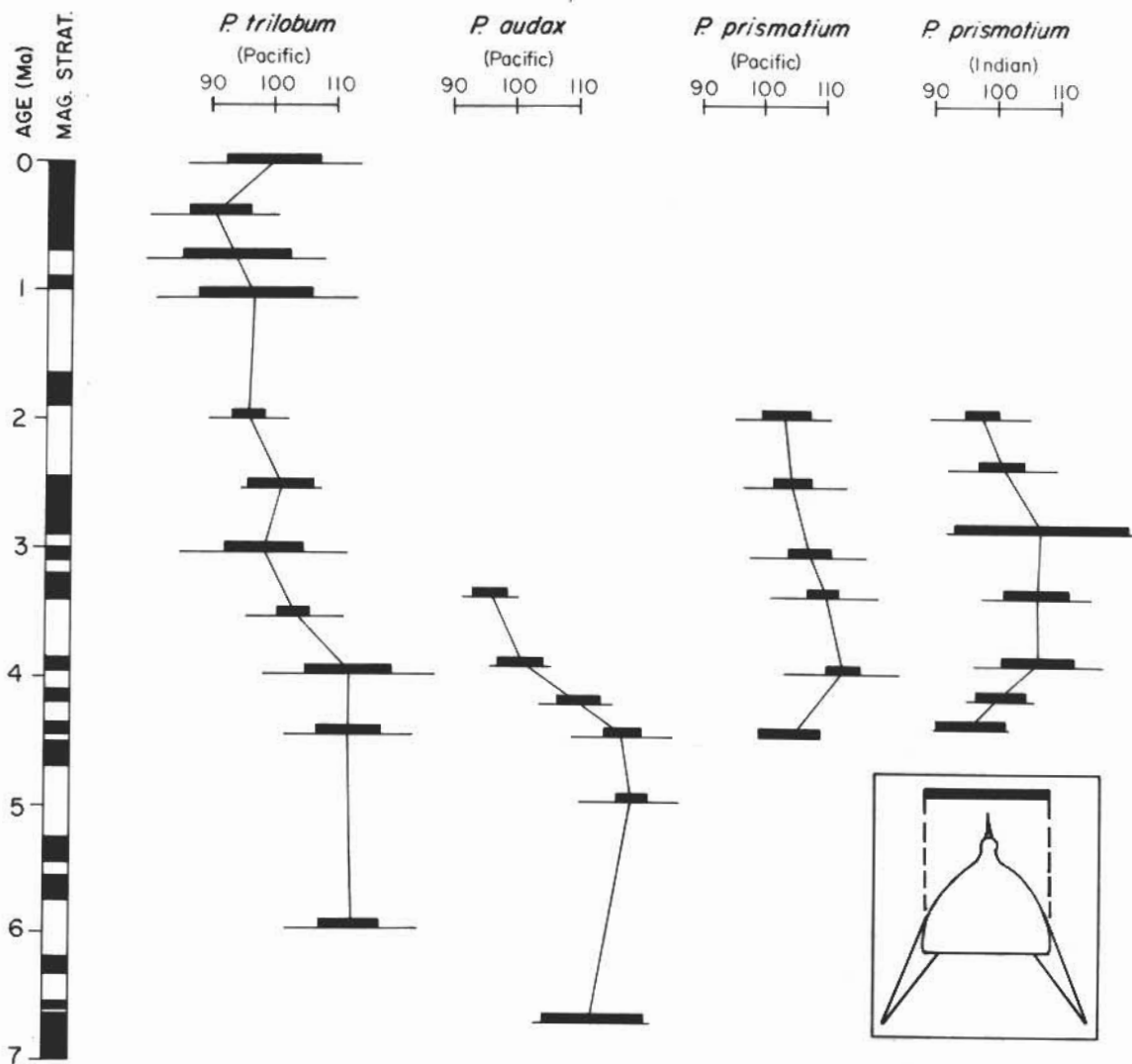


Figure 3 Gradual phyletic trends in mean thorax width of *Pterocanium* lineages. Narrow lines represent standard deviation of samples, heavy lines 95% confidence intervals of means. For sample locations and sizes see Figure 1.

logical patterns seen through the microscope. The measurements made however do indicate both the gradual rate of morphologic change and its reticulate nature. In *P. prismatium* (Figure 3) an initial increase in thoracic width in the early Pliocene is followed by a reversal in trend and a phyletic size decrease throughout the late Pliocene, eventually terminating in the abrupt extinction of the lineage at the base of the Pleistocene. Phyletic size decrease is also seen in the mean thoracic width of *P. audax*, and in the mean thoracic width of *P. trilobum* populations from the equatorial Pacific (Figure 3).

Variation in individual characters is very high for all radiolarian taxa examined, as is covariation. Size variation between individuals within a population is similar in one case to variation between taxa as well. This is shown in Figure 4, where nearly isometric axes of thoracic size variation in populations of *P. praetextum* and *P. trilobum* are colinear with the axis of between taxon differentiation. This uniformity of pattern however does not hold for comparisons of other taxa, for example *P. trilobum* to *P. prismatium* (Figure 4).

Apparent hybridization between the *P. praetextum* and *P. trilobum* lineages in the Pleistocene follow-

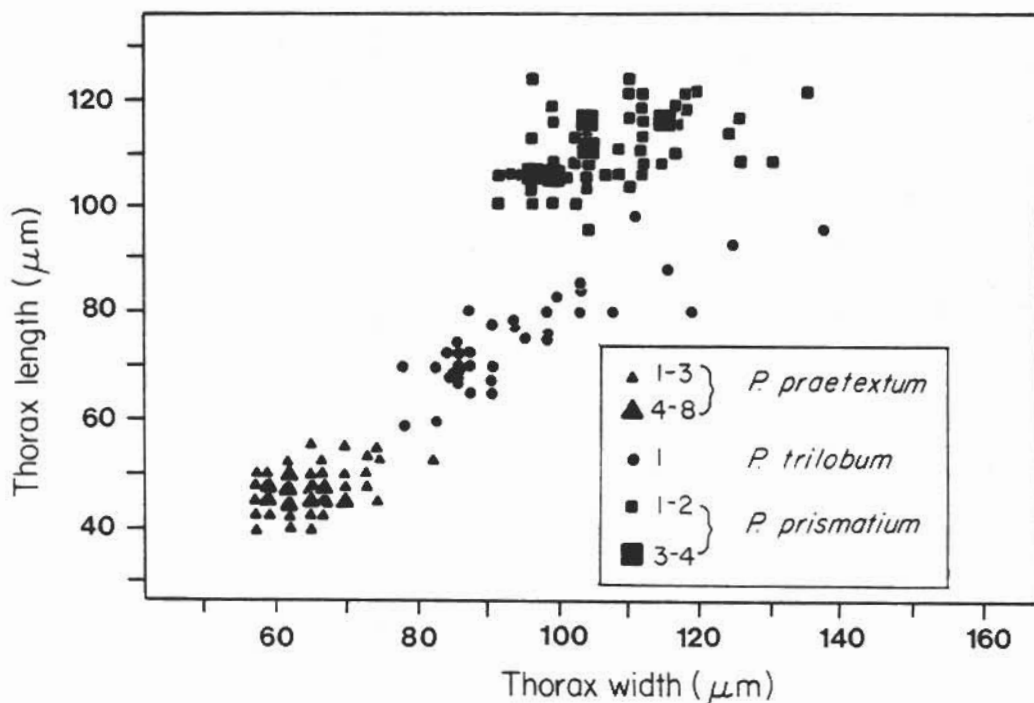


Figure 4 Scatterplots showing variation in thorax measurements for composite populations of *Pterocanium* species. *P. trilobum* and *P. praetextum* data is late Pleistocene, *P. prismatium* late Pliocene. Intermediates between *P. trilobum* and *P. praetextum* (shown on Figure 5) not plotted here for sake of clarity. Number of specimens represented by each plotted point is indicated by the size of the symbol, as shown.

ing differentiation in the Pliocene is indicated in Figure 5. Initially distinct, these two taxa become progressively harder to distinguish as intermediates become more common. Convergence is seen not only in size, but in many other diagnostic characters as well. Despite this phenomenon, recent populations of these lineages still display two distinct modes.

#### DISCUSSION

Certain generalizations about planktonic marine protistan evolution may be drawn from our study of *Pterocanium*. The tempo of evolution is very gradual, both during phyletic change and during speciation. The phylogenetic pattern observed is at least sometimes reticulate. Eldredge and Gould's (1972) hypothesis that most evolution is saltatory - i.e. that it is produced primarily by Mayrian speciation of small peripheral isolates, followed by stasis - does not seem to hold for these planktonic, deep-sea organisms. Possible reasons for this may be found in the distinctive biological characteristics of this group of protists.

Many workers have previously noted that in deep-sea holoplankton, a fluid environment with continual mixing results in huge populations, spread over vast areas - not small (a few square kilometers) scattered isolates which are stable over hundreds of years. These relatively large populations are

therefore not as likely to undergo rapid evolutionary modification as would smaller ones, which are more uniform and more subject to chance phenomena.

Isolation may be difficult to achieve for reasons of population structure as well. Complex geographic variation is quite marked in protistan holoplankton (in the Foraminifera, for example, see Kennett, 1976). This, together with observations of common hybridization and reticulate evolution (particularly in Radiolaria - e.g. Goll, 1976; this study) implies that most planktonic marine microfossil groups possess a typically protistan population structure of syngens, or perhaps a plant-like one of syngameons (Grant, 1971). The evolution of reproductive isolating mechanisms in (relatively) simple protists may therefore be more difficult than in more complex metazoan organisms.

Eldredge and Cracraft (1980) have argued that within-species trends may not be related to higher-level, macroevolutionary patterns. Gradual, within-species phyletic size decrease is common to most *Pterocanium* lineages studied. This is similar to a larger-scale trend towards smaller taxa in *Pterocanium*, created by the extinctions of relatively large *P. audax* and *P. prismatium*, and the origin of relatively small *P. praetextum*. Although 'micro' and 'macro' evolutionary trends are similar in our data, more characters

and more taxa are required to definitively test this model.

In conclusion, both empirical observations of microfossil evolution and theoretical considerations suggest that evolution in marine protistan holoplankton generally does not proceed by the rapid development of discrete species in small, isolated environments. Allopatry is an important mechanism of evolution in the deep-sea, but the relative rarity of allopatric events, and the huge size of the populations involved, distinguish it from the model used by Eldredge and Gould. Parapatric and clinal models of evolution by contrast are largely independent of absolute population size, nor do they require complete geographic isolation to operate (Endler, 1977). These models of speciation may often be more appropriate than allopatric ones for studying protistan evolution in the planktonic marine realm.

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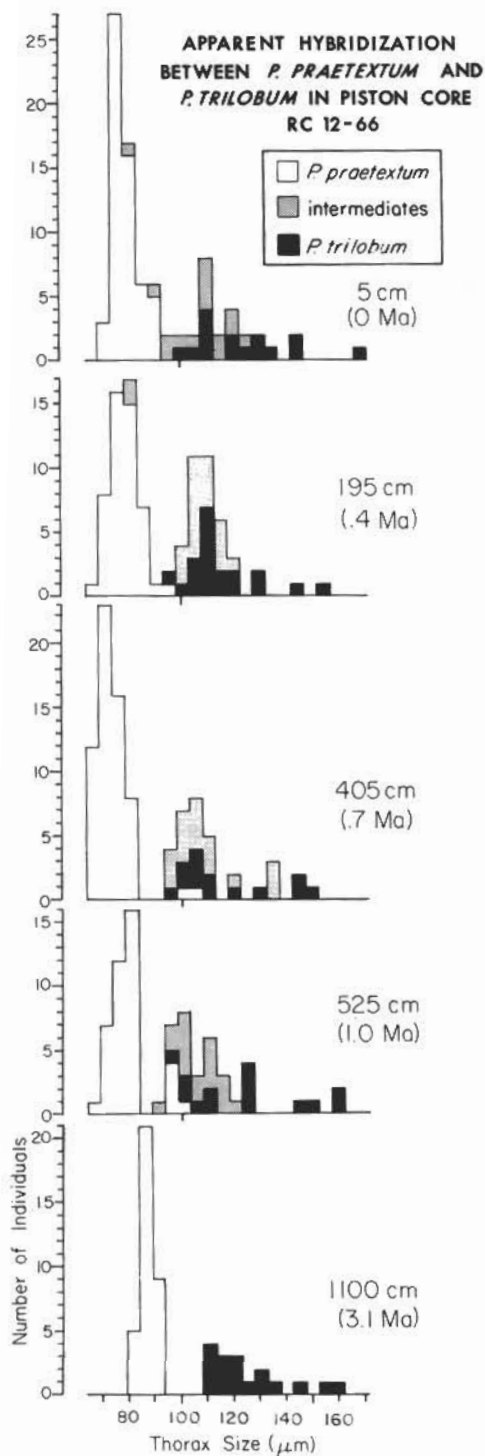


Figure 5 Histograms of thorax size distribution in equatorial Pacific populations of *P. trilobum*, *P. praetextum*, and intermediate forms. Classification of specimens based on several criteria other than thorax size (see Table 2). 'Size' defined as: square root(thorax length<sup>2</sup> + thorax width<sup>2</sup>) and is approximately colinear with the primary axis of variation shown in Figure 4.

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