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The Thecosomatous Pteropods: a contribution toward the Cenozoic Tethyan paleobiogeography

Maria Pia BERNASCONI Elio ROBBA

Dipartimento di Scienze della Terra
Università di Milano

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KEY WORDS — Thecosomatous Pteropods, Cenozoic, Tethys, Paleobiogeography.

SUMMARY — The Tethyan seaway seems to have had a rather low efficiency on the migration of Pteropods from Atlantic-Mediterranean toward Indo-Pacific and vice versa. The faunal interchanges between Caribbean-Mediterranean-Paratethys were active by the Oligocene and extended to Asia Minor as well during Middle Miocene; migration seems to have occurred from West toward East. Pteropods have been especially confined to the Atlantic-Mediterranean area until the entire Miocene at least; their Recent wide dispersal and ranges of species came to a definitive settlement during the Pleistocene.

RIASSUNTO — [Gli Pteropodi Thecosomati: un contributo alla paleobiogeografia cenozoica della Tetide] — *Sulla base dei dati esistenti, viene discussa la distribuzione geografica degli Pteropodi, dalla loro comparsa nell'Eocene ad oggi; le principali conclusioni sono le seguenti.*

La Tetide sembra essere stata poco efficace quale via di migrazione tra l'area Atlanto-Mediterranea e quella Indo-Pacifica. Se è corretta l'ipotesi che l'Atlantico sia stato il luogo di origine degli Pteropodi, va tenuto presente che il flusso della corrente nella via d'acqua della Tetide era da Est verso Ovest.

Gli scambi tra Caraibi, Mediterraneo e Paratetide sono stati attivi a partire dall'Oligocene e si sono estesi all'Asia Minore durante il Miocene Medio. Le migrazioni sono avvenute più che altro da Ovest verso Est, sfruttando il circuito Nord-Atlantico.

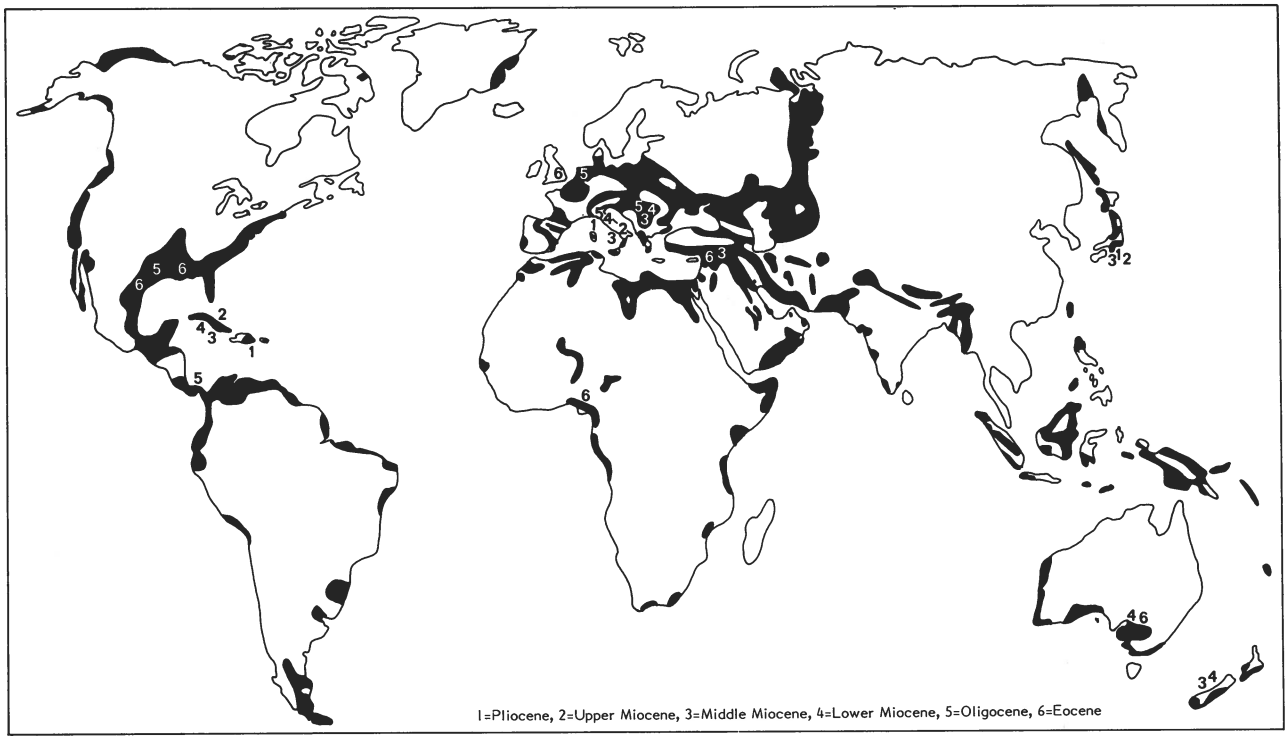
Pare che gli Pteropodi siano rimasti confinati più che altro nell'area Atlantica e Mediterranea almeno fino a tutto il Miocene. La loro dispersione in tutti gli oceani si è realizzata durante il Pleistocene.

INTRODUCTION

Thecosomata are planktonic Gastropods whose earlier members are known from the Lower Eocene and seem to have had a relatively rapid evolution onward.

The present-day Pteropods consist of approximately 30 species, some of them including subspecies, and grouped into 8 genera. They are present in the World oceans where their distribution is mainly controlled by the surface temperature, salinity and circulation patterns. The latter factor seems to have played the most significant role during Paleogene and Miocene, when the climate was rather uniform within the latitudinal range (text-fig. 1) occupied by Pteropods.

Data about fossil Thecosomata are so far rather scanty as well as discontinuous, due to the scarce attention given to this group and to their aragonitic shells which are easily susceptible to dissolution. For these reasons, the remarks exposed in the present paper might be modified by new informations. In any case, it seems not to be fortuitous that almost all the records concerning fossil Pteropods are within a latitudinal band which virtually coincides with the Tethyan Realm (Text-fig. 1). The spreading which brought them to the present-day worldwide distribution (high latitudes included) took place in the near past, possibly during Pliocene and Pleistocene.



Text-fig. 1 - Distribution of marine Tertiary sediments (after Adams, 1973) and of fossil records.

EOCENE

Twenty Eocene species are well known. Sixteen out of them are from the Central-North Atlantic area, being distributed in Great Britain (Curry, 1965), Nigeria (Curry, 1965), Texas and Alabama (Collins, 1934); 2 have been described from Asia Minor (Avnimelech, 1945); 2 occur in Southern Australia (Buonaiuto, 1979) (*).

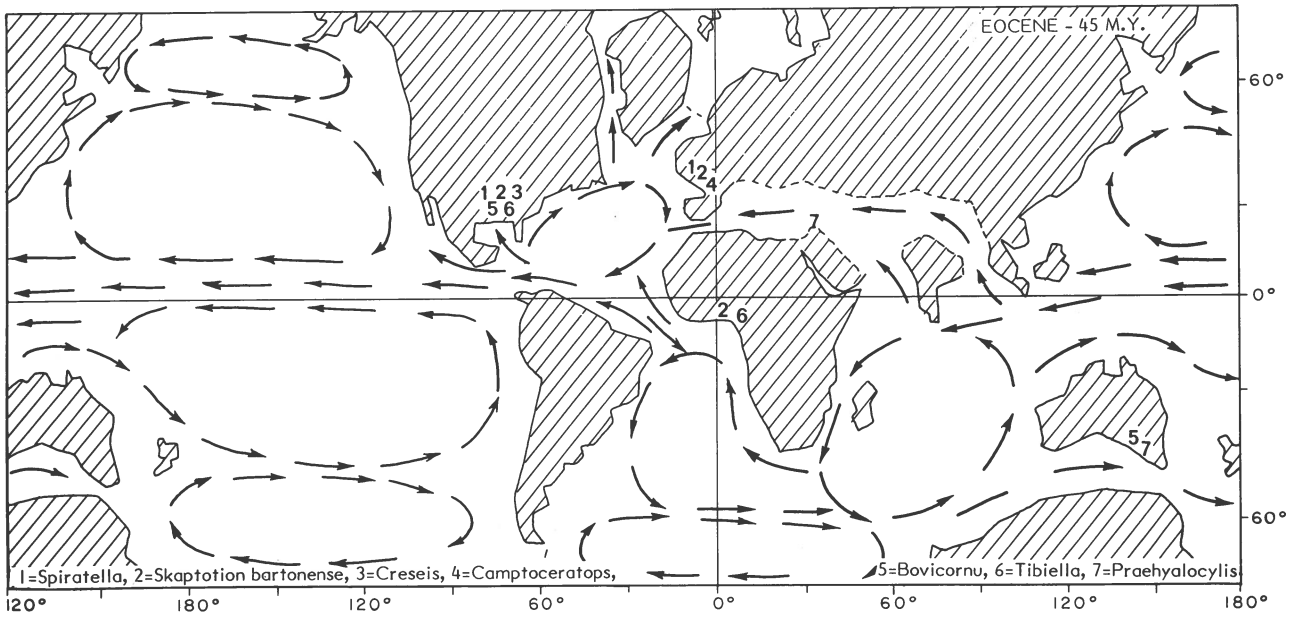
Table I, which summarizes the data here considered, seems to suggest a consistent difference between the areas taken into account, both at the genus and species level. In particular, *Creseis* Rang is only recorded in the United States and *Camptoceratops* Wenz only in Great Britain. The fact is quite possibly the consequence of scantiness of data because the paleocirculation patterns (Text-fig. 2), as inferred by Berggren and Hollister (1974, 1977) and Kennett (1982), should have favoured the dispersal of planktonic organisms and, thence, a higher similarity of the assemblages. The Gulf Stream and the North Equatorial Current were active agents of faunal dispersion in the Atlantic (Berggren and Hollister, 1974); as a matter of fact, *Skaptotion bartonense* Curry occurs in Great Britain, United States and Nigeria. Moreover, the Atlantic South Equatorial Current, flowing from West Africa straight to the Caribbean (McKenzie, 1973), may account for the presence of *Tibiella marshi* (Meyer) both in Nigeria and the Gulf Coast area. The Tethyan seaway is possibly responsible for the occurrence of *Praehyalocylis* Korobkov & Makarova in Asia Minor and of *Praehyalocylis* and *Bovicornu* Meyer in Southern Australia.

The marked difference between the number of recorded species in the Central-North Atlantic area and in the eastern oceans, if not completely due to the inadequacy of data, might support Van der Spoel's suggestion (1967) that the Atlantic is the presumable birthplace of Pteropods.

(*) The genus *Euchiloteca* Cossmann is not considered in this report, due to its uncertain systematic position; in fact, it is regarded by many authors as a member of family Cecidae and not as a Pteropod (Buonaiuto, 1979).

U.S.A. (Texas & Alabama)	NIGERIA	GREAT BRITAIN (London Clay)	TURKEY & PALESTINE	SOUTHERN AUSTRALIA
Spiratella choctavensis (Aldrich)				
Spiratella elongatoides (Aldrich)				
		Spiratella mercinensis (Watelet & Lefevre)		
		Spiratella nemoris Curry		
		Spiratella pygmaea (Lamarck)		
		Spiratella taylori Curry		
		Spiratella tutelina Curry		
Skaptotion bartonense Curry	*Skaptotion bartonense* Curry	*Skaptotion bartonense* Curry		
Creseis corpulenta (Meyer)				
Creseis hastata (Meyer)				
Creseis simplex (Meyer)				
		Camptoceratops prisca (Godwin-Austen)		
Bovicornu eocenense Meyer				
Bovicornu gracile Meyer				*Bovicornu robbai* Buonaioto
Tibiella marshi (Meyer)	*Tibiella marshi* (Meyer)			
Tibiella texana Collins				
				Praehyalocylis annulata (Tate)
			Praehyalocylis cretacea (Blanckenhorn)	
			Praehyalocylis eufratensis (Avnimelech)	

Table I - EOCENE



Text-fig. 2 - Distribution of Eocene genera (inferred circulation patterns from Kennett, 1982).

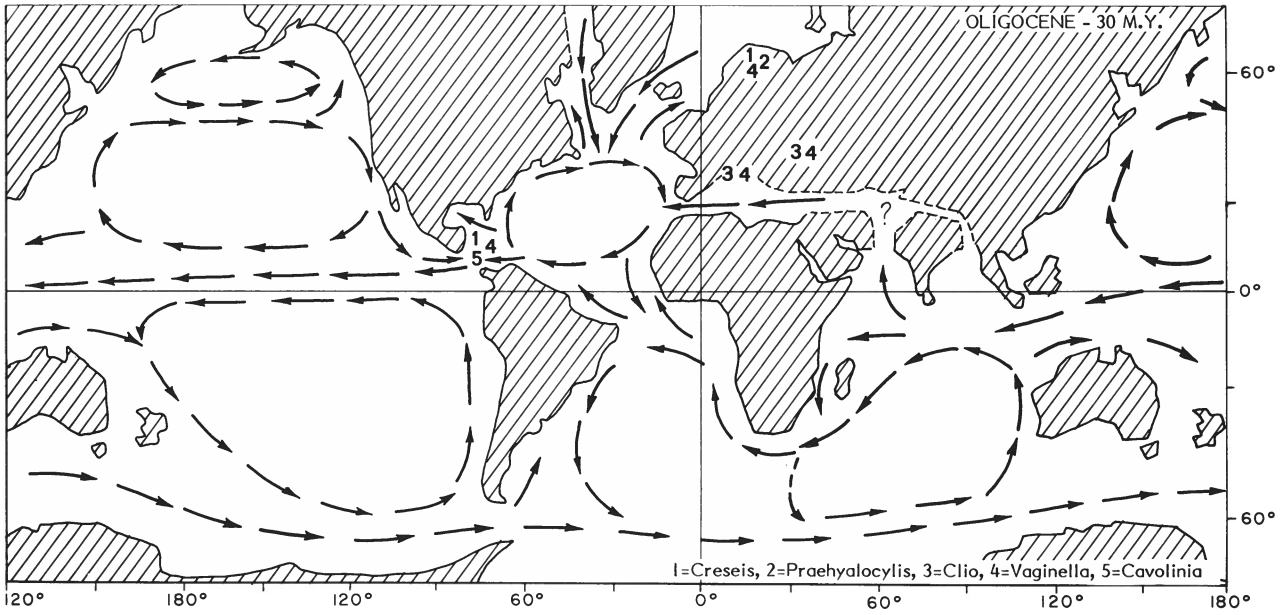
OLIGOCENE

The Eocene-Oligocene boundary is characterized by a drastic change in the Pteropod assemblages. Most of the Eocene genera had become extinct, *Creseis* Rang and *Praehyalocylis* Korobkov & Makarova being the only survivors; the former will evolve onward till to Recent, the latter is reported for the last time from the Middle Oligocene of Germany. New genera appeared that is to say *Clio* Linneaeus, *Vaginella* Daudin and *Cavolinia* Abildgaard; their members were concentrated mainly in the North Atlantic as well as in the Western Tethys areas which seem to have been the place of active evolutionary events.

As can be seen from Table II, the greatest affinity was between Italian and South-East European faunas: *Clio coebana* Robba, *Clio pedemontana* (Mayer) and *Vaginella calandrellii* (Michelotti) are common to both areas. The fact supports faunal interchanges between Western Tethys and Paratethys, where open marine conditions developed, as already stated by Steininger and Rögl (1979). Western Tethys continued to mantain open connections with the Caribbean, via the

CARIBBEAN	ITALY	SOUTH-EASTERN EUROPE	NORTHERN EUROPE
Creseis hastata (Meyer)			
			Creseis sp.n. (in Kuster-Wendenburg, 1971)
			Praehyalocylis maxima denseannulata (Ludwig)
			Praehyalocylis maxima laxeannulata (Ludwig)
	Clio carinata Audenino		
	Clio coebana Robba	*Clio coebana* Robba	
	Clio lavayssei Rutsch		
	Clio pedemontana (Mayer)	*Clio pedemontana* (Mayer)	
	Clio triplicata Audenino		
	Clio sp.n. (in Robba, 1972)		
	Vaginella calandrellii (Michelotti)	*Vaginella calandrellii* (Michelotti)	
	Vaginella depressa Daudin		
			Vaginella lanceolata (Boll)
	Vaginella lapugyensis Kittl		
Vaginella lophota Woodring	*Vaginella sp.* (in Robba, 1972)		
		Vaginella tenuistriata Semper	
	Vaginella testudinaria (Michelotti)		
	Vaginella sp. 2 (in Robba & Spano, 1978)		
Cavolinia xenica Woodring			

Table II - OLIGOCENE



Text-fig. 3 - Distribution of Oligocene genera (inferred circulation patterns from Kennett, 1982).

Atlantic Ocean (Berggren and Hollister, 1974, 1977). In this respect, data from the Carribean and Gulf Coast area are scarce, however, it is pointed out that *Vaginella lophota* Woodring is exactly the same as *Vaginella* sp. which has been reported by Robba (1972) for the Piedmont Basin. No Oligocene Pteropods have been found East of the Mediterranean. The fact is rather surprising because connections were still operative between Mediterranean and Indo-Pacific (Steininger and Rögl, 1979).

Text-fig. 3 depicts the distribution of Oligocene genera related to the paleocirculation patterns.

LOWER MIOCENE

Lower Miocene assemblages appear to have been richer in species than the Oligocene ones. The greatest diversity is to be noted in the Caribbean as well as in the Mediterranean, where evolutionary events were still very active. *Styliola* Gray made its first appearance in the Caribbean. *Cavolinia* Abildgaard, already present in the Caribbean Oligocene, entered the Mediterranean where it is recorded by the very Early Miocene. *Vaginella* Daudin is reported from all the areas where Pteropods have been found.

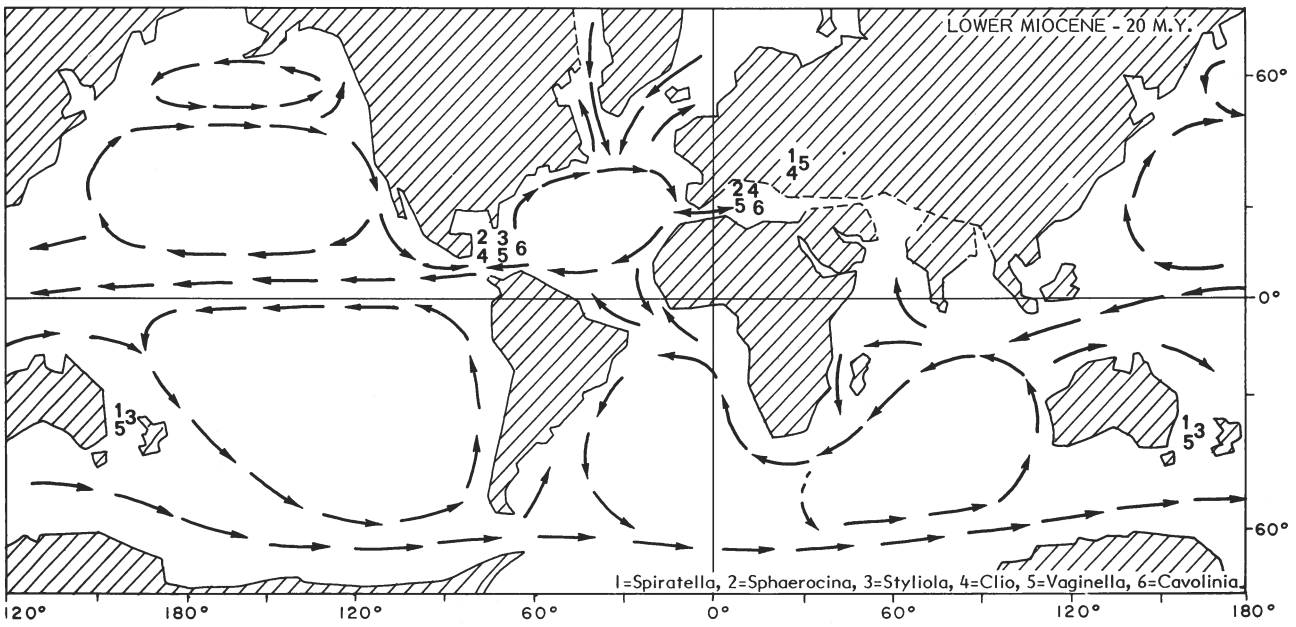
CARIBBEAN	MEDITERRANEAN	PARATETHYS	AUSTRALIA & NEW ZEALAND
		Spiratella andrussovi (Kittl)	
			Spiratella atypica Laws
			Spiratella ferax Laws
		Spiratella tarchanensis (Kittl)	
			Spiratella tertiaria (Tate)
		Spiratella valvatina (Reuss)	
Sphaerocina formae (Audenino)	*Sphaerocina formae* (Audenino)		
			Styliola rangiana Tate
Styliola sulcifera Gabb			
✱*Clio bellardii* Audenino			
	Clio carinata Audenino		
		Clio fallauxi (Kittl)	
Clio lavayssei Rutsch	*Clio lavayssei* Rutsch		
Clio pedemontana (Mayer)	*Clio pedemontana* (Mayer)	*Clio pedemontana* (Mayer)	
✱*Clio pulcherrima* (Mayer)			
	Clio triplicata Audenino	*Clio triplicata* Audenino	
	Clio sp.n. (in Robba, 1972)		
			Vaginella aucklandica Clarke
Vaginella floridana Collins	*Vaginella austriaca* Kittl	*Vaginella austriaca* Kittl	
Vaginella bicostata (Gabb)			*Vaginella bicarinata* (Tate)
	Vaginella calandrellii (Michelotti)		
Vaginella chipolana Dall			
	Vaginella depressa Daudin		
Vaginella cf. depressa (in Jung, 1971)			
			✱*Vaginella eligmostoma* Tate
Vaginella grenadinarum Jung			
	Vaginella lapugyensis Kittl	*Vaginella lapugyensis* Kittl	
Vaginella cf. lapugyensis (in Jung, 1971)	*Vaginella sp. 1* (in Robba & Spano, 1978)		
	Vaginella rotundata Blanckenhorn		
	Vaginella rzehaki Kittl	*Vaginella rzehaki* Kittl	
	Vaginella testudinaria (Michelotti)		
			Vaginella torpedo Marshall
Vaginella aff. undulata (in Jung, 1971)			
Vaginella venezuelana Collins			
	Vaginella sp. (in Robba, 1972)		
	Vaginella sp. 2 (in Robba & Spano, 1978)		
✱*Cavolinia audeninoi* Vinassa de Regny			
	Cavolinia interrupta (Bellardi)		
Cavolinia pycna Jung			
Cavolinia regulae Jung			
Cavolinia cf. vendryesiana (in Jung, 1971)			

Table III - LOWER MIOCENE

Table III shows that 5 species, that is to say *Sphaerocina formae* Audenino, *Clio lavayssei* Rutsch, *Clio pedemontana* (Mayer), *Vaginella austriaca* Kittl (= *floridana* Collins) and *Vaginella* sp. *1* Robba & Spano (= cf. *lapugyensis* Kittl, *in* Jung, 1971), are listed for the Caribbean as well as the Mediterranean, being about 30% of each assemblage.

As far as relationships between Western Tethys and Paratethys are concerned, 5 species are in common: *Clio pedemontana* (Mayer), *Clio triplicata* Audenino, *Vaginella austriaca* Kittl, *Vaginella lapugyensis* Kittl and *Vaginella rzehaki* Kittl; they make over 50% of the entire Paratethyan assemblage. The fact is a good evidence of open marine connections and faunal interchange with the Mediterranean. Some *Spiratella*'s species were definitely restricted to the Paratethys, where it seems that an endemic stock begun to develop.

The closure of the Tethyan seaway took place about 18 m.y. ago, during the Burdigalian, due to the junction of Africa and Eurasia, so that the connections with Indo-Pacific ceased to be operative (Berggren and Hollister, 1974, 1977; Steininger and Rögl, 1979; Kennett, 1982). As a matter of fact, no similarity at all does exist between the Mediterranean assemblages and those found in Australia and New



Text-fig. 4 - Distribution of Lower Miocene genera (inferred circulation patterns from Berggren and Hollister, 1977; Kennett, 1982).

Zealand. *Vaginella bicostata* (Gabb) recorded in the Caribbean and the Australian species *Vaginella bicarinata* (Tate) seem to be synonymous; if it is true, the possible dispersal routes between the two areas are to be considered. Due to the closure of the Tethyan seaway, the more logical connection should have been the Atlantic-Pacific North Equatorial Current, flowing in an East-West direction via Central America (Berggren and Hollister, 1977).

Text-fig. 4 depicts the distribution of Lower Miocene genera in reference with the paleocirculation patterns.

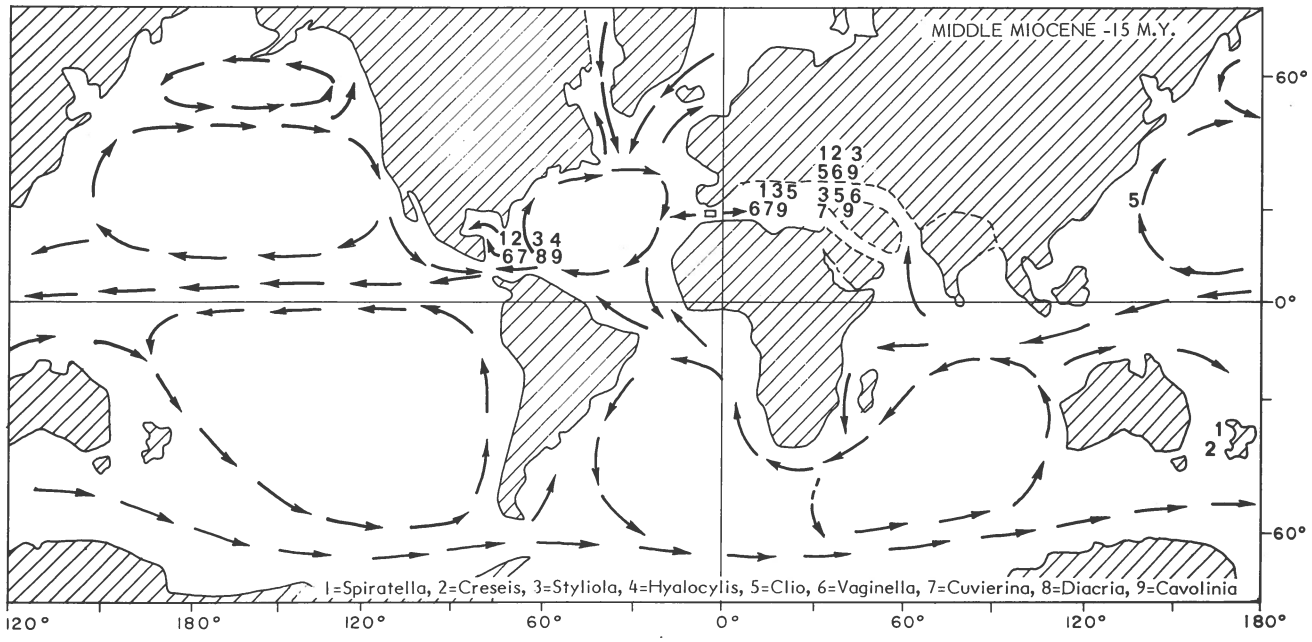
MIDDLE MIOCENE

During the Middle Miocene the total number of known species increases of about 50% in comparison with that recorded for the Lower Miocene. The greatest diversity is observed in Western Tethys and Paratethys.

Text-fig. 5 depicts the distribution of different genera; the most significant events are as follows. *Diacria* Gray makes its first appearance in the Caribbean; this genus will enter the Mediterranean later, during the Late Miocene. *Hyalocylis* Fol is recorded for the first time in the Caribbean; it is a probable discendent of the Paleogene genus *Praehyalocylis* Korobkov & Makarova (Buonaiuto, 1979) and its absence from Lower Miocene assemblages seems more the consequence of insufficient records. *Cuvierina* Boas is a new genus which shows a wide distribution, ranging from the Caribbean to Asia Minor. *Creseis* Rang appears to be the more widespread, being found in the Caribbean, Paratethys and New Zealand as well.

As can be seen from Table IV, the highest similarity is between assemblages from Western Mediterranean, Paratethys and Asia Minor which have 6 species in common. Ten species out of 13 listed from Asia Minor are recorded in Western Mediterranean too. Twelve *Spiratella*'s species appear to be confined to the Paratethys, where the endemic stock outlined formerly, during the Lower Miocene, seems to have reached its highest development. Apart from *Spiratella*, 13 other species are reported; 8 are in common with Western Tethys and 6 out of these have been found in Asia Minor as well. From the above it results that active faunal interchange should have existed between the considered areas. Flooding of Central and Eastern Paratethys reached the greatest expansion about 15 m.y. ago and open marine conditions established over wide areas (Steininger and Rögl, 1979). A self contained system possibly settled in far Eastern Paratethys toward the Russian platform, where the endemic fauna was particularly well developed (Rögl, Steininger and Müller, 1978).

The similarity between Western Tethys and Caribbean appears consistently low: the only sure occurrence in both areas concerns *Styliola subula* (Quoy & Gaimard) which, however, is represented by different subspecies. It is to be noted that *Clio bellardii* Audenino, *Clio pulcherrima* (Mayer) and *Cavolinia audeninoi* Vinassa de Regny, present in the Caribbean during the Lower Miocene, entered the Mediterranean where they are recorded by the very early Middle Mio-



Text-fig. 5 - Distribution of Middle Miocene genera (inferred circulation patterns from Berggren and Hollister 1977; Kennett, 1982).

CARIBBEAN	MEDITERRANEAN	PARATETHYS	ASIA MINOR	NEW ZEALAND	JAPAN
		Spiratella andrussovi (Kittl) *Spiratella carinata* Stancu			
				Spiratella ferax Laws	
	Spiratella cf. globulosa (Seguenza)				
		Spiratella hospes (Rolle) *Spiratella koeneni* (Kittl) *Spiratella konkensis* (Shizhchenko) *Spiratella inflata volhinica* Stancu *Spiratella lata* Krach *Spiratella nucleata* (Shizhchenko) *Spiratella stenogyra* (Philippi) *Spiratella subtarchanensis* (Shizhchenko) *Spiratella tarchanensis* (Kittl) *Spiratella valvatina* (Reuss) *Spiratella variabilis* (Friedberg)			
Spiratella inflata (d'Orbigny) *Spiratella inflata elevata* (Collins)					
	Spiratella zibinica Dieci				
Creseis acicula (Rang)					
		Creseis olteanui Stancu			
				Creseis urenuiensis (Suter)	
Styliola subula sulcifera Gabb *Hyalocylis haitensis* Collins	*Styliola subula lamberti* (Checchia Rispoli)	*Styliola subula lamberti* (Checchia Rispoli)	*Styliola aff. subula* (Quoy & Gaimard)		
	Clio aichinoi Checchia Rispoli *Clio bellardii* Audenino *Clio braidensis* (Bellardi) *Clio caralitana* Robba & Spano *Clio carinata* Audenino *Clio distefanoi* Checchia Rispoli		*Clio braidensis* (Bellardi)		
		Clio carinata Audenino	*Clio carinata* Audenino		
		Clio fallauxi (Kittl)			
	Clio garganica Sirna *Clio guidottii* Simonelli *Clio pedemontana* (Mayer) *Clio pulcherrima* (Mayer) *Clio pyramidata* Linnaeus *Clio saccoi* Checchia Rispoli *Clio sinuosa* (Bellardi) *Clio sturanii* Robba	*Clio pedemontana* (Mayer)	*Clio pedemontana* (Mayer) *Clio pulcherrima* (Mayer)		
					Clio hatai (Noda)
	Vaginella austriaca Kittl	*Vaginella austriaca* Kittl *Vaginella austriaca brevior* Krach *Vaginella calandrellii* (Michelotti)	*Vaginella austriaca* Kittl *Vaginella calandrellii* (Michelotti)		
Vaginella caribbeana Collins					
	Vaginella eligmostoma Tate				
			Vaginella labiata Blanckenhorn		
	Vaginella lapugyensis Kittl *Vaginella rotundata* Blanckenhorn *Vaginella rzehaki* Kittl	*Vaginella lapugyensis* Kittl *Vaginella rotundata* Blanckenhorn *Vaginella rzehaki* Kittl *Vaginella testudinaria* (Michelotti) *Vaginella triangularis* Stancu	*Vaginella rotundata* Blanckenhorn *Vaginella rzehaki* Kittl		
Vaginella undulata (Gabb)	*Vaginella varanica* Sirna				
Cuvierina globosa Collins	*Cuvierina columnella urceolaris* (Mörch)				
	Cuvierina grandis D'Alessandro & Robba				
	Cuvierina paronai Checchia Rispoli		*Cuvierina intermedia* (Bellardi) *Cuvierina paronai* Checchia Rispoli		
Cuvierina tubulata Collins *Diacria digitata* (Guppy) *Diacria trispinosa* (Lesueur) *Cavolinia triaspis* Woodring					
	Cavolinia audeninoi Vinassa de Regny *Cavolinia aurita* (Bellardi) *Cavolinia bisulcata* (Kittl) *Cavolinia cookei* Simonelli	*Cavolinia bisulcata* (Kittl)	*Cavolinia audeninoi* Vinassa de Regny		
Cavolinia mexicana Collins *Cavolinia ventricosa* (Guppy)					

Table IV - MIDDLE MIOCENE

cene. Berggren and Hollister (1974) pointed out that the generation of the Gibraltar Sill, about 15 m.y. ago, brought to the complete cessation of interchanges between Western Tethys and Caribbean. This is possibly true as far as deep pelagic organisms are concerned, but surface plankton would have been able to pass through the Gibraltar portal.

Vaginella eligmostoma Tate, which is a Lower Miocene Australian species, is recorded from number of Middle Miocene localities in Western Mediterra-

nean. Indo-Pacific connections (Text-fig. 5) of the Mediterranean might account for its occurrence. These connections proved to be re-opened since Langhian until Middle Serravallian at least. Evidences on this subject, both faunal and floral, have been reported by Rögl, Steininger and Müller (1978), Hsü *et al.* (1978), Steininger and Rögl (1979) and Hoffman (1979).

Clio sinuosa (Bellardi) is exceedingly similar to *Clio hatai* Noda and it is not unlike that they are synonymous (Robba, 1977). If this assumption is correct, the occurrence of the same species in Western Tethys and in Japan seems to be related with the seaway just mentioned.

CARIBBEAN	MEDITERRANEAN	JAPAN
✱*Creseis acicula* (Rang)		
Styliola subula sulcifera Gabb	*Styliola subula* (Quoy & Gaimard)	
Clio pyramidata Linnaeus	*Clio pyramidata* Linnaeus	
	Vaginella caribbeana Collins	
Bowdenatheca jamaicensis Collins		
	Cuvierina intermedia (Bellardi)	
	Cuvierina aff. tubulata Collins	
✱*Diacria digitata* (Guppy)		
	Diacria sangiorgii Scarsella	
Diacria trispinosa (Lesueur)	*Diacria trispinosa* (Lesueur)	
Cavolinia floridana Collins		
	Cavolinia gypsorum (Bellardi)	
✱*Cavolinia tridentata* (Niebuhr)		*Cavolinia tridentata* (Niebuhr)
Cavolinia vendryesiana (Guppy)		
Cavolinia ventricosa (Guppy)		

Table V - UPPER MIOCENE

HAITI	ITALY	JAPAN (Okinawa)
	Creseis acicula (Rang)	
	Creseis virgula (Rang)	
	Styliola subula (Quoy & Gaimard)	*Styliola subula* (Quoy & Gaimard)
		Hyalocylis striata (Rang)
Clio pyramidata Linnaeus	*Clio pyramidata* Linnaeus	*Clio okinawana* (Noda)
	Clio cuspidata (Bosch)	
	Cuvierina astesana (Rang)	
	Cuvierina intermedia (Bellardi)	
	Diacria digitata italica Grecchi	
	Diacria trispinosa (Lesueur)	*Diacria trispinosa* (Lesueur)
	Cavolinia cf. interrupta (Bellardi)	
		Cavolinia okinawana Noda
Cavolinia cf. tridentata (Niebuhr)	*Cavolinia tridentata* (Niebuhr)	*Cavolinia tridentata* (Niebuhr)
	Cavolinia uncinata (Rang)	

Table VI - PLIOCENE

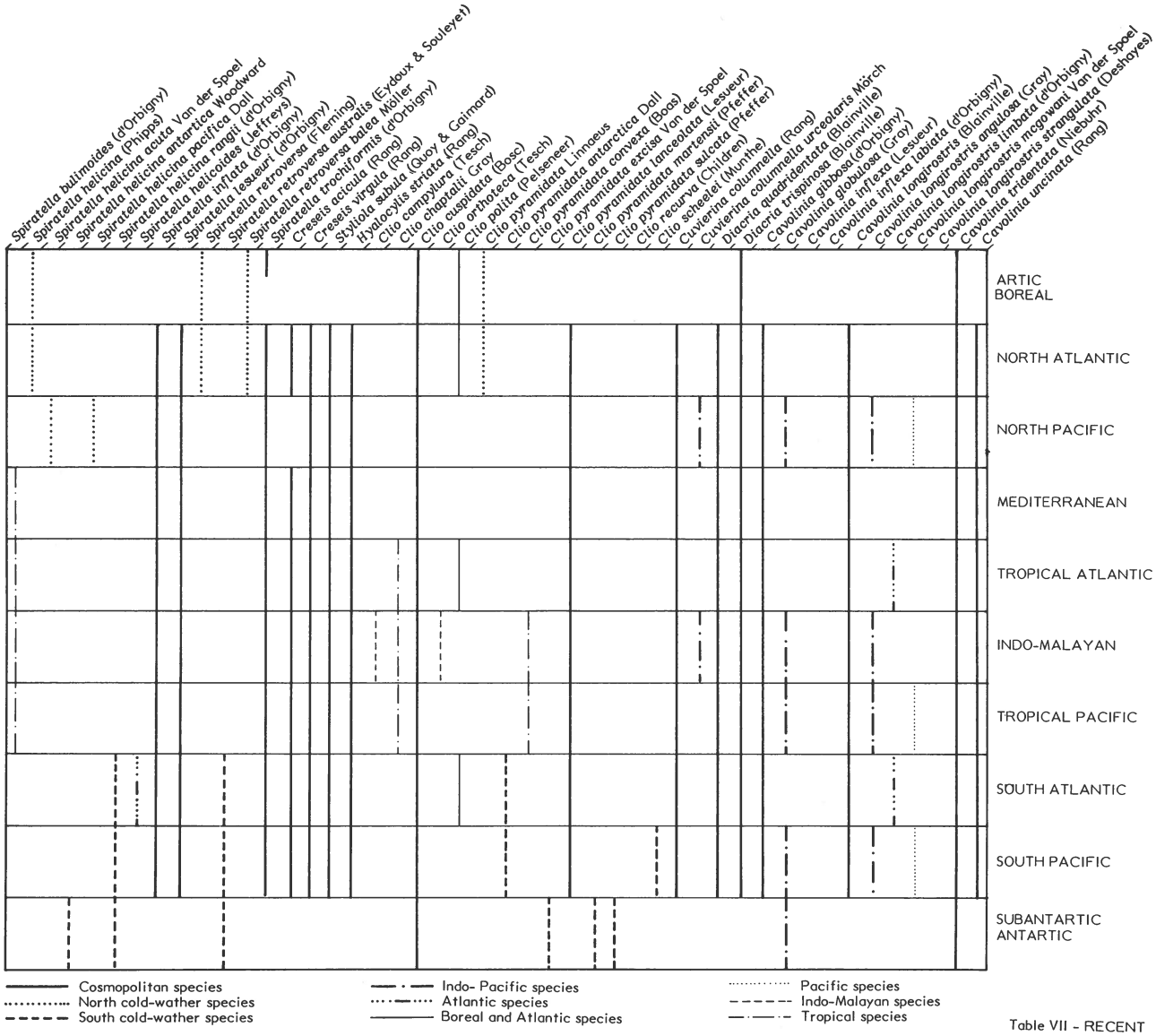


Table VII - RECENT

UPPER MIOCENE

The records are consistently less numerous and, thence, there is a drastic drop down of the total number of species listed so far; this is the main reason foı the very few remarks which follow. It is to be noted that the available data from the Mediterranean concern the Messinian assemblages from Northern Italy only.

It is well known that about 7-5 m.y. ago, during the Messinian, the Western Tethys was cut off intermittently from communication with Atlantic Ocean (Cita, 1973; Berggren and Hollister, 1974, 1977). In any case, interchanges between Mediterranean and Caribbean seem to have been mantained even during the Messinian; in fact, some species that is to say *Styliola subula* (Quoy & Gaimard), *Clio pyramidata* Linnaeus and *Diacria trispinosa* (Lesueur) and, possibly, *Cuvierina tubulata* Collins which appeared in the Caribbean during the Middle Miocene, entered the Mediterranean at an undetermined time within the Late Miocene; they were surely present during the Early Messinian (Pavia and Robba, 1979). The Mediterranean underwent complete isolation, due to the salinity crisis, between 5.5 and 5 m.y. ago (Cita, 1979).

Cavolinia tridentata (Niebuhr) seems to have had an already wide distribution, Atlantic-Pacific at least.

PLIOCENE

Records are so far scanty and mainly concern the Western Mediterranean area and Japan (Table VI); we

only point out the following. *Creseis acicula* Rang, *Cavolinia tridentata* (Niebuhr) and *Diacria digitata* (Guppy), previously present elsewhere, entered the Mediterranean.

It seems reasonable that the Pteropod's spreading could have begun during Pliocene. Data in this respect are exceedingly scarce; however, some species result to be quite widely distributed. Pteropods appear to have firmly settled in the Pacific; in fact, it is the first time that a diverse assemblage is found in Japan.

CONCLUDING REMARKS

The Tethyan seaway seems to have had a rather low efficiency on the migration of Pteropods from Atlantic-Mediterranean toward Indo-Pacific and vice versa. As a matter of fact, similarity between Eastern and Western assemblages remains consistently low or does not exist at all during the time span elapsed between Eocene and Middle Miocene. If it is correct to assume the Atlantic as the birthplace of Pteropods, one should have in mind that the flow of current in the Tethyan seaway was in an East-West direction (Berggren and Hollister, 1974, 1977; Kennet, 1982).

The faunal interchanges between Caribbean-Mediterranean-Paratethys were active by the Oligocene and extended to Asia Minor as well during Middle Miocene. Migration seems to have occurred from West toward East; evidence in this respect is the successive appearances both of genera and species or lower taxa in the Mediterranean, which were previously present in the Caribbean.

Pteropods seem to have been especially confined to the Atlantic-Mediterranean area until the entire Miocene at least; records in the Indo-Pacific, concerning the same time span, are quite scanty and primarily refer to Australia and New Zealand. It is within the Pliocene that Pteropods spread over the World oceans finally becoming rather diversified in the Pacific as well. Van der Spoel (1967) pointed out that the number of present-day species and lower taxa found in the latter ocean is smaller than the number in the Indian and Atlantic oceans; he suggested that possibly the Pacific would have been separated for a longer time from the birthplace of Pteropods. Surprisingly the development of Pteropods in the Pacific coincided with and followed the emergence of the Isthmus of Panama; in this latter area Atlantic-Pacific connections were previously operative (Atlantic-Pacific North Equatorial Current), allowing faunal interchanges.

Pteropods' Recent wide dispersal and ranges of species (Table VII) came to a definitive settlement during the Pleistocene, as already stated by Van der Spoel (1967).

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