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THE TRAPEZIIDAE AND DOMECIIDAE (DECAPODA: BRACHYURA: XANTHOIDEA) IN THE FOSSIL RECORD AND A NEW EOCENE GENUS FROM BAJA CALIFORNIA SUR, MEXICO

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ABSTRACT

Reconsideration of all fossils formerly referred to the Trapeziidae Miers, 1886, suggests that both the Trapeziidae and the morphologically similar Domeciidae Ortmann, 1893, are represented in the fossil record. Two fossil species formerly considered to be trapeziids are referred to the domeciid genus *Jonesius* Sankarankutty, 1962. New combinations include *J. oligocenicus* (Beschin *et al.*, 2001) and *J. planus* (Müller, 1996); thus, the recognized geologic record of the Domeciidae extends from the Oligocene to Recent. The Trapeziidae is known from three Eocene genera, including the new genus and species described here, *Archaeotetra inornata*. Other Eocene occurrences include two species of *Eomaldivia* Müller and Collins, 1991, and one species of *Tetralia* Dana, 1851. A few Miocene species of *Trapezia* Latreille, 1828, and a Pleistocene occurrence have been reported. Members of both families are symbiotic with cnidarians, and this relationship appears to have been established by the Eocene in the case of the Trapeziidae and the Oligocene for the Domeciidae, based upon the tropical to subtropical distribution and the occurrence of the fossils in each family in coral-bearing rocks. Coevolutionary processes appear to have resulted in high degrees of specialization in some genera within the Trapeziidae.

The fossil record of the various families within the Xanthoidea MacLeay, 1838, has received renewed attention in recent years (Schweitzer, 2000; Guinot and Tavares, 2001; Schweitzer and Feldmann, 2001; Karasawa and Kato, 2003a, b; Schweitzer, 2003a, b; Schweitzer and Karasawa, 2004; Karasawa and Schweitzer, 2004; Schweitzer, 2005), resulting in some major revisions of the classification of extinct xanthoid taxa. Attention in the last three decades to collecting in fossil reef environments, where preserved brachyurans are typically tiny and difficult to see (Müller, 2004), has led to the description of members of the Trapeziidae Miers, 1886, in the fossil record. The Trapeziidae have thus been known to occur as fossils in rocks at least as old as Eocene (Müller, 2004). Herein, the fossil record of both the Trapeziidae and the Domeciidae is examined, and a new genus and species of the Trapeziidae from Baja California Sur, México, is described. It appears that the symbiotic relationships with cnidarians within both families appeared early on in their history; further, the antiquity of these lineages should be acknowledged in phylogenetic studies of the Xanthoidea. Herein, the term "symbiotic" and its derivatives are used *sensu* Castro (1988, p. 161), who, in a review of symbiotic relationships in coral reef communities, defined symbioses as "close heterospecific associations irrespective of harm or benefit to the partners."

SYSTEMATIC PALEONTOLOGY

Order Decapoda Latreille, 1802
Infraorder Brachyura Latreille, 1802
Section Heterotremata Guinot, 1977
Superfamily Xanthoidea MacLeay, 1838
Family Domeciidae Ortmann, 1893

Included Genera.—*Domecia* Eydoux and Souleyet, 1842; *Jonesius* Sankarankutty, 1962 (fossil and extant); *Maldivia* Borradaile, 1902; *Palmyria* Galil and Takeda, 1986 (fossil and extant). List from Davie (2002); all are exclusively extant unless otherwise indicated.

Diagnosis.—Carapace hexagonal or ovate, wider than long, length averaging about 80 percent maximum carapace width, position of maximum width about 40 percent the distance posteriorly on carapace; regions poorly defined; front bilobed, sometimes granular or spinose, about half maximum carapace width; orbits shallow, semi-circular, directed forward, fronto-orbital width averaging about 80 percent maximum carapace width; anterolateral margin extending obliquely and distally from the outer-orbital corner, often spinose; merus of third maxilliped short, much wider than long; "second maxilliped with endopod having propodus and dactylus fused into a very large endite" (Davie, 2002, p. 152); chelipeds unequal, usually strongly granular or spinose, merus short; pereiopods 2–5 "with dactylo-propodal articulation formed by rounded prolongation of propodal lateral margin sliding against and beneath a projecting button situated proximally on lateral margin of dactylus" (Davie, 2002, p. 152); male abdomen with somites 3–5 fused, sutures may be visible, third somite in some taxa much wider than other somites (diagnosis after Davie, 2002; Poore, 2004; Castro *et al.*, 2004).

Discussion.—Genera currently embraced within the Domeciidae were previously placed within the Trapeziidae as a separate subfamily (Serène, 1984), and this has been maintained by some authors (Sakai, 2004). Davie (2002) elevated the subfamily to family status based upon what he considered to be great differences in external morphology between the Trapeziidae *sensu stricto* and the domeciids, and this action was subsequently supported (Castro, 2003; Castro *et al.*, 2004; Poore, 2004). Members of both families inhabit corals, and morphological similarities between them have been suggested to be a result of convergence due to adaptation to this habit (Davie, 2002). The main morphological

Table 1. Measurements (in mm) taken on the dorsal carapace of species referrable to the Domeciidae or the Trapeziidae. L/W = maximum length divided by maximum width; FOW/W = fronto-orbital width divided by maximum width; † indicates species that are extinct.

Taxon	Reference	L/W	FOW/W
Domeciidae			
Domecia glabra Alcock, 1899	Sakai, 1976, pl. 173, fig. 1	0.81	0.88
Domecia hispida Eydoux and Souleyet, 1842	Sakai, 1976, pl. 173, fig. 2	0.79	0.91
Domecia hispida	Davie, 2002, p. 152	0.73	0.7
Domecia hispida	Rathbun, 1930, pl. 227, fig. 3	0.75	0.86
Palmyria palmyriensis (Rathbun, 1923)	Galil and Takeda, 1986, fig. 7	0.8	0.8
Palmyria palmyriensis	Dai and Yang, 1991, pl. 48, fig. 5	0.8	0.76
Jonesius triunguiculatus (Borradaile, 1902)	Sakai, 1976, pl. 173, fig. 4	0.76	0.7
Jonesius triunguiculatus	Galil and Takeda, 1986, fig. 3	0.79	0.67
Jonesius triunguiculatus	Dai and Yang, 1991, pl. 48, fig. 4	0.73	0.69
†*Jonesius oligocenicus* (Beschin et al., 2001)	Beschin *et al.*, 2001, pl. 3, fig. 2	0.85	0.71
†*Jonesius planus* (Müller, 1996)	Müller, 1996, pl. 2, fig. 7	—	0.7
†*Jonesius planus*	Müller, 1996, pl. 2, fig. 8	—	0.64
Maldivia symbiotica Borradaile, 1902	Borradaile, 1902, fig. 60	0.97	0.86
Trapeziidae			
Trapezia cymodoce (Herbst, 1801)	Rathbun, 1930, pl. 228, fig. 2	0.86	0.86
Trapezia cymodoce	Rathbun, 1930, pl. 228, fig. 4	0.88	0.96
Trapezia cymodoce	Davie, 2002, p. 493	0.83	0.94
Trapezia digitalis Latreille, 1828	Rathbun, 1930, pl. 228, fig. 5	0.81	0.95
Hexagonalia brucei Galil, 1986	Galil, 1986, fig. 1A	0.8	0.84
Hexagonalia laboutei Galil, 1997	Galil, 1997, fig. 1A	0.86	0.86
Hexagonalia laboutei	Galil, 1997, fig. 1C	0.79	0.83
Quadrella nitida Smith, 1869	Rathbun, 1930, pl. 229, fig. 1	0.85	0.89
Quadrella nitida	Rathbun, 1930, pl. 229, fig. 2	0.92	0.84
†*Eomaldivia trispinosa* Müller and Collins, 1991	Müller and Collins, 1991, pl. 6, fig. 8	0.88	0.94
†*Eomaldivia pannonica* Müller and Collins, 1991	Müller and Collins, 1991, pl. 6, fig. 10	0.74	0.96
†*Archaeotetra inornata* new species	this paper	0.86	0.9
Tetralia cavimana Heller, 1861	Galil, 1988, fig. 1a	0.92	0.96
Tetralia fulva Serène, 1984	Galil, 1988, fig. 1b	0.96	0.88
Tetralia rubridactyla Garth, 1969	Galil, 1988, fig. 1d	0.88	0.92
†*Tetralia loerentheyi* (Müller, 1975)	Müller and Collins, 1991, pl. 6, fig. 9	0.83	0.95
Tetraloides nigrifrons (Dana, 1852)	Galil, 1985, fig. 1A	0.91	1

differences between the two families, as reported by Davie (2002), who separated them, are in the nature of the second and third maxillipeds. The former have not ever been reported in fossil brachyurans, and the latter are not commonly encountered; none is known in either the Domeciidae or the Trapeziidae. Other differences appear to lie in the nature of the basal antennal article joint and the endostome (Davie, 2002), which are rarely observed in fossils.

Members of the Domeciidae can be readily distinguished from the Trapeziidae in the fossil record by several means using the method of establishing proxy characters of the dorsal carapace (Schweitzer, 2003a) (Tables 1, 2). In the fossils herein referred to these two families, only the dorsal carapace is preserved. Several features of the dorsal carapace, orbits, and chelae may be used to distinguish between the two families in extant taxa (Table 2). In addition, if the male abdomen is preserved, it appears that, at least in *Domecia hispida* Eydoux and Souleyet, 1842, which is the only taxon for which it is illustrated (Rathbun, 1930, pl. 227, fig. 6), there is a laterally expanded somite 3, which does not appear to occur in the Trapeziidae.

It is important to note that while the average fronto-orbital width to maximum width ratios and length to width ratios in the two families are quite different, there is a small degree of overlap in the range of ratios present in each family among individual species (Table 1). Thus, it is necessary to use several characters together, as has been previously suggested for other members of the Xanthoidea (Schweitzer, 2003a; Schweitzer and Karasawa, 2004), to place fossils into these families. When this is done, however, the two families appear to be readily separable on external morphological grounds.

Maldivia has been described from the Oligocene of Italy (Beschin *et al.*, 2001) and the Miocene of Poland (Müller, 1996). Both occurrences appear to be legitimate members of the Domeciidae but are better placed within *Jonesius*. Both *Maldivia oligocenica* Beschin *et al.*, 2001, and *M. plana* Müller, 1996, exhibit an ovate-hexagonal carapace that is about 75 percent as long as wide, a fronto-orbital width occupying about 70 percent the maximum carapace width, three small anterolateral spines, and weakly domed cardiac and protogastric regions (Sakai, 1976; Beschin *et al.*, 2001), all of which are typical of *Jonesius* (Galil and Takeda, 1986). By contrast, *Maldivia* exhibits a fronto-orbital width occupying about 85 percent of the maximum carapace width and a length that is nearly equal to the width (97 percent). Thus, *Jonesius* appears to be the best placement for these fossil species. Karasawa (2000) reported *Maldivia palmyriensis* (Rathbun, 1923) from the Pleistocene of Japan; that species is now referred to *Palmyria* within the Domeciidae. Thus, two genera within the Domeciidae are known from the fossil record.

Castro *et al.* (2004) placed *Eomaldivia* within the Domeciidae. I do not concur. That genus is characterized by a fronto-orbital width to maximum width ratio of 0.95 and a length to width ratio of about 81 percent; neither is

Table 2. Dorsal carapace characters and other characters useful in distinguishing between fossil specimens of the Domeciidae and Trapeziidae. Trapeziidae and Tetraliidae *sensu* Castro *et al.* (2004) are separated so that the reader can see differences between the two groups; however, they are recognized as a single family herein. Characters from "Frontal margin" to the end of the table after Castro *et al.* (2004). * except *Hexagonalia* and *Quadrella*, in which they are at a very high angle.

Character	Domeciidae	Trapeziidae *sensu* Castro *et al.* (2004)	Tetraliidae *sensu* Castro *et al.* (2004)
Dorsal carapace shape	hexagonal	cordate or ovate	cordate or ovate
Orbits	directed forward	directed anterolaterally	directed anterolaterally
Fronto-orbital width/ maximum width	average of 80 percent	average of 91 percent	average of 94 percent
Orbit placement	not at anterior corners	at anterior corners	at anterior corners
Anterolateral margin	longer, oblique to anterior margin of carapace	short, nearly perpendicular to anterior margin of carapace*	short, nearly perpendicular to anterior margin of carapace
Length/width	average of 80 percent	average of 86 percent	average of 94 percent
Chela ornamentation	spiny, with large tubercles, or coarsely granular	smooth or with fine granules	smooth or with fine granules
Frontal margin	straight, smooth or serrate	straight, with 4 lobes or spines	straight, serrate
Anterolateral ornamentation	2 or more spines or small tubercles	smooth or with 1 or 2 spines	no spine or tubercles in adults, 1 in juveniles
Thoracic sternites 1 and 2	fused, as wide as high	fused, much wider than high	fused, as wide as high
Suture between sternites 2 and 3	absent	present	absent
Basal antennal article	slender, not expanded	slender, not expanded	laterally expanded
Merus of third maxilliped	narrow, much shorter than ischium	nearly square, shorter than ischium	nearly round, shorter than ischium
Third maxilliped ischium	elongated, smooth inner margin, lower inner margin oblique	rectangular, denticulate inner margin, inner margin at nearly 90 degree angle	elongated, smooth inner margin, lower inner margin oblique
Second maxilliped endopod	fused dactylus, propodus in *Domecia* only, 4 distinct segments in others	4 distinct segments	4 distinct segments
Pereiopod 2–Pereiopod 5 dactyli	curved	pointed tip or hoof-like tip	hoof-like tip
Male abdomen	somites 3–5 fused, sutures visible	somites 3–5 fused, faint sutures visible	all somites free
Gonopod 1 (G1)	stout, slightly sinous, blunt tip, truncated	slender, slightly sinuous or straight, tip pointed	short, stout, slightly sinuous or straight, tip rounded or pointed
Gonopod 2	proximally thick, about half length of G1	stout, slightly curved or nearly straight, spoon-like tip, less than half length of G1	stout, slightly curved, spoon-like tip, less than half length of G1

typical of the Domeciidae but both are typical of the Trapeziidae. *Eomaldivia* has a straight front and two anterolateral spines, typical of the Domeciidae, but members of the Trapeziidae may also have two anterolateral spines. The anterolateral margins in *Eomaldivia* are parallel to one another as is typical of trapeziids and not of the domeciids. Thus, *Eomaldivia* is herein placed within the Trapeziidae.

Based upon the fossil occurrences of *Jonesius*, the Domeciidae had appeared in the Tethys by Oligocene time. The family apparently had already adapted to living in association with corals, as suggested by the occurrence of both fossil species of *Jonesius* in coral-rich rocks. The Pleistocene occurrence in coral-rich rocks of Japan (Karasawa, 2000) supports a Tethyan distribution and continued coral association. Interestingly, members of the family are no longer found in the Mediterranean region but do exhibit a relict Tethyan distribution, being known from the Caribbean, tropical east Pacific, and Indo-Pacific regions (Rathbun, 1930; Sakai, 1976; Davie, 2002; Poore, 2004).

Family Trapeziidae Miers, 1886

Included Genera.—*Archaeotetra* new species (fossil only); *Eomaldivia* Müller and Collins, 1991 (fossil only); *Hexagonalia* Galil, 1986 (extant only); *Quadrella* Dana, 1851b (extant only); *Tetralia* Dana, 1851a (fossil and extant); *Tetraloides* Galil, 1985 (extant only); *Trapezia* Latreille, 1828 (fossil and extant). List after Castro (2000), Davie (2002), and Castro *et al.* (2004).

Diagnosis.—Carapace cordate, not much wider than long, length averaging about 86 percent maximum carapace width, position of maximum width about half the distance posteriorly on carapace; carapace regions not defined; front weakly bilobed, four-lobed, serrate, or nearly straight, about half maximum carapace width; orbits deeply excavated, positioned at corners of frontal margin of carapace, directed anterolaterally, fronto-orbital width about 90 percent or more maximum carapace width; anterolateral margins short, usually oriented nearly perpendicular to frontal margin of carapace or oriented at very high angle to frontal margin, entire or with one or two spines; chelae unequal, smooth or weakly granular, merus of cheliped extending beyond carapace margins when folded; pereiopods 2–5 "with dactylo-propodal articulation formed by rounded prolongation of propodal lateral margin sliding against and beneath a projecting button situated proximally on lateral margin of dactylus" (Davie, 2002, p. 493); basal antennal article slender; efferent channels defined by well-developed endostomal crests; merus of third maxilliped shorter than ischium, about as wide as long; endopod of second maxilliped composed of four separate segments; male abdomen with somites 3–5 fused with visible sutures or with all somites free (after Galil, 1986/1987, 1987; Davie, 2002; Poore, 2004).

Discussion.—Castro *et al.* (2004) performed a phylogenetic analysis of genera traditionally placed within the Trapeziidae and the Domeciidae using adult morphological characters, many of which are preservable in the fossil record. Their analysis supported the elevation of the Domeciidae to family status and also suggested that two genera, *Tetralia* and *Tetraloides*, be separated from the Trapeziidae and placed within a new family, Tetraliidae. It had previously been noted that the Trapeziidae was a somewhat heterogeneous group, based largely upon differences among members of the group in the degree and nature of fusion of male abdominal somites (Ng, 1998; Ng and Clark, 2000).

Castro *et al.* (2004) included within the analysis as members of the Trapeziidae *sensu lato* the three genera *Calocarcinus* Calman, 1909; *Philippicarcinus* Garth and Kim, 1983; and *Sphenomerides* Rathbun, 1987; these genera had historically been included in the group (Serène, 1984). Jamieson *et al.* (1993) reported that *Calocarcinus* was aligned with other xanthoids, but was no closer to the Trapeziidae than to any other xanthoids. Castro (1997, p. 61) placed *Calocarcinus* in the Trapeziidae apparently based upon historical precedent, although he remarked that the placement had "never been critically examined." Tudge *et al.* (1998) suggested that *Calocarcinus* was probably a member of the Bythograeidae Williams, 1980, based upon spermatozoal architecture and the lack of morphological similarity of *Calocarcinus* with the Trapeziidae. The dorsal carapace morphology of *Philippicarcinus* and *Sphenomerides* is in many ways similar to the Trapeziidae (smooth, unornamented). However, the fronto-orbital width to maximum width ratio of these two genera is well below 90 percent as in the Trapeziidae *sensu lato*, for example, and the length to width ratios are well below that for the Trapeziidae as well (see plate 4, Castro *et al.*, 2004). Even more significantly, none of these three genera has the horizontal rows of feeding setae on the pereiopods so important for mucous gathering in members of the Trapeziidae *sensu lato*. This feeding strategy is extremely important for the Trapeziidae *sensu lato* (they are obligate symbionts), and the fact that these three genera lack these structures suggests that they are not part of the same lineage. Further, *Philippicarcinus* and *Sphenomerides* are not known to inhabit cnidarians, also extremely important because the Trapeziidae *sensu lato* are obligate symbionts on cnidarians, which seems to be a defining factor for the group. I suggest that *Calocarcinus*, *Philippicarcinus*, and *Sphenomerides* be reinvestigated in order to determine whether in fact they truly belong within the Trapeziidae; I do not include them in the family herein based upon these very important differences. *Tanaocheles* Kropp, 1984, had also been previously referred to the Trapeziidae but was subsequently removed to the Pilumnidae (Ng and Clark, 2000).

The strong similarities between the Trapeziidae (which embraced *Calocarcinus*, *Philippicarcinus*, and *Sphenomerides*) and the Tetraliidae *sensu* Castro *et al.* (2004) were suggested to be a result of convergence because of their habit of living associated with corals. I suggest that it is just the reverse—the Trapeziidae and Tetraliidae *sensu* Castro *et al.* (2004) are closely related, and *Calocarcinus*, *Philippicarcinus*, and *Sphenomerides* are possibly convergent with them; this is probably true at least for *Calocarcinus* which lives associated with cnidarians (Castro *et al.*, 2004). Unfortunately, little is known about the ecology of the other two genera. Another possibility is that they are all in fact related, but that *Calocarcinus*, *Philippicarcinus*, and *Sphenomerides* diverged very early in their evolutionary history (as in pre-Eocene), before the appearance of the very specialized feeding setae on the pereiopods. Sadly, there is no fossil record for these three genera.

It is probable that these three genera grouped along with the other trapeziid genera in the study of Castro *et al.* (2004) for several reasons. These include the smooth, glabrous carapace; the number of anterolateral spines (two); and fused male abdominal somites 3–5, which were in fact given double weight in the analysis as they were scored as somites 3–4 fused and 4–5 fused (Castro *et al.*, 2004, p. 11), essentially scoring the same character twice. There are very few cases in which male abdominal somites 3–4 are fused and 4–5 are not or in which the reverse is true. For example, there is one genus within the Hexapodidae Miers, 1886, in which this is the case (Manning and Holthuis, 1981). There are a few other cases in which somites 3–4 are fused and 4–5 are movable (i.e., Mathildellinae Karasawa and Kato, 2003a). If there had been the possibility of such gradations in the taxa under study here, scoring abdominal somites 3–4 and 4–5 as fused separately would have been useful, but in fact there are no grades within the genera studied by Castro *et al.* (2004). Either somites 3–5 are fused or they are all free. Thus, it seems as if this character did receive extra weight in the analysis.

The fossil record supports the view that the Trapeziidae should be recognized as a single family embracing all of the genera listed above. When examining fossil forms, extending as far back as the Eocene, the dorsal carapace morphology overlaps the morphology seen in the Trapeziidae and Tetraliidae *sensu* Castro *et al.* (2004) (Tables 1, 2). For example, fossil species of *Tetralia* are much like the Tetraliidae *sensu* Castro *et al.* (2004) except in their possession of two anterolateral spines, in which they are more like the Trapeziidae *sensu* Castro *et al.* (2004). Species of *Eomaldivia* are much like the Tetraliidae *sensu* Castro *et al.* (2004) in their fronto-orbital width/maximum width ratio (0.95) and straight front but more like the Trapeziidae *sensu* Castro *et al.* (2004) in their possession of two anterolateral spines and length to width ratio (0.81). They differ from both in having a smooth, straight front. The new genus described here similarly exhibits features of both families *sensu* Castro *et al.* (2004) and also some unique features.

Thus, I suggest that the ancestral form of the Trapeziidae *sensu lato*, based on fossil occurrences, was very much like that exhibited by species of *Trapezia*, *Tetralia*, and *Tetraloides* in modern oceans. The ancestral form probably exhibited a straight front, possibly with a central notch, based upon the oldest known (Eocene) occurrences of the group and either exhibited two anterolateral spines or none. This variability in anterolateral spines is not problematic, as extant members of the Tetraliidae *sensu* Castro *et al.* (2004)

possess one anterolateral spine as juveniles which they later lose, and variations in the number of anterolateral spines within genera and even species of other xanthoids have been discussed at length previously (Guinot, 1989; Schweitzer, 2000). However, as only the dorsal carapace is known among fossil specimens, recovery of the ventral aspect of the fossils could help to reinforce this hypothesis.

It is quite likely that genera referred to the Trapeziidae *sensu* Castro *et al.* (2004) have experienced specialization in more recent geologic time. Huber (1985) suggested that species of *Trapezia* had speciated relatively recently, perhaps as recently as the Pleistocene and possibly influenced by coral extinctions and recolonizations due to climatic changes. Glynn (1983a) reported that members of *Trapezia* had more specialized adaptations (chelae) and behaviors for living associated with corals than did species of *Tetralia*. For example, he noted that species of *Tetralia* defended the corals much less successfully against predators than did *Trapezia*. Galil (1987, p. 83) noted that the setae on the appendages of species of these two genera and others within the Trapeziidae were different in structure from one another and considered that those of *Trapezia* were "more evolved."

There remains the issue of the degree of fusion of male abdominal somites 3–5, which in the Trapeziidae *sensu* Castro *et al.* (2004) are fused and in the Tetraliidae *sensu* Castro *et al.* (2004) are fused but with visible sutures. The morphological feature of fusion in male abdominal somites has taken on supreme importance in the neontological literature. The relative significance for functionality of varying degrees of fusion has not been discussed in the literature. It is possible that the state of being fused with clear sutures is a grade, and that any fusion, visible sutures or not, will have some effect on the abdomen, permitting it to function differently than an abdomen with no fusion. Fusion of abdominal somites is surely an important character, and one that is useful in the fossil record because the ventral portion of brachyurans is sometimes preserved. I suggest it is possible that, at least in this particular grade of fusion (visible sutures vs. no visible sutures), the difference may not be great enough to dictate family-level differences based primarily on just this one character.

Thus, it is possible that eventually a case may be made that the Trapeziidae *sensu* Castro *et al.* (2004) should be recognized as a separate, more specialized family, very well-adapted morphologically and behaviorally to association with corals and other cnidarians. The ancestral forms probably lived associated with corals, as suggested by the occurrence of fossil trapeziids *sensu lato* in coral-rich rocks, but the relationship may not have been an obligate symbiotic one. That aspect of the association may have evolved much more recently and most especially within *Trapezia*, and the evolutionary processes leading to the appearance of a possible new family *sensu* Castro *et al.* (2004) may well parallel the coevolutionary process discussed below. However, more evidence is needed to test these hypotheses, and the taxa referred to the Trapeziidae need to be better constrained. For now, I maintain one family, the Trapeziidae *sensu lato*, for all of these genera.

The Trapeziidae as herein recognized is a small family, comprised of tiny, obligate symbionts on cnidarians, usually corals (Davie, 2002). Most modern forms inhabit the tropical Indo-Pacific region, although there are some occurrences in the eastern Pacific Ocean (Rathbun, 1930; Castro, 2000; Davie, 2002). The number of included extant genera is small; only the five listed above are recognized. Castro (2000) provided an extensive list of recognized extant species within the extant genera of Trapeziidae which need not be repeated here.

The fossil record of the family is also sparse. Only three genera are known from the fossil record, two from late Eocene deposits of Hungary (Müller and Collins, 1991) and the new genus described here. *Eomaldivia* and its two species are placed within the family based upon their broad fronto-orbital width to maximum width ratio; the placement of the orbits at the frontal corners of the carapace; the anterolateral margin situated nearly perpendicular to the frontal margin of the carapace; and the cordate shape of the carapace. *Tetralia loerenthyi* (Müller, 1975) exhibits all of these characters plus the serrate frontal margin typical of the genus; thus, these three previously described fossil species are clearly embraced by the Trapeziidae. One species referred to *Trapezia* has been described from Miocene rocks of Hungary, *Trapezia glaessneri* Müller, 1975. That species appears to have six lobes on the frontal margin (Müller, 1984, pl. LXXXV, fig. 2), while other species of *Trapezia* have four; examination of type material will be necessary to determine whether this species should be referred to a different genus. It is clearly a trapeziid based upon its cordate shape; anterolaterally directed orbits placed at the distal margins of the anterior margin of the carapace; and perpendicular anterolateral margins. *Trapezia brevispinosa* Karasawa, 1993, and *Trapezia* sp. *in* Karasawa (1993) are known from Miocene rocks of Japan, and *Trapezia digitalis* Latreille, 1828, was reported from Pleistocene rocks of the Ryukyu Islands of Japan (Karasawa, 2000).

Amydrocarcinus Schweitzer *et al.*, 2002, was suggested to possibly be a member of the Tetraliidae *sensu* Castro *et al.* (2004). That genus was referred to the Goneplacidae (Schweitzer and Karasawa, 2004). Members of *Amydrocarcinus* are an order of magnitude larger than trapeziids; exhibit a serrate anterolateral margin unknown in any trapeziids; and exhibit male abdominal somites that clearly appear to have been unfused. Castro *et al.* (2004) noted the difficulties with determining whether abdominal somites in the fossil record were fused with clear sutures or free. That problem has been noted in terms of fossil specimens (Schweitzer *et al.*, 2004a), and there have even been difficulties in reporting on this feature in the neontological literature (Schweitzer, 2003a). This indeed can be a problematic issue, but the somites in *Amydrocarcinus* exhibit displacement in some specimens, suggesting that they were in fact free. Thus, its placement within the Goneplacidae is maintained.

The new genus and species described below marks the earliest known published occurrence of the family in the fossil record, although a possible earlier occurrence is currently being described (Müller, 2004). Thus, the Trapeziidae was established at least by the middle Eocene. The occurrence in Baja California is consistent with its modern distribution, which includes eastern Pacific locations (Rathbun, 1930). The Hungarian and Japanese occurrences suggest that the family had a Tethyan distribution early in its history, and the modern distribution of occurrences in the Indo-Pacific and eastern Pacific (Castro, 2000) is probably a relict Tethyan pattern.

Genus ***Archaeotetra*** new genus

Type species.—Archaeotetra inornata new species.

Diagnosis.—As for species.

Description.—As for species.

Etymology.—The genus name is derived from the Greek words *archaios,* meaning old or beginning, and *tetra,* meaning four, alluding to the quadrate nature of the carapace and the fact that it is thus far the oldest known member of the family. The gender is feminine.

Discussion.—The new specimen is referrable to the Trapeziidae based upon its cordate shape, broad front, orbits placed at the anterior corners of the carapace, broad fronto-orbital width, high length to width ratio, smooth dorsal carapace, and anterolateral margins that are nearly parallel to one another. No other family can accommodate a brachyuran of this morphology.

The new specimen cannot be accommodated by any existing genus within the Trapeziidae, due to its lack of spines or serrations on both the front and anterolateral margins. Generic and species-level determinations within the Trapeziidae can be difficult in fossils within this family, because many of the characters that serve to distinguish species within a genus and genera within the family are based upon color, antennal articles, the third maxillipeds, and the chelae (Davie, 2002). Unfortunately, the chelae, which of the four morphological features have the best possibility of fossilization, have never been found fossilized in this group. Thus, the nature of the anterolateral margins and front, which also appear to be of fundamental importance at the generic level, has been given primary importance.

Archaeotetra inornata new species
Fig. 1C

Diagnosis.—Carapace wider than long, widest about 40 percent the distance posteriorly on carapace; regions very poorly defined; front just over half maximum carapace width, very weakly biconvex, with shallow notch axially; orbits positioned at edges of anterior border of carapace; fronto-orbital width about 90 percent maximum carapace width; anterolateral margin short, formed into thickened rim.

Description.—Carapace wider than long, L/W = 0.86, widest about 40 percent the distance posteriorly on carapace, narrowing considerably posteriorly; weakly vaulted transversely, moderately vaulted longitudinally; regions smooth, very poorly defined.

Front broad, just over half maximum carapace width, very weakly biconvex, with shallow notch axially. Orbits positioned at edges of anterior border of carapace, semicircular, directed anterolaterally, most deeply excavated axially, very weakly rimmed; fronto-orbital width about 90 percent maximum carapace width. Anterolateral margin very short, formed into thickened rim. Posterolateral margin long, initially weakly convex, then becoming weakly concave near posterior corner. Posterior margin concave, about one-third maximum carapace width.

Regions poorly defined; protogastric regions and anteriormost mesogastric region weakly inflated to form broadly domed area; urogastric and cardiac regions defined laterally by branchiocardiac grooves.

Remainder of carapace and appendages unknown.

Measurements.—Measurements (in mm) taken on the dorsal carapace of MHN-UABCS/BA12-5: maximum carapace width = 7.4; maximum carapace length = 6.4; fronto-orbital width = 6.6; frontal width = 4.1; posterior width = 2.3; length to position of maximum width = 2.5.

Type.—The holotype and sole specimen, MHN-UABCS/BA12-5, is deposited in the Museo de Historia Natural, Universidad Autónoma de Baja California Sur, La Paz, Baja California Sur, México.

Etymology.—The trivial name is derived from the Latin word *inornatus,* meaning unadorned, referring to the lack of spines, projections, or serrations on both the front and anterolateral margins, unusual in the family.

Occurrence.—The specimen was collected at waypoint 29 of other publications (Schweitzer *et al.*, in press), in the Bateque Formation, Lat. 26°57′16.1″N, Long. 113°03′44.6″W, near the village of San Ignacio, Baja California Sur, México (Fig. 1A, B, near Laguna San Ignacio location).

Discussion.—The new taxon is known only from one specimen, possibly a molt because it consists only of the dorsal carapace. Its occurrence in a clastic facies suggests that it was transported out of the habitat in which it lived. That the specimen was transported is also supported by its occurrences with hundreds of brachyuran specimens representative of a variety of habitats, ranging from coral reefs (*Calappa* Weber, 1795, other Xanthoidea); deep-water environments (Homolidae de Haan, 1839; Raninidae de Haan, 1839); and cool-water, moderate-depth habitats (Cancridae Latreille, 1802) (Tucker, 1998; Schweitzer and Feldmann, 2000a, b; Schweitzer, *et al.*, 2004b). The deposit in which the specimen of *Archaeotetra* was recovered appears to represent a thanatocoenosis, possibly deposited by gentle currents in a near shore area where buoyant decapod molts could accumulate. Other facies within the Bateque Formation have yielded eight colonial coral species, four solitary coral species, one gorgonian, and one helioporid octocoral in other facies (Squires and Demetrion, 1992); thus, there are several possible host organisms that could have housed *Archaeotetra inornata* in a nearby environment.

Discussion

Evolutionary Relationships

Recent phylogenetic analyses generally place *Trapezia* or other trapeziid genera as a sister-group to members of the Xanthidae MacLeay, 1838 *sensu stricto*, and the Panopeidae Ortmann, 1893; to the freshwater crabs and thoracotreme crabs; or to a clade with all of these groups (Jamieson, 1993; von Sternberg *et al.*, 1999; Schubart *et al.*, 2000; von Sternberg and Cumberlidge, 2001; Brösing, 2002; Wetzer

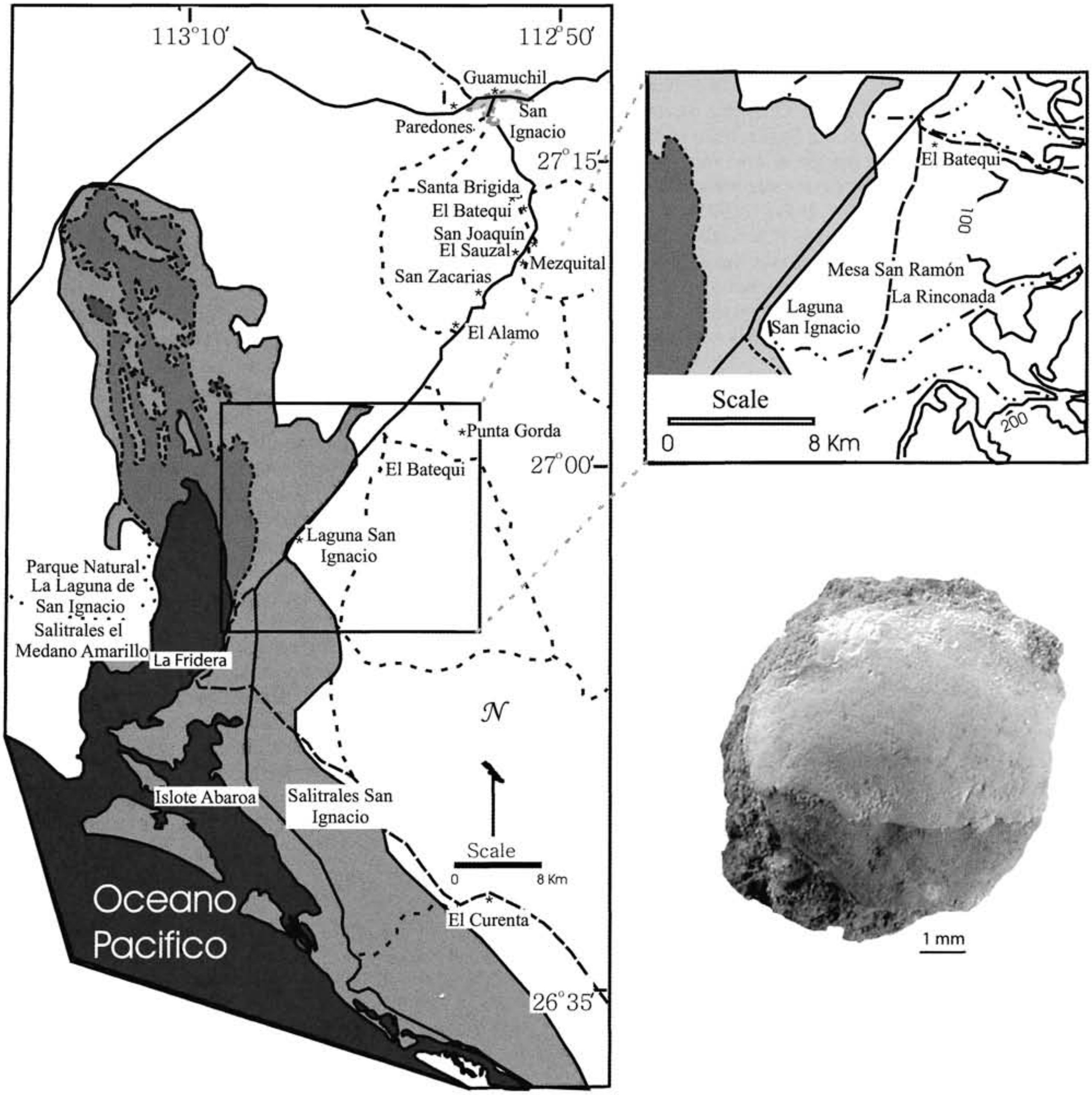

Fig. 1. *Archaeotetra inornata* new genus and species. A, Generalized location map of the Pacific coast of Baja California Sur, México, near San Ignacio. Medium gray area surrounded by dashed line represents areas inundated during high tides; light gray area surrounded by solid line represents transitional zone inundated during exceptional spring tides, salt pans, small dunes, and buttes, all less than 20 m above sea level. Other solid and dashed lines that do not bound shaded blocks are roads and trails. B, Enlargement of area near collecting locality waypoint 29, located near Laguna San Ignacio designation. C, Dorsal carapace of holotype and sole specimen, MHN-UABCS/Ba12-5. Scale bar = 1 cm.

et al., 2003; Castro *et al.*, 2004). In one analysis based upon mitochondrial DNA, *Trapezia* was part of an unresolved polytomy in a sister-group relationship to several xanthoid taxa arrayed within the Xanthidae *sensu stricto*, Panopeidae, and Eriphiidae MacLeay, 1838, as well as the Ocypodoidea Rafinesque, 1815 (Wetzer *et al.*, 2003). Another analysis using mitochondrial DNA placed the Trapeziidae as a sister group to a clade containing the Xanthidae *sensu stricto* and the Panopeidae (Schubart *et al.*, 2000). Jamieson (1993) suggested a similar phylogeny to that of Wetzer *et al.* (2003), based upon spermatozoan structure, in which the Trapeziidae was a neighboring taxon to a group containing the Panopeidae, Xanthidae *sensu stricto*, and several thoracotreme groups. An analysis using adult morphological characters placed *Trapezia* as a sister-group to a clade containing members of the Xanthidae MacLeay, 1838 *sensu stricto*, and the Panopeidae Ortmann, 1893 (von Sternberg and Cumberlidge, 2001). Phylogenetic analysis based upon morphology of foregut ossicles placed members of the Trapeziidae in a sister-group position to a large clade including members of the Hexapodidae Miers, 1886; Retroplumidae Gill, 1894; several families known from freshwater environments, and the Thoracotremata Guinot, 1977 (Brösing, 2002). Another study based upon adult morphology also demonstrated a sister-group relationship of members of the Trapeziidae to freshwater crab families and thoracotreme crabs (von Sternberg *et al.*, 1999). Only one recent analysis has included the Domeciidae; the Domeciidae and Trapeziidae *sensu lato* were sister groups to one another, and that larger clade was sister to the freshwater crabs (Castro *et al.*, 2004). Coelho and Coelho Filho (1993) placed the Trapeziidae as a subfamily of the Pilumnidae, based upon numerical taxonomy, but their analysis was based upon use of *Domecia acanthophora* (Desbonne and Schramm, 1867), a member of the Domeciidae. The position that the domeciids should be referred to the Pilumnidae has not subsequently been upheld.

Regardless of the group to which the Trapezidae eventually turn out to be the sister-group, the identification of Eocene trapeziids (Müller, 2004; herein) suggests that their common ancestor must have existed during Eocene or earlier time. The fossil record of some of the possible trapeziid sister-groups is known to extend into Eocene time, including the Panopeidae (Glaessner, 1969; Schweitzer, 2003b), but that of the Xanthidae *sensu stricto* is still under study. If the trapeziids are a sister-group to the Xanthidae *sensu stricto*, the latter's record must extend into the Eocene. Retroplumids are known from the Cretaceous (Schweitzer *et al.*, 2002). Freshwater crabs of the Potamoidea Ortmann, 1896, and Pseudothelphusoidea Ortmann, 1893, have a limited fossil record that extends into the Miocene (Pretzmann, 1972; Morris, 1976; Rodriguez and Diaz, 1977; Carriol and Secretan, 1994); if they are in fact the sister-group to the Trapeziidae, fossil freshwater crabs should be expected from Eocene or older rocks. Several thoracotreme groups have a fossil record, including the Grapsidae MacLeay, 1838 *sensu lato*, which extend into the Eocene (Glaessner, 1969; Karasawa and Kato, 2001; Schweitzer and Karasawa, 2004); the Pinnotheridae, which make their earliest known occurrence in the Danian of Greenland (Collins and Rasmussen, 1992; Schweitzer and Feldmann, 2001); the Camptandriidae Stimpson, 1858, which are recorded in the Miocene of Austria (Müller, 1998); and the Ocypodidae Rafinesque, 1815, which extend into the Miocene (Casadío *et al.*, unpublished). Clarification of the xanthoid fossil record continues to push the fossil record and the timing of major evolutionary events within the Brachyura further and further into the Paleogene.

Paleoecology

Members of the Domeciidae have been described as typically associated with coral (Davie, 2002) or as facultative symbionts of coral (Coles, 1982). They seem to prefer the coral families Acroporidae and Pocilliporidae (*Domecia*) and octocorallian gorgonians (*Maldivia*) (Castro, 1976; Patton, 1994) or are described simply as inhabiting corals or scleractinian corals (*Jonesius*, *Palmyria*) (Galil and Takeda, 1986; Castro, 1999). There is little mentioned about the impact of domeciid crabs on corals, but it has been reported that in the Domeciidae, hollowed-out areas developed in the corals as a response to contact with the crabs (Castro, 1976). Individuals of *Jonesius triunguiculatus* (Borradaile, 1902) were described as inhabiting a sizeable number of the chambers on live heads of the coral *Porites lobata* and that individuals might also inhabit dead coral (Coles, 1982). The fact that they can inhabit dead coral probably accounts for their being described as facultative symbionts, apparently not being dependent on the live coral for subsistence.

Members of the Trapeziidae have been described as "obligate ectoparasites," "obligate symbionts" or "obligate commensals" on various types of cnidarians (Patton, 1966, 1994; Knudsen, 1967; Castro, 1976, 1982, 1997; Galil, 1987; Galil and Takeda, 1985; Pratchett, 2001). Some workers have shifted to the use of the term "mutualists" (Stimson, 1990). The trapeziids have been deemed as obligate symbionts apparently because they are always found associated with live corals. Species and genera within the family tend to be host specific, generally preferring certain genera within the coral families Acroporidae and Pocilliporidae (*Trapezia*, *Tetralia*, *Tetraloides*) (Castro, 1976; Patton, 1994; Davie, 2002) but also inhabiting octocorallians including alcyonaceans (soft corals), antipatharians (black coral), and ahermatypic scleractinian corals (*Quadrella*) (Galil, 1986/1987; Davie, 2002) and hydrozoans of the family Stylasteridae (Galil, 1987, 1997).

It is apparently not known exactly why members of the Trapeziidae are obligate symbionts on various cnidarian groups. That the crabs are obligate symbionts seems to be a reasonable supposition, because they are always found on live cnidarians, but the exact biochemical or behavioral relationship that makes the relationship obligate for the crabs has not been explored. In addition, the mechanism by which the crabs have developed an immunity to the nematocysts of the cnidarians that they inhabit has not been explained (Castro, 1976). Several species within the Trapeziidae have been examined and have been found to feed almost exclusively on the nutrient-rich mucous secreted by corals, at times stimulating the corals to produce more mucous (Galil, 1987). Some types of corals have been shown to secrete lipid-rich structures in their mucous in the presence of crabs, which the crabs then eat (Stimson, 1990). It is possible that the crabs are dependent biochemically on this mucous for some reason such that they are obligate symbionts on their cnidarian hosts. Another possibility is that biochemicals associated with the cnidarians are necessary to trigger larval development of members of the family, which could explain their association with corals since at least the Eocene. A third possibility is that the gut structures of the Trapeziidae are uniquely modified to subsist only on coral mucous; phylogenetic analysis of foregut ossicles of a large array of members of the Brachyura grouped three species within the Trapeziidae together as a single clade (Brösing, 2002). A fourth possibility is that morphological limitations in cheliped or carapace size may restrict these organisms to inhabiting corals; however, the very broad geographic distribution of even individual species of members of the Trapeziidae (Galil, 1987; Castro, 1996, 2000) suggests that the limiting factor may have more to do with larval development and dispersal, biochemistry, or gut morphology than external size or morphology. Broad geographic and geologic distribution suggests that, other things being equal, these animals could survive in numerous environments with small hiding places (i.e., sponges, rocky areas, oyster banks, etc.), although note that those environments are not protected by nematocyst-bearing animals. In addition, the Domeciidae and other xanthoid crabs, with external morphology similar to the Trapeziidae and adapted for living in tiny places (Patton, 1994), are apparently not obligate symbionts on corals.

There have been varying reports as to whether corals of the families Acroporidae and Pocilliporidae benefit from the association with trapeziid crabs. Some reports suggest that the coral might actually be damaged by the association, because the mucous which the crabs scrape away to eat serves to protect the coral from dessication and against smothering by sedimentation (Knudsen, 1967; Glynn, 1983b; Galil, 1987). Other studies have demonstrated that the coral benefits directly from the crab association; trapeziids reduce predation by the echinoderm *Acanthaster planci* (Linnaeus), the crown-of-thorns starfish, by attacking its tubefeet (Castro, 1976; Glynn, 1976, 1983a; Ross, 1983; Patton, 1994). Glynn (1983a, b) reported an extensive study in which it was clearly demonstrated that corals housing trapeziid crabs exhibited better survivorship against such starfish than those without. Later studies have corroborated this finding (Stimson, 1990; Pratchett, 2001). Glynn (1983b) also reported that crustacean symbionts remove a variety of materials that settle on corals, thus helping to clean the coral. Based on this evidence, it seems most likely that the relationship is indeed mutually beneficial. However, note that the trapeziid crabs appear to be obligate symbionts, whereas the cnidarians can survive without the presence of the trapeziid crabs (Glynn, 1983a).

Glynn (1983a) believed that the trapeziids exhibited coevolution with corals in the family Acroporidae but seemed less inclined to the notion that corals had coevolved with the crabs. However, in the same paper, he described a scenario for coevolution between corals and crabs: "mucus production would support crustaceans which would benefit the coral ... [a]nd the coral would produce more and possibly higher quality mucus ..." (Glynn, 1983a, p. 169). Indeed, corals of the Pocilloporidae all seem to have crab inhabitants in the Indo-Pacific region (Glynn, 1983a), suggestive of a coevolutionary relationship. The Trapeziidae are adapted to life within corals, exhibiting modifications of the claws such that they can cling to the corals (Jeng, 1994) and highly modified appendages to stimulate production and promote gathering of mucous (Glynn, 1983a; Galil, 1987). The defensive behavior of the crabs suggests that they actively guard their food resource, although the degree to which this occurs is variable by genus (Glynn, 1983a). Coral mucous is apparently very difficult to metabolize, containing nematocysts (Glynn, 1983a), which also suggests a high degree of specialization in crabs that feed on it (and which also might somehow explain their immunity to the nematocysts).

There seems to be ample evidence that the corals have coevolved in response to the crabs. As discussed by Glynn (1983a), the corals may have had certain preadaptations, such as tightly packed branches, that made them amenable to housing crab symbionts. In the presence of trapeziid crabs, both pocilloporid and acroporid corals secrete more protein and lipid-rich mucous than if these crabs are not present (Glynn, 1983b; Stimson, 1990). The lipids are apparently in excess of the corals' own metabolic needs (Stimson, 1990). The fact that these corals can secrete more food resources when properly stimulated than they themselves need is strongly suggestive of a coevolutionary relationship. There seems to be little advantage for the coral in retaining this ability unless it is to respond to crustacean symbionts, who provide the coral with the valuable service of cleaning and protection from predators in exchange for the food resource. While it has clearly been demonstrated that the corals are not obligate symbionts, dependent on the crustaceans for survival, as say, plants and insect pollinators may be obligately codependent, this does not exclude a coevolutionary relationship. The genetic material that facilitates the response in the coral to secrete excess food resources must be selected for and retained because it is beneficial to the animal. This must be regarded as coevolution on the part of the coral.

Many authors have speculated that the trapeziids have undergone relatively recent speciation (Glynn, 1983a; Huber, 1985, 1987; Castro, 1988). Glynn (1983a) suggested that the presence of trapeziids and other crustacean symbionts probably had nothing to do with the radiation of reef-building corals in the Late Tertiary and Quaternary. However, the fossil record for the group challenges at least the former hypothesis. It may be true that speciation events within a single genus have been relatively recent, but radiation within the family must be an older event. Further, the origins of the symbiotic relationship of the Trapeziidae with the corals, and the coevolutionary relationship between the corals and the trapeziids, does in fact have a geological history based upon the fossil record. Glynn (1983a, p. 168) provided an elegant discussion of how host protection may have evolved in the Trapeziidae by looking at modern examples; looking to the fossil record, and finding more, and more complete trapeziid fossils with preserved chelae for example, could help test his notions.

The small number of genera in both the Domeciidae and the Trapeziidae in the fossil record and modern oceans may well be due to the specialized habit of members of the families as symbionts. This probably limits their diversity and undoubtedly limits their geographic range, as their main host organisms, hermatypic corals, live only in tropical oceans. However, note that the Tethyan, i.e., tropical, fossil distribution of each family suggests that the symbiotic relationship for each began early in their history. This is further supported by their occurrrences in either rocks with preserved coral reefs (Müller and Collins, 1991) or rocks with coral fragments and possible coral reef structures preserved in them (this occurrence; see Squires and Demetrion, 1992). The persistance of both families in Recent oceans suggests that this is a highly successful, long-lasting, faunal association.

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