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Phylogenetic and systematic position of the *Penaeus* subgenus *Litopenaeus* (Decapoda: Penaeidae)

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Abstract: Ten synapomorphies are demonstrated to separate the closed thelyca *Penaeus* subgenera (*Farfantepenaeus*, *Fenneropenaeus*, *Marsupenaeus*, *Melicertus*, and *Penaeus s.s.*) from the open thelycum subgenus *Litopenaeus*. The phylogenetic position of *Litopenaeus* was investigated within the context of the tribe Penaeae (genera *Funchalia*, *Heteropenaeus*, *Pelagopenaeus*, and *Penaeus*; Burkenroad 1936). A cladistic analysis using general genital characters positioned *Litopenaeus* basal within the tribe; cladistic analysis based upon genital and key somatic characters allowed several hypotheses of relationships to be developed. The first of these hypotheses, one compatible with the current classification, juxtaposed *Litopenaeus* and the closed thelyca *Penaeus* subgenera as sister taxa, proposing that the stem *Litopenaeus* species underwent reversals to ancestral character states (atavisms). The other hypotheses were congruent with the hypotheses based upon genital characters.

Key words: *Penaeus*, *Litopenaeus*, tribe Penaeae, phylogenetic analysis.

Marine shrimps of the genus *Penaeus* Fabricius (1798) constitute one of the most significant decapod crustacean groups. Shrimps in this genus comprise a global fishery with some of the 28 species intensively cultured (Dall *et al.* 1990). Indeed, many Latin American and Asian economies depend heavily upon *Penaeus* fisheries and aquaculture for revenue.

Penaeus shrimps are also important from a phylogenetic standpoint. Penaeids, indeed all dendrobranchiates (aristeids, solenocerids, sergestids, *etc.*), exhibit a number of plesiomorphic character states (*e.g.* naupliar larvae) pointing to a basal position in decapod phylogeny (Burkenroad 1981, Felgenhauer and Abele 1983, Bauer 1986). The somatic morphology of these shrimps is conservative although dendrobranchiate taxa display a diversity of genital structures (Bauer 1986, 1991). And some genera, *e.g. Penaeus*, have flourished since the early Mesozoic (Glaessner 1969, Dall *et al.* 1990) with only slight morphological change, relative to other decapod taxa.

Despite the importance of *Penaeus*, the systematics of this taxon has rarely been investigated within an evolutionary framework and the classification of penaeids is typological. The classification of species and subgenera in this genus was formulated without indicating genealogical relationships (Pérez Farfante 1969). The commonly accepted subgeneric divisions of *Penaeus* [6 subgenera: *Farfantepenaeus* Burokovskii (1972), *Fenneropenaeus* Pérez Farfante (1969), *Litopenaeus* Pérez Farfante (1969), *Marsupenaeus* Tirmizi (1971), *Melicertus* Rafinesque (1814), and *Penaeus s.s.* Fabricius (1798)] were based upon details of carapace sculpturing and genital structure (Pérez Farfante 1969), valid criteria, although only a search for synapomorphies can determine whether these species groupings are natural. Penaeid systematics has emphasized anatomical details of the highly modified endopods of the male first pleopods (petasma) and the female posterior thoracic somites XII - XIV used in sperm storage and transfer (thelycum), which constitute the genitalia in these decapods (Bauer 1994). Distinct morphological trends have been noted in the elaboration of these structures and it has been proposed that aspects of penaeid genital complexity can serve as a qualitative indicator of phylogenetic position (Bauer 1986, 1991). It is interesting to note that all *Penaeus* subgenera except *Litopenaeus* have an apomorphic closed thelycum where the spermatophores are enclosed in a seminal receptacle shielded by lateral plates after insemination. Fig. 1 presents a schematic of thelycal structure differences between open and closed thelycal *Penaeus* taxa. The morphological 'compactness' of the closed thelyca subgenera, by virtue of their unique genital structures, strongly suggest they constitute a monophyletic group. Inclusion of the open thelycum *Litopenaeus* in the genus *Penaeus*, a subgenus with a distinctly plesiomorphic genital form, suggests that *Penaeus* is a paraphyletic taxon.

The purpose of this paper is to apply an explicit methodology to determine the phylogenetic and systematic position of the *Penaeus* subgenus *Litopenaeus*. Following Burkenroad's classification (1936, 1983), the putative sister taxa of *Penaeus* are the genera *Funchalia* Johnson (1867), *Heteropenaeus* de Man (1896), and *Pelagopenaeus* Burkenroad (1934). The *Penaeus* sister taxa have open or semiclosed thelyca (*i.e.* lateral plates partially covering sternite XIV but not forming seminal receptacles) and exhibit a thelycal morphology intermediate that of *Litopenaeus* and the closed thelyca *Penaeus* subgenera. The specific aims of this study were: 1) to explicate phylogenetically significant character state differences between *Litopenaeus* and the closed thelyca *Penaeus* subgenera, 2) to examine genital character state transitions between *Litopenaeus* and the tribe Penaeae, and 3) to examine phylogenetic hypotheses of the tribe Penaeae using genital characters and genital plus key somatic structures. This is an initial attempt to understand *Penaeus* evolution within the context of other penaeid genera.

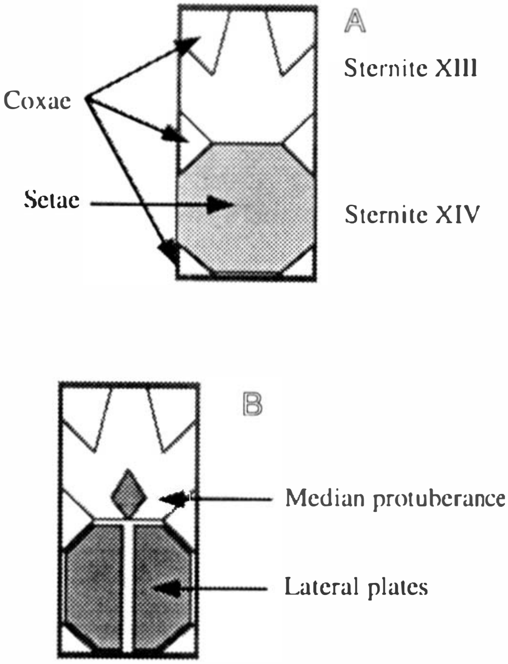

Fig. 1. Schematic representation of open and closed thelycal morphologies in the genus *Penaeus*. A. An open thelycum based upon *P.* (*L.*) *occidentalis*. B. A closed thelycum based upon *P.* (*P.*) *monodon*.

MATERIALS AND METHODS

Specimens of *Litopenaeus* [*P.* (*L.*) *occidentalis* Streets (1871), *P.* (*L.*) *schmitti* Burkenroad (1936), *P.* (*L.*) *setiferus* Linnaeus (1767), *P.* (*L.*) *stylirostris* Stimpson (1871), and *P.* (*L.*)*vannamei* Boone (1931)], *Farfantepenaeus* [*P.* (*F.*) *brasiliensis* Latreille (1817), *P.* (*F.*) *californiensis* Holmes (1900), *P.* (*F.*) *duorarum* Burkenroad (1939), *P.* (*F.*) *notialis* Pérez Farfante (1967), and *P.* (*F.*) *subtilis* Pérez Farfante (1967)], *Fenneropenaeus* [*P.* (*F.*) *orientalis* Kishinouye (1896)], *Marsupenaeus* [*P.* (*M.*) *japonicus* Bate (1888)], and *Penaeus s.s.* [*P.* (*P.*) *monodon* Fabricius (1798)] were examined from the collections of the Centro Nacional de Acuicultura e Investigaciones Marinas (CENAIM), Ecuador, Department of Biological Sciences, Florida International University, and the University of Miami Rosenstiel School of Marine and Atmospheric Science. Published descriptive material (Burkenroad 1934, 1936, Dall *et al.* 1990) on members of the tribe Penaeae was used to supplement examination of the materials. Specimens of the subgenus *Melicertus* were not examined as they differ rather slightly from members of *Farfantepenaeus*. The penaeid *Penaeopsis serrata* Bate (1888) was used to aid in character state polarization by outgroup comparison because this species exhibits a generalized penaeid morphology.

I have followed the argumentation of Bauer (1986, 1991) concerning morphological trends in penaeid shrimps. All available evidence points to open thelyca, complex spermatophores, open petasmata, etc., as plesiomorphic character states and closed thelyca, simpler spermatophores, semiclosed or closed petasmata as apomorphic character states. Given the importance of genital morphology in penaeid systematics, general aspects of thelycal, spermatophore, and petasmal structure were focused on in this study.

Readers are referred to Pérez Farfante (1969) and Bauer (1994) for terminology concerning penaeid genital structures.

The manual cladistic approach of Christoffersen (1987) was used to construct and test phylogenetic hypotheses. This methodology was chosen because it allowed a stepwise testing of hypotheses and the elimination of competing hypotheses by the identification of robust synapomorphies. The cladistic hypotheses were then expanded using PAUP 3.0 (Swofford 1990). The data matrix is presented in Table 3. Tree lengths (L), consistency indices (CI), and rescaled consistency indices (RC) are presented for the computer generated cladograms. The tree topologies presented differ from the computer generated cladograms because many obvious synapomorphies (*e.g.*, simplified spermatophores or thelycal lateral plates) linking taxa were designated as character state reversals for the outgroup by the software; that is, some synapomorphies were presented as plesiomorphies for the tribe with the primitive character state presented as an apomorphy (because a unique reversal) for the outgroup.

RESULTS

Phylogenetic Analysis: Phylogenetic comparison of the *Penaeus* subgenera with the outgroup taxon *Penaeopsis serrata* revealed eight genital synapomorphies which separate the subgenera *Farfantepenaeus*, *Fenneropenaeus*, *Marsupenaeus*, *Melicertus*, and *Penaeus* from *Litopenaeus*. Table 1 lists the synapomorphies separating the closed thelyca taxa from *Litopenaeus*. Some of the plesiomorphic character states exhibited by *Litopenaeus* are more similar to those possessed by open thelyca penaeid, aristeid, and solenocerid genera than to those exhibited by the closed thelyca *Penaeus* taxa. Inclusion of nongenital characters, *i.e.*, postlarval thoracic sternal spine formulae and the conjunction of moulting and insemination in closed thelyca taxa (Table 1; Dall *et al.* 1990), supported the genital distinction of the open and closed thelyca *Penaeus* taxa (see also Sternberg and Motoh 1995).

The information presented in Table 1 presents no evidence that *Litopenaeus* should be included in the genus *Penaeus*. To test the monophyly of *Penaeus*, *Litopenaeus* and the closed thelyca subgenera were phylogenetically compared within the context of the tribe Penaeae. A cladistic analysis of *Litopenaeus*, *Funchalia*, *Heteropenaeus*, *Pelagopenaeus*, and the closed thelyca *Penaeus* taxa genital morphologies revealed an interesting taxonomic distribution of character states. (See Table 2 for a listing of plesiomorphic and apomorphic character states in the tribe.) Fig. 2 presents modified PAUP generated cladograms (L = 10, CI = 1, RC = 1) of Penaeae relationships based upon general genital characters. [The phylogenetic hypotheses presented are not necessarily the most parsimonious; they are presented, however, to emphasize alternatives in the evolution of thelycal plates and, possibly, the development of seminal receptacles (see below).]

Like *Litopenaeus*, the genus *Funchalia* has an open thelycum and a moderately open petasma (characters 1 and 2). (Petasmata that are flexible and which can be easily opened are referred to here as 'moderately open' in contrast to the truly open petasmata of, *e.g.*, the aristeids. Moderately open petasmata may or may not have the ventral costae meeting along the midline. Petasmata that are compressed and less easily opened are here designated as semiclosed.) *Funchalia*, however, differs from other tribe members in having an asymmetrical petasma, an apomorphic character state (character 3). A trend toward a more advanced genital character state can be detected in the taxa

TABLE 1

Genital character state differences between Litopenaeus *and the closed thelyca* Penaeus *taxa*

Litopenaeus	**Other *Penaeus* subgenera**
A. Lateral plates absent	Broad lateral plates covering the ventral surface of sternite XIV
B. Seminal receptacles absent	Seminal receptacles present
C. Sternites XIII-XIV with pronounced prominences and setae for spermatophore attachment	Absence of prominences or setae on sternites XIII-XIV for spermatophore attachment.
D. Median protuberance absent or deeply concave	Median protuberance on posterior margin of sternite XIII always present and nonconcave
E. Spermatophore with complex articulations (flaps, flanges, ridges, *etc.*) (Pérez Farfante 1975)	Spermatophore a simpler, pod-like or round structure
F. Petasma moderately open	Petasma semiclosed
G. Petasmal ventral costae short	Petasmal ventral costae long
H. Median protuberance, when present, a unified, concave structure	Median protuberance divided into anterior and posterior processes
I. Postlarval thoracic sternal spine formula 0 + 0 + 0 + 1 + 0 (Dall *et al.* 1990)	0 + 0 + 0 + 1 + 1
J. Spermatophore implantation does not occur just after moulting (Dall *et al.* 1990)	Spermatophore implantation occurs just after moulting

TABLE 2

Key structures in penaeid shrimps and their plesiomorphic and apomorphic character states in the tribe Penaeae

Genital

1. Thelycum: Open (0), closed with seminal receptacles (1).
2. Petasma (I): Moderately open (0), semiclosed (1).
3. Petasma (II): Symmetrical (0), asymmetrical (1).
4. Lateral plates of thelycum: Absent (0), rudimentary, forming U-shaped rim around the central surface of sternite XIV (1), partially covering sternite XIV (2), completely covering sternite XIV (3).
5. Median protuberance on posterior margin of sternite XIII (I): Present (0), absent (1).
6. Median protuberance on posterior margin of sternite XIII (II): Unified, concave structure (0), differentiated into anterior and posterior processes (1).
7. Spermatophore: Complex with flaps, ridges, flanges, *etc.* (0), simpler, pod-like or round (1).
8. Sternites XIII-XIV: Prominences for spermatophore attachment (setae, protuberances, lamellae, *etc.*) (0), lacking prominences (1).

Somatic

9. Epipods on the 3rd thoracic somites: absent (0), present (1).
10. Pleurobranchs on the 8th thoracic somite: absent (0), present (1).
11. Pleurobranchs on the 7th thoracic somite: absent (1), present (0).
12. Ventral teeth on rostrum: Absent (0), present (1).
13. Integument: Pubescent (0), smooth (1).
14. Lateral ridges on integument: Absent (0), present (1).
15. Pits on integument: Absent (0), present (1).
16. Setae emerging from pits on integument: Absent (0), present (1).
17. Rostrum: Long (0), short (1).
18. Branchiostegal spine: Present (0), absent (1).
19. Dorsal carina on abdomen: 4th to 6th (0), 5th to 6th (1).
20. Basal spines on the 2nd pereopods: Absent (0), present (1).
21. Branchiocardiac carina: Absent (0), present (1).
22. Pterygostomial spine: Present (0), absent (1).
23. Ecology: Benthic, epibenthic (0), pelagic (1).
24. Fixed spines on telson: Present (0), absent (1).

TABLE 3

Data matrix used for cladistic (PAUP) analysis

Taxa	
Penaeopsis	000000000000000000000000
Litopenaeus	000010001101100001110101
Funchalia	001100111110010010011010
Funchalia danae	001200111110010010011010
Heteropenaeus	000200111111001101101101
Pelagopenaeus	000200111111110000011010
Penaeus	110301111101100001110101

Funchalia danae Burkenroad (1940), *Heteropenaeus*, and *Pelagopenaeus* which have thelyca with no seminal receptacles and with lateral flaps but possessing moderately open petasmata. The development of lateral plates is considered important as these structures appear to have been a precedent for the evolution of seminal receptacles in *Penaeus*. The taxa *F.danae*, *Heteropenaeus*, *Pelagopenaeus*, and *Penaeus* (exclusive of *Litopenaeus*) have lateral plates which cover the seminal receptacles on sternite XIV (*Penaeus*); or lateral plates which partially cover sternite XIV (*F.danae*, *Heteropenaeus*, and *Pelagopenaeus*) (character 4). The possible rudiments of lateral plates can be detected in the open thelyca *Funchalia* taxa. *Funchalia* has a U-shaped rim or margin surrounding the central surface of sternite XIV with the bottom of the U the posterior border of the sternite. The lateral plates of *F.danae*, *Heteropenaeus*, *Pelagopenaeus*, and *Penaeus* can be considered derivations of the U-shaped thelycal rim (Burkenroad 1936). In addition, the taxa *Funchalia*, *Heteropenaeus*, *Pelagopenaeus*, and *Penaeus* have well developed median protuberances on the posterior margin of sternite XIII (character 5). The presence of a median protuberance in this position is not an apomorphic character state as *Penaeopsis serrata* also has a similarly positioned structure. A median protuberance on the posterior margin of sternite XIII is absent in all *Litopenaeus* species except *P.* (*L.*) *vannamei*; the absence of this structure is the derived condition.

The median protuberance of *Penaeus* show moderate to pronounced differentiation into anterior and posterior processes, an advanced character (6).

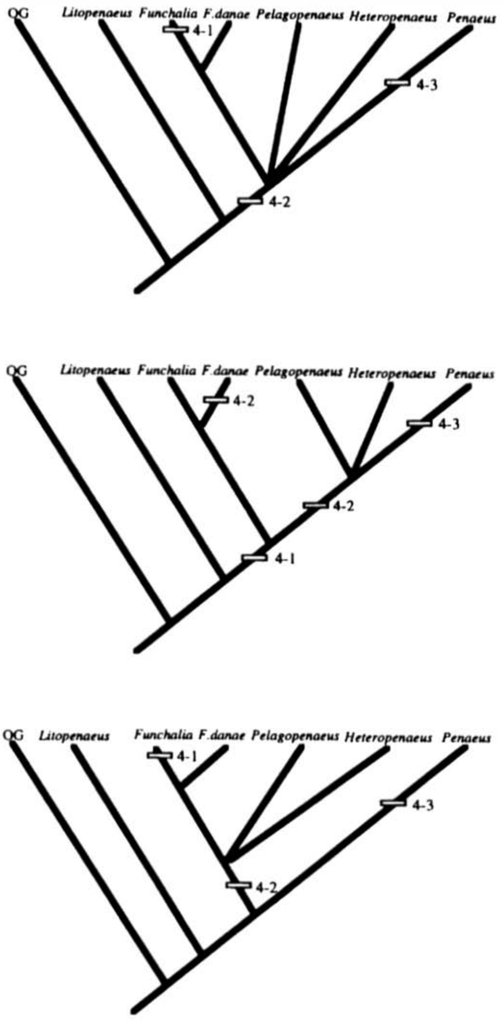

Fig. 2. Phylogenetic hypotheses of taxic relationships in the tribe Penaeae (Burkenroad 1936, 1983) based upon genital characters. Possibilities in the evolution of character 4 (lateral plate development) are emphasized. OG indicates the outgroup taxon (*Penaeopsis serrata*).

The closed and semiclosed thelyca taxa can be distinguished from *Litopenaeus* by the simpler, pod-like or round spermatophores (7). In *Litopenaeus*, as in other penaeoid taxa, the spermatophores exhibit complex prominences (*e.g.* flaps) for attachment to the thelycum (Pérez Farfante 1975). Furthermore, these taxa lack prominences on the ventral surface of sternites XIII and XIV for spermatophore attachment (8) which are present in *Litopenaeus*.

Based upon the characters stated above, all parsimonious hypotheses places *Litopenaeus* in a basal position within the tribe and points to the paraphyly of *Penaeus* (Fig. 2). Fig. 3 presents polarities in genital character state evolution in the tribe based upon the cladograms in Fig. 2. The hypothesis proposed here is that the transition from an open to semiclosed or closed thelycum was a unidirectional process (Fig. 3A). However, it should be noted that the computer generated hypotheses present *Funchalia* taxa as having lost the lateral plates (Fig. 3B).

The exclusive emphasis upon gross genital characters states overlooks many somatic features used in penaeid systematics. Fig. 4 presents schemata of relationships (equally parsimonious) in the Penaeae based upon genital and key somatic characters. All characters being of equal weight and unordered, the first modified PAUP hypothesis (L = 34, CI = 0.765, RC = 0.529) denotes *Litopenaeus* as the sister taxon to *Penaeus* , a placement congruent with the current implied classification of the tribe (Fig. 4A). However this hypothesis postulates that the progenitor to the *Litopenaeus* clade underwent several reversals to the penaeid morphological groundstate (atavisms). Fig. 5 presents a scheme of evolutionary events that are demanded by phylogenetically placing *Litopenaeus* adjacent to *Penaeus*.

The second modified PAUP hypothesis presented in Fig. 4B (L = 34, CI = 0.765, RC = 0.529) is congruent with the basal placement of *Litopenaeus* in the Penaeae based soley upon genital characters (Fig. 2). This second hypothesis presents genital character states as 'flickering on and off' in penaeid phylogeny (*i.e.* parallel evolution) in that the absence of defined lateral plates in *Funchalia* is presented as a character state reversal (4-2 to 4-1 transition; Figs. 3B and 4B). The hypothesis argued for here is that lateral plates evolved from a *Funchalia*-like groundstate, not the reverse (Fig. 3A; Burkenroad 1936). If this second hypothesis is correct then the semiclosed thelycum of *F.danae* and possibly *Pelagopenaeus* would have been acquired independently of other taxa in the tribe Penaeae. Fig. 4C presents a modified strict consensus tree of Penaeae relationships based upon the cladistic information presented in Figs. 4A and 4B. This hypothesis postulates the irreversibility of thelycal evolution from primitive (4-0, 4-1) to derived (4-2, 4-3) character states (Fig. 3A).

Bauer (1986, 1991) has made a convincing case that genital morphology is a key indicator of phylogenetic position. Whether the plesiomorphic character states exhibited by *Litopenaeus* denote a basal phylogenetic position (Figs. 2, 3, 4B, and 4C) or are atavisms (Figs. 4A and 5), the distinctions separating this genus from *Penaeus* are qualitative and profound.

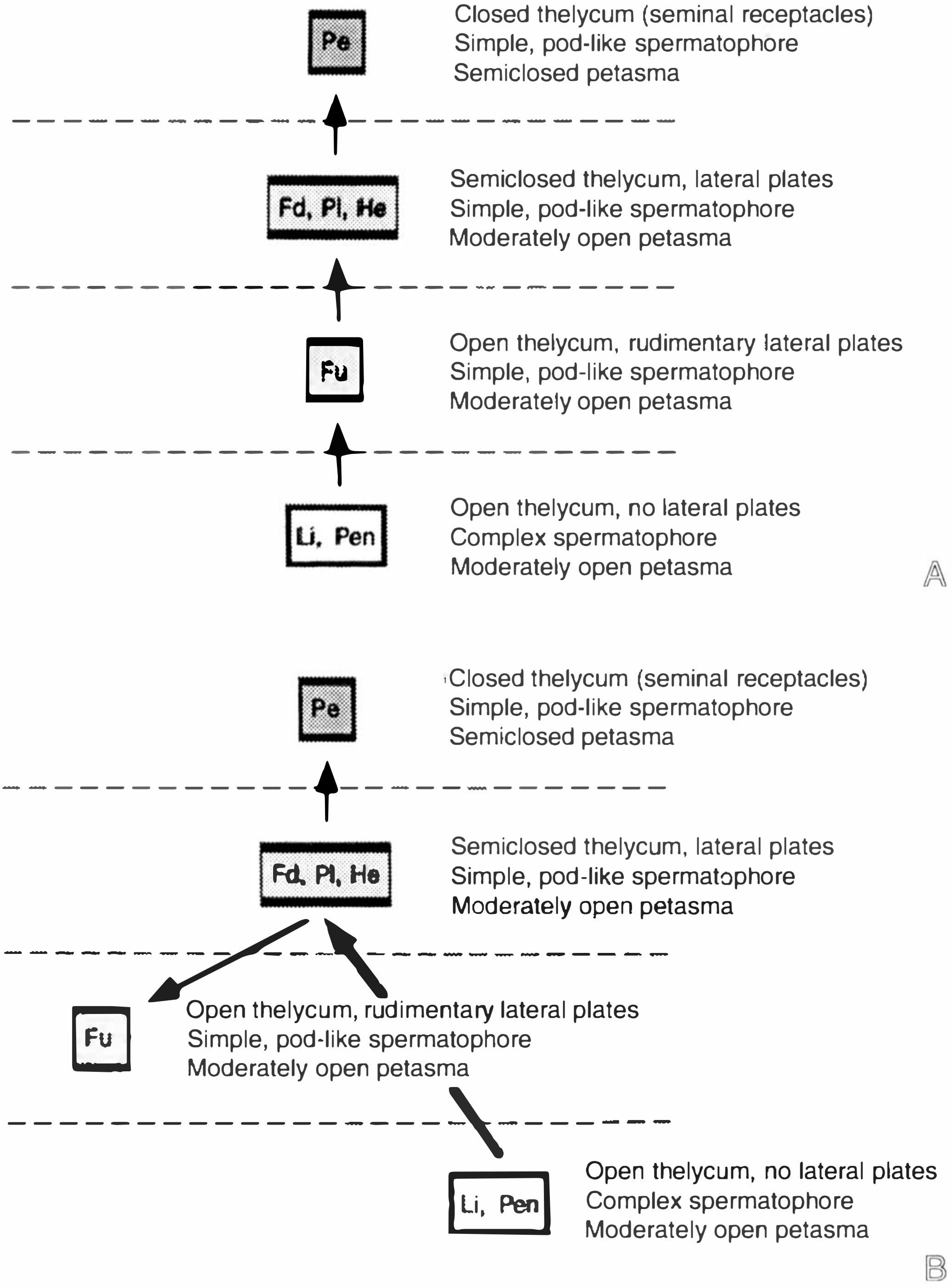

Fig. 3. Schemata of genital character state polarity in the tribe Penaeae based upon the cladograms in Fig. 2. Arrows denote character transitions from an open thelycum, complex spermatophore, and moderately open petasma to a closed thelycum, simple spermatophore, and semiclosed petasma. In this scheme *Litopenaeus* (Li) possesses the character groundstates (as do the taxa *Funchalia* (Fu) and *Penaeopsis* (Pen)) and is separated from *Penaeus* restricted (Pe) by 'intermediate' taxa [*F. danae* (Fd), *Pelagopenaeus* (Pl), and *Heteropenaeus* (He)].

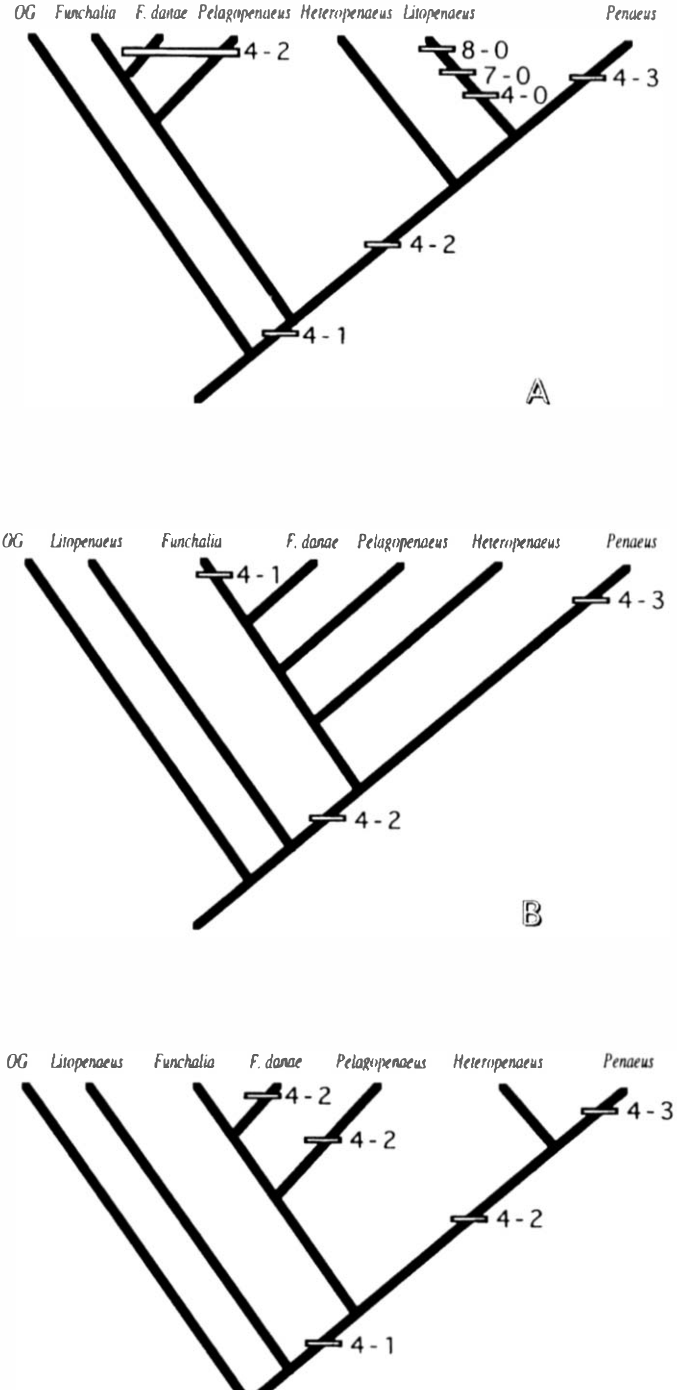

Fig. 4. **A - C**. Phylogenetic hypotheses of taxic relationships in the tribe Penaeae based upon genital and key somatic character states. Possibilities in the evolution of character 4 (lateral plate development) and character state reversals are emphasized. OG indicates the outgroup taxon (*Penaeopsis serrata*).

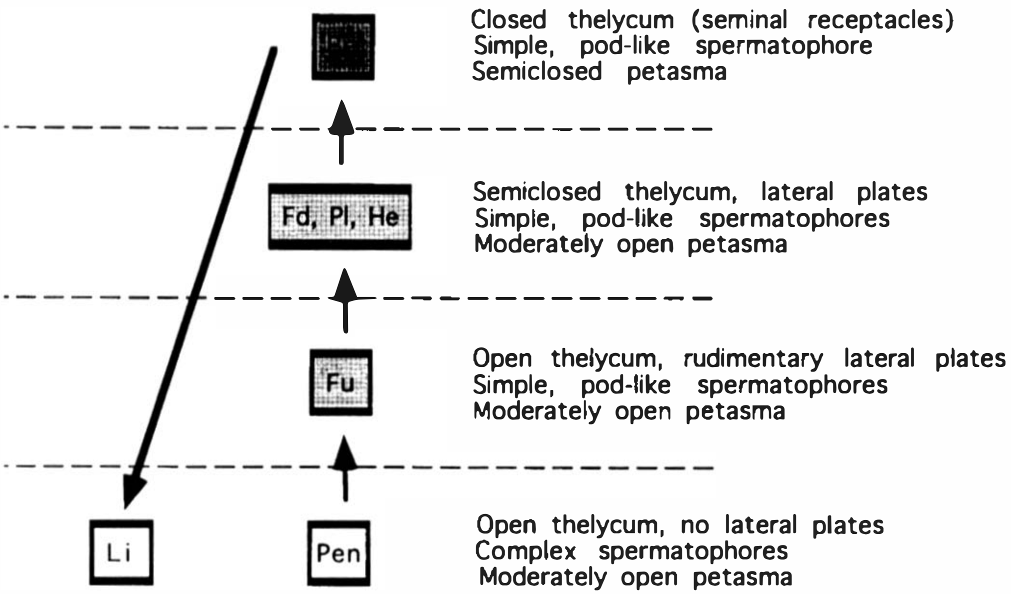

Fig. 5. Trends in penaeid genital structure evolution with character state reversals based upon the cladogram in Fig. 4A. Legend for scheme same as for Fig. 3. Large arrow denotes 3 large character state reversals in the stem *Litopenaeus* clade after separation from the *Penaeus* restricted clade. This scheme of character state polarity depicts the evolutionary events implied in the current classification of the genus *Peneaus* and the tribe Penaeae.

DISCUSSION

The underlying purpose of this paper has been to examine the phylogenetic and systematic position of the penaeid taxon *Litopenaeus* relative to other *Penaeus* subgenera. A total of ten key character states were identified which separate the closed thelycum *Penaeus* from the open thelycum *Litopenaeus* (Table 1). Eight of the ten putative synapomorphies concern aspects of genital form and function; no intermediate genital morphologies bridge the two genera. Pérez Farfante was the first penaeid systematist to stress the taxonomic weight of genital characters. She noted that the "...subgenus *Litopenaeus*...differ markedly from other members of the genus in characters of the external genitalia..." (Pérez Farfante 1969). She and subsequent workers noted the strikingly plesiomorphic character states typical for *Litopenaeus* but nevertheless maintained this taxon with the advanced closed thelycal taxa.

The large differences separating *Litopenaeus* and *Penaeus* can be explained within the context of the tribe Penaeae. If we consider only genital characters in our phylogenetic analysis of the tribe then *Litopenaeus* occupies a distant position from *Penaeus* as this taxon holds a basal position within the tribe (Fig. 2); the somatic similarities shared by the two genera would thus represent parallelisms. On the other hand, if we consider genital and somatic characters, several phylogenetic reconstructions can be generated (Fig. 4). One hypothesis juxtaposes *Litopenaeus* and *Penaeus* with *Litopenaeus* having undergone reversals to the plesiomorphic genital character states (atavisms). This phylogenetic hypothesis is less tenable than the ones presented in Figs. 2 and 4B and the modified consensus tree in Fig. 4C. This hypothesis proposes that the ancestral *Litopenaeus* lost the lateral plates and seminal receptacles, acquired articulations, prominences, setae, *etc.*, on sternites XIII and XIV, acquired complex spermatophores and so on after separating from the *Penaeus* clade. The fact that this hypothesis postulates large character state reversals is not the major reason for rejecting the 'atavism' hypothesis. First, the large genital differences separating or grouping taxa are qualitatively distinct from the somatic features. Second, many somatic characters may be adaptations to a benthic, epibenthic, or pelagic lifestyle. Thus relatively simple characters, *e.g.*, smooth *versus* pubescent integument, may be the result of convergence. Third, Bauer (1986, 1991) has pointed out that male and female genitalia and spermatophores in penaeoids have coevolved and reveal ordered morphoclines. Genital morphology is less likely to be shaped by convergent evolution to similar habitats and reflects the internal dynamics (mating behavior, aspects of spermatophore attachment, petasmal function, *etc.*) of the clade. The reader should note that the phylogenetic hypotheses are tentative and auxillary to the evidence underscoring the gulf between *Litopenaeus* and *Penaeus* (Table 1). Unlike the traditional approaches to penaeid systematics based upon overall similarity, the phylogenetic arguments presented here are subject to direct falsification. Additional information, particularly concerning the ontogeny of penaeid genitalia and the functional aspects of various genital and somatic structures will aid in modifying and/or refuting the hypotheses presented.

The tribe Penaeae, defined by two putative synapomorphies (retention of 3rd maxilliped epipodites and last pereomere pleurobranchs; Table 2 and Burkenroad 1983), provides a 'snapshot' of evolutionary trends within the Penaeoidea. This tribe encapsulates a 'primitive' organizational stage of penaeid female genitalia with no seminal receptacles and no lateral plates (*Litopenaeus*), the development of lateral plate progenitor structures (*Funchalia*), the acquisition of lateral plates but with no seminal receptacle development (*F. danae*, *Heteropenaeus*, and *Pelagopenaeus*), and the emergence of seminal receptacles covered by lateral plates (closed thelycum; *Penaeus*). Similarly, the transition from complex spermatophores (*Litopenaeus*) to simpler, pod-like or round spermatophores (*Funchalia*, *Heteropenaeus*, *Pelagopenaeus*, and *Penaeus*) and from moderately open petasmata (*Litopenaeus*, *Funchalia*, *Heteropenaeus*, and *Pelagopenaeus*) to semiclosed petasmata (*Penaeus*) is observed. My observations, as they relate to Bauer's hypotheses of trends in penaeoid evolution (1986, 1991), lead me to suggest that complexification of the genitalia is a trend occurring parallel in penaeid lineages. The asymmetrical petasma of *Funchalia*, for example, was acquired independently of that exhibited by *Metapenaeopsis* Bouvier (1905) (in the tribe Parapenaeae). In other words, genital complexification is indicative of an overall phylogenetic tendency in the penaeids but one that is realized independently in clades.

Inasmuch as *Litopenaeus* and *Penaeus* are important decapod taxa from the ecological, commercial, phylogenetic, and systematic perspective, reluctance in accepting the implied generic separation of *Litopenaeus* from *Penaeus* is expected. Arguments *contra Litopenaeus* deserving generic status can, I think, take only two forms: a) the shared *habitus* of the two genera and b) the argument for tradition *qua* convenience.

The first possible counter argument can be removed by reinterpreting the generic characters formerly used to separate *Penaeus* from other members of the tribe Penaeae (Burkenroad 1983) as symplesiomorphies. Many of the characters used in penaeid systematics need to be reexamined as some character states used as key generic indicators are undoubtedly symplesiomorphies shared with other penaeid taxa (*e.g.* smooth integument or teeth on the lower rostral margin; Fig. 4). In other words, overall morphological similarity may mask profound phylogenetic differences. Strict Hennigian reasoning dictates that a monophyletic taxon be recognized as one based on shared derived characters; hence, ascribing systematic weight to genital characters *and* uniting open and closed thelyca taxa in one genus is contradictory. The synapomorphies linking the closed thelyca *Penaeus* taxa suggests that further division of the genus is unwarranted.

The second possible counter argument, *i.e.*, tradition, can be opposed as it promotes unnatural, subjective classifications. For example, Dall *et al.* (1990) have stated concerning *Penaeus* "In a genus with only 27 (*sic*) species it is difficult to see the justification for creating six subgenera...there seems little point in complicating the taxonomy in this way." Such an argument overlooks the significant character states uniting some *Penaeus* taxa and the gaps between *Litopenaeus* and *Penaeus*. Furthermore, such an argument conflates species number with morphological diversity.

It is helpful to place the distinctions between *Litopenaeus* and *Penaeus* in the broader context of decapod crustacean systematics. One need only note the role of gonopod morphology in freshwater crab systematics (Rodríguez 1982) or the importance placed upon gonopore position for the suprafamilial classification of brachyurans (Guinot 1978, 1979). Relative to other characters used for decapod generic distinction, *e.g.*, carapace shape, chelae morphology, straight *versus* curved gonopods (some ocypodid crab taxa; Manning and Holthuis 1981), *etc.*, *Litopenaeus* can justifiably be removed from the taxon *Penaeus*.

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