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MOLECULAR SYSTEMATICS OF THE GONODACTYLIDAE (STOMATOPODA) USING MITOCHONDRIAL CYTOCHROME OXIDASE C (SUBUNIT 1) DNA SEQUENCE DATA

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A B S T R A C T

A molecular phylogenetic analysis of the stomatopod family Gonodactylidae and selected representatives of the superfamily Gonodactyloidea was conducted using 649 base pairs of DNA sequence data from mitochondrial cytochrome oxidase C subunit 1 (CO-I). Results showed the family Gonodactylidae is not monophyletic ($P < 0.0001$). Within the Gonodactylidae, results are inconclusive as to whether *Gonodactylellus*, *Gonodactylinus*, and *Gonodactylus* represent distinct monophyletic taxa or should be collapsed into a single genus *Gonodactylus*. Results strongly indicate that *Gonodactylellus* is polyphyletic; four of the five *Gonodactylellus* species examined formed a monophyletic clade which was closely related to *Gonodactylus* and *Gonodactylinus*, while *Gonodactylellus hendersoni* was found to be deeply divergent from its congeners and formed a strong monophyletic group with members of *Gonodactylopsis* and *Hoplosquilla*. The genus *Gonodactylaceus* was found to be monophyletic and highly divergent from the other gonodactylid genera. The species *Gonodactylaceus aloha* is shown to be a synonym of *G. mutatus*. Finally, although our analysis suggests a close relationship of *Odontodactylus* and *Hemisquilla*, high levels of nucleotide substitution saturation prevented the resolution of deep (family level) branches within the phylogenetic structure of this relatively old stomatopod lineage.

Stomatopods are benthic marine crustaceans of the class Malacostraca, subclass Hoplocarida. Commonly known as mantis shrimps, they are both behaviorally complex and taxonomically diverse. More than 400 extant species are currently recognized from over 100 genera, representing 19 families arranged into 5 superfamilies: Bathysquilloidea Manning, Squilloidea Latreille, Erythrosquilloidea Manning and Bruce, Lysiosquilloidea Geisbrecht, and Gonodactyloidea Geisbrecht (Manning, 1995; Ahyong, 1997). Alpha taxonomy of the stomatopods has intensified greatly in the past half-century; by comparison, Kemp (1913) recognized only 126 species in 6 genera, all in the family Squillidae Latreille. While this increase in our understanding and appreciation of stomatopod diversity and systematics has been partly a result of increased sampling intensity in cryptic habitats, it is perhaps most attributable to the tireless work of Raymond Manning, who has singly, or with coauthors, described approximately one half of all known stomatopod species and is largely responsible for the systematic framework of stomatopod families and superfamilies which are now recognized. We present this paper in his honor.

Within the five superfamilies of extant stomatopods, the Gonodactyloidea have received much attention recently owing to their complex ecology, elaborate behavioral repertoire (Caldwell, 1988, 1991), acute color vision (Cronin and Marshall, 1989), and potential for use as bioindicators of marine pollution stress (Erdmann and Caldwell, 1997). The Gonodactyloidea are highly diverse; Manning (1995) recognized 33 genera in nine gonodactyloid families. This group has the highest familial diversity within the five extant superfamilies and is second only to the Squilloidea in both species and generic diversity (Manning, 1995). Additionally, the Gonodactyloidea is a relatively old lineage. Like the other superfamilies, the Gonodactyloidea is considered to have Cretaceous origins (Schram, 1986; Hof, 1998). The oldest known fossil stomatopod assigned to one of the extant superfamilies, *Palaeosquilla brevicoxa* Schram, is believed to be a gonodactyloid from the middle Cretaceous (Schram, 1968).

Of the nine recognized gonodactyloid families, the type family Gonodactylidae is by far the most diverse, with ten described genera. Taxonomic revisions have been common in the Gonodactylidae. Manning (1995) split the formerly speciose genus of *Gonodactylus* into five genera: *Gonodactylaceus, Gonodactylellus, Gonodactylinus, Gonodactylus*, and *Neogonodactylus*, although he expressed reservation with regard to the phylogenetic basis for this division. Recently, Erdmann and Manning (1998) described five new species of gonodactylid from Indonesia.

Although evolutionary relationships within the Stomatopoda have been implicitly proposed in systematic descriptions and even explicitly discussed in a number of studies (e.g., Brooks, 1886; Schram, 1986; Manning, 1969a), modern cladistic methods (using morphological data) have only recently been applied to the analysis of stomatopod phylogenetics (Ahyong, 1997; Hof, 1998). Although several workers are currently involved in extending cladistic techniques to stomatopods using molecular sequencing data (Ahyong, in prep.; Harling, in prep.), the present paper is the first to attempt a molecular phylogenetic analysis of the Gonodactylidae.

In the last ten years the use of mitochondrial DNA sequence data in systematics has become commonplace. Molecular data have been used to corroborate morphological systematics and taxonomy as well as help resolve questions unanswered by morphological studies (e.g., Brown *et al.,* 1994; Arndt *et al.,* 1996; Itagaki *et al.,* 1998). DNA sequence data from CO-I has been used in systematic studies ranging from family- to subspecies-level relationships (e.g., Gleason *et al.,* 1997; Davis *et al.,* 1998; Foighil *et al.,* 1998) and even intraspecific phylogeography (e.g., Juan *et al.,* 1998). This study applies molecular systematic techniques to questions of stomatopod evolution. The goals of this study are threefold: (1) determine whether phylogenetic analysis using DNA sequence data supports the currently proposed systematic classification of the Gonodactyloidea in general and the Gonodactylidae in particular; (2) evaluate the validity and taxonomic placement of five new gonodactylid species described in Erdmann and Manning (1998); and (3) evaluate the long-disputed validity of *Gonodactylaceus aloha* (Manning and Reaka, 1981) as a distinct species from *G. mutatus* (Lanchester, 1903).

Materials and Methods

Taxon Sampling

Samples were obtained from 33 individuals of 28 species within the superfamily Gonodactyloidea (Table 1). Within the family Gonodactylidae, 17 species representing seven of the ten described genera in the family were sampled (*Gonodactylaceus* Manning $n = 3$; *Gonodactylellus* Manning $n = 5$; *Gonodactylinus* Manning $n = 1$; *Gonodactylopsis* Manning $n = 1$; *Gonodactylus* Berthold $n = 4$; *Hoplosquilla* Holthuis $n = 1$; *Neogonodactylus* Manning $n = 2$). Additionally, taxa from five of the eight other recognized families within the Gonodactyloidea were included (Table 1). A representative of the Lysiosquilloidea (*Parvisquilla multituberculata* Borradaille), recognized by Ahyong (1997) as a sister clade to the Gonodactyloidea, was included as an outgroup taxon. Finally, multiple samples of several species (*Gonodactylaceus mutatus* Lanchester $n = 2$, *Gonodactylellus hendersoni* Manning $n = 2$, and *Gonodactylus childi* Manning $n = 4$) were included to examine the depth of divergence between geographically distant populations of the same species. Note that although Manning (1995) synonymized *G. childi* as being based on *Gonodactylellus incipiens* (Lanchester), it has since been clearly shown to represent a distinct species (Erdmann, 1997; Erdmann and Manning, in prep.).

DNA Extraction, Amplification, and Sequencing

Total DNA was extracted from abdominal wall muscle tissue of specimens preserved in 70–95% ethanol, using a 5% Chelex® (Biorad) solution (Walsh *et al.,* 1991). For those specimens where fresh tissue was available (indicated in Table 1), a single pereiopod was clipped from living specimens, and mitochondrial DNA was extracted and purified using Wizard Minipreps® (Promega Corporation) following the methods of Beckman *et al.* (1993).

A 649 bp fragment of the mitochondrial cytochrome oxidase-1 gene was amplified via the polymerase chain reaction (Saiki *et al.,* 1988) using primers HCO–2193 and LCO–1490 designed by Folmer *et al.* (1994). Hot-start thermocycling was done in a Perkin-Elmer 9600 using Amplitaq Gold® (Perkin-Elmer Corp.) and began with an initial 10-min denaturation at 94°C to activate the enzyme, followed by 42 cycles of 94°C/1 min, 45°C/1 min, 72°C/1.5 min, and finished with a 3-min final extension at 72°C. Double-stranded PCR products were electrophoresed on TAE agarose gels then excised from the gel and purified with Ultraclean 2® (Invitrogen). Cleaned PCR products were sequenced via cycle sequencing (Amplicycle®, Perkin-Elmer Corp.) under manufacturer-recommended reaction conditions, using P^{33} radiolabeled d-ATP, followed by electrophoresis and autoradiography.

Data Analyses

Sequences were manually entered into the alignment program Seqapp 1.9 (Gilbert, 1995). Pairwise comparison of sequence variation was performed using test version 4.0d64 of PAUP*, written by David Swofford. The presence of phylogenetic signal in the data set was evaluated by examining the skewness of a tree-length distribution of 10^6 randomly generated trees (Hillis, 1991; Hillis and Huelsenbeck, 1992). To test for saturation of nucleotide substitutions

Table 1. Material from which mitochondrial DNA was extracted for study. Classification follows Manning (1995). Location of collection is indicated for each specimen, as is the type of material examined (F = fresh material from clipped pereiopod; E = ethanol-preserved specimen). Note: *P. ciliata* was obtained from a live animal trader; probable location Hawaii, but not known with certainty.

Species	Collection locale	Type of material
Family Gonodactylidae Geisbrecht, 1910		
Gonodactylaceus aloha (Manning and Reaka, 1981)	Hawaii, USA	F
Gonodactylaceus mutatus Q (Lanchester, 1903)	Queensland, Australia	E
Gonodactylaceus mutatus S (Lanchester, 1903)	S. Sulawesi, Indonesia	E
Gonodactylaceus glabrous (Brooks, 1886)	S. Sulawesi, Indonesia	E
Gonodactylellus affinis (de Man, 1902)	S. Sulawesi, Indonesia	E
Gonodactylellus annularis Erdmann and Manning, 1998	S. Sulawesi, Indonesia	E
Gonodactylellus caldwelli Erdmann and Manning, 1998	Queensland, Australia	F
Gonodactylellus hendersoni J (Manning, 1967)	Java, Indonesia	E
Gonodactylellus hendersoni S (Manning, 1967)	S. Sulawesi, Indonesia	E
Gonodactylellus rubriguttatus Erdmann and Manning, 1998	Komodo, Indonesia	E
Gonodactylinus viridis (Serène, 1954)	S. Sulawesi, Indonesia	E
Gonodactylopsis komodoensis Erdmann and Manning, 1998	Komodo, Indonesia	F
Gonodactylus childi S Manning, 1971	S. Sulawesi, Indonesia	E
Gonodactylus childi Q Manning, 1971	Queensland, Australia	E
Gonodactylus childi M Manning, 1971	Moorea, F. Polynesia	F
Gonodactylus childi T Manning, 1971	Talaud, Indonesia	E
Gonodactylus chiragra (Fabricius, 1781)	Java, Indonesia	F
Gonodactylus platysoma Wood-Mason, 1895	Dravuni, Fiji	F
Gonodactylus smithii Pocock, 1893	Irian Jaya, Indonesia	E
Hoplosquilla said Erdmann and Manning, 1998	C. Sulawesi, Indonesia	E
Neogonodactylus bredini (Manning, 1969)	Belize	F
Neogonodactylus oerstedii (Hansen, 1895)	Belize	F
Family Hemisquillidae Manning, 1980		
Hemisquilla ensigera californiensis Stephenson, 1967	California, USA	F
Family Odontodactylidae Manning, 1980		
Odontodactylus scyllarus (Linnaeus, 1758)	Komodo, Indonesia	F
Family Protosquillidae Manning, 1980		
Chorisquilla excavata (Miers, 1880)	Moorea, F. Polynesia	F
Chorisquilla spinosissima (Pfeffer, 1888)	Queensland, Australia	F
Haptosquilla glyptocercus (Wood-Mason, 1875)	S. Sulawesi, Indonesia	E
Haptosquilla hamifera (Odhner, 1923)	S. Sulawesi, Indonesia	E
Haptosquilla pulchella (Miers, 1880)	S. Sulawesi, Indonesia	E
Haptosquilla stoliura (Müller, 1886)	S. Sulawesi, Indonesia	E
Haptosquilla trispinosa (Dana, 1852)	Queensland, Australia	F
Family Pseudosquillidae Manning, 1977		
Pseudosquilla ciliata (Fabricius, 1787)	Hawaii?, USA	F
Family Takuidae Manning, 1995		
Taku spinosocarinatus (Fukuda, 1909)	Queensland, Australia	F
Superfamily Lysiosquilloidea, Family Coronididae Manning, 1980		
Parvisquilla multituberculata (Borradaile, 1898)	N. Sulawesi, Indonesia	E

in the data set (Berbee *et al.*, 1995), percentage uncorrected sequence divergence (p-distance) was plotted against percentage sequence divergence corrected for multiple hits using Kimura 2-parameter distance (Kimura, 1980) for first-, second-, and third-position transitions and transversions.

Various character-weighting schemes were explored. Analyses were run with all characters unweighted, and with transitions downweighted (ts:tv = 1:2, 1:3, 1:4, 1:5) with respect to transversions. A final weighting scheme employed a codon-specific weighting that corrects for multiple substitution events, transition/transversion bias, and differential proportions of first-, second-, and third-position changes (Albert and Mishler, 1992; Albert *et al.*, 1993). All phylogenetic analyses were conducted with test version 4.0d64 of PAUP* using *Parvisquilla multituberculata* as an outgroup. Parsimony analyses using all weighting methods were conducted via the heuristic search option, implementing step-wise addition with 1,000 random addi-

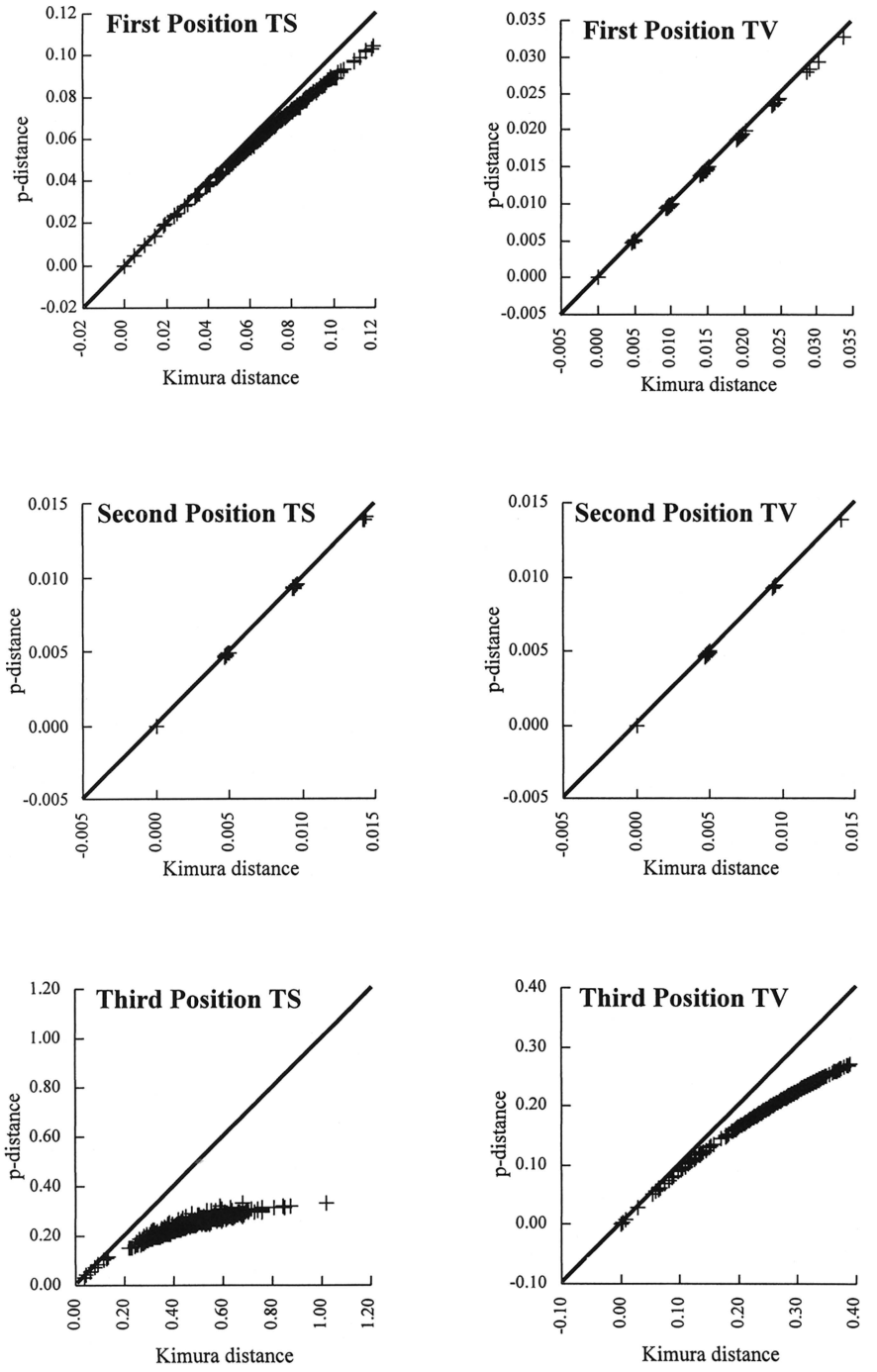

Fig. 1. Plot of uncorrected p-distance vs. Kimura 2-parameter distance (1980) for 1st-, 2nd-, and 3rd-position transitions and transversions from 649 base pairs of mitochondrial cytochrome oxidase (subunit 1). Lines are slope x = y. Evidence of saturation is revealed in all third-position transitions and transversions as well as first-position transitions.

tion replicates (Maddison, 1991), random addition of taxa, TBR branch swapping, zero-length branches collapsed to yield polytomies, and steepest descent option not in effect. Bootstrapping with 1,000 replicates (Felsenstein, 1985) and a decay analysis (Bremer, 1988, 1994) were performed to test the robustness of the resulting phylogenies. A Kishino-Hasegawa test (Kishino and Hasegawa, 1989) was performed in PAUP* on the resulting trees in an at-

Table 2. Pairwise uncorrected p-distance (top diagonal) and absolute distances (lower diagonal) calculated from 649 base pairs of mitochondrial cytochrome oxidase c (subunit 1) obtained from 22 samples representing 17 taxa from family Gonodactylidae plus 12 outgroup taxa.

		1	2	3	4	5	6	7	8	9
1	*G. aloha*	—	0.054	0.014	0.138	0.178	0.181	0.178	0.171	0.190
2	*G. mutatus* Q	35	—	0.054	0.133	0.176	0.182	0.178	0.184	0.184
3	*G. mutatus* S	9	35	—	0.143	0.178	0.181	0.174	0.175	0.191
4	*G. glabrous*	89	86	92	—	0.185	0.184	0.194	0.199	0.204
5	*G. affinis*	111	110	111	116	—	0.139	0.126	0.211	0.185
6	*G. annularis*	114	115	114	116	87	—	0.130	0.183	0.174
7	*G. caldwelli*	113	113	110	123	79	82	—	0.204	0.179
8	*G. hendersoni* J	110	119	113	129	132	116	129	—	0.140
9	*G. hendersoni* S	120	116	120	129	116	110	113	89	—
10	*G. rubriguttatus*	106	116	107	125	93	84	80	122	121
11	*G. viridis*	102	105	99	116	101	101	96	108	115
12	*G. komodoensis*	106	108	105	129	119	111	114	89	92
13	*G. childi* S	100	99	97	119	100	99	105	117	121
14	*Go. childi* Q	107	108	107	134	114	108	105	119	124
15	*G. childi* M	108	111	106	136	112	105	105	119	122
16	*G. childi* T	111	112	109	132	111	105	109	125	125
17	*G. chiragra*	102	107	101	118	102	97	106	107	113
18	*G. platysoma*	114	121	114	113	102	100	98	114	114
19	*G. smithii*	107	111	105	117	109	113	111	114	114
20	*H. said*	117	115	114	121	118	108	117	96	92
21	*N. bredini*	94	105	95	111	117	116	118	108	105
22	*N. oerstedii*	97	102	97	114	117	104	116	99	102
23	*H. ensigera*	131	128	129	131	130	130	122	131	133
24	*O. scyllarus*	128	127	126	127	129	126	121	126	119
25	*C. excavata*	96	94	96	112	110	102	108	105	109
26	*C. spinosissima*	99	93	98	111	112	109	114	100	119
27	*H. glyptocercus*	104	104	103	108	116	112	118	100	115
28	*H. hamifera*	103	105	100	111	112	109	111	105	108
29	*H. pulchella*	91	99	90	101	109	109	110	99	109
30	*H. stoliura*	95	95	96	108	115	103	112	98	112
31	*H. trispinosa*	107	105	108	115	105	93	110	114	105
32	*P. ciliata*	110	116	106	128	121	117	125	103	120
33	*T. spinosocarinatus*	98	96	97	112	113	108	100	110	104
34	*P. multituberculata*	97	105	93	112	108	112	108	120	118

		10	11	12	13	14	15	16	17	18
1	*G. aloha*	0.166	0.162	0.165	0.160	0.168	0.168	0.172	0.158	0.177
2	*G. mutatus* Q	0.180	0.167	0.167	0.158	0.169	0.172	0.173	0.166	0.187
3	*G. mutatus* S	0.167	0.158	0.163	0.155	0.167	0.164	0.169	0.156	0.177
4	*G. glabrous*	0.194	0.185	0.199	0.190	0.209	0.210	0.204	0.182	0.174
5	*G. affinis*	0.149	0.162	0.190	0.159	0.182	0.179	0.177	0.163	0.163
6	*G. annularis*	0.133	0.162	0.176	0.158	0.173	0.166	0.167	0.154	0.159
7	*G. caldwelli*	0.127	0.153	0.180	0.167	0.166	0.165	0.172	0.167	0.155
8	*G. hendersoni* J	0.189	0.172	0.138	0.187	0.186	0.184	0.193	0.165	0.176
9	*G. hendersoni* S	0.192	0.185	0.146	0.193	0.198	0.193	0.198	0.179	0.181
10	*G. rubriguttatus*	—	0.160	0.182	0.172	0.174	0.169	0.171	0.165	0.166
11	*G. viridis*	100	—	0.164	0.158	0.164	0.162	0.165	0.154	0.150
12	*G. komodoensis*	117	103	—	0.166	0.175	0.173	0.175	0.154	0.187
13	*G. childi* S	107	99	104	—	0.038	0.043	0.021	0.133	0.176
14	*G. childi* Q	111	103	112	24	—	0.025	0.033	0.142	0.180
15	*G. childi* M	109	102	112	27	16	—	0.043	0.136	0.182
16	*G. childi* T	110	104	113	13	21	28	—	0.142	0.181
17	*G. chiragra*	106	97	100	83	91	88	92	—	0.150
18	*G. platysoma*	107	94	121	110	115	118	117	97	—
19	*G. smithii*	107	97	101	98	109	107	106	87	96
20	*H. said*	124	114	82	110	120	115	120	106	123
21	*N. bredini*	120	109	105	109	119	117	117	111	108
22	*N. oerstedii*	119	101	100	105	108	108	110	119	99
23	*H. ensigera*	133	121	128	114	120	124	124	122	120
24	*O. scyllarus*	141	121	119	119	123	127	123	120	119
25	*C. excavata*	109	106	111	95	101	105	104	109	106
26	*C. spinosissima*	108	92	102	97	103	101	107	86	102
27	*H. glyptocercus*	111	92	117	105	104	108	109	97	107
28	*H. hamifera*	110	93	110	93	101	104	101	99	106
29	*H. pulchella*	115	99	108	100	105	107	111	103	104
30	*H. stoliura*	107	97	104	108	120	120	120	105	107
31	*H. trispinosa*	110	116	99	86	96	95	95	93	112
32	*P. ciliata*	127	110	108	101	106	105	108	101	123
33	*T. spinosocarinatus*	107	92	112	105	106	106	115	105	97
34	*P. multituberculata*	119	105	118	109	121	126	120	114	119

Table 2. Continued.

		19	20	21	22	23	24	25	26	27
1	*G. aloha*	0.166	0.182	0.146	0.151	0.204	0.199	0.150	0.154	0.162
2	*G. mutatus* Q	0.172	0.178	0.162	0.158	0.199	0.197	0.146	0.144	0.161
3	*G. mutatus* S	0.163	0.177	0.147	0.150	0.200	0.196	0.149	0.152	0.159
4	*G. glabrous*	0.181	0.188	0.171	0.176	0.203	0.197	0.174	0.173	0.167
5	*G. affinis*	0.174	0.189	0.187	0.187	0.208	0.206	0.176	0.179	0.186
6	*G. annularis*	0.179	0.171	0.184	0.165	0.206	0.200	0.163	0.174	0.178
7	*G. caldwelli*	0.175	0.185	0.187	0.183	0.193	0.191	0.171	0.180	0.186
8	*G. hendersoni* J	0.176	0.149	0.167	0.153	0.203	0.196	0.163	0.156	0.155
9	*G. hendersoni* S	0.181	0.146	0.167	0.162	0.211	0.189	0.174	0.190	0.183
10	*G. rubriguttatus*	0.166	0.193	0.186	0.185	0.207	0.220	0.170	0.169	0.173
11	*G. viridis*	0.154	0.181	0.174	0.161	0.193	0.192	0.169	0.147	0.147
12	*G. komodoensis*	0.156	0.127	0.162	0.155	0.198	0.185	0.172	0.158	0.181
13	*G. childi* S	0.156	0.176	0.175	0.168	0.182	0.190	0.152	0.155	0.168
14	*Go. childi* Q	0.170	0.188	0.186	0.168	0.188	0.193	0.158	0.161	0.163
15	*G. childi* M	0.165	0.179	0.181	0.167	0.192	0.197	0.163	0.157	0.167
16	*G. childi* T	0.164	0.186	0.181	0.170	0.192	0.191	0.162	0.166	0.169
17	*G. chiragra*	0.134	0.165	0.172	0.184	0.189	0.186	0.169	0.134	0.150
18	*G. platysoma*	0.148	0.191	0.167	0.153	0.186	0.185	0.165	0.158	0.165
19	*G. smithii*	—	0.171	0.175	0.178	0.198	0.193	0.168	0.162	0.164
20	*H. said*	110	—	0.178	0.166	0.215	0.205	0.159	0.151	0.186
21	*N. bredini*	113	115	—	0.130	0.199	0.188	0.174	0.176	0.169
22	*N. oerstedii*	115	107	84	—	0.175	0.176	0.162	0.166	0.170
23	*H. ensigera*	128	138	128	113	—	0.184	0.181	0.174	0.186
24	*O. scyllarus*	124	132	121	113	118	—	0.189	0.196	0.179
25	*C. excavata*	108	102	112	104	116	121	—	0.099	0.124
26	*C. spinosissima*	104	97	113	107	112	126	64	—	0.121
27	*H. glyptocercus*	106	120	109	110	120	115	80	78	—
28	*H. hamifera*	107	108	107	115	125	117	84	68	62
29	*H. pulchella*	100	106	107	98	123	106	75	80	69
30	*H. stoliura*	100	111	102	109	120	108	83	81	78
31	*H. trispinosa*	115	107	115	100	121	114	85	84	89
32	*P. ciliata*	121	115	96	99	126	128	100	98	101
33	*T. spinosocarinatus*	124	118	112	95	125	119	103	98	101
34	*P. multituberculata*	115	111	124	101	125	122	100	99	97

		28	29	30	31	32	33	34
1	*G. aloha*	0.160	0.143	0.149	0.167	0.171	0.152	0.151
2	*G. mutatus* Q	0.162	0.155	0.149	0.163	0.180	0.149	0.163
3	*G. mutatus* S	0.155	0.141	0.150	0.168	0.164	0.150	0.144
4	*G. glabrous*	0.172	0.159	0.169	0.179	0.198	0.173	0.173
5	*G. affinis*	0.179	0.174	0.184	0.168	0.194	0.180	0.173
6	*G. annularis*	0.173	0.173	0.163	0.149	0.186	0.172	0.178
7	*G. caldwelli*	0.175	0.173	0.176	0.174	0.197	0.158	0.171
8	*G. hendersoni* J	0.163	0.155	0.153	0.177	0.159	0.170	0.186
9	*G. hendersoni* S	0.172	0.173	0.178	0.168	0.191	0.165	0.188
10	*G. rubriguttatus*	0.171	0.182	0.169	0.172	0.198	0.166	0.185
11	*G. viridis*	0.148	0.158	0.154	0.185	0.175	0.146	0.168
12	*G. komodoensis*	0.170	0.169	0.163	0.154	0.167	0.173	0.183
13	*G. childi* S	0.149	0.160	0.172	0.138	0.162	0.168	0.175
14	*Go. childi* Q	0.158	0.166	0.190	0.150	0.165	0.165	0.189
15	*G. childi* M	0.160	0.168	0.188	0.147	0.162	0.164	0.195
16	*G. childi* T	0.156	0.174	0.188	0.148	0.167	0.178	0.186
17	*G. chiragra*	0.153	0.162	0.164	0.144	0.156	0.162	0.176
18	*G. platysoma*	0.164	0.163	0.168	0.174	0.190	0.150	0.184
19	*G. smithii*	0.165	0.157	0.157	0.179	0.187	0.192	0.178
20	*H. said*	0.168	0.167	0.174	0.167	0.178	0.183	0.172
21	*N. bredini*	0.166	0.168	0.160	0.179	0.149	0.173	0.192
22	*N. oerstedii*	0.178	0.154	0.171	0.155	0.153	0.147	0.156
23	*H. ensigera*	0.194	0.193	0.188	0.188	0.196	0.194	0.194
24	*O. scyllarus*	0.182	0.166	0.169	0.178	0.199	0.185	0.190
25	*C. excavata*	0.130	0.118	0.131	0.132	0.156	0.160	0.155
26	*C. spinosissima*	0.105	0.126	0.127	0.130	0.152	0.152	0.154
27	*H. glyptocercus*	0.096	0.108	0.122	0.138	0.157	0.156	0.150
28	*H. hamifera*	—	0.107	0.132	0.124	0.155	0.159	0.145
29	*H. pulchella*	68	—	0.107	0.126	0.179	0.163	0.145
30	*H. stoliura*	84	68	—	0.146	0.180	0.168	0.170
31	*H. trispinosa*	80	80	93	—	0.170	0.169	0.143
32	*P. ciliata*	100	114	115	109	—	0.167	0.178
33	*T. spinosocarinatus*	103	104	107	109	108	—	0.164
34	*P. multituberculata*	94	92	108	92	115	106	—

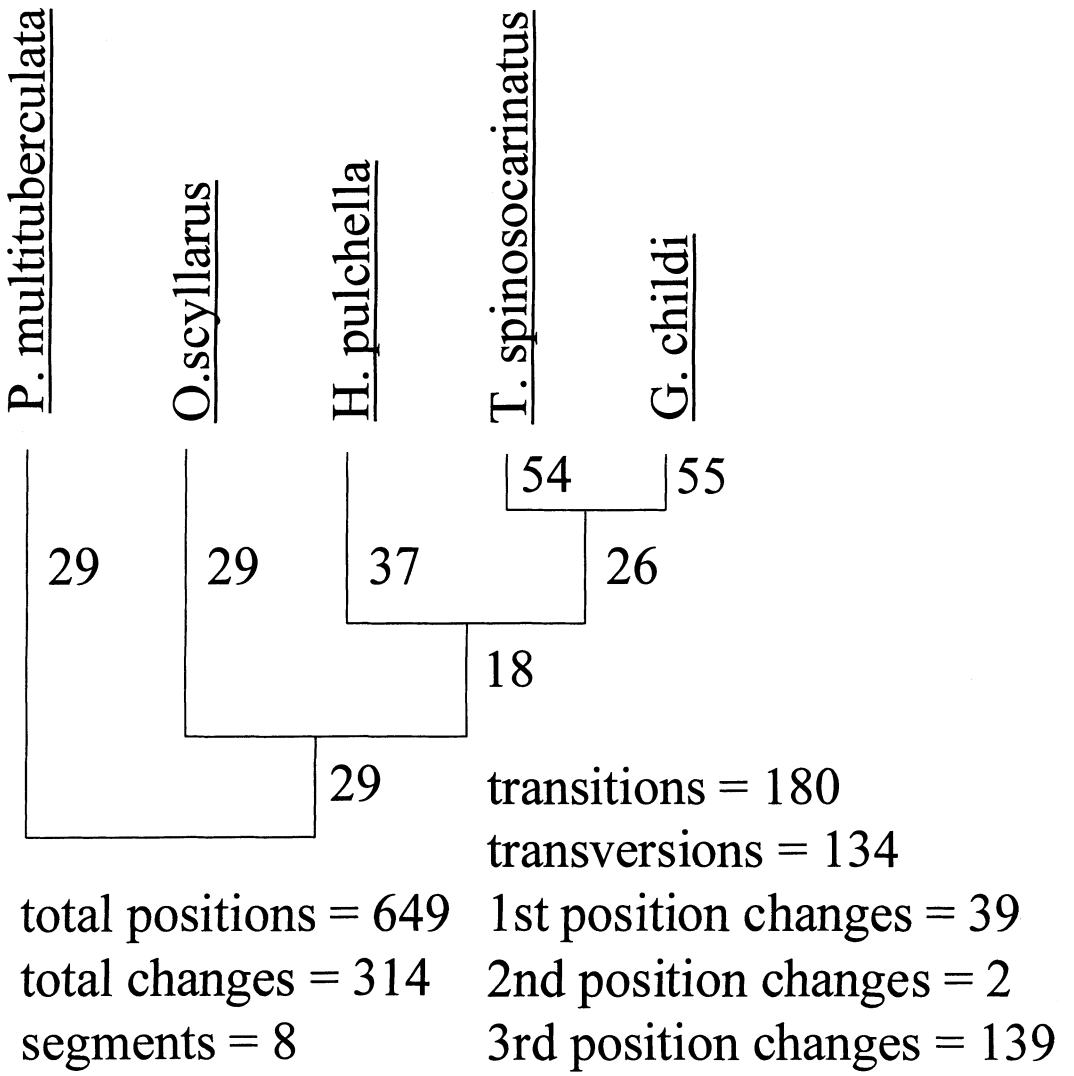

Fig. 2. Topology used to create a codon-specific weighting scheme following the methods of Albert and Mishler (1992), and Albert *et al.* (1993). This method corrects for multiple substitution events, transition/transversion bias, and differential proportions of first-, second-, and third-position changes (Albert and Mishler, 1992; Albert *et al.*, 1993). The basis of this topology was derived from a morphologically based systematic study by Ahyong (1997). Parameters were then calculated from the topology using the sequence data obtained.

tempt to statistically differentiate between trees produced by the various weighting methods. To determine the sensitivity of tree topologies to weighting, a strict consensus tree was constructed using all of the most parsimonious trees obtained from each weighting method.

Results

Sequence Data

The 649 bp fragment of mitochondrial cytochrome oxidase I revealed high levels of sequence divergence between taxa (Table 2). The average uncorrected percentage sequence difference was 16.7% and ranged from 1.4% between *Gonodactylaceus aloha* and *G. mutatus* to 22% between *Odontodactylus scyllarus* Linnaeus and *Gonodactylellus rubriguttatus* Erdmann and Manning. A total of 45 of 277 variable sites resulted in non-silent substitutions. The transition/transversion ratio was 2.3:1. Base composition was A = 27.6%, C = 19.9%, G = 19.5%, and T = 33.0%.

Plotting uncorrected p-distance against Kimura 2-parameter distance revealed complete saturation of third-position transitions,

Table 3. Results of Kishino-Hasegawa test of 11 most parsimonious trees obtained under different weighting schemes. Trees 1–11 were obtained by weighting transitions-transversions differentially. Trees 10–11 were obtained by employing a codon-specific (C.S.) weighting that corrects for multiple substitution events, transition/transversion bias, and differential proportions of first-, second-, and third-position changes (Albert and Mishler, 1992; Albert *et al.*, 1993). Tree 12 is a tree that constrains the Gonodactylidae to monophyly. Likelihood scores were obtained allowing for among-site rate variation, using empirical base frequencies. Rates were assumed to follow a gamma distribution with shape parameter estimated via maximum likelihood with settings for discrete gamma approximation. Number of rate categories = 4. Average rate for each category represented by mean. Transition/transversion ratio estimated via maximum likelihood. Starting branch lengths obtained using Rogers-Swofford approximation method. Molecular clock was not enforced.

Tree	Weighting	–Ln L	Diff –ln L	SD(diff)	*T*	*P*
1	1:1	7520.86	19.67	13.38	1.47	0.14
2	1:1	7517.73	16.54	12.68	1.30	0.19
3	1:1	7518.44	17.26	13.29	1.30	0.19
4	1:1	7515.46	14.28	12.45	1.15	0.25
5	1:2, 1:3	7501.78	0.60	2.17	0.27	0.78
6	1:2, 1:3	7504.17	2.98	3.20	0.93	0.35
7	1:3, 1:4, 1:5	7501.19	(best)			
8	1:3, 1:4, 1:5	7503.46	2.27	2.24	1.01	0.31
9	1:5	7503.85	2.66	2.68	0.99	0.32
10	C.S.	7515.93	14.74	13.12	1.12	0.26
11	C.S.	7513.75	12.57	12.92	0.97	0.33
12	Monophyly	7584.89	83.70	19.60	4.269	<0.0001*

moderate saturation of third-position transversions and some saturation of first-position transitions (Fig. 1). To compensate for this, several weighting schemes were explored for down-weighting transitions (ts:tv = 1:2, 1:3, 1:4, 1:5) with respect to transversions. A sixth weighting scheme employed codon-specific weighting following the methods of Albert and Mishler (1992) and Albert *et al.* (1993). To create the codon-specific weights, data from a subset of the taxa used in this study were constrained to the tree topology of Ahyong (1997). Transition and transversion ratios, as well as number of character-state changes were then estimated from the tree (Fig. 2). Aligned sequences have been deposited into GenBank (accession no. AF205224–AF205257).

Phylogenetics

Phylogenetic analysis implementing six different weighting schemes yielded a total of 11 unique, most parsimonious trees (Table 3). The topology with the lowest Ln likelihood score (ln L = –7,501.19) was obtained under the 1:3, 1:4, and 1:5 transition/transversion-weighting methodologies (Fig. 3), but the Kishino-Hasegawa test (Kishino and Hasegawa, 1989) was unable to statistically differentiate between the resulting topologies. However, the Kishino-Hasegawa test did indicate that all 11 trees obtained under the different weighting methods were significantly shorter than the tree wherein Gonodactylidae was constrained to monophyly ($P < 0.0001$). Bootstrapping and decay analyses were performed using the 1:3 ts/tv weighting. This weight was chosen because it was the lowest weighting that still yielded the most likely tree topology.

A strict consensus tree of the four trees produced with a 1:3 weighting yielded a well-resolved topology (Fig. 4). Much of this structure, however, had relatively low decay values (< 5) and bootstrap support (< 75%), particularly the deeper branches of the topology. Additionally, the strict consensus of all 11 most parsimonious trees produced under the six different weighting schemes (Fig. 5) indicated that the phylogenetic placement of many of the taxa outside the family Gonodactylidae was highly sensitive to the weighting method used. Because of this, many of the deeper phylogenetic relationships implied by the topology must be interpreted with extreme caution.

Five major phylogenetic groupings were found within the sampled genera (Fig. 4). Clade 1 consisted of *Gonodactylus, Gonodactylellus, Gonodactylinus* and *Taku* Manning; clade 2 included *Gonodactylopsis, Hoplosquilla, Gonodactylellus, Pseudosquilla* Manning, and *Neogonodactylus;* clade 3 consisted of the *Gonodactylaceus;* clade 4 was com-

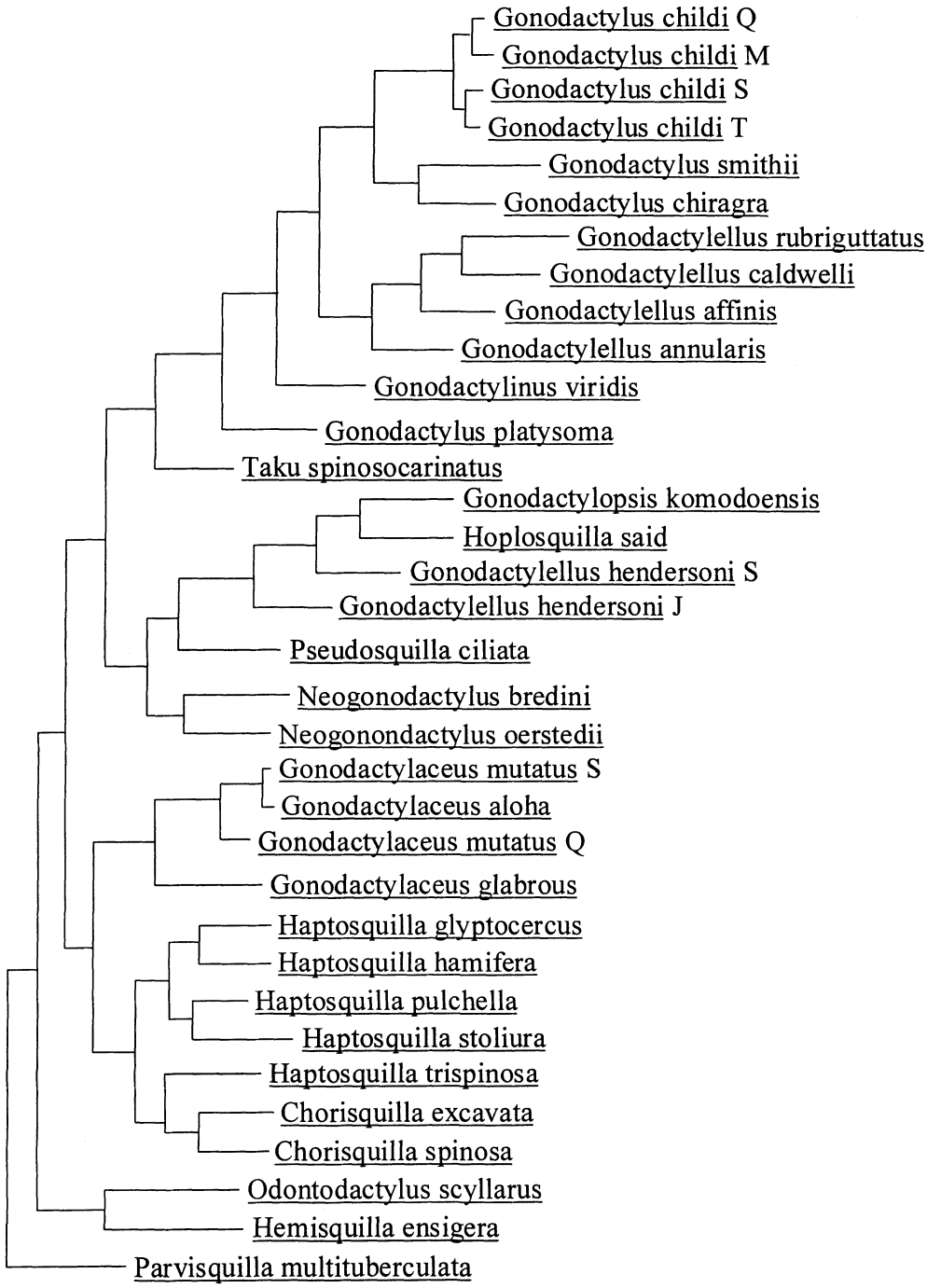

Fig. 3. A phylogram of the best parsimony-based topology of 17 taxa of Gonodactylidae and 12 outgroup taxa as determined by a Kishino-Hasegawa test (Kishino and Hasegawa, 1989). This topology was not significantly shorter ($P > 0.05$) than 10 other trees obtained via parsimony. Tree length is 1,741, CI = 0.274 and RI = 0.494.

posed of *Haptosquilla* Manning and *Chorisquilla* Manning; and clade 5 consisted of *Odontodactylus* Manning and *Hemisquilla* Hansen.

Within clade 1, the majority of *Gonodactylus* species formed a monophyletic group. The four specimens of *G. childi* formed a strongly-supported group (bootstrap 100%, de-

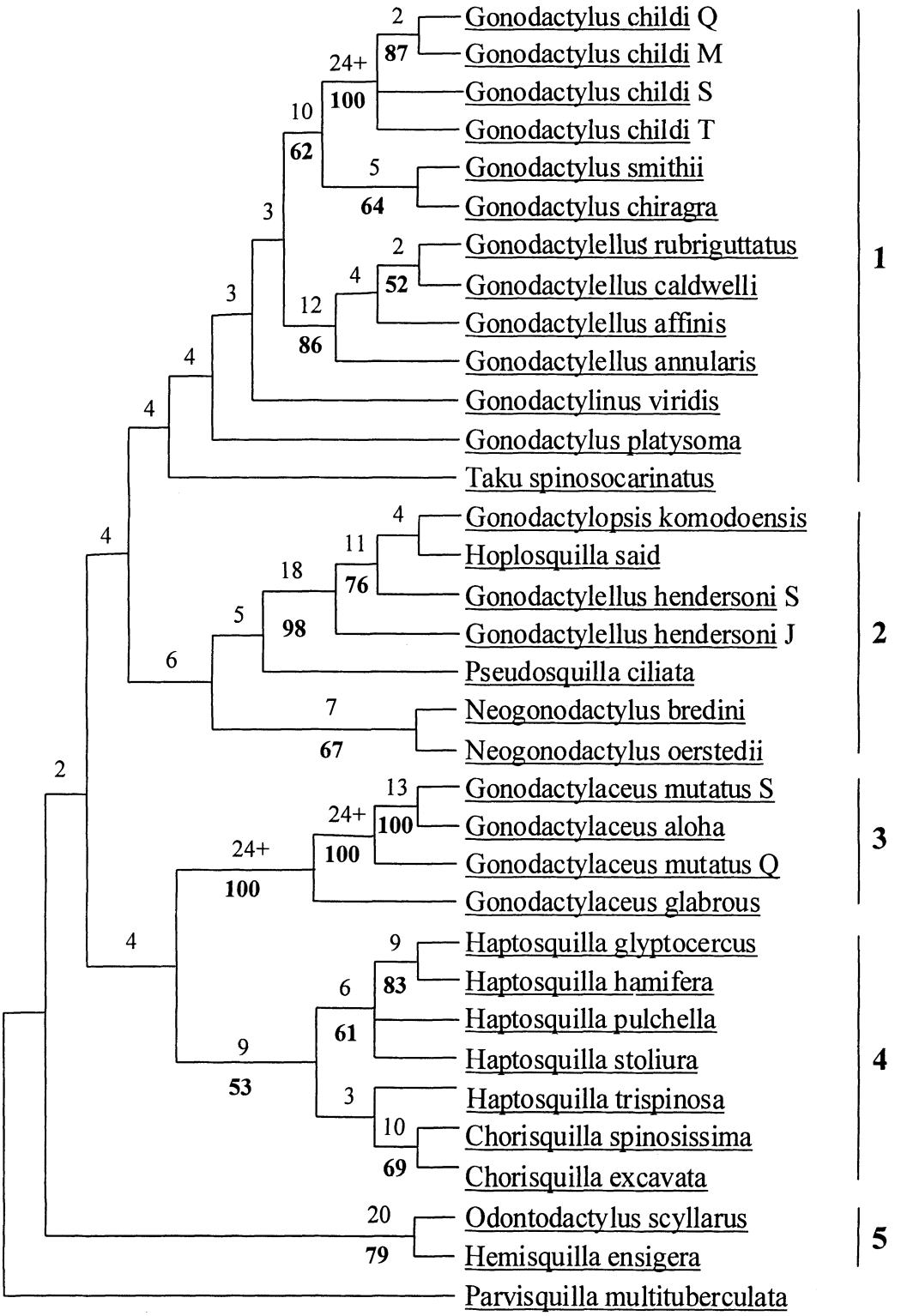

Fig. 4. A strict consensus of four most parsimonious trees of the Gonodactylidae and outgroup taxa obtained from a 3:1 downweighting of transitions with respect to tranversions. Numbers above the nodes are decay values. Numbers in bold below the nodes are bootstrap values (1,000 replicates). Values below 50% are not reported. Numbered bars refer to clades discussed in the text.

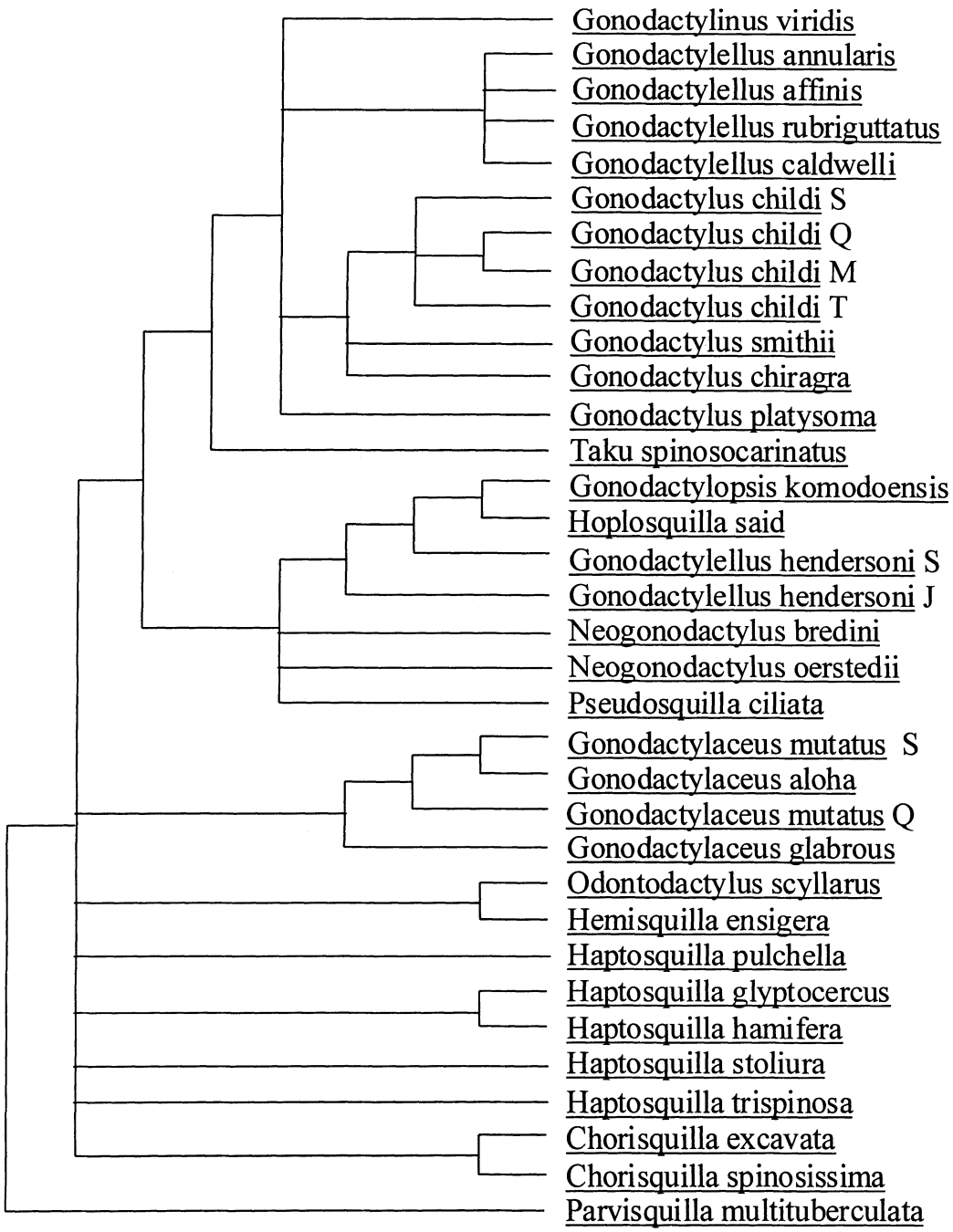

Fig. 5. A strict consensus of eleven most parsimonious trees of the Gonodactylidae and outgroup taxa obtained under six different methods of differentially weighing transitions and trasversions as listed in Table 2.

cay value 24+), with the two south Pacific specimens (Queensland, Australia and Moorea, French Polynesia) more closely related to each other than to specimens from eastern Indonesia. The species *G. childi, G. smithii* Pocock and *G. chiragra* Fabricius are part of a moderately-supported clade of *Gonodactylus* (bootstrap 62%, decay value 10) that was found under all weighting schemes. The remaining species of *Gonodactylus* included in this analysis, *G. platysoma* Wood-Mason, was not part of this clade, and in fact

was found to be more distant from this group than were *Gonodactylinus viridis* Serène and several *Gonodactylellus* species (*G. affinis* de Man, *G. annularis* Erdmann and Manning, *G. caldwelli* Erdmann and Manning, and *G. rubriguttatus* Erdmann and Manning).

In the remainder of clade 1, the four sampled species of *Gonodactylellus* (*G. affinis, G. annularis, G. caldwelli*, and *G. rubriguttatus*) formed a well-supported clade (bootstrap 86%, decay value 12) that is the sister clade of *Gonodactylus* (excepting *G. platysoma*). This clade was recovered under all weighting schemes, although the topology within the group varied. This result supports the taxonomic placement of the three *Gonodactylellus* species recently described by Erdmann and Manning (1998). The next most closely related taxon to the *Gonodactylellus* clade was *Gonodactylinus viridis*, followed by *Gonodactylus platysoma* and *Taku spinosocarinatus* Fukuda. Again, clade 1 was found under all character weightings, although the positions of the basal branches varied.

In clade 2, *Hoplosquilla said* Erdmann and Manning and *Gonodactylopsis komodoensis* Erdmann and Manning formed an extremely well-supported clade (bootstrap 98%, decay value 18) with two individuals of *Gonodactylellus hendersoni* (from Sulawesi and Java). However, the *G. hendersoni* did not form a clade and were found to be highly divergent (14.1% uncorrected sequence divergence). These groupings were unaffected by different character weightings. *Pseudosquilla ciliata* Fabricius was the next most closely related taxon to the above clade, followed by a moderately supported (bootstrap = 67%, decay value = 7) monophyletic grouping of *Neogonodactylus bredini* Manning and *N. oerstedii* Hansen. Like clade 1, clade 2 was found under all character weightings.

Clade 3 was a strongly supported (bootstrap = 100%, decay value = 24+) grouping of *Gonodactylaceus mutatus, G. aloha,* and *G. glabrous* that was found under all weighting schemes. Although the phylogeny indicated that the *Gonodactylaceus* clade was more closely related to *Haptosquilla* and *Chorisquilla* than to the other gonodactylid genera, this relationship was not well supported (bootstrap < 50%, decay value 4) and was highly sensitive to character weighting. Within this clade, *G. mutatus* S from Indonesia was more closely related to *G. aloha* (bootstrap = 100%, decay value = 13) than it was to *G. mutatus* Q from Australia.

Clade 4 consisted of a grouping of the seven members of Protosquillidae examined in this study. Within this clade, *Chorisquilla* was monophyletic. *Haptosquilla* was monophyletic with the exception of *H. trispinosa* Dana, which was the sister taxon of *Chorisquilla*. The placement of *H. trispinosa* within the *Chorisquilla* had low bootstrap and decay analysis support, and likely represents a poorly resolved phylogenetic branch, especially since this relationship was not found under all character weightings.

Clade 5 consisted of a well-supported (bootstrap = 79%, decay value = 20), weighting-insensitive grouping of *Odontodactylus scyllarus* and *Hemisquilla ensigera californiensis* Stephenson. This clade was more distantly related to the Gonodactylidae than were Pseudosquillidae, Protosquillidae, and Takuidae.

Discussion

The high levels of nucleotide substitution saturation (Fig. 1) indicate that CO-I has limited utility in resolving deep phylogenetic structure within the relatively old gonodactyloid stomatopod lineage, and likely within the order Stomatopoda in general. The deeper branches of the topology were highly sensitive to character weighting (Fig. 5) and generally had low decay and bootstrap support (Fig. 4). This result is not surprising given the age of the Gonodactyloidea and the fact that CO-I is a relatively rapidly-evolving mitochondrial gene. Because of the difficulties mentioned above, the deeper phylogenetic relationships indicated in Fig. 4 should be interpreted with caution. For instance, Fig. 4 indicates that the Gonodactylidae are polyphyletic, with members of the Takuidae and Pseudosquillidae being placed within the greater gonodactylid clade, while the gonodactylid genus *Gonodactylaceus* is the sister taxon of Protosquillidae. This result has limited bootstrap and decay-analysis support and is morphologically tenuous. Although previous authors have considered the Takuidae to be a close sister group with the Gonodactylidae (Manning, 1969a; Ahyong, 1997), it is difficult to accept that the morphologically divergent Takuidae are more closely related to *Gonodactylus* than are the *Neogonodactylus*, which are morphologically

extremely similar to *Gonodactylus*. However, the results of the Kishino-Hasegawa test indicate that the data are not concordant with a monophyletic Gonodactylidae ($P < 0.0001$). This result suggests that although it is highly unlikely that the Gonodactylidae form a monophyletic group, the precise relationships that lead to this conclusion cannot accurately be determined.

The relationships between the Gonodactylidae and the Pseudosquillidae, Odontodactylidae and Hemisquillidae also generally received weak bootstrap and decay analysis support, and are difficult to reconcile with current systematic thinking (Fig. 4). Certainly, the evolutionary affinities of these families have long been a subject of speculation. Manning (1968, 1969a) divided the Gonodactylidae (which at that time would have included all gonodactyloid species analyzed herein) into two broad sections, the *Pseudosquilla* section and the *Gonodactylus* section, and he aligned both *Hemisquilla* and *Odontodactylus* with the *Gonodactylus* section, based on overall body shape and the basally-inflated dactylus. Manning (1977) included *Hemisquilla* in the family Pseudosquillidae, but later split the Hemisquillidae from the Pseudosquillidae, citing the differences of large size, globular eye, and unarmed dactylus of *Hemisquilla* as justification (Manning, 1980). Recently, Ahyong's (1997) phylogenetic analysis placed the Hemisquillidae between the Pseudosquillidae and the Odontodactylidae, with the Odontodactylidae closest to the Gonodactylidae. This result was based primarily upon presumed evolutionary changes in the raptorial claw leading from a spearing morphology in the pseudosquillids to the smashing type in the hemisquillids, odontodactylids, and gonodactylids.

Unfortunately, the present analysis provides limited additional information for resolving the relationships between these families. Our analysis provides evidence of a close relationship between *Odontodactylus* and *Hemisquilla*. This result also has both a morphological and ecological basis; members of both taxa have relatively large and robust bodies, with large globular eyes, and are highly colorful subtidal burrow-builders, actively foraging outside of these burrows and using their hardened dactyls to smash prey (Erdmann, personal observation; Caldwell, personal communication). However, *Pseudosquilla* also appears more closely related to the gonodactylids than are *Hemisquilla*, *Odontodactylus*, or even the Protosquillidae (Fig. 4), a result that is difficult to reconcile with the respective morphologies of these taxa. Because of the low support for these branches, we have little confidence in the family-level relationships described in Fig. 4 beyond the close relationship of *Odontodactylus* and *Hemisquilla*.

Despite the limits of CO-I in resolving the deeper relationships among stomatopod lineages, a number of interesting and well-supported relationships at the generic and species level were revealed. Manning's (1995) division of *Gonodactylus* into the five genera *Gonodactylus, Gonodactylaceus, Gonodactylellus, Gonodactylinus*, and *Neogonodactylus* received limited support from the molecular analysis. The results provide strong evidence that *Gonodactylaceus* and *Neogonodactylus* (and the clade including *Gonodactylellus hendersoni*) are each monophyletic and genetically divergent from *Gonodactylus*, and should be considered distinct genera as proposed by Manning (1995). However, the relationships between *Gonodactylinus*, *Gonodactylellus*, and *Gonodactylus* are less clearly defined. Results indicate that *Gonodactylinus* and four of the five species of *Gonodactylellus* analyzed (*G. affinis, G. annularis, G. caldwelli*, and *G. rubriguttatus*) are more closely related to the primary *Gonodactylus* clade (including *G. childi, G. chiragra* and *G. smithii*) than is *Gonodactylus platysoma* (Figs. 3, 4). This suggests that either *G. platysoma* has been incorrectly assigned to the genus *Gonodactylus* or that perhaps *Gonodactylus, Gonodactylinus,* and *Gonodactylellus* (with the exception of *Gonodactylellus hendersoni*) should be collapsed into a single monophyletic genus, *Gonodactylus*.

Morphologically, the latter conclusion is plausible. Manning (1995: 66) himself had expressed reservation at erecting a new genus for *Gonodactylinus viridis*, based primarily on its narrow ocular scales and smaller overall size than the other members of *Gonodactylus*. Similarly, *Gonodactylellus* (formerly the *G. demanii* group of *Gonodactylus,* Manning, 1967b), was also differentiated from *Gonodactylus* based primarily upon its smaller ocular scales and diminutive size. Despite these considerations, bootstrap and de-

cay-analysis support for a single inclusive genus *Gonodactylus* is relatively low, as evidenced by the unresolved polytomy shown for this group in the strict consensus tree (Fig. 5). While our analysis does imply that most analyzed species of *Gonodactylellus* form a natural group, further evidence will be required to determine whether *Gonodactylus*, *Gonodactylellus,* and *Gonodactylinus* are valid genera or if they should be collapsed into *Gonodactylus*.

The results clearly show that *Gonodactylellus* Manning, 1995, is not monophyletic. While the four species discussed above formed a strong monophyletic grouping, two samples of *G. hendersoni* were highly divergent from this group and aligned closely with *Gonodactylopsis komodoensis* and *Hoplosquilla said*. This result is not an indication that the latter two species were improperly assigned to their respective genera; *G. komodoensis* is clearly a member of *Gonodactylopsis* (Manning, 1969b) based upon its sharply trispinous rostral plate, inwardly-curved uropodal endopod, and unusual uropodal setation. Similarly, *H. said* conforms well to the criteria for *Hoplosquilla* (Holthuis, 1964), including no mandibular palp and the unique fixed teeth on the inner margin of the uropodal endopod and exopod. Rather, this genetic grouping indicates that perhaps the morphological characters that are used to separate these taxa have been overly emphasized to the exclusion of the characters that unite them. Manning (1969a) commented that *Gonodactylopsis* and *Hoplosquilla* were morphologically quite similar. Erdmann (1997) listed a number of characters that are shared by these taxa. These characters include: 1) a unique setation pattern on the uropods (no setae on the inner margin of the endopods and the distal segment of the exopod, and incomplete setation on the outer margin of the endopod); 2) a broad telson with three tumescent bosses, each with posterior spines; 3) sharply set-off lateral telson teeth; and 4) a unique inflated boss at the base of each of the submedian and intermediate telson teeth. The strong bootstrap and decay-analysis support for this group suggests that the relationship between *Gonodactylellus hendersoni, Gonodactylopsis komodoensis,* and *Hoplosquilla said* should be formally recognized. Further genetic analysis utilizing other gene regions and increased taxon sampling within these genera should determine whether these taxa should be collapsed into a single genus or perhaps represent a unique family.

As shown above, *Gonodactylaceus* is a strongly supported monophyletic genus, and its placement in the tree topology (Fig. 4) indicates that this group likely split from the other gonodactylids deep in the history of the lineage. This conclusion is concordant with morphology; although *Gonodactylaceus* shares the overall gonodactylid morphology, the five telson carinae and the proximal lobe(s) between spines of the basal prolongation of the uropod clearly separate them from all other gonodactylids. Although *Gonodactylaceus* ranks as the sister taxon to the protosquillids (Fig. 4), there is little support for this grouping in the analysis (bootstrap < 50%, decay index = 4), and such a relationship is inconsistent with morphology.

Within the *Gonodactylaceus*, the results provide strong evidence that *G. aloha* is a synonym of *G. mutatus*. The 1.4% sequence divergence between *G. aloha* and *G. mutatus* S from Indonesia was the lowest encountered in this study (including between the four populations of *Gonodactylus childi*), and all topologies examined support a closer relationship of *G. mutatus* S to *G. aloha* than to its conspecific *G. mutatus* Q. These results are concordant with Kinsey's (1968, 1984) hypothesis that the Hawaiian *G. aloha* simply represents a population of *Gonodactylus falcatus* (now considered *Gonodactylaceus mutatus*) introduced to Hawaii in the 1950s by World War II barges towed from southeast Asia. Manning and Reaka (1981) originally separated *G. aloha* from *G. mutatus* based primarily on perceived color differences. Kinzie (1984) later criticized this, claiming that color evaluations are useless in defining new species. Erdmann (1997) showed that the described color characteristics for *G. aloha* were actually well within the range of color variation observed for over 600 live specimens of *G. mutatus* from Indonesia, and suggested that *G. aloha* be synonymized as *G. mutatus*. The present genetic analysis supports this synonymization.

Although Kinsey (1968) was supported regarding the specific status of *G. aloha*, his 1984 general assertion that color differences are useless for differentiating stomatopod species is not supported by our analysis. The results of the genetic analysis indicate that

Gonodactylellus rubriguttatus and *G. affinis*, two species that were first recognized as distinct by meral-spot color differences (Erdmann and Manning, 1998), are clearly distinct species (14.9% sequence divergence). Consistent color differences between populations can provide evidence of divergence, and the present analysis shows that genetic comparisons can be an excellent tool for substantiating species differences when morphological differences are minimal.

The percentage sequence differences between conspecific representatives of geographically separate populations were substantial and indicated significant genetic population structure within widespread species, although these differences were relatively low compared to the average 16.7% interspecific sequence difference. Percentage sequence differences between the four specimens of *Gonodactylus childi* ranged 2–4.3%, and indicated a closer relationship between the two South Pacific populations than the two Indonesian populations despite the significantly greater distance between Queensland and Moorea. Further testing with multiple specimens from each locality will be required to determine whether this pattern is an artifact of low sample size or possibly an effect of differences in current-mediated larval dispersal within these two regions.

Similarly, percentage sequence differences were also relatively low in the three specimens of *Gonodactylaceus mutatus* examined (including *G. aloha*). Differences here ranged 1.4–5.4%. In contrast, 14.1% sequence difference was found between *Gonodactylellus hendersoni* from Java and Sulawesi. The level of sequence variation found in *G. hendersoni* is similar to that found between congeners in this study, which ranged 9.6–14.6% between the five species of *Haptosquilla* examined, up to 15% between *Gonodactylus chiragra* and *G. platysoma*. It also falls within the observed range of variation seen between species of different genera, which ranged from 10.6% between *Chorisquilla spinosissima* and *Haptosquilla hamifera* to 22% between *Odontodactylus scyllarus* and *Gonodactylellus rubriguttatus*. These results suggest that the two specimens of *Gonodactylellus hendersoni* likely represent two different species, and a detailed morphological comparison of specimens from the Sulawesi and Java populations is currently underway to determine if consistent morphological differences can be documented. Furthermore, the extremely high percentage sequence difference between the two *Gonodactylellus hendersoni* specimens and the four other *Gonodactylellus* species examined (17.4–21.1%) strongly argues for separate generic status for the *G. hendersoni* specimens.

Molecular phylogenetic analysis of DNA sequence data from CO-I provided important insights into the evolutionary relationships among gonodactyloid stomatopods, especially at the species and generic level. However, CO-I had only limited utility in resolving relationships of higher-level taxa. A more conserved gene region, such as the mitochondrial 12s or 16s ribosomal RNA genes, may provide more phylogenetically useful information for resolving deeper relationships. A repeat phylogenetic analysis of the taxa examined herein is currently underway using these alternative markers to help clarify the questionable deep relationships suggested here.

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