

Phylogeny of Mantodea based on molecular data: evolution of a charismatic predator

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Abstract. The previously unknown phylogenetic relationships among Mantodea (praying mantids) were inferred from DNA sequence data. Five genes (16S rDNA, 18S rDNA, 28S rDNA, cytochrome oxidase II and histone 3) were sequenced for sixty-three taxa representing major mantid lineages and outgroups. The monophyly of mantid families and subfamilies was tested under varying parameter settings using parsimony and Bayesian analyses. The analyses revealed the paraphyly of Hymenopodidae, Iridopterygidae, Mantidae, and Thespidae and the monophyly of the Amorphoscelidae subfamily Paraoxyphilinae. All represented subfamilies of Iridopterygidae and Mantidae appear paraphyletic. Mantoididae is sister group to the rest of the sampled mantid taxa. Lineages congruent with current subfamilial taxonomy include Paraoxyphilinae, Hoplocoryphinae, Hymenopodinae, Acromantinae and Oligonicinae. The mantid hunting strategy is defined as either generalist, cursorial or ambush predators. By mapping hunting strategy onto our phylogeny, we reconstructed the ancestral predatory condition as generalist hunting, with three independent shifts to cursorial hunting and one shift to ambush hunting, associated with the largest radiation of mantid species.

Introduction

Comprising 2300 described species distributed in 434 genera (Ehrmann, 2002), Mantodea is a predatory insect group, the members of which occupy a diverse array of widely distributed habitats (Hurd, 1999). Some groups live in dense tropical rainforests distributed around the equator, whereas others reside in arid forests and deserts from Africa to Australia. Mantids show considerable diversification in morphology, hunting strategy and habitat specialization. Despite considerable popularity and their consistent presence in the history of humanity (Prete & Wolfe, 1992), praying mantids have received surprisingly little attention from a phylogenetic or evolutionary standpoint.

With extensive morphological variation, many groups are remarkable in appearance. For example, the arid-dwelling family Eremiaphilidae have reduced wings and elongated legs suitable to their cursorial lifestyles. Females and nymphs of *Nesoxypilus*, a genus of Amorphoscelidae, resemble and live among terrestrial foraging ants (*Rhytidoponera*) in Australia (Milledge, 1990). *Metallyticus* is the only mantid group to

possess metallic coloration (Mukherjee *et al.*, 1995). Species of *Hymenopus*, otherwise known as orchid mantids, are some of the most remarkably camouflaged insects. Besides mimicking ants and flowers, mantids may also resemble brown or green leaves, twigs, tree bark, grass, or have cryptic coloration to hide on the forest floor.

The monophyly of Mantodea is well supported by the presence of raptorial forelegs, a well-defined postclypeus, femoral brush, lamella system, the loss of one denticle in the gizzard and abdominal neuromeres II and III fused to the complex of neuromeres in thoracic segment III and abdominal segment I (Klass, 1998, 1999; Roy, 1999). Although it is clear that Mantodea and the orders Blattaria (cockroaches) and Isoptera (termites) form a monophyletic group, called Blattopteroidea by Hennig (1981) but generally known as Dictyoptera (Kevan, 1977; Richards & Davies, 1977), the relationship between mantids and these other orders has been controversial. A review by Eggleton (2001) outlined the main hypotheses based on molecular and morphological analysis: (1) Mantodea + (Isoptera + Blattaria) (Kristensen, 1995); (2) Isoptera + (Mantodea + Blattaria) (Thorne & Carpenter, 1992; Wheeler *et al.*, 2001); and (3) Mantodea + (Blattaria + (*Cryptocercus* + Isoptera)) (Maekawa *et al.*, 1999; Klass, 2000; Lo *et al.*, 2000; Terry *et al.*, in preparation). This last hypothesis, which places the subsocial cryptocercid cockroaches as sister group to termites, has received the most support in recent analyses.

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Early taxonomic work completed on Mantodea by Beier (1964, 1968) established eight families (Chaeteessidae, Mantoididae, Metallyticidae, Amorphoscelidae, Eremiaphilidae, Hymenopodidae, Empusidae, and Mantidae) and twenty-eight subfamilies, of which twenty-one are included in the largest family Mantidae. The ambiguous grouping of subfamilies in Mantidae and alternative interpretations of taxonomic characters have subsequently spurred several reorganizations, most notably by Roy (1987) and Wang (1993). A new taxonomic scheme proposed by Ehrmann (2002) elevated several mantid subfamilies to familial rank and reorganized the positions of many genera to create a new classification composed of fifteen families and forty-eight subfamilies. In particular, the mantid subfamilies Iridopteryginae, Thespinae, Sibyllinae, Toxoderinae, Liturgusinae, and Tarachodinae were elevated to familial status. Ehrmann (2002) draws attention to the conflict between alternative classification schemes, indicating the confusion which exists in establishing a natural classification for these insects. Although Ehrmann's revision represents the most recent statement on mantid classification, which we follow in this study, this classification, and those which preceded it, was based on no phylogenetic framework. Our work represents the first formal quantitative analysis of mantid phylogeny, and allows us to test the classification scheme put forth by Ehrmann (2002).

Previous work on mantid phylogeny was based only on morphological characters and was untested by formal phylogenetic analysis. Beier (1968) proposed Mantoididae, Chaeteessidae, and Metallyticidae as the 'most basal' families based on similar plesiomorphic character states (e.g. wing venation; Smart, 1956). Similarly, Klass (1997) proposed the same three families as being most basal to the rest of Mantodea, although the study offered resolution to the 'basal splitting events' among these groups. For instance, the topology presented placed Mantoididae as the most basal mantid family (Mantoididae + (Chaeteessidae + (Metallyticidae + other Mantodea))). Additionally, early splitting events among families of Mantodea have been hypothesized using untested scenarios of character evolution. For instance, one such case has been the assumption that basal mantids possess a short prothorax, with the elongation of the thorax occurring only in the more derived taxa (Roy, 1999). Consequently, five mantid families with a short prothorax are grouped together as the most 'primitive' lineages (Chaeteessidae, Mantoididae, Amorphoscelidae, Eremiaphilidae, and Metallyticidae). Roy (1999) proposed that prothoracic elongation progressed gradually in different lineages with possible secondary shortening in some groups. Roy (1999) placed the three families Mantidae (*sensu* Beier, 1968), Hymenopodidae and Empusidae within the superfamily Mantoidea, based on the presence of a relatively elongate pronotum and a clear supracoxal enlargement. However, it is unclear whether this group and its constituent families are monophyletic, and these hypotheses of relationship and character evolution remain to be tested by phylogeny.

Hunting strategies vary greatly among mantids, and the precise hunting style a mantid species employs may depend on habitat selection, geographical location and/or phylogenetic constraints. For example, cursorial mantids actively run on the ground intercepting prey items (Milledge, 1990; Balderson, 1991). Open forest floors and desert habitats are conducive to this strategy, and subsequently most cursorial mantids employ active hunting. Alternatively, the majority of arboreal mantids are ambush predators (Matsura & Inoue, 1999). The chaotic nature of vegetation prevents arboreal mantids from actively pursuing their prey; so waiting for prey items to approach suits an environment that restricts fast locomotion.

Some mantids fit neither ambush nor cursorial lifestyles, but exhibit a wider range of habitat utilization and a more opportunistic hunting strategy. Mantid species which use both ambush and cursorial strategies are generalist mantids. For example, members of the family Iridopterygidae occur on open tree trunks, bare branches, twigs and sometimes on the ground and are generalist predators. Likewise, species of *Bolbe* (Haplomantinae) are found in trees where they may ambush or pursue prey, but in many instances were observed running on open ground far from any trees. Mantids strictly living and actively hunting on the ground will be referred to as 'cursorial', mantids living in vegetation (bushes, trees, grass) and strictly ambushing prey will be referred to as 'ambush', and mantids utilizing both cursorial and ambush lifestyles will be referred to as 'generalists'.

The three main classes of hunting strategy exhibited by mantids have never been investigated from a phylogenetic standpoint to determine whether these strategies are phylogenetically constrained or evolutionary labile. For instance, what is the ancestral hunting strategy? Are ambush mantids derived from cursorial mantids or from more generalist mantids? By addressing hunting strategies in a phylogenetic context we attempt to provide insight into the evolution of mantid predation.

This work presents the first formal phylogeny of Mantodea based on a quantitative analysis of character data. A robust phylogeny based on molecular data allows us to: (1) test the monophyly of mantid families and subfamilies; (2) evaluate the classification scheme of Ehrmann (2002) based on this phylogeny, and (3) evaluate phylogenetic patterns of mantid hunting strategies.

Materials and methods

Outgroup exemplars include five species of Blattaria from four families and three species of Isoptera from three families. Fifty-five ingroup species were selected as exemplars from Mantodea, including Mantoididae (one species), Amorphoscelidae (six species), Hymenopodidae (five species), Empusidae (one species), Liturgusidae (one species), Iridopterygidae (ten species), Thespidae (six species) and Mantidae (twenty-five species) (Table 1). These species represent twenty subfamilies and forty genera. Our distribution of mantid samples is approximately proportional to the

Table 1. List of taxa used in this analysis, with hunting strategies and GenBank accession numbers (absent sequence data are listed as NA).

Family, Subfamily	Species	16S rDNA/18S rDNA/28S rDNA/Cytochrome Oxidase II/ Histone 3	Hunting strategy
Blaberidae	<i>Gromphadorhina portentosa</i>	GPU17787/AY491145/AY491207/AY491266/AY491322	NA
Blatellidae	<i>Supella longipalpa</i>	NA/AY491146/AY491208/NA/AY491323	NA
Blattidae	Blattidae sp.1	NA/AY491147/AY491209/AY491267/AY491324	NA
Blattidae	Blattidae sp.2	CPU38411/AY491148/NA/AY491268/AY491325	NA
Cryptoceridae	<i>Cryptocercus punctulatus</i>	AY491095/AY491149/AY491210/AY491269/AY491326/	NA
Kalotermitidae	<i>Cryptotermes</i> sp.	NA/AY491150/NA/NA/NA	NA
Mastotermitidae	<i>Mastotermes darwinensis</i>	NA/AY491151/AY491211/NA/NA	NA
Termitidae	<i>Nasutitermes</i> sp.	AF262618/AY491152/NA/AF189108/NA	NA
Amorphoscelidae, Paraoxyphilinae	<i>Paraoxyphilus tasmaniensis</i> (Saussure)	AY491096/AY491153/AY491212/AY491270/AY491327	Generalist
Amorphoscelidae, Paraoxyphilinae	<i>Paraoxyphilus</i> sp.2	AY491097/AY491154/AY491213/AY491271/AY491328	Generalist
Amorphoscelidae, Paraoxyphilinae	<i>Gyromantis</i> sp.2	AY491098/AY491155/AY491214/NA/NA	Generalist
Amorphoscelidae, Paraoxyphilinae	<i>Cliomantis obscura</i> (Hinton)	NA/AY491156/AY491215/AY491272/AY491329	Cursorial
Amorphoscelidae, Paraoxyphilinae	<i>Cliomantis cornuta</i> (Giglio-Tos)	AY491099/AY491157/AY491216/AY491273/AY491329	Cursorial
Amorphoscelidae, Paraoxyphilinae	<i>Gyromantis occidentalis</i> (Sjöstedt)	AY491100/AY491158/AY491217/AY491274/AY491331	Cursorial
Empusidae, Empusinae	<i>Gonygylus gonyglodes</i> (Linné)	NA/AY491159/AY491218/NA/AY491332	Ambush
Hymenopodidae, Acromantinae	<i>Acromantis</i> sp.	AY491101/AY491160/AY491219/AY491275/AY491333	Ambush
Hymenopodidae, Acromantinae	<i>Chrysomantis</i> sp.	NA/AY491161/AY491220/AY491276/AY491334	Ambush
Hymenopodidae, Epaphroditidae	<i>Phyllocrania paradoxa</i> (Burmeister)	NA/AY491162/AY491221/AY491227/AY491335	Ambush
Hymenopodidae, Hymenopodinae	<i>Hymenopus coronatus</i> (Olivier)	AY491102/AY491163/AY491222/AY491278/AY491336	Ambush
Hymenopodidae, Hymenopodinae	<i>Pseudocrobotra ocellata</i> (Palisot de Beauvois)	AY491103/AY491164/AY491223/AY491279/AY491337	Ambush
Iridopterygidae, Hapalomantinae	<i>Bolbe</i> sp.1	AY491104/AY491165/AY491224/AY491280/AY491338	Generalist
Iridopterygidae, Hapalomantinae	<i>Bolbe</i> sp.2	AY491105/AY491166/AY491225/AY491281/AY491339	Generalist
Iridopterygidae, Hapalomantinae	<i>Taruchinu</i> sp.	AY491106/AY491167/AY491226/AY491282/AY491340	Cursorial
Iridopterygidae, Nanomantinae	<i>Calogulcinia australis</i> (La Greca)	AY491107/AY491168/AY491227/AY491283/AY491341	Generalist
Iridopterygidae, Nanomantinae	<i>Ima</i> sp.	AY491108/AY491169/AY491228/AY491284/AY491342	Generalist
Iridopterygidae, Nanomantinae	<i>Ima fusca</i> (Tindale)	AY491109/AY491170/AY491229/AY491285/AY491343	Generalist
Iridopterygidae, Nanomantinae	<i>Calofulcinia paraoxyphila</i> (Tindale)	AY491110/AY491171/AY491230/AY491286/AY491344	Generalist
Iridopterygidae, Nanomantinae	<i>Fulcinia punctipes</i> (Werner)	NA/AY491172/AY491231/AY491287/AY491345	Generalist
Iridopterygidae, Tropidomatinae	<i>Chloromantis rhombica</i> (Giglio-Tos)	AY491111/AY491173/AY491232/AY491288/AY491346	Generalist
Iridopterygidae, Tropidomatinae	<i>Neomantis hyalina</i> (Tindale)	AY491112/AY491174/AY491233/AY491289/AY491347	Generalist
Liturgusidae, Liturgusinae	<i>Ciulfina</i> sp.	AY491113/AY491175/AY491234/AY491290/AY491348	Generalist
Mantidae, Amelinae	<i>Amantis reticulata</i> (De Haan)	AY491114/AY491176/AY491235/AY491291/AY491349	Generalist
Mantidae, Amelinae	<i>Litaneutria minor</i> (Scudder)	AY491115/AY491177/AY491236/AY491292/AY491350	Cursorial
Mantidae, Choeradodinae	<i>Choeradodis rhombicollis</i> (Latreille)	AY491116/AY491178/AY491237/AY491293/AY491351	Ambush
Mantidae, Mantinae	<i>Tenodera aridifolia</i> (Stoll)	AY491117/AY491179/AY491238/AY491294/AY491352	Ambush
Mantidae, Mantinae	<i>Tenodera australasiae</i> (Leach)	AY491118/AY491180/AY491239/AY491295/AY491353	Ambush
Mantidae, Mantinae	<i>Plistospilota</i> sp.	AY491119/AY491181/AY491240/AY491296/AY491354	Generalist
Mantidae, Mellerinae	<i>Melliera brevipes</i> (Beier)	AY491120/AY491182/AY491241/AY491297/AY491355	Ambush
Mantidae, Orthoderinae	<i>Orthodera</i> sp.	AY491121/AY491183/AY491242/AY491298/AY491356	Ambush
Mantidae, Oxythessinae	<i>Heterochaetula</i> sp.	AY491122/AY491184/AY491243/AY491299/AY491357	Cursorial
Mantidae, Paramantinae	<i>Mantis religiosa</i> (Linné)	AY491123/AY491185/AY491244/AY491300/AY491358	Ambush
Mantidae, Paramantinae	<i>Archimantis</i> sp.	AY491124/AY491186/AY491245/AY491301/AY491359	Ambush
Mantidae, Paramantinae	<i>Sphodromantis viridis</i> undet. subspecies	AY491125/NA/NA/AY491302/NA	Ambush
Mantidae, Paramantinae	<i>Sphodromantis lineola</i> (Burmeister)	AY491126/AY491187/AY491246/AY491303/AY491360	Ambush
Mantidae, Paramantinae	<i>Rhombodera stalii</i> (Giglio-Tos)	AY491127/AY491188/AY491247/AY491304/AY491361	Ambush
Mantidae, Paramantinae	<i>Hierodula</i> sp.2	AY491128/AY491189/AY491248/AY491305/AY491362	Ambush
Mantidae, Paramantinae	<i>Tamolonica tumolana</i> (Branesik)	NA/AY491190/AY491249/AY491306/AY491363	Ambush
Mantidae, Paramantinae	<i>Tamolonica denticulata</i> (Krauss)	AY491129/AY491191/AY491250/AY491307/AY491364	Ambush
Mantidae, Paramantinae	<i>Hierodula schultzei</i> (Giglio-Tos)	AY491130/AY491192/AY491251/AY491308/AY491365	Ambush
Mantidae, Paramantinae	<i>Statilia apicalis</i> (Saussure)	AY491131/AY491193/AY491252/AY491309/AY491366	Ambush
Mantidae, Paramantinae	<i>Statilia apicalis</i> (Saussure)	AY491132/AY491194/AY491253/AY491310/AY491367	Ambush
Mantidae, Stagmomantinae	<i>Stagmomantis carolina</i> (Johansson)	AY491133/AY491195/AY491254/AY491311/AY491368	Ambush
Mantidae, Stagmomantinae	<i>Stagmomantis vicina</i> (Saussure)	AY491134/AY491196/AY491255/NA/AY491369	Ambush
Mantidae, Stagmomantinae	<i>Stagmomantis limbata</i> (Hahn)	AY491135/AY491197/AY491256/AY491312/AY491370	Ambush
Mantidae, Vatinae	<i>Vates pectinicornis</i> (Stöl)	AY491136/AY491198/AY491257/AY491313/AY491371	Ambush
Mantidae, Vatinae	<i>Phyllovates chlorophaea</i> (Blanchard)	AY491137/AY491199/AY491258/AY491314/NA	Ambush
Mantoididea	<i>Montoida schraderi</i> (Rehn)	AY491138/AY491200/AY491259/AY491315/AY491372	Unknown
Thespidae, Hoplocoryphinae	<i>Hoplocorypha</i> sp.1	AY491139/AY491201/AY491260/AY491316/AY491373	Cursorial
Thespidae, Hoplocoryphinae	<i>Hoplocorypha</i> sp.2	AY491140/AY491202/AY491261/AY491317/AY491374	Cursorial
Thespidae, Oligonicinae	<i>Bantia</i> sp.1	AY491141/AY491203/AY491262/AY491318/AY491375	Generalist
Thespidae, Oligonicinae	<i>Bantia</i> sp.2	AY491142/AY491204/AY491263/AY491319/NA	Generalist
Thespidae, Pseudomipteriginae	<i>Anumiopteryx</i> sp.2	AY491143/AY491205/AY491264/AY491320/AY491376	Ambush
Thespidae, Pseudomipteriginae	<i>Anumiopteryx</i> sp.1	AY491144/AY491206/AY491265/AY491321/AY491377	Ambush

percentage of species found in the mantid families represented in our study: Mantoididae » 0.4% of species ~ 1.8% of samples; Amorphoscelidae » 3.6% of species ~ 10.9% of samples; Hymenopodidae » 9.6% of species ~ 9.0% of samples; Empusidae » 2.2% of species ~ 1.8% of samples; Liturgusidae » 3% of species ~ 2% of samples; Iridopterygidae » 5.4% of species ~ 18% of samples; Thespidae » 8.3% of species ~ 11% of samples; and Mantidae » 49% of species ~ 45% of samples. Seven families were not included (Chaeteessidae, Eremiaphilidae, Metallyticidae, Acanthopidae, Tarachodidae, Toxoderidae, Sibyllidae) due to difficulty in acquiring specimens suitable for DNA extraction. These families are relatively small groups and specific taxa have been difficult to acquire, but efforts are underway to include these taxa in a subsequent analysis. Two families (Chaeteessidae and Metallyticidae) necessary for inclusion in future analyses are important given their putative plesiomorphic morphological characters. Without the inclusion of these two families we cannot identify the deepest/earliest branching relationships. Specimens were identified using current taxonomic keys and the collaborative assistance of several colleagues (see Acknowledgements). In some cases, specimens could not be identified to species and/or genera due to the lack of thorough monographic work on mantids, and therefore are treated as morphospecies with vouchers retained. Mantids were classified as cursorial, ambush or generalist hunters (Table 1) based on reports in the literature for amorphoscelids (Balderson, 1991) or field observations (remaining taxa).

Thoracic and profemoral muscle tissue was excised from specimens preserved in 100% ethanol. DNA was extracted using the Qiagen DNeasy (Valencia, California, U.S.A.) protocol for animal tissue. Specimen and DNA vouchers are deposited in the Insect Genomics Collection (IGC), M. L. Bean Museum, Brigham Young University. Five genes

were targeted for amplification and sequencing: 16S ribosomal DNA (16S rDNA, ~440 bp), 18S ribosomal DNA (18S rDNA, ~1800 bp), 28S ribosomal DNA (28S rDNA, ~2800 bp), histone 3 protein coding for the nucleosome (H3, 329 bp) and cytochrome oxidase II (COII, 600 bp). The primers and protocol utilized for 18S and 28S amplifications are given in Whiting (2002). Additional primer sequences and amplification protocols for 16S rDNA, COII and H3 are provided in Table 2.

DNA regions of the five targeted genes were amplified via the polymerase chain reaction (PCR) on a DNA Engine DYAD™, Peltier Thermal Cycler. The PCR products were visualized using gel electrophoresis to verify amplification and contamination via negative controls. Amplicons were purified via the Montage PCR₉₆ Cleanup Kit (Millipore®) and cycle sequenced with ABI Prism Big Dye® version 3 dye terminator chemistry. Sequencing reactions were column purified with Sephadex™ G-50 Medium and fractionated with an ABI 3730xl DNA analyser. Gene regions were sequenced with complements and sufficient overlap with adjacent regions to ensure the accuracy of sequence data. Sequence data were imported into SEQUENCHER® 4.0 (Genecodes, 1999) for nucleotide editing and contig assembly. Missing data for Isoptera and Blattaria were augmented by four sequences downloaded from GenBank for *Mastotermes darwiniensis* (16S rDNA and COII; Thompson *et al.*, 2000), *Cryptocercus punctulatus* (16S rDNA; Kambhampati *et al.*, 1996) and *Gromphadorhina portentosa* (16S rDNA; Kambhampati, 1995). Genes were initially manually aligned in SEQUENCHER® 4.0 and partitioned into regions at the conserved domains in order to speed up the alignment search strategy. This resulted in multiple gene partitions: 16S rDNA – two regions, 18S rDNA – four regions (congruent with the G, A–D, B–C and E–F domains of 18S), 28S rDNA – seven regions

Table 2. (a) Primer sequences.

Gene	Primer	Sequence
16S	16Sa	5'- CGC CTG TTT ATC AAA AAC AT -3'
	16Sb	5'- CTC CGG TTT GAA CTC AGA TCA -3'
COII	COII 2a	5'- ATA GAK CWT CYC CHT TAA TAG AAC A-3'
	COII Flue	5'- TCT AAT ATG GCA GAT TAG TGC -3'
	COII 9b	5'- GTA CTT GCT TTC AGT CAT CTW ATG -3'
	COII R-lys	5'- GAG ACC AGT ACT TGC TTT CAG TCA TC -3'
H3	HexAF	5'- ATG GCT CGT ACC AAG CAG ACG GC -3'
	HexAR	5'- ATA TCC TTG GGC ATG ATG GTG AC -3'

Table 2. (b) Amplification profiles.

	Hot start	Denature	Anneal	Extension	Final extend	Cycles
16S	95° (12 min)	94° (30 s)	54° (30 s)	72° (1 min)	72° (5 min)	40
COII	95° (12 min)	94° (1 min)	52° (1 min)	72° (1 min 15 s)	72° (1 min)	40
H3	95° (12 min)	94° (1 min)	54° (1 min)	72° (1 min)	72° (10 min)	40

COII, cytochrome oxidase II; H3, histone 3.

(congruent with the A, B1, B2, C, D, E and F domains of 28S), COII – one region and H3 – one region. All partitioned regions were combined in the analyses.

Partitioned gene regions were analysed via direct optimization in *POY* (Gladstein & Wheeler, 1997) and implemented in parallel on an IBM SP-2 supercomputer (<http://marylou.byu.edu/resources.htm>) containing 316 power3 processors (375 MHz). The *POY* search parameters are as follows for equivalent cost ratios '-fitchtrees -maxprocessors 3 -onan -onannum 1 -parallel -noleading -norandomizeoutgroup -impliedalignment -sprmaxtrees 1 -tbrmaxtrees 1 -maxtrees 5 -holdmaxtrees 50 -slop 5 -checkslop 10 -buildspr -buildmaxtrees 2 -random 20 -stopat 25 -multirandom -treefuse -fuselimit 10 -fusemingroup 5 -fusemaxtrees 100 -numdriftchanges 30 -driftspr -numdriftspr 10 -drifttbr -numdrifttbr 10 -slop 10 -checkslop 10 -molecularmatrix 111.txt -seed -1'.

Multiple cost parameters were employed to test the sensitivity of the phylogenetic conclusions to perturbations in parameter values. The goal of sensitivity analysis is not to determine the 'true' analytical parameters *per se*, as these are unknown and unknowable, but rather to test the sensitivity of the phylogenetic conclusions to a wide range of biologically meaningful analytical parameters. We varied the cost ratios for gap insertion, transversion and transition from identity to treating gaps and transversions as four times the cost of transitions (Wheeler, 1995; Wheeler *et al.*, 2001). This resulted in twenty combinations of parameter

values evaluated across the parameter landscape. Additionally, we used the Incongruence Length Difference metric (ILD; Mickevich & Farris, 1981) to measure congruence among data partitions across the range of cost parameters (Table 3). The combination of cost parameter values which maximized dataset congruence by minimizing the ILD value, was retained as the best justified parameter values for phylogenetic estimation (Wheeler *et al.*, 2001), and thus underwent a more exhaustive search (100 random additions for individual gene analyses, 1200 random additions for the total combined analysis). The trees were rooted to Blattaria.

Nodal support was calculated for the combined dataset. Partitioned Bremer support values (Baker & DeSalle, 1997) were calculated from *POY*'s implied alignment using *TREEROT v2b* (Sorenson, 1999) and *PAUP 4.0b10* (Swofford, 2002). Although the implied alignment of *POY* is not intended to be the same as a standard multiple alignment, it is nonetheless the best estimate of a minimal cost multiple alignment and is useful for further phylogenetic investigation. Nonparametric bootstrap values were also calculated using the implied alignment from *POY* (1000 replicates, fifty random additions per replicate, gaps treated as fifth state) in *PAUP 4.0b10*.

The data were also analysed under the maximum likelihood criterion. The best fit likelihood model for the implied alignment of the total combined dataset was determined using *MODELTEST 3.06 PPC* (Posada & Crandall,

Table 3. Lengths for data partitions across twenty cost parameter sets (gap cost : transversion cost : transition cost) and Incongruence Length Difference (ILD) values.

	110	111	210	211	221	310	311	331	410	411
16S	801	1384	927	1520	2212	1019	1615	3033	1109	1706
18S	282	535	407	671	835	521	791	1125	632	905
28S	1780	3076	2554	3983	4974	3218	4718	6797	3849	5411
Ribosomal	2978	5117	4051	6321	8228	4995	7337	11225	5860	8295
Ribosomal ILD	0.039	0.024	0.040	0.023	0.025	0.047	0.029	0.024	0.046	0.033
COII	1326	2854	1324	2850	4230	1324	2853	5570	1325	2853
H3	313	793	313	793	1126	313	793	1446	313	793
Total	4715	8916	5825	10133	13828	6791	11175	18591	7680	12157
Molecular ILD	0.0452	0.0307	0.0515	0.0312	0.0326	0.0583	0.0362	0.0333	0.0589	0.0402

	421	441	621	631	821	841	931	1231	1241	1641
16S	2462	3851	2666	3398	2839	4322	3684	3942	4707	5048
18S	1095	1414	1332	1512	1546	1926	1864	2189	2388	2824
28S	6647	8591	8060	9222	9387	11812	11326	13271	14588	17153
Ribosomal	10517	14240	12506	14593	14337	18672	17523	20213	22519	26091
Ribosomal ILD	0.030	0.027	0.036	0.032	0.039	0.033	0.037	0.040	0.037	0.041
COII	4227	6901	4227	5570	4224	6896	5567	5569	6905	6907
H3	1126	1763	1126	1446	1126	1763	1446	1446	1763	1763
Total	16133	23334	18178	21984	20055	27825	24988	27764	31827	35480
Molecular ILD	0.036	0.035	0.042	0.038	0.047	0.040	0.044	0.049	0.046	0.050

COII, cytochrome oxidase II; H3, histone 3.

1998). A Bayesian analysis was performed with MRBAYES 2.01 (Heulsenbeck & Ronquist, 2001) using model parameters from the calculated best fit model (generations = 1 000 000). The first 80 000 generations were treated as the burn-in and discarded.

Results

Equally weighted gaps, transitions and transversions resulted in the minimal ILD score among datasets for all parameters tested (0.0307; Table 3). This result is consistent with other studies which demonstrate that for complex datasets, treating parameter cost ratios as identity (gap : transversion : transition ratio equals 1) in POY results in the greatest congruence among datasets (Robertson *et al.*, 2004; Whiting *et al.*, 2003). A more thorough search with parameter values set to identity resulted in a single topology accepted as the preferred tree for subsequent analyses and discussion (length = 8913, consistency index = 0.4490, retention index = 0.5908; Fig. 1).

Sensitivity analyses were performed to test the stability of certain nodes to variations in cost parameter values. The results from these analyses are reported in the phylogeny (Fig. 2). These results suggest that some of the deep level relationships (e.g. Mantodea, clades 1 and 2) are stable across a wide range of parameter values, whereas others are stable only under a more narrow range. Overall, the shallow nodes are more stable to parameter perturbations than are the deeper nodes in the topology, suggesting that this topology is moderately stable to fluctuations in parameter values across the landscape.

Nonparametric bootstraps and partitioned Bremer calculations show high levels of nodal support throughout the topology. Based on Bremer and partitioned Bremer values (Table 4), 28S rDNA expressed the majority of signal for all nodes (48%) and provided the greatest signal for deeper level relationships (53%) of any data partition. The majority of signal from 16S (22%) was at the inter- and intrafamilial level. Although 28S rDNA supplied sufficient support at deeper nodes and the terminals to recover the majority of the total combined topology, this gene alone could not recover relationships at the tips of the tree. Besides 28S, subfamilial and terminal relationships were best supported by COII (19%) and similarly by 16S rDNA (17%) and H3 (16%). Both H3 and COII provided their best support for terminal relationships (16 and 19%, respectively) while providing little support for deeper level nodes (12 and 5%, respectively). 18S provided consistently weak support throughout the topology, but was best at recovering deeper level relationships (8%). Of fifty-four nodes on the topology, forty-one were supported by values of 90% or higher for the nonparametric bootstrap, indicating the relative robustness of the topology.

The Bayesian analysis resulted in a topology highly congruent with the parsimony analysis. The major incongruence between Bayesian and parsimony topologies was caused by the inconsistent placement of *Amantis reticulata*,

which is resolved as sister to Iridopterygidae + Liturgusidae + Amorphoscelidae in the Bayesian analysis, but is sister to all ingroup taxa except *Mantoida schraderi*, *Bantia* sp. 1 & 2, and *Plistospilota* sp. in the combined POY analysis (Fig. 1). The position of this taxon finds only weak support in both maximum likelihood and parsimony. Additionally, the Bayesian analysis resolved *Choeradodis rhombicollis* as sister to *Orthodera* sp. The posterior probabilities calculated for the topology were 90% or greater for forty-five of the fifty-four nodes (Fig. 1). The nodes not supported by the Bayesian analysis are labelled as DNS (does not support, Fig. 1).

Mantoida schraderi (Mantoididae) is strongly supported as sister to the rest of the ingroup taxa. Direct optimization produced a topology with basal *Mantoida schraderi* supported by all genes except H3, which expressed a minor (-2) conflicting signal and a bootstrap of 100%. The Bayesian analysis recovered a basal *Mantoida schraderi* with a posterior probability of 100%. The monophyly of Paraoxyphilinae is supported by 18S, 28S and H3 whereas both 16S and COII provide no support, but the placement of Amorphoscelidae is not at the base of Mantodea as predicted by Roy (1999), but rather is nested in a paraphyletic assemblage of Iridopterygidae and Liturgusidae.

Mantidae is a grossly paraphyletic assemblage regardless of whether one follows the classification of Beier (1968) or Ehrmann (2002), who raised many Mantidae subfamilies to a familial level. In fact, a monophyletic Mantidae was found in no sensitivity analysis. Of the seven mantid families included in this analysis, only five had multiple exemplars, and of these five only one (Amorphoscelidae) is potentially monophyletic, which can be tested with the inclusion of taxa from Amorphoscelinae and Perlamantinae in future analyses. Of the twenty subfamilies included in this analysis, fourteen had multiple exemplars, and of these fourteen, five are monophyletic (Hymenopodinae, Acromantinae, Paraoxyphilinae, Oligonicinae and Hoplocoryphinae).

Discussion

Our phylogenetic analysis of Mantodea provides insight into the naturalness of the classification suggested by Ehrmann (2002). Our results suggest that the majority of families and subfamilies are paraphyletic, and that some characters used in current mantid classification are homoplasious. For example, Roy (1999) considered Mantoididae and Amorphoscelidae to be primitive mantid lineages based on the short prothorax. Although the basal position of *Mantoida schraderi* agrees with previous studies (Beier, 1968; Klass, 1997; Roy, 1999), the more apical placement of Paraoxyphilinae (Amorphoscelidae) contradicts Roy's (1999) notion that these characters indicate a primitive mantid lineage. According to our results, the short prothorax in Paraoxyphilinae was derived secondarily, perhaps in association with lifestyle. Therefore, prothorax length is a homoplasious character and classifications using this character should be considered suspect. The

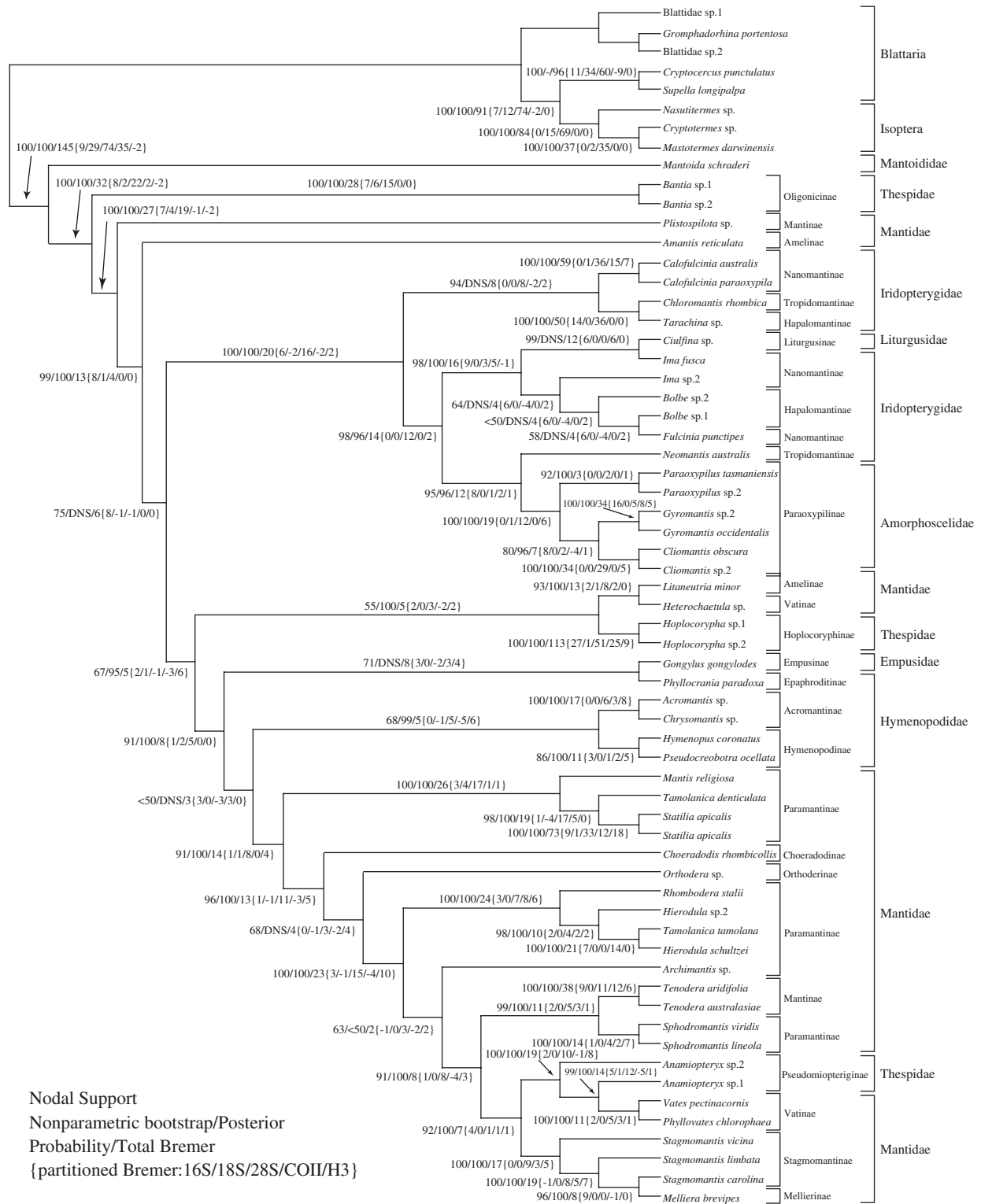


Fig. 1. Direct optimization topology based on five genes (16S rDNA + 18S rDNA + 28S rDNA + cytochrome oxidase II + histone 3) (length = 8913, consistency index = 0.4490, retention index = 0.5908). This topology is largely congruent with the Bayesian analysis topology except for nodes labelled as DNS (does not support). Nodal support is presented in terms of nonparametric bootstraps, followed by posterior probabilities, followed by total Bremer support values. The numbers in parentheses refer to the partitioned Bremer support values given in the order 16S/18S/28S/cytochrome oxidase II/histone 3.

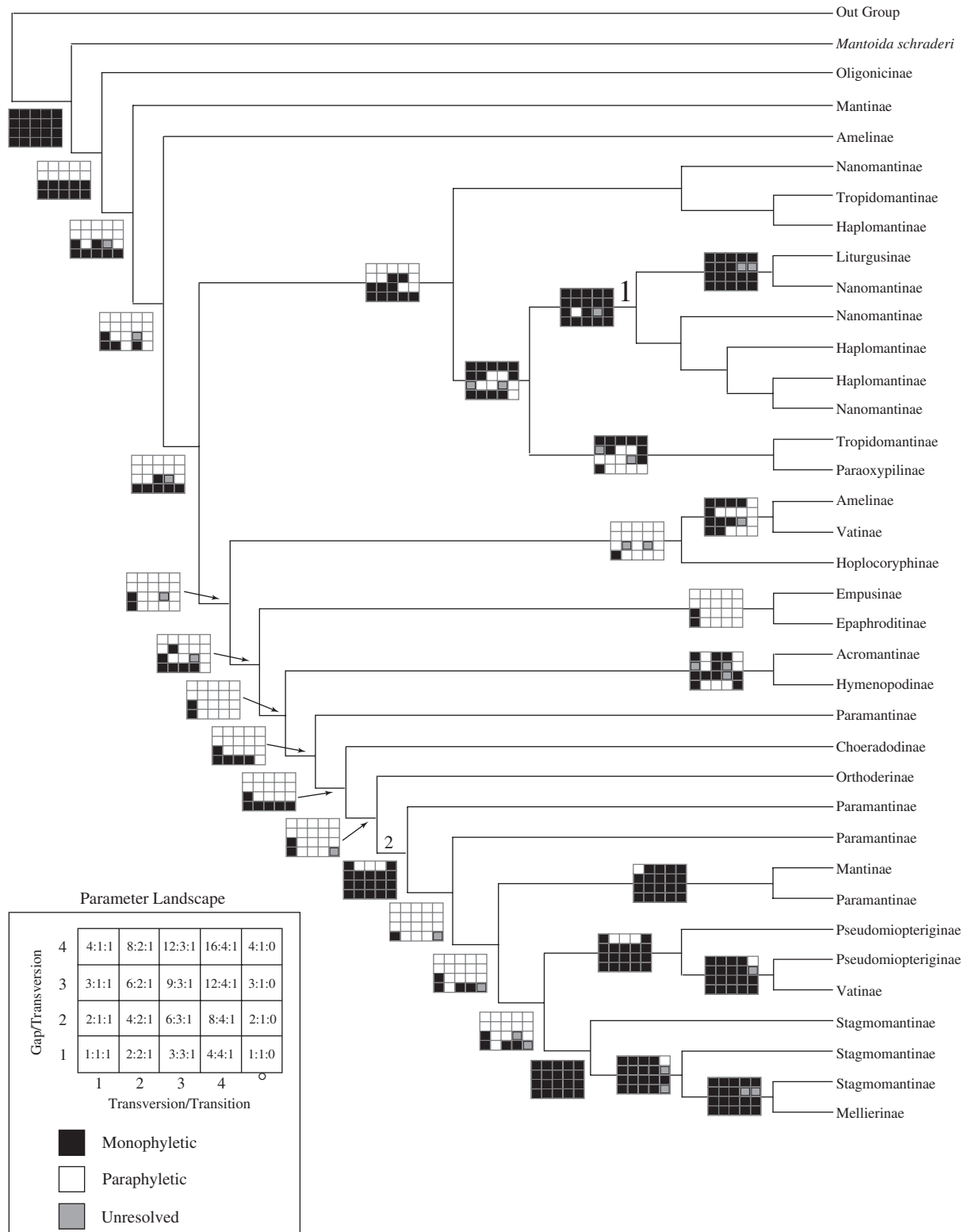


Fig. 2. Direct optimization topology as given in Fig. 1, but with terminals combined at the subfamilial level, with parameter landscapes depicting the results of the sensitivity analysis for deeper nodes. The landscape depicts cost parameter values for twenty parameter combinations, with the monophyly, paraphyly or unresolved status of each node for every combination indicated on the corresponding landscape.

Table 4. Sums of Bremer and partitioned Bremer support values across the topology in Fig. 1.

Nodes	Total Bremer support	Total support					Percentage support				
		16S	18S	28S	COII	H3	16S	18S	28S	COII	H3
Ingroup	1134	238	45	547	141	163	21	4	48	13	14
Interfamilial	418	90	35	223	22	48	22	8	53	5	12
Intrafamilial	716	148	10	324	119	115	21	1	45	17	16
Intrasubfamilial	561	98	10	257	108	88	17	2	46	19	16

COII, cytochrome oxidase II; H3, histone 3.

potential plasticity of prothorax length also leads us to believe that trends in prothorax lengthening are mostly meaningless across the topology. Instead, accurate trends may only be uncovered with thorough taxon sampling.

Hymenopodidae is paraphyletic due to the placement of the empusid *Gongylus gongyloides* as sister to the hymenopodid *Phyllocrania paradoxa*. Support for this relationship is mainly from 16S, COII and H3, whereas 28S provides a conflicting (–2) signal. In the Bayesian analysis, *Gongylus gongyloides* nests within Acromantinae along with Epaphroditinae, making the Hymenopodidae + Empusidae clade monophyletic, although additional sampling from both families is needed to test this relationship.

Our finding that Mantidae is a grossly paraphyletic lineage is not particularly surprising, as this family has historically been a taxonomic ‘grab-bag’ of many divergent taxa including ~80% of the described species (Beier, 1968). A major innovation in Ehrmann’s (2002) work was to raise a number of Mantidae subfamilies to familial status, and to describe additional subfamilies within Mantidae. Ehrmann (2002) elevated the subfamilies Iridopteryginae, Thespiinae, Sibyllinae, Toxoderinae, Liturgusinae and Tarachodinae, formerly placed within Mantidae, to familial status. In addition, the Mantidae was reorganized to include twenty subfamilies. These new families (Iridopterygidae, Thespiidae and Liturgusidae) nest in positions more basal to the majority of the other Mantidae, which appear on the more apical portions of the tree. However, Thespiidae appears to be grossly paraphyletic, with the three representative subfamilies (Hoplocoryphinae, Oligonicinae and Pseudomiopteriginae) broadly separated on the tree. The placement of these taxa make sense in light of predatory strategies (described below) in that Pseudomiopteriginae are ambush mantids which nest among the other ambush mantids, Hoplocoryphinae are cursorial mantids which nest among the other cursorial mantids and Oligonicinae are generalist predators which nest among the other generalist predators in our topology. Our sampling of Liturgusidae is not sufficient to conclude anything about its status as a valid family. For those subfamilies within Mantidae and Iridopterygidae, which include multiple exemplars, none is monophyletic. These results suggest that even the revised classification of Ehrmann (2002) needs further revision to represent mantid phylogeny more accurately.

The evolution of hunting strategy

Although detailed analyses of hunting strategy have yet to be undertaken for a wide variety of mantid species, our analysis shows some broad patterns in the evolution of mantid predation. As described above, the sister group to Mantodea is Blattaria (with Isoptera nested as a subordinate cockroach lineage), and roaches are generalist feeders and scavengers. The ancestral condition within Mantodea appears to be generalist predators which employ a diverse range of strategies for capturing prey. The specific hunting strategy used by the mantid placed basal in our topology (*Mantoida schraderi*) is unknown, but the topology predicts that it should also be a generalist predator.

Generalist mantids originated at the most basal dichotomy within Mantodea, but the largest monophyletic radiation of generalist mantids is exemplified in clade 1 (Fig. 3) which includes an assemblage of three diverse families (Iridopterygidae, Amorphoscelidae and Liturgusidae). If clade 1 is also recovered in future analyses with additional representatives of these three families, then this will represent the largest radiation of generalist predators within Mantodea. Species from this clade live on the bare surfaces of trees on the main trunk or branches. They exhibit cryptic behaviour, holding still to avoid detection, but resort to fast bursts of speed to capture prey. The behaviour of these mantids appears more advantageous to a smooth, unhindered environment as opposed to the complex tangle of vegetation characteristic of ambush mantids.

Within the generalist mantids there are three independent origins of the cursorial strategy, where mantids are restricted to actively hunting on the ground by intercepting prey. Within clade 1 (Fig. 3), the cursorial lifestyle evolved once within the genus *Cliomantis* and once within the clade *Tarachina* + *Chloromantis*. The arid habitat of these three genera suggests that both groups are probably derived from ancestors living on dry scrubland trees. The sister group to *Cliomantis* is *Gyromantis*, and we have observed *Gyromantis* utilizing both tree surface and ground habitats as generalist predators. There appears to be differing degrees of ground utilization throughout Amorphoscelidae, and the group seems to exhibit an intermediate predatory strategy, by searching for prey both on trees and on the ground. Within clade 2, the cursorial predatory strategy was derived once

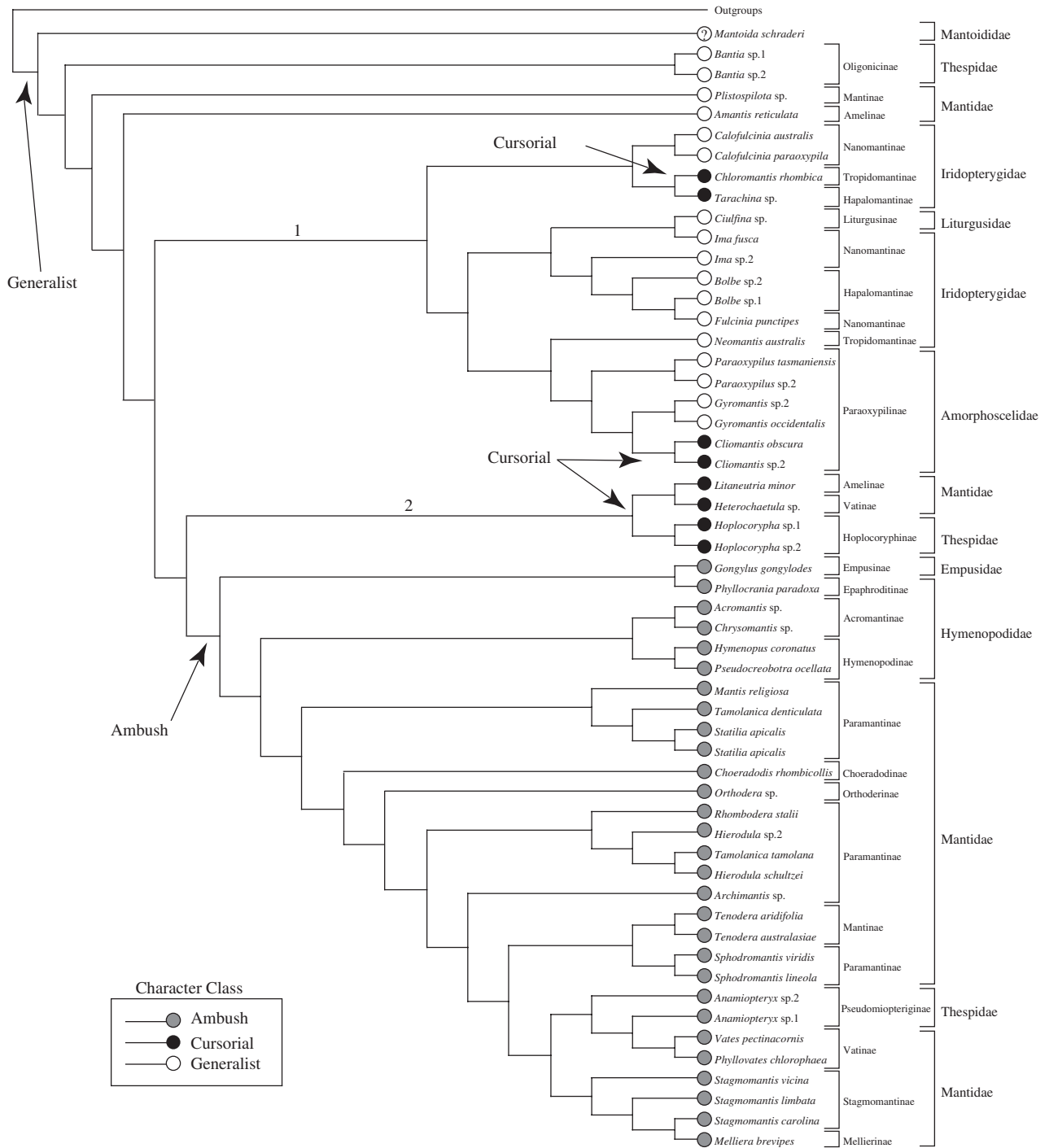


Fig. 3. Direct optimization topology with predatory strategy indicated on the topology and mapped on the nodes. The ancestral condition in mantids is generalist, with two shifts to cursorial strategy in clade 1 and one shift in clade 2. This topology supports a single origin of the ambush strategy. The strategy of *Mantoida schraderi* is unknown.

within the clade comprising *Hoplocorypha*, *Heterochaetula* and *Litaneutria*. Members of this clade are all considered strict cursorial specialists. These taxa are found in the same sort of arid habitat as the other cursorial taxa, suggesting

that these multiple shifts from bark surface dwelling to cursorial specialization are associated with habitat.

All mantids which possess the ambush strategy form a monophyletic group whose apical placement suggests that

this is the most derived hunting strategy. The majority of mantid species fit within this category, suggesting that the shift from generalist to ambush predators was a major innovation in mantid diversification. Hymenopodidae and Empusidae are sister to the rest of the ambush mantids, and both exhibit some of the most specialized morphological adaptations (e.g. *Hymenopus coronatus*, the orchid mantid). It is perhaps significant that we see no shift from ambush predators to cursorial predators, or reversals to the generalist strategy, further indicating that this was an important life shift in the evolution of mantids. We suspect that a shift also occurred in the mantid visual systems, as ambush predators have to orientate to prey in three dimensions, whereas the generalist and cursorial predators essentially hunt in two dimensions. This potential shift will be investigated in a subsequent study which will examine many facets of mantid visual systems.

We have presented the first formal quantitative analysis of mantid phylogeny based on any character system. Although our results are preliminary, and would certainly benefit from the addition of representatives of other mantid lineages, our study suggests that our topology is robust and that mantid classification needs further revision. The majority of families and subfamilies are paraphyletic, and there is a need to score both morphology and molecular data across a wider range of taxa. The predatory strategies employed by mantids appear more congruent with our topology than the current taxonomy, and the shift to ambush predators appears to be a major innovation in the evolution of mantids, leading to a greater diversification of species. Mantids are a fascinating but neglected group of insects, and further work deciphering their phylogenetic relationships will undoubtedly provide valuable insights into the evolution of these charismatic predators.

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