Mantodea vs. BlattodeaA Comprehensive Comparative Analysis

Morphology, Ecology, Behavior, and Molecular Phylogeny within Superorder Dictyoptera

Document Type: Formal Academic Comparative Analysis | Archive Reference: Dictyoptera-CCA-2026

Classification: **Order Mantodea** (praying mantises) & **Order Blattodea** (cockroaches & termites)

Prepared: Friday, 12 June 2026 | Time: 14:29 CDT | Location: Groves, TX, United States

Abstract

This document presents a structured comparative scientific analysis of two orders constituting Superorder Dictyoptera: Mantodea (praying mantises, ~2,400 described species) and Blattodea (cockroaches and termites, ~7,400 described species including Isoptera). Despite sharing a common Dictyopteran ancestor in the Permian (~280–320 Ma), these sister orders have followed profoundly divergent evolutionary trajectories. Mantodea evolved extreme predatory specialization — raptorial forelegs, stereoscopic 3D vision unique among invertebrates, and an unpaired metathoracic ultrasound ear — at the cost of ecological breadth. Blattodea pursued generalist omnivory, high reproductive flexibility, gut microbiome symbioses, and ultimately the evolution of eusociality (termites). All major morphological, ecological, behavioral, and molecular evidence is synthesized, with reference to landmark phylogenomic studies including Schwarz & Roy (2019), Evangelista et al. (2019), and Misof et al. (2014). Open phylogenetic questions and comparative genomics opportunities are

identified.

Keywords: Dictyoptera; Mantodea; Blattodea; Isoptera; raptorial forelegs; ootheca; molecular phylogeny; metathoracic ear; eusociality; Blattabacterium; hemimetabolism; comparative morphology; divergence time estimation

Praying mantis (Order Mantodea) — large compound eyes, raptorial forelegs, elongated prothorax

Figure 1. Representative taxa. Left: A large green mantis (Order Mantodea), illustrating the raptorial foreleg, triangular head with large compound eyes, and elongated prothorax. Right: Blattella germanica (Order Blattodea), illustrating the dorsoventrally flattened body, shield-like pronotum, cursorial legs, and multisegmented cerci.

SECTION 1: INTRODUCTION — THE DICTYOPTERA FRAMEWORK

1.1 Superorder Dictyoptera

Superorder **Dictyoptera** Leach, 1815 is a holophyletic clade of hemimetabolous insects comprising three extant orders: *Mantodea* Burmeister, 1838 (praying mantises), *Blattodea* Brunner von Wattenwyl, 1882 (cockroaches), and *Isoptera* Brullé, 1832 (termites) — the latter now firmly established as a derived, eusocial lineage nested within *Blattodea* rather than a separate order. The superorder is well-supported as monophyletic by both nuclear and mitochondrial molecular markers, and constitutes one of the clearest examples of disparate morphological and ecological divergence from a shared insect ground-plan.

Parameter	Mantodea	Blattodea (incl. Isoptera)
Authority	Burmeister, 1838	Brunner von Wattenwyl, 1882

Parameter	Mantodea	Blattodea (incl. Isoptera)
Accepted classification authority	Schwarz & Roy (2019)	Evangelista et al. (2019)
Approximate described species	~2,400 spp. in ~430 genera, 29 families	~4,600 spp. cockroaches; ~3,100 spp. termites; total ~7,400
Common names	Praying mantises, praying mantids	Cockroaches, termites (white ants)
Development mode	Hemimetabolous (incomplete metamorphosis)	Hemimetabolous (incomplete metamorphosis)
Estimated divergence from sister order	200–260 Ma (Triassic–Jurassic boundary)	200–260 Ma (Triassic–Jurassic boundary)
Dictyoptera crown age	280–320 Ma (Permian) — Misof et al. (2014)	

Current consensus places Dictyoptera as part of the larger clade Polyneoptera, with debated sister-group relationships to *Orthoptera* in some analyses. Monophyly of Dictyoptera is strongly supported by multiple synapomorphies including ootheca production, the unique wing-folding mechanism (tegmina + membranous hindwing), and the 5-5-5 tarsal formula, as well as by comprehensive molecular phylogenomic datasets (Misof et al., 2014).

1.2 Purpose of This Comparison

The scientific rationale for comparing *Mantodea* and *Blattodea* is threefold. First, as confirmed sister groups, they represent the most direct evolutionary comparison possible within Dictyoptera — any differences between them are the product of divergence from a shared common ancestor, not of independent origins. Second, the contrast between the two orders is extraordinarily stark: mantises are specialized sit-and-wait predators with advanced sensory and locomotor adaptations for prey capture, while cockroaches are generalist detritivores and omnivores whose ecological success depends on reproductive

flexibility, chemical communication, and, in the case of termites, extreme social organization. Third, both orders represent important systems for studying fundamental questions in insect biology: the evolution of raptorial appendages, stereoscopic vision in invertebrates, ultrasound hearing, eusociality, gut microbiome evolution, and Hox gene regulation of segment identity.

Key Evolutionary Dichotomy

From a shared Permian ancestor, **Mantodea** specialized as predators (narrow diet, advanced sensory systems, elaborate mimicry), while **Blattodea** diversified as generalists (broad diet, social complexity, gut symbioses, high reproductive output). These two trajectories illuminate the range of evolutionary solutions available to a hemimetabolous insect body plan.

SECTION 2: MORPHOLOGICAL COMPARISON

2.1 Comprehensive Character Comparison Table

The following table presents a systematic comparison of major morphological characters across both orders. Characters are drawn from adult morphology unless otherwise noted. Scientific names follow Schwarz & Roy (2019) for *Mantodea* and Evangelista et al. (2019) for *Blattodea*.

Morphological Character	Mantodea	Blattodea	Notes / Significance
Head orientation	Hypognathous; highly mobile; unique 300°	Prognathous or hypognathous; limited lateral	*Mantodea* unique among Hemimetabola for

Morphological Character	Mantodea	Blattodea	Notes / Significance
	rotation possible	mobility	extreme head mobility
Compound eyes	Large, widely separated, with binocular overlap anteriorly; 3D stereoscopic vision documented (Nityananda et al., 2018)	Moderate size; widely separated on sides of head; primarily motion-detecting	*Mantodea* possess far superior visual acuity; only invertebrate with confirmed 3D vision
Ocelli	3 simple ocelli present in most species; positioned on frons	3 ocelli typically present; reduced or absent in some cave/burrowing species	Plesiomorphic condition; both orders largely retain ocelli
Antennae	Filiform (thread-like); bipectinate (comb-like) in male Empusidae	Filiform; very long; multisegmented (up to 100+ segments)	Similar basic structure; Empusidae elaboration unique to *Mantodea*
Prothorax	Greatly elongated; cylindrical to dorsoventrally flattened; leaf-like in some; varies by family	Short; broad shield-like pronotum; often covers or conceals head from above	Contrasting strategies: mantid elongation for reach; cockroach head-shielding for protection
Forelegs (T1)	Raptorial: coxa elongated (up to 1/3 body length); femur with rows of spines; tibia closes against femur in rapid grasping strike (<60 ms)	Cursorial: standard ambulatory walking leg; no raptorial modifications	**Most diagnostic morphological character separating the orders**
Middle and hind legs (T2, T3)	Ambulatory; slender; unmodified for speed; used for perching and ambush position	Cursorial; spiny; strongly built for rapid running; *Periplaneta americana* achieves ~1.5 m/s	Cockroaches among fastest running insects relative to body size

Morphological Character	Mantodea	Blattodea	Notes / Significance
Wings	Tegmina (leathery forewings) + membranous hindwings; many species brachypterous or apterous (especially females); wing venation taxonomically important	Tegmina + membranous hindwings; many species brachypterous; secondary winglessness common in Blaberidae; some apterous burrowing forms	Both orders show frequent, independent wing reduction; flight rare or weak in many taxa
Abdominal segmentation	10 visible segments; abdomen relatively stiff; less flexion	10 visible segments; abdomen more flexible; allows tighter body compression for crevice entry	Cockroach body flexibility an adaptation to concealed habitats
Cerci	1-segmented; short; limited sensory function	Multisegmented (up to 8 segments); long; highly mechanosensory; detect air movement (wind-sensitive filiform hairs)	Cockroach cerci key anti-predator organ; trigger escape response in <15 ms of air movement
Ootheca (egg case)	Universal; produced by all species; proteinaceous foam hardens to protective case; shape highly variable and taxonomically diagnostic	Present in basal families (Blattidae, Ectobiidae); many families evolved ovoviviparity or viviparity as derived conditions	Shared plesiomorphic character; *Blattodea* shows more derived, varied reproductive modes
Body size range	1 cm (*Bolbe pygmaea*, Amorphoscelidae) to ~17 cm (*Ischnomantis gigas*)	~0.5 cm to ~9 cm (*Macropanesthia rhinoceros*, giant burrowing cockroach)	Both orders span broadly similar size ranges

Morphological Character	Mantodea	Blattodea	Notes / Significance
Body shape	Highly variable: stick-like, leaf-like, elongated, robust, bark-mimicking; enormous variation across families	Generally dorsoventrally flattened; ovoid or elongated; less varied body plan overall	*Mantodea* show greater morphological disparity; cockroaches more stereotyped
Coloration	Highly cryptic: green, brown, bark-textured, sand-colored; some species with flash coloration (blue or purple hindwings)	Typically brown, black, or tan; some tropical species (Blaberidae) colorful; generally less elaborate crypsis	*Mantodea* have more elaborate crypsis and aggressive mimicry (flower-mantids)
Tibial spurs	Present on mid and hind legs	Present; often more robust; aid in rapid locomotion	Present in both; functional context differs
Tarsal formula	5-5-5 (5 tarsomeres on all three leg pairs)	5-5-5	Identical; shared plesiomorphic (ancestral) character within Dictyoptera
Prosternal stridulatory ridge	Present in some Mantidae; used in threat displays	Absent	Autapomorphic feature present in some mantid lineages
Metathoracic ear (tympanal organ)	Present (unpaired "cyclopean" ear) in many lineages; detects bat echolocation ultrasound; evolved independently ≥4 times	Absent; no homologous auditory structure	Unique to *Mantodea*; one of the most remarkable convergent evolutionary origins in insects

2.2 Morphological Synapomorphies (Shared Derived Characters)

The following characters are interpreted as synapomorphies (shared derived traits) supporting the monophyly of Dictyoptera, present in both orders:

Dictyoptera Synapomorphies

- Ootheca production (proteinaceous egg case secreted by accessory glands; secondarily modified or lost in derived Blattodea)
- Hemimetabolous development (three-stage: egg → nymph → adult; no pupal stage)
- 5-5-5 tarsal formula across all leg pairs
- Tegmina (hardened or leathery forewings) protecting membranous hindwings at rest
- Triangular head (broader and more flattened in *Blattodea*; more acute in *Mantodea*)
- Multifaceted compound eye structure with typical ommatidial organization
- Three simple ocelli present in the ancestral ground plan
- Cursorial or pre-cursorial hind leg ground plan (modified to raptorial in *Mantodea*)

2.3 Morphological Autapomorphies (Unique Derived Characters)

Mantodea Autapomorphies

- **Raptorial prolegs (T1):** Greatly elongated coxa; spined femur-tibia grasping mechanism; strike velocity <60 ms — the defining functional character of the order
- **Extreme head mobility:** Up to 300° rotation of the head on the neck; unique in Hemimetabola; enables prey tracking without body movement
- **Metathoracic cyclopean ultrasound ear:** Unpaired tympanal organ in the ventral metathorax; detects bat echolocation; evolved independently ≥4 times (Yager, 1999)
- **Stereoscopic 3D vision:** Binocular overlap in anterior visual field; confirmed by Nityananda et al. (2018) using 3D cinema glasses; unique among all invertebrates
- **Aggressive mimicry apparatus:** Leg-lobe petal mimicry in Hymenopodidae (e.g., *Hymenopus coronatus*); attracts pollinating insects as prey
- **Elongated prothorax (pro-mesothoracic ratio):** Unique among Dictyoptera; enables reach extension during prey capture strike

Blattodea Autapomorphies

- **Flat, rapid-running body plan:** Dorsoventral flattening; cursorial leg modifications; *Periplaneta americana* up to ~1.5 m/s; can traverse vertical surfaces
- **Multisegmented wind-sensitive cerci:** Primary anti-predator sensory organ; triggers escape response in <15 ms
- **Shield-like pronotum:** Covers and protects the head from above;

absent in *Mantodea*

- **Eusocial organization (Isoptera):** Evolved once within *Blattodea*; represented by ~3,100 species of termites with castes, colonies, and division of reproductive labor
- **Ovoviviparity and viviparity:** Multiple independent evolutionary origins within *Blattodea*; absent in *Mantodea*
- ***Blattabacterium* gut endosymbiont:** Obligate nitrogen-recycling endosymbiont; universal in cockroaches; absent in *Mantodea*
- **Gut microbiome for lignocellulose digestion:** Symbiotic bacteria, protozoa, and archaea enabling wood digestion (especially in Cryptocercidae and Isoptera)
- **Greater relative gut length:** Supports detritivore and omnivore ecology; lacks the simplicity of carnivore-adapted mantid gut

SECTION 3: ECOLOGICAL COMPARISON

3.1 Feeding Ecology

Ecological Character	Mantodea	Blattodea
Dietary guild	Obligate carnivore / predator — live animal prey only	Omnivore and detritivore (primarily); occasionally predatory
Diet breadth	Very narrow; restricted to living, moving prey	Extremely broad: decaying matter, dung, fungi, plant material, stored products, carrion, other insects,

Ecological Character	Mantodea	Blattodea
		wood (termites)
Primary prey / food types	Arthropods (insects, spiders); vertebrates (small lizards, frogs, hummingbirds) in large species	Decaying organic matter; stored food products; cellulose and lignin (termites via symbiotic gut fauna)
Gut symbiosis	Minimal to none; simple carnivore-adapted digestive tract	Extensive: *Blattabacterium* (nitrogen recycling); protozoa and archaea in Cryptocercidae & termites (cellulose digestion)
Trophic position	Secondary or tertiary consumer	Primary decomposer; secondary consumer occasionally
Biocontrol / pest value	Documented arthropod pest control (e.g., *Tenodera sinensis* marketed as biocontrol agent); minor economic value	Major urban and stored-product pest species (*Blatta orientalis*, *Periplaneta americana*, *Blattella germanica*); simultaneously vital ecological decomposers
Nutrient cycling role	Minor; mortality returns nutrients through predator excretion	Major; termites among the most important decomposers in tropical ecosystems; contribute to soil aeration and nitrogen cycling
Foraging mode	Sit-and-wait ambush predation; rarely pursuit predation	Active search; central place foraging (termites return to nest); scavenging

3.2 Habitat Use

Habitat Type	Mantodea	Blattodea
Tropical forest	Primary diversity center; maximum	Primary diversity center; enormous

Habitat Type	Mantodea	Blattodea
	species richness in tropical rainforest; foliage, bark, and leaf-litter strata occupied	species richness; all microhabitats occupied from canopy to soil
Desert / arid	Eremiaphilidae: major specialist radiation (~100+ spp.); sand-running, flightless, heat-adapted	Widespread; numerous desert-adapted genera across multiple families
Temperate zone	Present but reduced diversity: *Mantis religiosa*, *Tenodera sinensis*, *Stagmomantis* spp.	Very widespread; most urban pest species are temperate-adapted or cosmopolitan
Cave environments	Absent or exceedingly rare; no confirmed troglobitic mantises	Present; specialized troglobitic cockroaches (e.g., *Nocticola*); blind, depigmented cave-adapted species known
Bark surfaces	Major adaptive zone: Liturgusidae, Metallyticidae, Amorphoscelidae all bark-dwelling	Some species occupy bark; not a primary radiation zone
Urban / synanthropic	Rare; occasional garden visitors; not adapted to human structures	Dominant pest group; *Blattella germanica*, *Periplaneta americana*, *Blatta orientalis* globally distributed via human transport
Soil / burrowing	Absent; no confirmed burrowing mantis species	Present: *Macropanesthia rhinoceros* constructs deep burrows; multiple other burrowing genera
Aquatic / semi-aquatic	Absent	Absent (though some species inhabit moist forest floor near water)

3.3 Activity Patterns

Mantodea are predominantly **diurnal**; most ambush predation occurs during daylight when visual hunting is effective. Males of many species engage in nocturnal dispersal flights, during which the metathoracic ear plays an important bat-evasion role. Conversely, **Blattodea** are predominantly **nocturnal** and strongly photophobic; most foraging and social activity occurs in darkness or in concealed microhabitats. Cave and soil species are entirely non-photic, with no circadian light dependency.

3.4 Population Ecology

Mantodea are characteristically **solitary**, occurring at low population densities. Intraspecific encounters frequently result in cannibalism, reinforcing spacing behavior. No aggregation pheromones are known. In contrast, **Blattodea** are **gregarious to eusocial**: aggregation pheromones (e.g., the aggregation pheromone complex in *Blattella germanica*) promote group formation, high local densities, and resource sharing. Termites represent the pinnacle of social evolution within the order, with colonies of millions of individuals organized into reproductive, worker, and soldier castes.

SECTION 4: BEHAVIORAL COMPARISON

4.1 Anti-Predator Strategies

Anti-Predator Strategy	Mantodea	Blattodea
Crypsis	Highly elaborate: leaf mimicry (*Deroplatys*), bark mimicry, flower mimicry (*Hymenopus*), twig mimicry, grass	Simpler: brown, dark or mottled coloration; flattened silhouette aids concealment; less elaborate

Anti-Predator Strategy	Mantodea	Blattodea
	mimicry; primary defensive strategy	
Thanatosis (death feigning)	Documented in several species; may hold cryptic posture for extended periods	Documented in some species
Deimatic (startle) display	Wing spread revealing bright hindwing patterns; abdomen upturned; rocking display; aimed at vertebrate predators	Minimal; some species produce hissing sounds (e.g., *Gromphadorhina portentosa*)
Chemical defense	Absent; no known chemical defensive secretions	Present in some species: *Diploptera punctata* secretes quinones; defensive glands in some genera
Speed / escape flight	Variable; many species fly poorly; primary escape is crypsis + stillness	Rapid running (up to ~1.5 m/s) primary escape mechanism; cerci detect predator air movement and trigger reflex escape in <15 ms
Stridulation	Present in some species via prosternal ridge rubbing against foreleg coxa	Present in some species; *Gromphadorhina* hissing is well-known
Ultrasound bat evasion	Metathoracic ear detects bat echolocation; triggers power dive or spiral escape flight maneuver (Yager, 1999)	Absent; no tympanal auditory organ
Social alarm response	Absent; solitary; no conspecific alarm	Present in termites: soldier-produced alarm pheromones mobilize nest defense; some cockroaches show aggregation disruption responses

4.2 Reproductive Behavior

Reproductive Character	Mantodea	Blattodea
Mate-finding	Male visual search supplemented by female-produced sex pheromone; females largely stationary	Pheromone-based signaling; sometimes acoustic; aggregation pheromones facilitate encounters
Courtship behavior	Male approaches with characteristic rocking/swaying motion; antenna waving; abdominal displays	Variable by species; typically less elaborate than mantids; stridulation in some
Sexual cannibalism	Present; estimated ~25–35% of wild encounters result in female consuming male; male continues copulation after decapitation (Prete et al., 1999)	Absent in *Blattodea*
Mating system	Largely promiscuous; brief pair bond; no lasting pair relationship	Variable; promiscuous in most cockroaches; strict monogamy in reproductive termite pairs (king and queen)
Egg packaging	Universal ootheca; proteinaceous foam that hardens; shape highly variable and family-diagnostic	Ootheca present in basal families; derived groups evolved ovoviviparity (retain ootheca internally) or viviparity (live birth)
Egg number per ootheca	10–400 eggs depending on species and body size	Typically 10–50 eggs per ootheca in oviparous species
Parental care	None post-oviposition; female deposits ootheca and departs	Present in some cockroaches: *Cryptocercus* (subsocial wood roach) shares hindgut symbionts with nymphs via proctodeal trophallaxis; termites: extensive brood care by

Reproductive Character	Mantodea	Blattodea
		workers
Eusociality	Absent	Present: Isoptera (termites) — most elaborate insect society; overlapping generations, reproductive altruism, caste differentiation, cooperative brood care

4.3 Sensory Biology

Sensory Modality	Mantodea	Blattodea
Vision	Highly developed; large compound eyes with wide binocular overlap; 3D stereoscopic depth perception confirmed (Nityananda et al., 2018); tracks moving prey visually; fovea-like region of higher acuity	Moderate compound eyes; primarily motion detection; limited acuity; many species functionally rely on other senses over vision
Mechanoreception	Body hair sensilla (trichobothria) on abdomen and legs; cerci limited; less emphasis than in cockroaches	Multisegmented cerci bearing wind-sensitive filiform hair sensilla; extremely sensitive to air disturbance; primary near-distance predator detector
Chemoreception	Antennal olfaction for prey, mates, and habitat; well-developed but less complex than cockroach chemosensory system	Highly developed; antennal olfaction mediates food finding, aggregation, sex pheromones, trail pheromones (termites), alarm pheromones; among most complex insect chemosensory systems

Sensory Modality	Mantodea	Blattodea
Audition	Ultrasound detection via metathoracic tympanal ear; sensitive to 25–45 kHz bat echolocation; triggers evasive flight maneuver	No formal tympanal ear; some species detect substrate-borne vibrations via subgenual organs in legs; no airborne acoustic organ
Thermoreception	Poorly studied; thermoreceptors likely present on antennae	Present in some species; temperature gradient detection guides habitat selection and thermoregulatory behavior
Hygroreception	Present; humidity-detecting sensilla on antennae	Well-developed; strongly guides habitat selection; cockroaches preferentially aggregate in humid microhabitats

SECTION 5: MOLECULAR PHYLOGENY AND SYSTEMATICS

5.1 Phylogenetic Position within Insecta

Superorder Dictyoptera is placed within the larger clade **Polyneoptera**, which also includes Orthoptera, Phasmatodea, Dermaptera, Plecoptera, and others. The sister-group relationship between *Mantodea* and *Blattodea* is strongly supported across all modern molecular datasets. The precise sister group of Dictyoptera within Polyneoptera remains debated — Orthoptera is a frequent placement in molecular studies, but topologies vary with taxon sampling and analytical method.

A pivotal modern consensus point is that *Isoptera* (termites) are not a separate order but are nested within *Blattodea* as a derived eusocial lineage most closely related to the wood-feeding cockroach genus *Cryptocercus*. This finding, first strongly supported by Lo et al. (2000) and confirmed by all

subsequent molecular analyses, has fundamentally restructured our understanding of social insect evolution.

5.2 Key Molecular Phylogenetic Studies

Study	Year	Key Findings and Contribution
Kristensen, N.P.	1991	Foundational morphological framework placing Dictyoptera within Polyneoptera; established Mantodea + Blattodea as sister groups using morphological characters
Lo, N. et al.	2000	First strong molecular evidence (18S rRNA, 28S rRNA, CO2 mtDNA) placing Isoptera nested within Blattodea; confirmed *Cryptocercus* as closest cockroach relative to termites
Inward, D. et al.	2007	Comprehensive Dictyoptera molecular phylogeny; provided first robust divergence date estimates for Mantodea–Blattodea split (200–260 Ma); confirmed Isoptera-within-Blattodea
Svenson, G.J. & Whiting, M.F.	2009	First comprehensive molecular phylogeny of Mantodea; key family-level placements; challenged traditional morphological classifications; identified homoplasy problems in external morphology

Study	Year	Key Findings and Contribution
Misof, B. et al. (1KITE)	2014	Landmark phylogenomics study of 1,478 insect species; confirmed Dictyoptera monophyly; robust Polyneoptera topology; estimated Dictyoptera crown at 280–320 Ma; most comprehensive insect phylogenomics dataset to date
Schwarz, C.J. & Roy, R.	2019	Comprehensive revised classification of Mantodea; 29 recognized families; used male genitalia morphology + molecular data; current accepted classification for the order; resolved multiple polyphyletic groupings
Evangelista, D.A. et al.	2019	First nuclear phylogenomic study of entire Blattodea; confirmed blaberoid sister relationships; proposed new clade names (Tutricablattae, Kittrickea, Solumblattodea); showed most Blattodea subgroups diverged in Cretaceous
Ma, Y. et al.	2023	Mitogenomic phylogeny of Mantodea (61 mitogenomes); dated Spinomantodea origin ~149 Ma (Late Jurassic); inferred hearing organ origin in Early Cretaceous (~119 Ma); refuted bat co-evolution hypothesis for ear origin

5.3 Divergence Time Estimates

Phylogenetic Node	Estimated Age	Method	Primary Reference(s)
Dictyoptera crown	280–320 Ma (Permian)	Molecular clock + fossil calibration	Misof et al. (2014)
Mantodea–Blattodea split	200–260 Ma (Triassic–Jurassic boundary)	Molecular clock (Bayesian relaxed)	Inward et al. (2007)
Mantodea crown	130–170 Ma (Jurassic–Cretaceous)	Fossil calibration + molecular clock	Grimaldi (2003); Svenson & Whiting (2009)
Blattodea crown	230–270 Ma (Triassic)	Molecular clock (Bayesian)	Evangelista et al. (2019)
Isoptera origin (within Blattodea)	170–220 Ma (Jurassic)	Molecular clock	Lo et al. (2000); Inward et al. (2007)
Spinomantodea origin	~149 Ma (Late Jurassic)	Mitogenomics + fossil calibration	Ma et al. (2023)
Metathoracic ear origin (Cernomantodea)	~119 Ma (Early Cretaceous)	Mitogenomics + molecular clock	Ma et al. (2023)
Modern Mantidae radiation	60–100 Ma (Cretaceous–Paleogene)	Molecular clock	Schwarz & Roy (2019)

5.4 Shared Molecular Signatures

- **Mitochondrial genome organization:** Both orders retain the standard arthropod mitochondrial gene order, with minor rearrangements independently evolved in each lineage
- **Transposable element (TE) landscape:** Both orders harbor similar classes of TEs; comparative TE analysis across Dictyoptera is an active research area

- **No confirmed Dictyoptera-specific horizontal gene transfers (HGT)** from bacteria have been published to date, though HGT in wood-digesting cockroaches (dehalogenase genes) is under investigation
- ***Blattabacterium* endosymbiont:** Universal in *Blattodea* cockroaches (lost in termites, which evolved alternative nitrogen-recycling strategies); entirely absent in *Mantodea* — a key metabolic synapomorphy of cockroaches

5.5 Convergent Molecular Evolution

- **Independent ootheca losses in *Blattodea*:** Ovoviviparity and viviparity evolved multiple independent times; correlated with changes in reproductive gene expression; *Mantodea* retain ootheca universally
- **Raptorial T1 leg development in *Mantodea*:** Hox gene (*Sex combs reduced*, *Antennapedia*) expression modification in the T1 (prothoracic) segment underpins foreleg raptorial specialization; no orthologous modification in *Blattodea* T1
- **Ultrasound ear evolution in *Mantodea*:** The metathoracic tympanal ear evolved de novo at least 4 independent times within the order; tympanum evolved from pleural sclerite tissue; no structural precursor identified in *Blattodea*
- **3D vision molecular basis:** Binocular integration in mantid visual system likely involves modifications in visual processing neurons and opsin expression patterns; no comparative genomic study yet published

SECTION 6: MASTER SUMMARY COMPARISON TABLE

6.1 Comprehensive Character Matrix

The following table synthesizes all major morphological, ecological, behavioral, and molecular characters discussed above into a single master comparison. Characters are organized by category. "More Derived / Notable" indicates the order in which the character represents a more derived evolutionary state, or the order in which the character is most prominently expressed.

#	Character	Mantodea	Blattodea	Notable / More Derived
MORPHOLOGY				
1	Head mobility	Up to 300° rotation; unique in Hemimetabola	Limited; prognathous or hypognathous; fixed	**Mantodea**
2	Compound eye size and acuity	Large; binocular overlap; stereoscopic; 3D vision	Moderate; motion-detecting; limited acuity	**Mantodea**
3	Foreleg morphology	Raptorial: elongated coxa, spined femur-tibia grasping	Cursorial: standard ambulatory walking leg	**Mantodea**
4	Prothorax form	Greatly elongated; cylindrical to leaf-like	Short; broad; shield-like pronotum covers head	Both (contrasting)
5	Running speed	Slow; not specialized for speed	Fast; up to ~1.5 m/s; cursorial leg adaptations	**Blattodea**
6	Cerci form	1-segmented; short; limited sensory function	Multisegmented (up to 8); wind-sensitive; major anti-	**Blattodea**

#	Character	Mantodea	Blattodea	Notable / More Derived
			predator sensor	
7	Tarsal formula	5-5-5 (plesiomorphic)	5-5-5 (plesiomorphic)	Equal (shared)
8	Wing reduction	Frequent; especially in females; many wingless species	Frequent; secondary winglessness in Blaberidae and burrowing forms	Equal (frequent both)
9	Body shape disparity	Very high: stick, leaf, bark, twig, flower mimics	Lower: primarily flattened ovoid; less polymorphic	**Mantodea**
10	Metathoracic ear	Present; unpaired cyclopean tympanal organ; evolved ≥4×	Absent	**Mantodea**
11	Prosternal stridulatory ridge	Present in some Mantidae	Absent	**Mantodea**
12	Dorsoventral body flattening	Minimal; more cylindrical	Strong; enables entry into very narrow crevices	**Blattodea**
ECOLOGY				
13	Dietary guild	Obligate carnivore / predator	Generalist omnivore / detritivore	Both (contrasting)
14	Diet breadth	Very narrow: live prey only	Extremely broad: nearly any organic material	**Blattodea**
15	Trophic	Secondary/	Primary	Both

#	Character	Mantodea	Blattodea	Notable / More Derived
	position	tertiary consumer	decomposer; secondary consumer rarely	(contrasting)
16	Gut symbiosis	Absent / minimal	Extensive: *Blattabacterium*; protozoa; archaea	**Blattodea**
17	Cellulose digestion	Absent	Present via symbiotic gut fauna (Cryptocercidae, Isoptera)	**Blattodea**
18	Habitat breadth	Broad but absent from caves, soil, and urban environments	Extremely broad: all major terrestrial and subterranean habitats	**Blattodea**
19	Desert specialization	Eremiaphilidae: ~100 spp.; major specialist radiation	Numerous desert-adapted genera across multiple families	Both (significant)
20	Cave adaptation	Absent	Present; troglobitic species with eye reduction, depigmentation	**Blattodea**
21	Synanthropic (urban) success	Rare; not urban-adapted	Dominant pest guild globally; cosmopolitan species via human transport	**Blattodea**
22	Activity pattern	Predominantly diurnal	Predominantly nocturnal;	Both (contrasting)

#	Character	Mantodea	Blattodea	Notable / More Derived
			photophobic	
23	Population density	Low; solitary; territorial cannibalism	High; gregarious to eusocial; aggregation pheromones	**Blattodea**
24	Ecological decomposer role	Negligible	Critical; termites are among Earth's most important decomposers	**Blattodea**
BEHAVIOR				
25	Crypsis elaboration	Extremely elaborate: leaf, bark, flower, twig, grass morphs	Simpler: primarily cryptic coloration; flattened silhouette	**Mantodea**
26	Aggressive mimicry	Present: flower mantids (*Hymenopus coronatus*) lure prey; documented prey attraction	Absent	**Mantodea**
27	Deimatic display	Wing spread; colored hindwing flash; body rocking; abdomen lift	Minimal; *Gromphadorhina* hissing most notable	**Mantodea**
28	Chemical defense	Absent	Present in some; quinone secretions; defensive glands	**Blattodea**
29	Bat evasion	Active: ultrasound	Passive: speed,	**Mantodea**

#	Character	Mantodea	Blattodea	Notable / More Derived
		ear triggers evasive spiral/power-dive maneuver	crevice entry, cerci-triggered escape	
30	Sexual cannibalism	Present; ~25–35% of field encounters	Absent	**Mantodea**
31	Parental care	Absent post-oviposition	Present in some cockroaches (*Cryptocercus*); extensive in termites	**Blattodea**
32	Eusociality	Absent	Present: Isoptera; single origin; most complex insect societies	**Blattodea**
33	Pheromone communication	Sex pheromone only (female attractant for male)	Sex, aggregation, alarm, trail, and brood-care pheromones — highly complex pheromone repertoire	**Blattodea**
34	Social alarm	Absent	Present in termites (soldier alarm pheromones); aggregation cockroaches show disruption responses	**Blattodea**
REPRODUCTION				
35	Ootheca (egg case)	Universal; hard	Present in basal	Equal (plesiomorphi

#	Character	Mantodea	Blattodea	Notable / More Derived
		proteinaceous foam; shape family-diagnostic	families; secondarily modified in derived lineages	c)
36	Viviparity	Absent	Multiple independent origins in Blaberidae and other derived families	**Blattodea**
37	Eggs per ootheca	10–400; highly variable by species	10–50 typically; fewer in ovoviviparous species	**Mantodea (higher max)**
MOLECULAR AND PHYLOGENETIC				
38	*Blattabacterium* endosymbiont	Absent	Universal in cockroaches; absent in termites (replaced)	**Blattodea**
39	Hox gene T1 modification	Present: *Sex combs reduced* expression modified to produce raptorial T1 leg	Absent: T1 leg remains cursorial; standard Hox expression	**Mantodea**
40	Genome size (estimated)	~2.0–3.0 Gb (estimated; *Tenodera sinensis* sequencing underway)	~2.0–3.4 Gb (*Blattella germanica*: 3.4 Gb genome published 2018)	Comparable
41	Described species richness	~2,400 species in 29 families	~7,400 species including Isoptera;	**Blattodea**

#	Character	Mantodea	Blattodea	Notable / More Derived
			~4,600 cockroaches alone	
42	Cryptic species problem	Significant; morphologically conservative genera likely harbor many undescribed species	Significant; molecular barcoding revealing many cryptic species in widespread genera	Both (significant)
43	Fossil record quality	Moderate; Cretaceous amber inclusions abundant; oldest fossils ~140 Ma (Burmantis, Cretaceous)	Excellent; abundant Carboniferous–Permian roachoid fossils; one of oldest insect fossil records	**Blattodea**
44	Convergent evolution frequency	Very high: tympanal ear (≥4×); leaf mimicry (multiple); flower mimicry (multiple)	High: viviparity (multiple); winglessness (multiple); social behavior (subsocial→eusocial)	Both (extensive)
45	Conservation concern	Moderate; habitat specialists vulnerable; some CITES-listed	Generally robust; most species not threatened; some cave-endemic species at risk	**Mantodea (higher risk)**

6.2 Evolutionary Synthesis

> *From a common Dictyopteran ancestor in the Permian (~300 Ma),*
>
> Mantodea
>
> *evolved an extreme predatory specialization — the raptorial foreleg — paired with unmatched sensory innovations (3D stereoscopic vision unique among invertebrates, ultrasound bat-evasion hearing) and elaborate mimicry systems including flower mimicry, leaf mimicry, and bark mimicry, at the cost of reduced ecological breadth: mantises are obligate predators, occurring at low densities, absent from caves and soil, and largely excluded from synanthropic environments.*
>
> Blattodea
>
> *took the opposite evolutionary trajectory: generalist omnivory and detritivory, high reproductive rates with multiple independent evolutions of viviparity, social complexity culminating in eusociality (termites — the most architecturally sophisticated insect societies), cryptic nocturnal dispersal, gut microbiome partnerships enabling cellulose digestion, and a mechanosensory escape system (multisegmented cerci) unparalleled in speed — producing the most ecologically diverse and abundant detritivore insects on Earth. These two contrasting trajectories, arising from the same hemimetabolous ground plan, constitute one of evolutionary biology's most vivid demonstrations of divergent selection from a shared ancestor.*

SECTION 7: RESEARCH FRONTIERS AND OPEN QUESTIONS

7.1 Unresolved Questions in Mantodea

Open Mantodea Phylogenetic and Biological Questions

- **Placement of Metallyticidae:** Whether this morphologically divergent family represents the sister group to all remaining Mantodea (Schwarz & Roy, 2019) or is nested within Schizomantodea remains contested across analytical methods
- **Monophyly of Thespidae:** Strong evidence for polyphyly of this historically large catch-all family; multiple independent origins of the "thespid" morphology are supported by molecular data
- **Cryptic species diversity:** Morphologically conservative genera (e.g., *Rhombodera*, *Hierodula*) likely harbor substantial undescribed diversity; molecular barcoding surveys underway
- **Raptorial foreleg evolution:** Whether the full complement of raptorial modifications (elongated coxa + spined femur + closing tibia) arose in a single origin at the Mantodea crown, or involved parallel elaboration in multiple lineages, is not yet resolved at the genomic level
- **Metathoracic ear evolution:** Ma et al. (2023) provided dates for ear origin but the molecular genetic basis (which genes, which regulatory changes) remains unknown; no Mantodea genome annotation of tympanal organ development published
- **3D vision neural basis:** The retinal and central neural mechanisms underlying mantid stereopsis are under active investigation (Newcastle group); full connectome of the mantid visual system not yet published

7.2 Unresolved Questions in Blattodea

Open Blattodea Phylogenetic and Biological Questions

- **Exact position of *Cryptocercus* + Isoptera divergence:** Whether the termite-cockroach split occurred within a narrowly defined *Cryptocercidae*-sister clade or more broadly within the Kittrickea is not fully resolved (Evangelista et al., 2019)
- **Origins of eusociality:** A single origin of eusociality in the termite ancestor is the consensus, but the pathway from subsocial (*Cryptocercus*-like) to eusocial is debated; molecular correlates of the transition are incompletely known
- **Horizontal gene transfers in wood-digesting cockroaches:** Putative dehalogenase gene HGT events in Cryptocercidae and some Blattodea require verification with complete genome data
- **Blaberidae internal phylogeny:** Relationships within Blaberidae (the most speciose and morphologically diverse cockroach family) remain poorly resolved
- **Viviparity genetic basis:** The genes and regulatory networks underlying the multiple independent origins of viviparity in *Blattodea* are an active comparative genomics target
- **Lost *Blattabacterium* replacement in termites:** Termites lost *Blattabacterium* but retain nitrogen recycling via gut bacteria; the evolutionary transition pathway and gene transfers involved are incompletely characterized

7.3 Comparative Genomics Opportunities

The current state of Dictyoptera genomics presents major opportunities for comparative research. A reference genome for *Tenodera sinensis* (Chinese

mantis) is in progress (as of 2026), and a high-quality annotated genome of *Blattella germanica* (~3.4 Gb) was published in 2018. However, no formal comparative genomic study between a *Mantodea* and a *Blattodea* species has been published to date. Priority targets for comparative analysis include:

- **T1 (prothoracic) Hox gene expression:** Comparison of *Sex combs reduced*, *Antennapedia*, and downstream leg-patterning gene expression in mantid (raptorial) vs. cockroach (cursorial) T1 legs — a rare opportunity to study major functional leg morphology evolution at the molecular level
- **Visual system opsin and retinal gene comparison:** Mantid visual system genes vs. cockroach; expected major divergence in opsin complement and processing neuron gene expression
- **Chemoreceptor gene family evolution:** Cockroaches are predicted to have massively expanded olfactory receptor (OR) gene families relative to mantids, consistent with pheromone complexity difference
- **Tympanal organ development genes:** Identify the genetic toolkit underlying the ≥4 independent origins of the mantid metathoracic ear
- **Reproductive gene divergence:** Ootheca protein genes (mantids: all species); viviparity gene modifications (cockroaches: multiple lineages)

SECTION 8: REFERENCES

8.1 Primary Literature

Bell, W.J., Roth, L.M., & Nalepa, C.A. (2007). *Cockroaches: Ecology, Behavior, and Natural History.* Johns Hopkins University Press, Baltimore. 230 pp.

Evangelista, D.A., Wipfler, B., Béthoux, O., Donath, A., Fujita, M., Kohli, M.K., Legendre, F., Liu, S., Machida, R., Misof, B., Peters, R.S., Podsiadlowski, L., Rust, J., Schuette, K.,

Tollenaar, W., Ware, J.L., Wappler, T., Zhou, X., Meusemann, K., & Simon, S. (2019). An integrative phylogenomic approach illuminates the evolutionary history of cockroaches and termites (Blattodea). *Proceedings of the Royal Society B: Biological Sciences*, 286(1895), 20182076. https://doi.org/10.1098/rspb.2018.2076

Grandcolas, P. (1993). The origin of biological diversity in the family Blaberidae (Insecta, Dictyoptera, Blattaria): a phylogenetic analysis. *Journal of Zoological Systematics and Evolutionary Research*, 31(3), 169–182.

Grimaldi, D. (2003). A revision of Cretaceous mantises and their relationships, including new taxa (Insecta: Dictyoptera: Mantodea). *American Museum Novitates*, 3412, 1–47.

Grimaldi, D. & Engel, M.S. (2005). *Evolution of the Insects.* Cambridge University Press, Cambridge. 755 pp.

Inward, D., Beccaloni, G., & Eggleton, P. (2007). Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. *Biology Letters*, 3(3), 331–335. https://doi.org/10.1098/rsbl.2007.0102

Kristensen, N.P. (1991). Phylogeny of extant hexapods. In: CSIRO (Ed.), *The Insects of Australia* (2nd ed., Vol. 1, pp. 125–140). Melbourne University Press, Melbourne.

Lo, N., Tokuda, G., Watanabe, H., Rose, H., Slaytor, M., Maekawa, K., Bandi, C., & Noda, H. (2000). Evidence from multiple gene sequences indicates that termites evolved from wood-feeding cockroaches. *Current Biology*, 10(15), 801–804. https://doi.org/10.1016/S0960-9822(00)00561-3

Ma, Y., Zhang, L.P., Lin, Y.J., Yu, D.N., Storey, K.B., & Zhang, J.Y. (2023). Phylogenetic relationships and divergence dating of Mantodea using mitochondrial phylogenomics. *Systematic Entomology*, 48(4), 673–689. https://doi.org/10.1111/syen.12596

Misof, B., Liu, S., Meusemann, K., et al. (2014). Phylogenomics resolves the timing and pattern of insect evolution. *Science*, 346(6210), 763–767. https://doi.org/10.1126/science.1257570

Nityananda, V., Joubier, A., Rubin, S., Tarawneh, G., & Read, J.C.A. (2018). A novel form of stereo vision in the praying mantis. *Current Biology*, 28(4), 588–593.e4. https://doi.org/10.1016/j.cub.2018.01.012

Prete, F.R., Wells, H., Wells, P.H., & Hurd, L.E. (Eds.) (1999). *The Praying Mantids.* Johns Hopkins University Press, Baltimore. 362 pp.

Schwarz, C.J. & Roy, R. (2019). The systematics of Mantodea revisited: an updated classification incorporating multiple data sources (Insecta: Dictyoptera). *Annales de la Société entomologique de France (N.S.)*, 55(2), 101–196. https://doi.org/10.1080/00379271.2018.1556567

Svenson, G.J. & Whiting, M.F. (2009). Reconstructing the origins of praying mantises (Dictyoptera, Mantodea): the roles of Gondwanan vicariance and morphological convergence. *Cladistics*, 25(5), 468–514. https://doi.org/10.1111/j.1096-0031.2009.00263.x

Yager, D.D. (1999). Structure, development, and evolution of insect auditory systems. *Microscopy Research and Technique*, 47(6), 380–400. https://doi.org/10.1002/(SICI)1097-0029(19991215)47:6<380::AID-JEMT3>3.0.CO;2-P

Yager, D.D. (1999). Hearing in mantises: structure, function, and evolution. In Prete, F.R. et al. (Eds.), *The Praying Mantids*. Johns Hopkins University Press, Baltimore. pp. 93–113.

8.2 Supporting References

Adis, J., Zompro, O., Moombolah-Goagoses, E., & Marais, E. (2002). Gladiators: a new order of insect. *Scientific American*, 287(5), 60–65.

Beccaloni, G.W. (2014). *Cockroach Species File Online*. Version 5.0. Available at: http://cockroach.speciesfile.org

Brannoch, S.K., Wieland, F., Rivera, J., Klass, K.D., Béthoux, O., & Svenson, G.J. (2017). Manual of praying mantis morphology, nomenclature, and practices. *ZooKeys*, 696, 1–100. https://doi.org/10.3897/zookeys.696.12542

Ware, J.L., Litman, J., Klass, K.D., & Spearman, L.A. (2008). Relationships among the major lineages of Dictyoptera: the effect of outgroup selection on dictyopteran tree topology. *Systematic Entomology*, 33(3), 429–450. https://doi.org/10.1111/j.1365-3113.2008.00424.x

Wieland, F. (2013). *The phylogenetic system of Mantodea (Insecta: Dictyoptera).* Species, Phylogeny and Evolution 3(1–2): 3–91. Pensoft Publishers, Sofia.

Zhou, X., Song, F., Cumming, R.T., et al. (2022). Wingless cockroach genomes illuminate the origins of the eusocial termites. *PNAS*, 119(15), e2110363119. https://doi.org/10.1073/pnas.2110363119
