

# INSECT MOUTHPARTS: Ascertaining the Paleobiology of Insect Feeding Strategies

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## ABSTRACT

One of the most intensively examined and abundantly documented structures in the animal world is insect mouthparts. Major structural types of extant insect mouthparts are extensive, consisting of diverse variations in element structure within each of the five mouthpart regions—labrum, hypopharynx, mandibles, maxillae, and labium. Numerous instances of multielement fusion both within and among mouthpart regions result in feeding organs capable of ingesting in diverse ways foods that are solid, particulate, and liquid in form. Mouthpart types have a retrievable and interpretable fossil history in well-preserved insect deposits. In addition, the trace-fossil record of insect-mediated plant damage, gut contents, coprolites, and insect-relevant floral features provides complementary data documenting the evolution of feeding strategies during the past 400 million years.

From a cluster analysis of insect mouthparts, I recognize 34 fundamental mouthpart classes among extant insects and their geochronological evolution by a five-phase pattern. This pattern is characterized, early in the Devonian, by coarse partitioning of food by mandibulate and piercing-and-sucking mouthpart classes, followed by a rapid rise in herbivore mouthpart types for fluid- and solid-feeding during the Late Carboniferous and Early Permian. Mouthpart innovation during the Late Triassic to Early Jurassic added mouthpart classes for fluid and aquatic particle-feeding. This ecomorphological expansion of mouthpart design was associated with the radiation of holometabolous insects, especially Diptera. The final phase of mouthpart class expansion occurred during the Late Jurassic and Early Cretaceous, with addition of surface-fluid-feeding mouthpart classes that

subsequently became important during the ecological expansion of angiosperms. Conclusions about the evolution of mouthpart design are based on the mapping of phenetic mouthpart classes onto (ideally) cladistic phylogenies of lineages bearing those same mouthpart classes. The plotting of phenetic and associated ecological attributes onto baseline phylogenies is one of the most important uses of cladistic data.

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## INTRODUCTION

One of the most intensively studied structures among animals is insect mouthparts. Although reasons for the extensive literature addressing insect mouthpart structure are as varied as insects themselves, three major aspects are central. First, because insects are ubiquitous residents of virtually all terrestrial and freshwater habitats and have elevated taxonomic diversity and ecomorphologic disparity, their mouthparts represent a broad spectrum of feeding modes that are ideal for comparative studies. Second, insect mouthparts represent one of the most externally complex, yet structurally integrated and homologous morphologies known (67, 206, 317), such that detailed studies can be made of element and multielement innovations in the conversion of one mouthpart type to another (65, 44) or in the convergence toward a mouthpart type among unrelated lineages (3, 185, 239). Third, considerable effort in understanding economically related consequences of insect feeding, particularly in agricultural fields such as pest control, crop pollination, and the transmission of insect-vectored diseases, historically has required a fundamental understanding of mouthpart structure and function. However, only recently have this complex structural system and its ecological correlates been placed in a phylogenetic context. In this review I provide a synopsis of the geochronologic deployment of insect mouthpart types and, in particular, detail the role that paleobiology has to offer in recapturing the pattern of the ecological partitioning of food resources by insects during the past 400 million years.

## INSECT MOUTHPARTS IN PERSPECTIVE

### *Basic Patterns of Insect Mouthparts*

The head capsule of insects appears to be subdivided into six regions that correspond to embryonic segments (215, but see 271), of which five bear mouthpart appendages that are relevant for documentation of insect mouthpart structure in the fossil record and the evolution of insect feeding strategies (43, 172). In a generalized mandibulate insect such as a grasshopper, the head capsule is characterized by two dorsolaterally placed compound eyes, three median ocelli

located frontally at the vertices of a small inverted triangle, and the anatomically ventral mouthparts borne on five regions. The most anteriorly positioned mouthpart is a median flap known as the labrum, which is the "upper lip" that contains an inner membranous surface rich in sensilla, the epipharynx. Posterior of the labrum is the centrally positioned, medial, and tongue-like hypopharynx, which is laterally encompassed by articulating mandibles. The two similar posteriormost regions consist of a pair of proximal and distal sclerites that are separate in the laterally positioned maxillae but fused in the posteriormost labium into a mesal "lower lip." Both the maxillae and the labium have laterally attached, multisegmented palps, fleshy inner lobes, and often sclerotized, sometimes elongated outer lobes. For the maxillae, these lobes are known respectively as the galeae and laciniae, whereas in the labium they are termed the glossae and paraglossae. Placement of mouthparts on the head ranges from the hypognathous condition described above to those that are angulated posteriorly, as in the opisthognathous mouthparts of cicadas, and those that are directed forward, such as prognathous ground beetles.

### *Interesting Deviations*

The generalized mandibulate condition, found in orthopteroid insects such as crickets and termites, or in holometabolous insects such as beetles and sawflies, is frequently modified so that mouthpart elements are co-opted in the formation of multielement complexes necessary for fluid feeding (43, 172, 319). Co-optation may include transformation and association of the labrum, hypopharynx, mandibles, and maxillary laciniae into interlocking stylets in extinct and nonhaustellate Paleozoic paleodictyopteroids (166), or into stylets housed within an enclosing labial sheath, or haustellum, formed by medial fusion of the labial palps as in nematocerous flies (43, 130). Other examples of the haustellate-stylet condition include thrips, homopterans, bugs, and fleas. In other taxa, such as proturans and certain small beetles, stylet mouthparts have originated from the prolongation of mouthpart elements, concomitant with a rotation of musculature to produce protracting/retracting stylets rather than mesially adducting/abducting mandibles or laciniae (65, 241). Both nonhaustellate and haustellate types of stylet mouthparts function by piercing and sucking and are involved overwhelmingly in invasive fluid feeding, principally of algal and fungal protoplasts, plant sap, and animal blood.

Noninvasive types of fluid feeding involve mouthpart modifications for surface feeding of exposed fluids such as honeydew, nectar, and exudates from animal wounds. In advanced flies, fused labial palpi form a sponging organ consisting of a fleshy labellum with a feeding surface of orally-directed pseudotracheae and miniscule sclerites for directing the capillary flow of fluid food (85, 106, 291). In advanced moths, fluid feeding is accomplished by medial

fusion of elongate maxillary galea to form a coiled siphon that is extended by hydraulic action (83, 146). By contrast, in advanced Hymenoptera, principally bees, the maxillae and labium form a joint labiomaxillary complex, characterized by prolongation of the labial glossa into a hirsute and often long organ for lapping fluids during extension. Upon glossal retraction, cupped lateral galeae and adpressed labial palps form an enclosed structure containing the glossa, on which fluid food ascends by capillary action and then is suctioned into the mouth by a pharyngeal pump (219, 319).

Mouthparts of subadult insects are equally varied, particularly those of holometabolous larvae (172). The unique labial mask of dragonfly naiads is folded into a Z-shaped configuration under the head when at rest (242) but can be protracted instantaneously by abdominal contraction (233) to extend a significant distance anteriorly beyond the head. The labial mask terminates in labial palps modified into clawed pincers (285, 331) that are responsible for securing and impaling prey. A similar structure with identical function occurs in some staphylinid beetle larvae (13), but instead of terminal pincers, adhesives on labial appendages stick to prey for its rapid retrieval into the pharynx. The larval mouthparts of flies, particularly Culicidae, Simuliidae, and Chironomidae (188, 232, 299), and of other orders such as mayflies (84) and beetles (282), are modified into elaborate setiferous fans, pilose brushes, grooved rakes, and other devices for passively filtering and actively sieving suspended organic matter (347). Terrestrial larvae of planipennians, by contrast, bear falcate, acuminate mandibles that are longitudinally channeled on the ventral surface and can be covered by the adjacent lacinial plate which, when articulated over the mandible, results in a closed canal for releasing proteolytic enzymes into a prey item (150, 284). After the prey is secure, a reversal of the direction of fluid flow results in imbibition of the liquefied contents of the prey item. An analogous feeding mechanism exists for several lineages of larval beetles, except that the tubular channel is contained within individual mandibles (44, 345).

Modifications of mandibulate mouthparts other than for the familiar deep-tissue and surface fluid feeding have occurred in some lineages. For example, adult beetle mouthparts are typically characterized as mandibulate, with powerful mandibles occurring especially in large species. However, several lineages of scarab beetles have evolved mouthparts incapable of chewing solid food (227) and have been modified into flexible flaps for procurement of honey (90), for pollen consumption (31), and for the likely absence of feeding altogether (210). Typical pseudotracheate and fleshy labella of flies have been modified into a rasping organ by conversion of typically nonabrasive prestomal sclerites into batteries of circumoral teeth. The armature of these teeth is used for predation on other insects, abrasion of fruit, and scarification of vertebrate integument for feeding on exuded fluids, including blood (364). This labellum type has originated independently at least several times in muscomorph flies

(85, 131), including the Muscidae (161), Scathophagidae (228), Glossinidae (250), and Tephritidae (80). A last example is the transformation of the noctuid moth siphon into a stylet, primarily by sclerotization of the siphon tip and tubular stiffening (9), a process that occurred independently in Southeast Asia and Africa (9, 322, 361). These stylate moths consume fruit or they pierce humans and the thinner integumentary regions of large ungulates.

## PALEOBIOLOGY AND EVOLUTIONARY BIOLOGY OF INSECT MOUTHPARTS

### *Approaches Centered on the Fossil Record*

The insect fossil record historically has been considered poor—overwhelmingly dependent on descriptions of wings (40, 41). However, this is a caricature. At the family level, 63% of modern families are represented as fossils (174), surpassing many invertebrate and vertebrate groups. Additionally, recent studies have revealed rich morphological detail from soft-part material in both sedimentary compression (10, 28, 97, 108, 196, 263) and amber (160, 245, 369) deposits. Moreover, investigations of the fossil history of plant-insect associations, including the record of insect-mediated plant damage (176, 179, 301, 302, 323), increasingly have been placed in an evolutionary context (177, 236), as have examination of plant tissues in coprolites (180, 283) and insect guts (34, 166, 265, 266), and understanding the origin and timing of floral features for the evolution of insect pollination syndromes (52, 53, 230, 355). These developments provide considerable and mutually independent data addressing the history of insect mouthpart design and, more broadly, the macroevolutionary history of insect feeding strategies.

**MOUTHPART STRUCTURE PRESERVED IN THE FOSSIL RECORD** Even in deposits with well-preserved, soft-part anatomy, detailed preservation of insect mouthparts is uncommon. However, during the past 15 years, particularly Mesozoic deposits (108, 127, 135, 203, 261, 263, 269, 350) have yielded sufficient mouthpart detail that direct evidence now exists for the occurrence of major mouthpart types in the pre-Cenozoic fossil record. In this section a brief summary is provided of some notable occurrences of fossil insect mouthparts, from which certain deductions can be made about feeding strategies and diets (23, 355). Most of the record of mouthpart structures is driven by exceptionally well-preserved deposits that are spatiotemporally scarce but reveal details of feeding mechanisms for many species.

*Paleozoic* From the Early Devonian, two deposits, at approximately 390 Ma, indicate that collembolans (125) and archaeognathans (175) bore distinctive mouthpart types, including primitive entognathous and ectognathous

mandibulate and possibly piercing-and-sucking types (175). The earliest known stratum for which there is abundant, well-preserved material occurs in the Late Pennsylvanian (Late Moscovian) age (307 Ma) ironstone nodules of Mazon Creek in north-central Illinois (273). This deltaic deposit contains mouthpart and head detail of primitively wingless forms, including large entognathous diplurans (165), and a monuran and thysanuran with broadly articulating, dicondylic mandibles and leg-like palps (165). Of the extinct paleodictyopteroids, paleodictyopterans have been described with long, robust beaks containing five unsheathed and interlocking stylets (165, 166), variously interpreted as imbibing small particulate matter such as lycopod spores (281, 310), fluidized endosperm from cordaite or pteridosperm seeds (307, 310), or sap from the vascular tissue of tree ferns (179). Megasecopterans with smaller, truncate beaks (179) are also known. Also documented are the ancestral hemipteroids *Eucaenus* with long and slender maxillary palps and a prominent clypeal dome (42; CC Labandeira, personal observation), and *Gerarus* (32, 165, 168), also with a combination of orthopteroid and primitive hemipteroid features. An undescribed endopterygote larva has been figured, apparently bearing mouthparts resembling an externally-feeding caterpillar (166). In slightly younger Late Pennsylvanian (Kasimovian) ironstone deposits at Commentry, France, the raptorial mouthparts of the protodonatan dragonfly *Meganeura monyi*, one of the largest known insects, had mandibles and maxillary lobes with sharp, terminal incisors for cutting prey (310). Equally impressive is the large paleodictyopteran *Eugereon boeckingii* from the lowermost Permian of Germany (224), with a beak 3.1 cm long (310), that probably fed on plant sap (179).

From younger, Lower Permian (264 Ma) marginal marine deposits at Elmo, Kansas, head and associated mouthpart structures are documented for several insects. These include a monuran (81), a diaphanopteroidean adult with a bulging clypeal pump and transverse linear depressions indicating dilator muscles (39), the rostrate psocopteran *Dichentomum* with terminally located mouthparts, including small, biting mandibles (37, 38, 166), and the prominent clypeus and beak with an enclosed stylet of an archescytinid homopteran (36). The Chekarda insect fauna, of Early Permian age (Kungurian; 258 Ma), near Perm, Russia, represents the most extensive documentation of Paleozoic insect mouthparts. From compressions in these fine-grained deposits, the mouthpart and head structure has been documented for a monuran (305) resembling that of modern archaegnathans. For paleodictyopteroids, documentation and reconstructions are available for the heads and mouthparts of paleodictyopterans (281), megasecopterans with more gracile beaks compared to their Carboniferous predecessors (169, 281), diaphanopteroideans, especially *Permuralia* (281, 163, 167), and the small, delicate, and acuminate beaks of a near dipterous

permothemistid (166). Generalized orthopterans with mandibulate mouthparts similar to those of modern grasshoppers are known (Sharov 1968). Ancestral hemipteroids such as *Synomaloptilia* bear a rostrate head with exerted, apically bifid lacinial blades and a clypeal dome (259, 281, 310)—features that have been interpreted as a strategy for feeding on gymnosperm megaspores (259). One of the earliest known homopterans, *Permocicada*, possessed a three-segmented opisthognathous beak, and a modest clypeal bulge on which occurred a battery of transverse ridges representing pronounced cibarial dilator muscles (16), indicating phloem feeding (309). An early endopterygote larva is known with head capsule and mandibular detail (21, 304). Two major Paleozoic mouthpart types—in paleodictyopteroids the unsheathed beak with interlocking stylets, and in ancestral hemipteroids the combination of mandibulate mouthparts, exposed lacinial blades, and a prominent clypeal dome (166)—have no modern analogs. In addition, the distinctive rostrate head bearing terminal mouthparts in the psocopteran *Dichentomum* may be unique to the Paleozoic.

*Triassic and Jurassic* Little is known of insect mouthparts or even head structures of well-preserved Triassic insects. The first documented appearances of modern taxa correspond with the near absence of Paleozoic-aspect taxa in better preserved Triassic deposits (97, 235). An assumption that the mouthpart structures of these Triassic lineages are similar to those of their modern descendants is supported by more extensive, better-preserved, and intensively collected Jurassic material containing the earliest known occurrences of many modern mouthpart types. From the Lower Jurassic (Hettangian, 203 Ma) shales of Issyk Kul in Kirghizstan (278) and better preserved material from various Early and Middle Jurassic localities in Siberia (142), several mouthpart types first occur in association with the radiation of nematoceran flies (278, 360). These include plumose and setose mouthparts modified for filtration and sieving of particulate matter by aquatic larvae (56, 142, 360), the cephalopharyngeal complex and associated, dorsoventrally articulating mouthhooks used for piercing by terrestrial larvae (142), various multistylate proboscides for piercing integument in adult blood feeding (140, 141, 151), a sponging labellum for adult surface fluid feeding (152, 153), and adults with rudimentary mouthparts indicating aphyagy (155). Additionally, this interval marks the appearance of weevil mouthparts (370), generally used for chewing through indurated substrates (58), and the distinctive labiomaxillary complex associated with the dominantly parasitic apocritan Hymenoptera (262).

Perhaps the most celebrated and best-preserved Jurassic insect deposit is the lacustrine shale at Karatau, Kazakhstan, dated as Oxfordian to Kimmeridgian in age ( $\approx 152$  to 157 Ma). Well-preserved insects from this deposit were initially described by Martynov in the 1920s, and subsequently specialists have

described a wealth of insect taxa (7, 279), including structural details of mouthparts. Prominent are cockroaches, which include ovipositor-bearing mesoblatinids with typical orthopteroid mouthparts (342), and an apparently oöthecate lineage of snakefly-mimics, possessing elongate, forwardly oriented heads and prolonged mandibulate mouthparts associated with long, gracile maxillary palps (343), evidently used in probing and feeding in concealed places. Also present are protopsyllidiid and other homopteran taxa (17, 18) with modest clypeal expansions that are similar to those of Paleozoic forms; some of the earliest fossils of extant phytophagous beetle lineages, such as alleculids (212), mordellids (58), and chrysomelids with robust, toothed mandibles (204, 211); the earliest diverse suite of weevils, representing several major lineages with rostra of various lengths and dorsoventral orientations (6, 170, 204, 369); orthophlebiid scorpionflies with rostrate heads and hypognathous mouthparts; and apparent nemestrinid flies with long proboscides (108, 280). Many of these mouthpart types indicate interaction with plants, which, judging from the Karatau floral record, consisted principally of ferns, caytonialeans, bennettitaleans, cycads, ginkgoaleans, and coniferaleans (73). From the Late Jurassic/Early Cretaceous boundary ( $\approx 145$  Ma), Kozlov (157) described the earliest known siphonate proboscis, possibly belonging to a ditrysian moth (177). If true, this find precedes the earliest known angiosperms by approximately 15 my. Nepticuloid leaf mines are documented in penecontemporaneous deposits from Australia (287), indicating that primitive siphonate mouthparts may have been present in another lepidopteran lineage (177).

*Cretaceous* The Cretaceous record, once considered depauperate (40, 41), has improved dramatically because of the discovery and description of insect taxa from several compression deposits of exceptional quality outside Europe and North America, and a significant rise in the number of insect taxa described from amber (174). During the Early Cretaceous, the coarse morphological spectrum of insect mouthparts converged on the Recent, and by approximately 80 million Ma, the modern spectrum of mouthparts was already deployed. Although the detail of Early Cretaceous compression fossils from fine-grained lacustrine shales and carbonates is not as impressive as that in Late Cretaceous amber from forested settings, the Early Cretaceous insect material provides insights into insect-bearing deposits that did not reappear until the Cenozoic.

The lithographic limestone of Lérída, Spain is one of the earliest, insect-bearing Cretaceous deposits, of Berriasian age (143 Ma). In this deposit are found the head and rostra of nemonychid weevils (350), heptageniid mayfly naiads with prominent maxillae and mandibular tusks (350), and one of the earliest known adult termites, bearing asymmetric but robust mandibles with conspicuously hardened incisors (183). Also known are dipteran larvae bearing



a cephalopharyngeal apparatus with parallel ventral impressions of mouthhooks (350).

Several uppermost Jurassic to mostly Lower Cretaceous localities ( $\approx$ 150 to 130 Ma) in Transbaikalian Russia have revealed siphonurid mayfly naiads with prominent labra and mandibles, an anthocorid hemipteran with trisegmented beak (252), aquatic hydrophilid beetles with prognathous mouthparts (248), an orthophlebiid scorpionfly with conspicuous rostrate and hypognathous mouthparts (327), and well-preserved nematocerous flies with both labellate and stylate proboscides (141, 154). A rare, externally feeding sawfly larva, *Kuengilarva*, bears a typical head capsule with mandibulate, albeit indistinct, mouthparts (264). The most enigmatic insect is *Saurophthirus*, evidently a panorpoid holometabolan (246) but ordinarily unplaced and interpreted by Ponomarenko (246, 247) as ectoparasitic on pterosaurs and related to fleas. It possesses an opisthognathous head bearing a pronounced cheek region and an elongated, palp-bearing proboscis that abruptly tapers distally into a terminus with exerted stylets.

Perhaps less enigmatic but equally controversial are the four taxa of presumed fleas from the Koonwarra Insect Bed, in Victoria, Australia, of Late Aptian age, dated at approximately 118 Ma (135). Two of these taxa have been assigned to the extant family Pulicidae (135, 275), and a third, *Tarwinia*, has a body facies and prolonged head shape with stylate mouthparts that converges on *Saurophthirus* and extant insects ectoparasitic on warm-blooded vertebrates (e.g. 189). The Koonwarra specimens possess heads that are modestly compressed laterally, and display mouthpart specializations that include elongate palps and long styliform structures interpreted as epipharynges and laciniae (135). Unlike other recently discovered Lower Cretaceous compression faunas, Koonwarra insects are of interest because of their unique taxonomic character and abundance of immature stages. Additional examples include a siphonurid mayfly naiad bearing spinose maxillary appendages and detail of mandibular dentition; mesophlebiid and coenagrionid dragonfly naiads with distinctive labial masks, one with stiff, parallel hairs on the labial palps; and exceptionally well-preserved mouthparts in a hydrophilid beetle larva, including a convex clypeal border, edentate, falcate mandibles and maxillae with a long palpus (135).

The Santana Formation, from northeastern Brazil, also of Late Aptian age, has yielded a diverse insect fauna (108, 109). It includes a dragonfly nymph with robust, inwardly curving antennae and a robust labial mask (35), an earwig with typical mandibulate mouthparts (249), and a diverse spectrum of homopterous Hemiptera (109, 115, 116) mostly preserved in lateral aspect, with evident but variously developed clypeal bulges and beak lengths indicating a variety of feeding strategies. Large insect-feeding robber flies with dagger-like, monostylate beaks have also been described (108, 109).

An insect fauna of Aptian to Albian age (124 to 100 Ma) from northwestern Mongolia taxonomically parallels that of Transbaikalia mentioned above (261). It includes a hexagenitid mayfly naiad (316) with distal mandibular and maxillary surfaces that indicate a scraping feeding strategy, a predatory odonatan naiad (255) with an unextended labial mask 0.8 cm long, a cicadelloid (308) exhibiting a pronounced clypeal expansion and muscle insertion chevrons indicating a powerful pump for imbibing deep-seated vascular fluids, and the aquatic corixid bug *Velocorixa* (251) that bears prothoracic legs with elongate, inwardly-directed, filiform hairs, and a short, truncate, three-segmented beak—structures indicating algivory. Also documented are nematocerous flies, some with prominent, elongate labial palps for piercing (Chaoboridae) and others with short, broader labellae for surface fluid feeding (Anisopodidae) (139), and the enigmatic *Saurophthiroides*, less well-preserved than its presumed Transbaikalian relative, *Saurophthiris* (247). Additionally the seeds of an extinct ginkgophyte were used by caddisfly naiads to construct cases (159). At Orapa, Botswana, dated as Cenomanian (93 Ma) in age, a glimpse into an early Late Cretaceous insect fauna reveals weevils with well-preserved, decurved beaks (171), staphylinid beetles with typical mandibulate mouthparts (269), and a tipulid fly (268) housing an elongate rostrum 0.3 cm long, the tip bearing elongate, five-segmented palps and a small labellum, interpreted as a modification for nectarivory (267, 268).

The record of mouthpart structures from predominately Late Cretaceous amber is equally informative, and complements the dominantly Early Cretaceous occurrences of compression deposits. The earliest documented amber with insect inclusions is Hauterivian in age ( $\approx 133$  Ma; 297), and contains thrips with a mouthcone, labial palps, and exerted mandibular stylets (370), phytophagous whitefly labial sheaths with enclosed stylets (296), a monotrisionian lepidopteran larva bearing a head capsule (DA Grimaldi personal communication), and nematoceran dipterans (297) including an phlebotomine fly with extruded stylate mouthparts (120). From New Jersey amber of Campanian age ( $\approx 80$  Ma), an early ant with a wasplike head and short, bidentate mandibles is known (359), as is a labellate phorid dipteran (107). Also present is the earliest known bee glossa, belonging to a meliponine bee, which reveals the distal margin of an apically dentate mandible, although other mouthpart structures are obscured (220). From known correlates between stylet dentition and palpal sensillae in modern ceratopogonid midges and their host preferences (208, 209, 286), Borkent (23) deduced that two and perhaps three ceratopogonid species from New Jersey and slightly younger Canadian ambers fed on exposed regions of the bodies of large vertebrates, specifically hadrosaurs, with accessible, vascularized integument (see also 76, 112, 141).

Siberian amber from the Taimyr Peninsula of Russia, of Santonian age (85 Ma) (369) has revealed the most diverse suite of Cretaceous insect mouthparts.

Included in this assemblage are a variety of aphidoids, particularly several extinct family-level lineages similar to modern phylloxerans (149), some with beaks exceeding the body in length and undoubtedly used for deep-seated vascular tissue feeding and probably capable of penetrating wood. Also present are adult caddisflies possessing well-preserved fluid-feeding haustella and associated labial and maxillary palps (25), ceratopogonids with robust, elongate proboscides and adjacent palps (270), bethylid and trigonalid wasps with unelongated mouthparts bearing prominent, apically dentate mandibles (92, 260) probably used for insect predation, and bombyliids with short labella for nectar feeding on bowl-shaped flowers (365), unlike subsequent Tertiary descendants with significantly more elongated labella for nectaring in flowers with tubular corollas.

*Cenozoic* The post-Cretaceous insect record improves dramatically, especially with reference to highly collected, specimen-rich, and taxonomically diverse faunas such as Baltic Amber (160) and the Green River shales of the western United States. However, this record is uninformative with regard to major mouthpart innovation, and it collectively mirrors the Recent. Essentially all major mouthpart types (172; 182) and feeding strategies (172) had occurred by the end of Cretaceous, and overwhelmingly during the earlier Mesozoic. For example Szadziowski (330) discussed the life habits of ceratopogonid flies, found in Baltic amber ( $\approx 37$  Ma), some of which pursued large mammalian hosts in ways similar to vertebrate-seeking Late Cretaceous ancestors (23). The Cenozoic record of insect mouthparts does reveal minor variations within previously established mouthpart types, such as modifications involved in faithful pollination of certain angiosperms (51, 54, 355) or fine-tuned ectoparasitic specializations for mammalian hosts (145, 198, 213, 340).

**THE RECORD OF INSECT-MEDIATED PLANT DAMAGE** Insects consume virtually all live and dead organic matter, including substances that are minimally rewarding nutritionally such as xylem sap (30) or those that are nonnutritive, such as wood, but are used indirectly as substrates for fungi or other saprophytic organisms to be consumed (12, 353). Virtually the entire fossil record of insect-organismic associations focuses on the interactions between insects and plants, preserved as trace fossils. Direct evidence of insect-fungal interactions (128, 352) are very rare but may be inferred from the presence of fossil taxa (134, 294) whose modern representatives are intimately coevolved with wood and fungi. Evidence for insect predation on animals has been derived principally from mouthpart morphology (23, 25, 141, 255).

The trace-fossil record of insect-plant interactions is largely decoupled from the record of insect body fossils (14), attributable to differing taphonomic circumstances in which insects and plants occur in the fossil record. Thus, inferences regarding plant associations have been made from insect body fossils

in one of three ways: by tight correspondences between the taxonomy and ecological attributes of relevant modern insect taxa (60), functional interpretation of unique or otherwise well-preserved mouthpart structure (268, 309), or, ideally, assignment of botanically identifiable gut or coprolite contents to known fossil insect taxa (197, 265). Similarly, from the often well-preserved trace-fossil record of insect-mediated plant damage, it is often difficult to circumscribe an insect culprit with any taxonomic reliability. In instances of excellent preservation of insect-mediated damage on known plant hosts, the taxonomic identities of insect herbivores can be made at the level of the family or genus, either by reference to highly stereotyped damage patterns inflicted by ancestors of modern lineages whose interactions with plants are well characterized in the agricultural and entomological literature (113, 191, 192, 243, 328), or for extinct lineages by functional inference from mouthpart-inflicted damage seen on anatomically preserved plant host tissue and cellular structure (179, 180).

In this context, the Paleozoic poses special challenges because it records plant damage attributable almost exclusively to extinct lineages (15), requiring dependence on the functional morphology of plant damage and the presence of requisite insects with appropriate mouthparts (8, 144). By contrast, in Cenozoic floras, functional-feeding-groups such as leaf-miners (236, 323, 324), gallers (69, 184, 222, 302), and highly stereotyped external feeders (102, 293, 323) have been assigned to modern taxa. Increasingly this appears possible, perhaps with a relaxing of the taxonomic level, for Cretaceous angiosperm-dominated floras (177, 178, 323). [But see Jarzembowski (134) and Rozefelds (287) for highly stereotyped feeding patterns on Late Jurassic to Early Cretaceous nonangiospermous hosts.]

In many instances the historical record of insect-plant associations parallels mouthpart evolution as reflected in the body-fossil records of insect herbivores. Ironically, in some instances the plant damage record can provide a better assessment of a clade's ecological presence and plant-host specificity than body fossils (156, 177, 323), particularly for poorly sclerotized taxa of low preservational potential that lack a significant mouthpart history. Major examples include endophytic larvae that leave highly distinctive feeding patterns in woody plants, especially lepidopteran leaf miners (122, 257, 320), cecidomyiid, cynipid, and other gallers (1, 313, 357), and some phytophagous coleopterans whose larvae and adults feed in highly patterned and recognizable ways (138, 240).

**GUT CONTENTS AND COPROLITES** The most direct way of establishing the diets of fossil insects is examination of well-preserved specimens with gut contents. This approach has not been used extensively, but recent examination of insects from a variety of Late Carboniferous to Miocene settings, including those in ironstone nodules, lacustrine shales, and amber have established that ingested

spores and pollen frequently are well preserved and identifiable to source plant taxa. By contrast, insect coprolites containing inclusions that are anatomically preserved with histological and cellular detail are commonly encountered only in permineralized coal-balls from the Euramerican Pennsylvanian (283, 303).

Documented gut contents of Paleozoic insects occur in the Late Carboniferous Mazon Creek locality in Illinois (274) and at Chekarda in Russia (265). Mazon Creek insects that possess gut content palynomorphs include a thysanuran (301), a diaphanopteroidean nymph (165), the adult ancestral hemipteroid *Eucaenus* (303), and an unidentified "protorthopteran" (303), all of which consumed spores and probably pollen, but only arborescent lycopod spores have been positively identified (303). In penecontemporaneous coal-swamp deposits 225 km from the clastic-swamp delta at Mazon Creek, abundant spore-bearing coprolites are found amid permineralized plant tissues (173). From the younger deposits at Chekarda, a more diverse assemblage of palynomorphs has been identified in the guts of an ancestral hemipteroid, a grylloblattid, and an unassigned species, collectively containing gastric residues of conifer, peltasperm, and glossopterid pteridosperm, and probably gnetalean pollen (217, 265, 266). Of these, only the unassigned species contains a monospecific pollen assemblage; the others were eclectic consumers of several gymnospermous pollen types.

It is notable that the two extinct mouthpart types associated with the Paleozoic insect fauna are also associated with pollinivory—the robust beak of palaeodictyopteroids and the lacinate mouthparts of ancestral hemipteroids. The mouthpart structure and inferred feeding mechanism of these insects has been discussed by several authors (168, 265, 281) who note the presence of a prolonged hypognathous head, rod-shaped maxillary laciniae, and a pronounced clypeal dome that indicate pollinivorous feeding habits. Modern psocopteran mouthparts (43, 205, 206) exhibit the closest similarities to Paleozoic hypoperlids. Both mechanisms of pollinivory independently have originated in modern taxa, including mandibulate beetles (31, 295) and adult syrphid flies (101, 126, 300) with tubular suction. A third major mechanism of pollen ingestion is the punch-and-suck mechanism of certain thrips (148), in which individual pollen grains are punctured by the single stout mandible, followed by adpression of the mouthcone over the pollen grain and suction of the internal contents; this method may have Paleozoic antecedents (344).

Post-Paleozoic examples of insect gut contents center on three major mandibulate taxa: beetles (268, 293, 355), sawfly hymenopterans (34, 158), and a katydid orthopteran (266). The earliest occurrence, a Late Jurassic katydid from Karatau, Russia, contains pollen from a cheirolepidaceous conifer (266). Early Cretaceous sawflies from Santana, Brazil, consumed winteraceous angiospermous pollen (34, 79), whereas at a slightly earlier locality in Transbaikalia,

Russia, three xyelid sawflies consumed pollen of pinaceous and other conifers (158). From Eocene deposits, buprestid beetles have been recovered at Messel, Germany, with well-preserved pollen (293), and a scaptiid beetle from Baltic amber was coated by a diverse assemblage of pollen types (354). Related examples of insects with body surfaces bearing various palynomorphs include an early Late Cretaceous beetle at Orapa, Botswana, with undetermined pollen on its abdomen (268), an apid bee from the Middle Eocene of Germany bearing *Tricolporopollenites* grains on its sternites and metatarsal brush (197), and, from Early Miocene Dominican amber, ambrosia beetles bearing ascomycetous spores in mycangial cavities as well as a meliponine bee covered with *Hymenaea* and with unidentified pollen on its abdomen (110).

After an intestinal bolus exits the insect body as a fecal pellet, it can be fossilized immediately into a coprolite, albeit with loss of the original taxonomic context of its fabricator. However, coprolite assemblages can provide unparalleled ecological information if they are sufficiently abundant, compositionally diverse, and well preserved, such as those present in coal-ball floras from Late Carboniferous Euramerican wetlands. Such assemblages are identified by coprolite types distinctive in size, shape, composition, and plant associations (14, 303), and they often are linked to insect taxa at higher levels (180, 181, 283, 301). Thus, evidence from coprolites containing anatomically pristine tissues—equivalent in histological detail to modern embedded and sectional fecal pellets—can be used to document and understand insect dietary strategies (173). For an insect body fossil record for Late Carboniferous coal-swamp deposits (14), detailed identification of coprolite contents offers much promise for documenting early dietary diversity of mandibulate insects.

**FLORAL STRUCTURE AND POLLINATION SYNDROMES** Much suggestive evidence indicates insect pollination of diverse Paleozoic gymnospermous plants, including pteridosperms, conifers, and cycadophytes (70). Among some Late Carboniferous medullosan pteridosperms, pollen is sufficiently large (70) that prepollen transfer was achieved probably by an insect vector (333). However, if sufficiently buoyant, *Medullosa* prepollen could move distances as much as 200 m with modest air currents (229). Certainly insects such as some large ancestral hemipteroids, orthopteroids bearing robust mandibles with shearing incisors, or paleodictyopteroids with stout, short beaks were capable of fragmenting and consuming medullosan prepollen of large size. Supplemental evidence of plant damage occurs in the form of a 1.2 cm-long beak probe, terminal feeding chamber, and associated reaction tissue in a bell-shaped medullosan pollen organ (298), wherein a paleodictyopteroid consumed prepollen and intercalated tissue while the organ was still alive (179, 272). The Early Permian conifer *Fergliocladus* of Argentina bore delicate, deliquescent tissue at the micropylar

apex of each platyspermic ovule, indicating formation of liquid that rose up the micropylar tube and into a circumapertural depression at the external surface (2). This condition may indicate insect pollination. Mamay (201) proposed a function for characteristic glandular bodies occurring on cycadophyte leaves and between the seeds of associated reproductive structures, in coeval strata from Texas. He proposed that such glands were attractants for fluid-feeding insects that would acquire pollen in the feeding process and pollinate adjacent or distant ovules (but see 15). If this interpretation is correct, likely pollinators would be mandibulate insects possessing hypognathous heads and pectinate or hirsute mouthparts for imbibing fluid and possibly pollen.

As illustrated above, it is difficult to evaluate from fossil material evidence for the existence of pollination syndromes. The evidence almost always is indirect, requiring evaluation of a suite of floral or other reproductive characters and the likely presence, with or without co-ordinate paleontomological evidence, of suitable insects vector to effect pollination. Such is the case for well-reasoned assessments inferring insect pollination of a Late Triassic gnetophyte and the angiosperm-like *Sanmiguelia* (46, 47). Although several modern gnetophytes are associated with pollinating insects (143, 214, 253, 341), the indirectness of this approach centers on specification of an insect to achieve pollination in return for a reward by the pollinated plant that benefits the insect (93, 314, 346). Alternatively, the presence of certain mouthpart structures known to effect pollination occur in a bewildering variety of modern insects (132), and similar mouthpart types present during the Middle and Late Jurassic can be interpreted as consuming plant substances that result in pollination. One example in the Late Jurassic Karatau insect fauna is beetles with mouthparts resembling extant boganiids, chrysomelids, and nemonychids (5, 6, 58, 59, 211, 212). Additionally, it is suggested that nemonychid weevils from these deposits (170) were inhabiting cycads in ways similar to some modern primitive weevils that occur in cycads (5, 6, 58), a conclusion supported by paleobotanical evidence documenting the presence of five cycad and allied genera (73).

Recent discoveries documenting extant beetle associations, in particular pollination of several cycad species (59, 95, 231, 332, 346), led to the conclusion that consumption by primitive beetles of cone axes, microsporophylls, pollen, and occasionally ovuliferous tissue is probably an ancient association (58, 60, 89, 223, 225). Evidence from the Early Cretaceous of a more or less related clade, the Cycadeoidea, reveals patterns of damage in the reproductive tissues of several specimens (50, 52, 58, 105) indicating that robust insects, undoubtedly beetles (58), were capable of entering the concealed interstices of a cycadeoid strobilus (cf 332) to consume interseminal scales and adjacent tissues (50). This resulted in a more extreme version of the "mess-and-soil" or cantharophilous pollination syndrome common to some extant beetles on magnolialean angiosperms (105, 336). A conclusion from these direct and indirect

examples suggests that primitive, beetle pollination syndromes existed during the Late Jurassic and Early Cretaceous on nonangiospermous seed plants (71, 105).

Some of the earliest, best-documented evidence for angiosperm-centered pollination syndromes comes from the Early Cenomanian (97 Ma) Dakota Formation, in which several flower morphotypes and dispersed pollen have been described and documented (11, 72). One of these, the "Rose Creek flower" is a bisexual, actinomorphic rosid with pentamerous and showy petals, an abbreviated style, and a robust and hypogynous receptacular disk possibly with nectaries. Judging by the pollinator spectra of equivalent modern flowers, this and other functionally similar magnoliid flowers with significant visual impact were probably pollinated predominantly by small to large mandibulate beetles (4, 63, 88, 99, 100) and medium-sized flies with sponging labella (78, 351). However, some early angiospermous flowers were small, simple, either sessile or closely attached to axes (53, 104), and characteristic of the myophilous pollination syndrome. These flowers resembled modern Winteraceae (86, 338), Chloranthaceae (87), and related families that are pollinated by small insects, especially flies (339, 351) and to a lesser extent thrips (86, 337, 338). Early Cretaceous lineages of nematoceros and plesiomorphic brachyceros Diptera occur in many insect faunas, although most modern representatives are generally considered hematophagous or saprophagous. These same clades sporadically have pollinating nectarivorous members today, including the Tipulidae (207, 277), Chironomidae (77, 195), Ceratopogonidae (33, 75, 292), Culicidae (114, 186, 335), Cecidomyiidae (94, 234, 363), Sciaridae (348) and Tabanidae (200), indicating that stylate mouthpart structure can be associated with nectarivory.

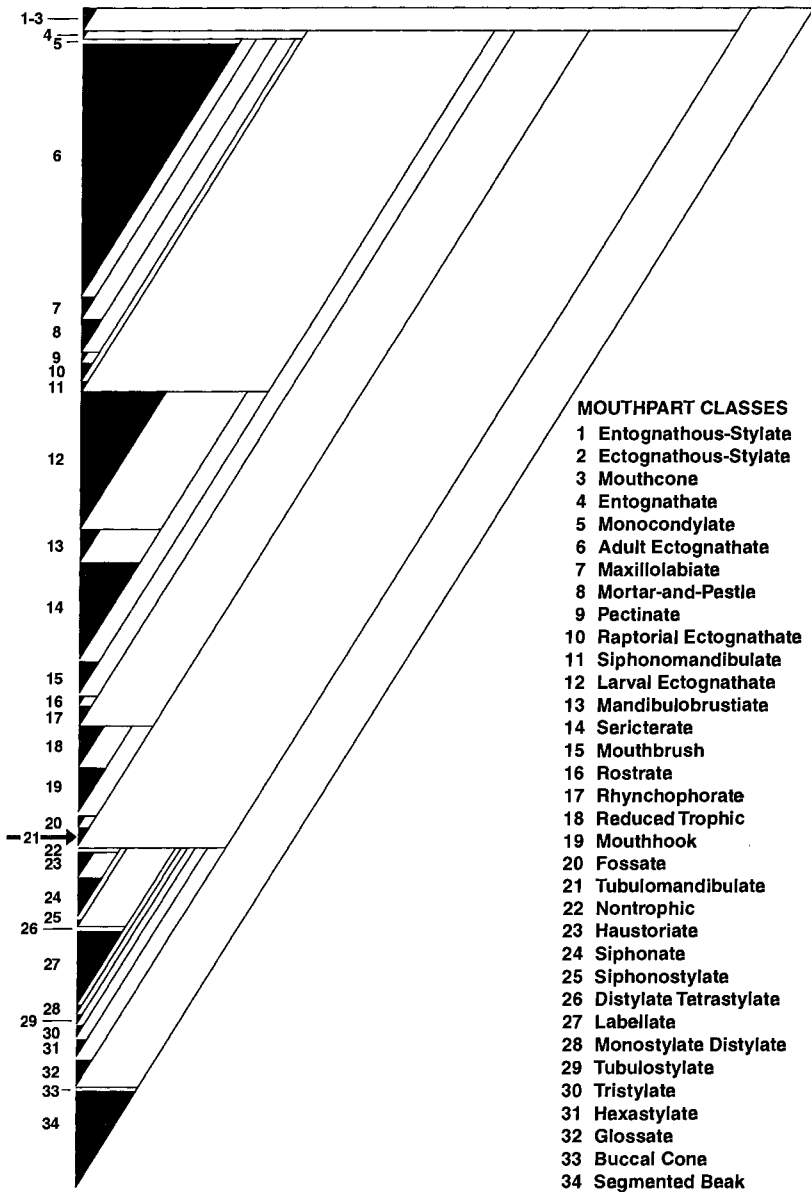
The radiation of the parasitoid Hymenoptera during the Jurassic (262) provided another pollinating insect group, since the labiomaxillary apparatus of small parasitoid wasps often is involved in nectaring (123, 136, 190, 256). Members of these clades entered a pollination syndrome, melittophily, involving further modification of the labiomaxillary complex into the glossate mouthparts of bees and its functional equivalent in some advanced wasps (172, 289, 290). Melittophily probably originated during the later Early Cretaceous (220). The phalaenophily of large moths and butterflies—but including long-tongued labellate flies that often hover, such as tabanids, nemestrinids, vermeleonids, and bombyliids (132, 200, 202, 326, 334)—was a Late Cretaceous or later development (82, 256) and is indicated by the fine-tuning of floral features to accommodate pollinator behavior and structure, such as zygomorphy, sympetaly, tubular corollas, and the presence of elaiophores (53, 355). Faithful modes of pollination, such as flowers with deep funnelform corollas and insects with significantly long mouthparts (200, 202), are probably post-Cretaceous (51, 52).



### *Mapping Mouthpart Classes onto Fossil-Calibrated Cladograms*

A conservative estimate of the number of primary literature papers published since 1880 on insect mouthparts is 2100. These articles can be divided into standard descriptions of head and mouthparts of selected insect species (68, 83, 137), examinations of specific homologous structures or mouthpart regions across a wide range of insect taxa (49, 91, 318), monographic comparisons of head and mouthpart structure within an insect order (55, 244, 321, 325), and biomechanical analyses of mouthparts, such as those involving labial mask extension in dragonfly naiads (233, 254, 285) or aquatic filter feeding (26, 27, 48, 299). A sample of 1200 mouthpart and head sources from the literature up to 1989 was used in a phenetic analysis of the structural diversity and fundamental types of modern insect mouthparts (Figure 1). This literature contains a wealth of data on the structure of insect heads and mouthparts in an area of research that has been largely abandoned (but see 19, 80, 193) except as a source of data for supplying characters and character-states for cladistic analyses (20, 117, 238, 315).

This phenetic summary of the insect mouthpart literature was accomplished by a cluster analysis of 1365 modern insect species, including noninsectan apterygotes (Figure 1; 172). Criteria for inclusion of literature-based sources included rejection of all groundplan or otherwise idealized or generalized abstractions, citation of a documented taxon to genus or species level, repeatability of data among investigators, and multiplicity of data sources. Variables consisted of qualitative descriptions and nonmeristic size and shape assessments of mouthpart elements and mouthpart complexes and head-associated structures that meaningfully could be compared across all insects. Clusters were determined objectively by dendrogram branch lengths, similarity levels, overall dendrogram topology, and absence of chaining, although cluster 1-3, expressed as a single cluster in Figure 1, consisted of three discrete clusters in subsequent analyses (172). After criteria were used for cluster delimitation, a mouthpart class was designated for each cluster. Post hoc justifications for each cluster included demonstration that they were internally consistent with common mouthpart features, structurally unique when compared with the 33 other clusters, and, in some instances, that they had been previously recognized in the mouthpart literature. The resulting 34 fundamental mouthpart clusters are thus defined by membership of a clade or, more often, multiple unrelated clades that converge on a particular suite of head and mouthpart features forming a discrete structural unit in nature. Most of these mouthpart classes were previously recognized informally in the mouthpart literature (67, 133, 216, 317), and a subsequent summary employing a classical morphological approach (318, 319) independently repeated many of the results (43).



The purpose of summarizing the extensive mouthpart literature by a cluster analysis was not only to determine the fundamental number and taxal composition of major extant mouthpart designs, but also to map each mouthpart class onto its constituent evolutionary lineages, calibrated by fossil occurrences (172). Thus patterns of taxal origination and diversification were assessed for the appearance and timing of mouthpart innovations. In addition, given an appropriate level of taxonomic analysis that ranges from the order to the genus, depending on the taxonomic scope of the mouthpart class, an assessment can be made of the degree of major mouthpart innovation within a monophyletic clade (e.g. 194), or alternatively of convergence toward a given mouthpart class in unrelated lineages (e.g. 3, 239). Thus, events such as the radiation of the Diptera during the Triassic and Early Jurassic (121, 278) is associated with the origin of six mouthpart classes; by contrast, the same mouthpart themes were repeated in two diverse clades, illustrated in the tubulomandibulate example of Figure 2. For the tubulomandibulates, which had arisen by the Late Triassic and radiated during the Jurassic, characteristic tubular mandibles originated from two to seven times within two major beetle clades (44, 66, 345, 366) as evaluated at the family level. It is possible that both clades may reveal additional convergences on the tubulomandibulate condition if the level of taxonomic resolution were increased to the genus or species levels. The defining feeding structure in tubulomandibulates is sickle-shaped, piercing mandibles that house tubular canals for ejection of proteolytic enzymes to liquefy insectan and invertebrate prey, as opposed to typical cutting mechanisms in mandibulate sister-group taxa.

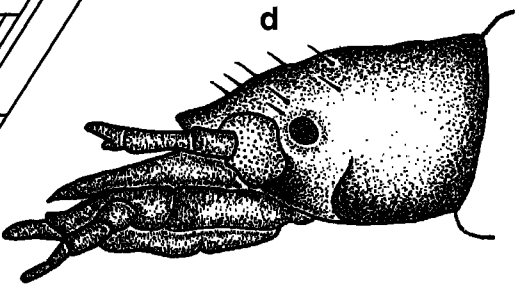
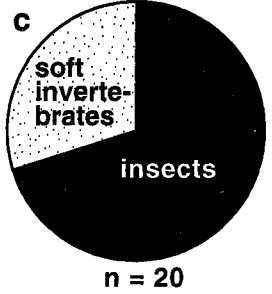
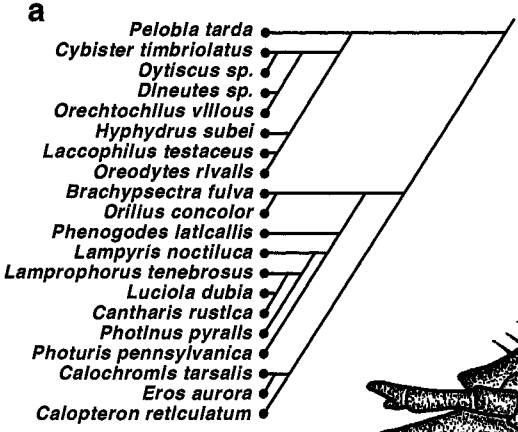
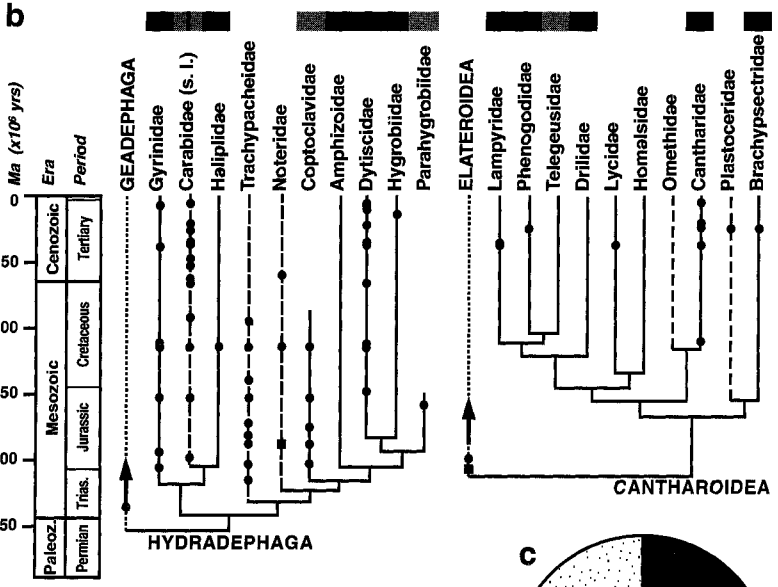
## A GEOCHRONOLOGIC HISTORY OF INSECT FEEDING STRATEGIES

When the method of analysis described above is applied to all 34 mouthpart classes, the result is a distinctive geochronological pattern of mouthpart class ap-

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*Figure 1* Resulting dendrogram from a cluster analysis of recent hexapod mouthparts. Literature-derived data for this analysis consisted of 49 qualitative variables with characters ranging from 3 to 19 states, and representing all mouthpart regions, major mouthpart elements, and associated cephalic structures. 1365 cases were used, representing a diversity of modern hexapod mouthpart structure, including all 33 conventional orders and 70% of all recognized families. A matrix inversion of the BMDP1M cluster analysis program (118) was used with a Jaccard similarity index and an average linkage clustering algorithm. The root of the dendrogram is at the upper right, and the horizontal positions of nodes that link clusters indicate phenetic similarity. The vertical length of each blackened cluster is proportional to the number of included species; for example, cluster 6 contains 291 species, whereas cluster 32 contains 29 species. *Arrow* designates cluster 21, the Tubulomandibulate Mouthpart Class, detailed in Figure 2. Additional details and elucidation of clusters are provided in Labandeira (172).

TUBULOMANDIBULATE MOUTHPARTS



pearances (Figure 3). These data are combined with occurrences from the physical mouthpart and plant-insect association records to yield a five-phase sequence of insect mouthpart innovation and associated feeding strategies (Figure 4, top). This history is based upon minimal dates of mouthpart class appearance, and occasionally on indirect inference regarding mouthpart presence attributable to sister-group relationships of mouthpart-bearing taxa and types of fossil evidence, indicated by the cross-hatched portions of the vertical bars. Two intervals of the insect fossil record provide no data or minimal data for resolution: a 60 my interval from the Middle Devonian to Early Carboniferous, and a 13 my interval during the Early and Middle Triassic.

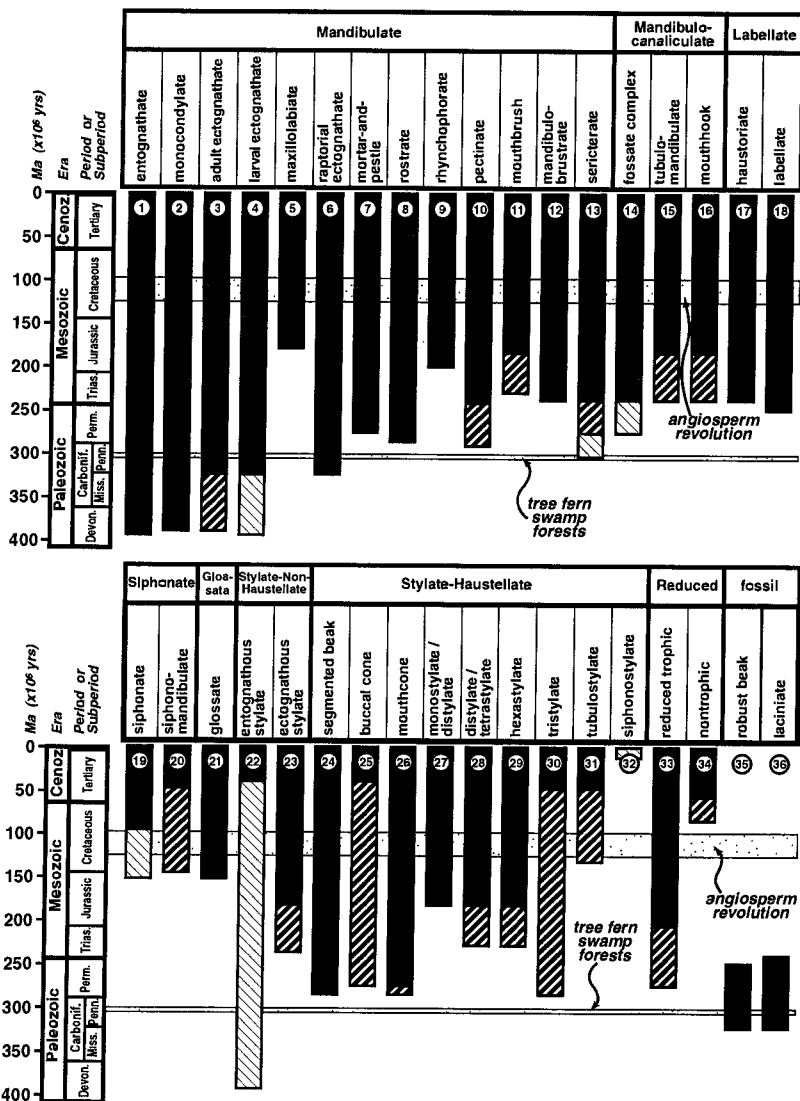
In Figure 4, morphological innovation of mouthpart types, expressed by the five-phased temporal pattern of mouthpart class diversity, is compared with family-level taxonomic diversity for the same geochronologic interval (174, 176, 182). The different forms of these two curves suggest that the evolution of distinctive mechanisms for processing food predates a rise in overall taxonomic diversity. Preliminary estimates of insect diversity at the genus level merely repeat the pattern observed at the family level.

### *Phase 1: Early Devonian*

Primitive modes of mandibulate feeding and undoubted piercing-and-sucking extend to the Early Devonian, indicating the coarsest possible partitioning of food resources. Mandibulate feeding was accomplished by three mouthpart types borne by small hexapods (175): the entognathate (103) and moncondylate (22) types of detritivory with weakly abducting, milling mandibles, and probably an unelaborated version of adult ectognathate mouthparts (98) characterized by dicondylic and muscularly more powerful mandibles (175). Entognathous-stylate mouthparts are found generally in proturans (96) and

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*Figure 2* The Tubulomandibulate Mouthpart Class. (a) Membership and inter-relationships of taxa comprising cluster 21 in Figure 1. Tubulomandibulates constitute those larval beetles with tubular mandibles used for fluid-feeding on live prey. Details are provided by Labandeira (172). (b) Phylogeny, calibrated by fossil occurrences, of family-level lineages comprising the taxa in (a). The fossil occurrences are represented by *circles* for reliable assignments and *squares* for less secure identifications; they are not necessarily a complete inventory of all known, relevant fossils. The *bar* at top indicates membership in the Tubulomandibulate Mouthpart Class (*black*) or probable membership for fossils lacking in mandibular detail or for extant taxa with undocumented mouthpart structure (*grey*). For the Carabidae, the tubulomandibulate condition is documented in one species (366). The phylogenies are after Beutel & Roughley (21) for Hydradephaga, and Lawrence (187) and Crowson (58) for the Cantharoidea. Abbreviations: Paleoz. = Paleozoic, Trias. = Triassic. (c) Dietary spectrum of taxa in (a). Soft invertebrates are primarily gastropods. (d) A representative member, the cantharid *Chauliognathus* sp. Note that this mouthpart class originated from two to seven times, when evaluated at the family level.



some collembolans, and evidence indicates that piercing-and-sucking occurred on primitive land plant stems (8, 179).

### *Phase 2: Pennsylvanian*

There is no insect record for the Late Devonian and Mississippian; apparently, several major additional mouthpart classes originated not long before the earliest Pennsylvanian. Raptorial ectognathate mouthparts (312) of adult protodonatan predators (29), possibly including adult ephemeropterans (164), represented active pursuit predation of other insects. In another paleopterous lineage, the distinctive robust beak mouthparts of paleodictyopteroids (28, 166) were an effective piercing-and-sucking mechanism for tissue penetration and stylet maneuverability. Evidence exists for plant damage caused by this mouthpart type (179, 272, 307). Lacinate mouthparts occurred in some ancestral hemipteroid lineages (168, 259, 281), providing a combination of lacinal puncturing of indurated food, mandibulate chewing capability, and a clypeal suction pump for ingestion. Perhaps dating to the Early Pennsylvanian (166), sericterate mouthparts of larval holometabolans (311) provided multiple feeding strategies, including external feeding of foliar material by caterpillar-like larvae (166) and consumption of stem and petiole parenchyma by endophytic apodous galls (180). Meanwhile, there was a continual expansion of lineages bearing adult ectognathate mouthparts, particularly orthopteroids.

### *Phase 3: Early Permian*

During the Early Permian, mouthpart classes increased from six to nine, attributable to the earliest documented appearances of true hemipteroids and holometabolans. Most of these mouthpart classes were innovations for fluid-feeding, whereas others represented new ways of consuming aquatic or terrestrial detritus. Among hemipteroids, the mortar-and-pestle mouthpart class of psocopterans (205) was a major modification of the lacinate condition.

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*Figure 3* The geochronologic distribution of modern mouthpart classes elucidated in Figure 1, including two extinct mouthpart classes not analyzed in Figure 1 but sufficiently distinctive for inclusion herein. Data is updated from Labandeira (172). *Solid black segments* of vertical bars indicate presence of a mouthpart class as body fossils in well-preserved deposits; *heavy slashed segments* indicate presence based on sister-group relationships when one lineage of a pair occurs as fossils and the sister lineage, whose modern representatives bear the mouthpart class in question, is inferred to have been present. The *lightly slashed segments* indicate more indirect evidence for presence, including trace fossil evidence and the documented occurrence of a mouthpart class in one life-stage of a species (e.g. larva) when the mouthpart class of interest is inferred to have been present in another life-stage (e.g. adult) that lacks a fossil record. Abbreviations: Devon. = Devonian, Carbonif. = Carboniferous, Miss. = Mississippian, Penn. = Pennsylvanian, Perm. = Permian, Trias. = Triassic, Cenoz. = Cenozoic.

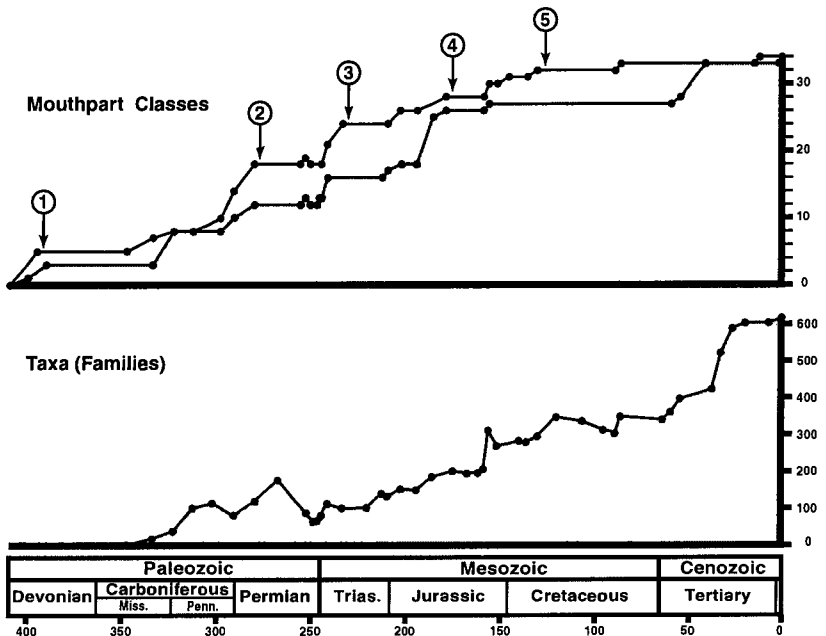


Figure 4 Comparison of mouthpart class diversity (*upper panel*) and family-level taxonomic diversity (*lower panel*) since the Early Devonian. Data for both graphs are resolved at the stage level, shown at bottom sequentially as data points but included in the *top panel* only to reflect diversity changes. For mouthpart diversity, *darker pattern* indicates strong evidence for presence (i.e. *black portion* of bars in Figure 3) and *lighter pattern* indicates less reliable evidence (*slashed patterns* of bars in Figure 3). Numbers attached to arrows refer to the five phases of mouthpart class diversification described in the text. Mouthpart data are an updated version of Labandeira (172), and taxonomic data are from Labandeira & Sepkoski (182), documented in Labandeira (174). Abbreviations: Miss. = Mississippian, Penn. = Pennsylvanian, Trias. = Triassic.

Mouthcone mouthparts (221) are found in lophioneurid thysanopterans, which bore an asymmetrical, hypognathously drawn head that apparently bore stylets (344) used for feeding on shallow plant tissues. Prosbolid and archescytinid homopterans with opisthognathous, segmented beaks (16) mark the appearance of segmented beak mouthparts; they probably were fluid feeders on more nutritionally rewarding and deeper-seated plant sap. Larvae of mandibulate planipennians, overwhelmingly fluid feeders on other insects, probably possessed the fossate complex mouthparts of recent forms (362) and were present during the Lower Permian (304). Adult mecopterans or their stem-group (358), which occur in Lower Permian deposits, bore a characteristic hypognathous rostrum with mouthparts attached posteroventrally to the head capsule (119); modern



forms are scavengers on detritus and dead insects. Indirect, sister-group evidence is present for buccal cone (124) and tristylate (349) mouthparts, both involved in the ectoparasitic extraction of blood from vertebrates, although it is equally likely that both lineages are more recently derived (121). The evidence for reduced trophic mouthparts (147) is indirect but centers on the presence of Permian coccoid homopterans, of which most modern adult males are non-feeding. Lastly, presence of aquatically filtering pectinate mouthparts (842) is assumed from Early Permian occurrences (162), although little is known of preadult ephemeropterans during the Permian, and the single well-documented Pennsylvanian form probably was predaceous (164).

#### *Phase 4: Late Triassic to Early Jurassic*

During the Late Triassic to Early Jurassic, there was an explosion in mouthpart innovation and feeding strategies, with approximately one third of all modern mouthpart classes coming into existence. Half of these 12 new mouthpart classes are attributable to the origin and ecological diversification of nematoceros Diptera (142, 278). This proliferation of new mouthpart designs included distinctive larval feeding apparatuses and in adults the combination of an elongate protractile labium surmounted by a fleshy labellum that enclosed piercing or cutting stylets of varying number and length (130, 244). Although most of these mouthpart types were designed for fluid feeding, ingestion was accomplished by sponging with a pseudotracheate labellum (291), by piercing and sucking with haustellate stylets (208, 329), or by laterally-to-dorsoventrally occluding falcate mouthhooks in larvae of some advanced lineages (276). Adult diets included vertebrate blood or insect haemolymph for those with hexastylate, distylate/monostylate, and monostylate/distylate mouthparts (112, 141). Labellates imbibed exposed plant, animal, and fungal fluids, including honeydew—polysaccharide containing secretions from extrafloral nectaries (78)—and protein- and lipid-rich exudates from carrion or exposed wounds. Mouthhook-bearing larvae were scavengers or predators principally on other insects. However, dipteran feeding strategies were successful not only on land—in freshwater habitats, modification occurred of labra, mandibles, and maxillary appendages into the penicillate or setate filtering structures of mouthbrush mouthparts (48, 64, 258)—and allowed for exploitation of particulate organic material suspended in the water or as epibenthic detritus (61). Early trichopteran lineages paralleled dipterans in that adults developed a fleshy, labellum-like sponging organ (55) in the form of haustoriolate mouthparts, and naiads similarly possessed seta- and hair-bearing mandibulobrustiate mouthparts designed for sieving or filtering particulate organic matter (24). In freshwater environments, a revolution occurred in the trophic partitioning of the water and upper benthic zones, with several diverse lineages of filterers,

scrapers, gatherers, and shredders (61, 62) appearing during this time interval (360).

The presence of new food resources was probably attributable to the emergence of several seed plant clades during the Triassic, leading to increased interactions with insects, examples of which include the earliest occurrence of leaf mining (as plant damage—288), surface fluid feeding and undoubtedly pollination. Nondipteran clades that participated in the exploitation of new food resources included the maxillolabiates, mostly diminutive adults of parasitoid Hymenoptera that possessed mandibles and a labiomaxillary apparatus (237) for chewing solid food and lapping fluids. Rhynchophorates appeared during the Late Triassic (368), becoming abundant during the Late Jurassic, and bore a characteristic decurved snout with terminal mandibulate mouthparts (74) designed for masticating hard substrates such as seeds, stem sclerenchyma, and wood. Both maxillolabiates and rhynchophorates could have fed on and pollinated Jurassic seed plants. The tubulomandibulate mouthpart class (345), consisting of specialized fluid-feeding predators on other invertebrates, originated in water initially during the Late Triassic and re-evolved during the Late Jurassic within the terrestrial Cantharoidea (57, 58). During the Triassic and Early Jurassic, several separate origins of small beetles characterized the ectognathous-stylate mouthpart class in which typical adducting/abducting mandibles become transformed into protracting/retracting stylets, with accompanying modifications in labral, maxillary, and labial structures (65, 241).

### *Phase 5: Late Jurassic to Early Cretaceous*

Almost all of the innovation in major mouthpart design occurred before the Cretaceous. Phase 4 of the earlier Mesozoic had broadened the repertoire of feeding to include noninvasive feeding on surface fluids by several mouthpart types. This was extended during the later Mesozoic to include the siphonate (157, 177) and glossate (220) mouthpart classes, which involved novel mechanisms in the imbibition of surface fluids (83, 218), becoming crucial during the Late Cretaceous by contributing members to major pollination syndromes with flowering plants (53, 256). By the Eocene, faithful modes of pollination were principally centered on these two speciose mouthpart types. The documentation of nontrophic mouthparts in the fossil record is spotty because it is difficult to ascertain even in modern insects whether vestigial mouthparts are capable of securing food, whether adults are truly nonfeeding or simply have not been observed to feed. Vestigial mouthparts occur sporadically in ephemeropterans (226), lepidopterans, and dipterans, and circumstantial evidence indicates that this mouthpart class originated during the Late Cretaceous, although it could have occurred significantly earlier for ephemeropterans.

Three other mouthpart classes have inadequately understood histories because their fossil records are missing or poorly documented. Siphonomandibulate mouthparts, in which maxillary galeae or palps are fused, originated independently among several genera, including meloid (111) and rhipiphorid (356) beetles, and probably certain bees with tubular maxillary proboscides (129, 185). Among three mid-Cenozoic occurrences of rhipiphorids (172), it is not known if they are siphonomandibulates; based on other evidence, this mouthpart class probably extends to the mid-Cretaceous. The fossil record of the tubulostylate mouthpart class is better, since glossinids occurred during the latest Eocene (45), and an Early Miocene hippoboscid is known (199). Siphonostylates consisting of multiple innovations of skin-piercing noctuid moths that puncture fruit (322, 361) and the integument of large, even pachydermous, mammals (9) are the only mouthpart class that probably originated during the Cenozoic.

## CONCLUSIONS

Insect mouthparts and associated head structures consist of distinctive, highly integrated structural units containing single and multiple elements that are coordinated in processing food. For foods different than those of generalized, solid-food feeding mandibulate insects, many subsequently originating mouthpart types broadened the spectrum of food available for consumption, such as organic particles and both exposed and tissue-bound fluids. These innovations involved significant multielement co-optation and modification between two or more mouthpart regions, resulting in major mouthpart types engaged in aquatic filter-feeding, piercing-and-sucking, sponging, siphoning, and lapping, among others.

The fossil insect mouthpart record occurs sporadically in approximately 40 exceptionally well-preserved deposits. This record provides detail for minimal dates of origin and the timing of diversification for the vast majority of modern mouthpart types; it also includes documentation of unique Paleozoic mouthpart types lacking modern analogs. Supplementing this body-fossil record is the trace-fossil record of mouthpart-mediated plant damage, insect gut and copro-litic contents, and floral and other plant features indicative of particular insect feeding styles.

In addition to the above approach centered on the fossil record, an objective classification of modern insect mouthparts into formal mouthpart classes was made, in which each mouthpart class was mapped onto its constituent lineage or lineages, calibrated by fossil occurrences. From a summary cluster analysis of modern insect mouthparts, 34 structurally defined mouthpart classes of insects and their apterygote relatives were recognized; most of these mouthpart classes have multiple origins among clades not sharing common ancestors.

The geochronologic record of mouthpart innovation, when supplemented by data on the effects of mouthparts on plants, indicates a fivefold phase in the evolution of feeding strategies, with all documentable mouthpart classes in the fossil record antedating the mid-Cretaceous. These five phases of mouthpart class origination—Early Devonian, Mississippian, Early Permian, Late Triassic to Early Jurassic, and Late Jurassic to Early Cretaceous—are characterized by successive partitioning of freshwater and especially terrestrial food resources, and a trend from solid-food feeding toward exposed- and tissue-bound fluid feeding and particle feeding. Major mouthpart innovations include a proliferation of mostly herbivorous mouthpart classes during the Pennsylvanian, expansion of fluid-feeding strategies during the Early Permian, a dramatic increase in several fluid-feeding and particle-capturing mouthpart classes associated with the radiation of the Holometabola, particularly Diptera, during the Late Triassic and Early Jurassic, and further expansion of surface-fluid feeding strategies during the Late Jurassic and Early Cretaceous. Many earlier Mesozoic mouthpart classes that were engaged in fluid-feeding subsequently became important as associates of angiosperms during the mid-Cretaceous.

An important consequence of a phenetic summary of the profuse literature of modern insect mouthparts is condensation of a wealth of morphological data into 34 basic entities. The macroevolutionary distribution of these 34 mouthpart classes is made meaningful only when they can be plotted on cladistic phylogenies of lineages bearing those mouthpart classes. This review suggests that one of the most important uses of cladograms is to provide an objective phylogenetic framework by which ecological attributes can be compared, particularly when both phylogenies and ecological data are anchored in a known fossil record.

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