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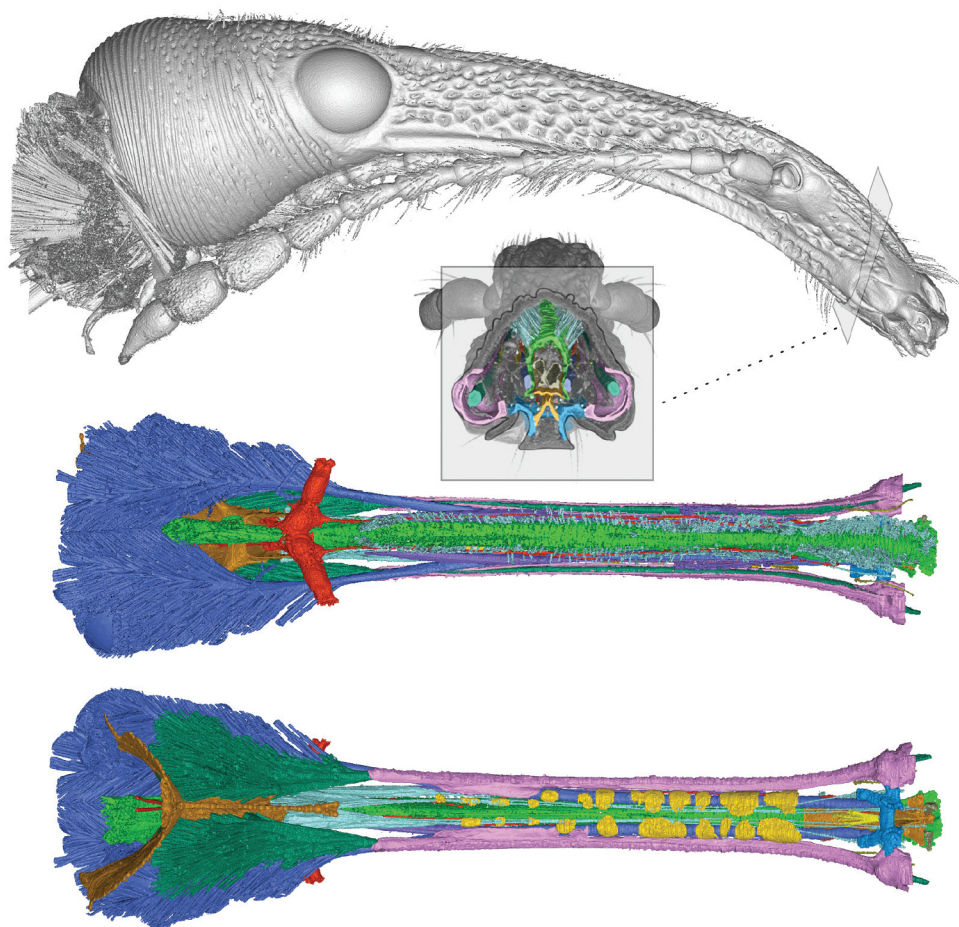
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THE WEEVIL ROSTRUM (COLEOPTERA: CURCULIONOIDEA): INTERNAL STRUCTURE AND EVOLUTIONARY TRENDS

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ABSTRACT

The current classification of weevils has witnessed vast improvements at higher phylogenetic levels, though much remains unstable at the lower levels. In order to develop a more robust morphological character system for cladistic analysis of the higher lineages and to gain a comprehensive understanding of the structure of a hallmark feature of weevils, a comparative study was conducted of rostra throughout Curculionoidea. Semithin sections were made of the rostra of 36 exemplar genera representing all seven currently recognized weevil families, as well as 19 of 21 subfamilies within the largest family, Curculionidae, and internal structures were examined for phylogenetically informative characters. While the morphological diversity of rostral forms is impressive, general trends are apparent with respect to life-history traits and modes of feeding. Exploration of internal rostral morphology has yielded valuable but previously unexplored characters that greatly complement the external characters of this structure. Together, these features provide new insight for settling current incongruence at the higher levels of classification.

KEY WORDS: morphology, histology, phylogeny, adult structure

INTRODUCTION

Weevils (Coleoptera: Curculionoidea) are one of the most diverse family-level groups of extant organisms, with approximately 60,000 described species (Anderson, 1995). They are extremely important agriculturally and economically, because they are associated with all major groups of plants and plant parts. The current classification of weevils, including numerous hypotheses on relationships, is relatively stable at the familial level but remains unstable at the middle to lower levels (e.g., subfamilial, tribal; Alonso-Zarazaga and Lyal, 1999; Oberprieler et al., 2014; Oberprieler, 2014a). The exploration of informative anatomy has not reached an asymptote for weevils, so this study was undertaken to deepen our knowledge of their morphology (see also Davis, 2014, for additional character systems). In order to develop a more robust morphological character system for cladistic analysis of the higher lineages and to gain a comprehensive understanding of rostrum structure (for current developmental work), a comparative study was conducted of rostrum structure throughout Curculionoidea. Semithin sections were made of the rostra of exemplar taxa (table 2) representing all seven weevil families, as well as 19 of 21 subfamilies within Curculionidae (see methods section below), and internal structures were examined for useful characters. Although the morphological diversity of rostral forms is vast, general trends in structure are apparent. Features

of internal rostral morphology provide a valuable complementary set of previously unexplored characters. Although this study includes relatively few taxa, it covers a fair range of rostral forms and taxonomic divisions, highlighting the major features apparent in weevil rostrum evolution and diversification. It will serve as a basis for continued exploration of rostrum structure throughout weevil subfamilies to determine the breadth of rostral architecture deviating from the generalized forms determined here. Lastly, this work addresses current incongruence at the higher levels of classification.

METHODS

Taxon Sampling

Semithin sections were produced for all seven of the currently recognized, extant families within Curculionoidea, and 19 of 21 subfamilies within Curculionidae (table 2). To adhere to a conservative assessment of current and evolving views in the classification, the sampling design followed that by Oberprieler et al. (2007, 2014) for families and and a combination of designs by Alonso-Zarazaga and Lyal (1999) and Oberprieler (2014a) for subfamilies (particularly within Curculionidae). To elucidate the variability of internal rostral morphology, sampling of more than one taxon was undertaken when possible, i.e., within the families Anthribidae, Belidae, Attelabidae, and Brentidae. Within Curculioni-

dae, sampling of more than one taxon was performed for a few subfamilies, including Brachycerinae, Dryophthorinae, Entiminae, Cryptorhynchinae, Scolytinae, Curculioninae, and Molytinae. Of course, it would be of great interest to extend this study to include a more diverse sampling, but the range covered herein is considered adequate to make many well-supported conclusions and hypotheses.

Histological Sectioning

Many adult taxa were acquired through personal field collecting; several were also sampled from dried and pinned collections. In the former case specimens were collected into 70% ethanol and later fixed in 4% paraformaldehyde before full dehydration in ethanol. In the latter case specimens were rehydrated by soaking them in warm water for ~1 hour and then dehydrated in ethanol. Although sectioning previously dried specimens is far from optimal for obtaining histological information, sclerotized structures are adequately preserved and were sufficient for this study. After weevil heads were dehydrated in 100% ethanol, infiltration of head tissue consisted of approximately 12 hour incubation periods through a series of 1:1 then 1:2 ethanol to LR White® (an acrylic resin) mixtures. Heads were placed in gelatin capsules and embedded in pure LR White®. Following thermal curing in an oven for 24 hours at 60° C, embedded heads were removed from the capsules and sectioned using a Leica EM UC6 ultratome and diamond knife, producing semithin sections ~5–6 µm thick. Sections were transferred to glass slides, stained in toluidine blue, air dried, mounted in Permount™, and digitally photographed with a Canon EOS-1 camera mounted on an Olympus BX51 compound microscope. A z-stack was acquired of several photomicrographs using the software CombineZ, and edited in Adobe Photoshop CS3.

Electron Microscopy

Scanning electron microscope (SEM) images were captured using a LEO 1550 FESEM (field emission scanning electron microscope). Heads were mounted on SEM stubs using Leit-C-Plast adhesive and an isopropanol-based colloidal graphite, and were then coated with gold.

Confocal Microscopy

Confocal microscopy was performed on dissected mouthpart components using a Zeiss LSM 710 and collecting green and red spectra from autofluorescence of the cuticle.

Microcomputed Tomography (µCT)

Select weevil scans were done from ethanol-preserved specimens that were subsequently chemically dried using HMDS (hexamethyldisilazane) and scanned using a GE Phoenix v-tome-x µCT; scanning parameters were as follows: voltage 70 kV, current 160 µA, number of images 1200, image acquisition time 333 ms, image averages 5, molybdenum target used. Reconstruction was done in GE Phoenix datosx 2 reconstruction software. Four separate scans were manually stitched in ImageJ, and segmentation done in Volume Graphics Studio MAX v3.0. A rendered µCT scan movie of the adult head of *Rhynchites auratus* (same as figures 1–7), showing internal anatomy, is available with this article online (https://doi.org/10.5531/sd.sp.27).

Phylogenetic Analysis

The morphological character matrix (table 1), consisting of 19 adult rostral characters coded for 36 taxa, was constructed in WinClada (Nixon, 1999b). Parsimony analyses were performed using Nona (Goloboff, 1999), in which the ratchet search algorithm (Nixon, 1999a) was implemented several times under different search configurations to maximize exploration of tree space and ensure convergence on a stable topology. Successive searches analyzed 8–14 characters for 500–4000 iterations using two simultaneous threads. The results presented here are based on analyses of 14 characters (equally weighted) for 2000 ratchet iterations using two simultaneous threads. Phylogenetic results essentially follow the contemporary classifications of Oberprieler et al. (2007) and Oberprieler et al.

TABLE 1

Morphological character matrix of 19 characters coded for 36 weevil taxa

Assigned polymorphisms are as follows: $ = 2, 4.

	5	1 0	1 5
Cimberis pilosa (Nemonychidae)	0000110000000000000		
Euparius paganus (Anthribidae)	0000100000000000000		
Ptychoderes sp. (Anthribidae2)	0000100000000000000		
Dicorydylus sp. (Belidae)	1120011000100000001		
Rhynchites auratus (Rhynchitinae)	0110101000110000101		
Attelabus sp. (Attelabinae)	0110100000110000101		
Caenominurus topali (Caridae)	1120100100110001101		
Ithycerus noveboracensis (Ithycerinae)	1120311000120111101		
Arrenodes minutus (Brentinae)	1120110000110111101		
Apion sp. (Apioninae)	1121111200110111101		
Nanophyes sp. (Nanophyinae)	1120310200110111101		
Brachycerus sp. (Brachycerini)	11203120000$1111111		
Gilbertiola sp. (Raymondionymini)	1120310000111111111		
Lissorhoptrus sp. (Erirhinini)	11203120001$1111111		
Sphenophorus sp. (Dryophthorinae1)	1120310000111112111		
Rhodobaenus sp. (Dryophthorinae2)	1120310000111112111		
Platypus sp. (Platypodinae)	1------000111112111		
Bagous restrictus (Bagoinae)	1122112011141111111		
Hypera eximia (Hyperinae)	1120311011141112111		
Cyrtepistomus castaneus (Entiminae)	1120210011221112111		
Listronotus sp. (Cyclominae)	1120213011221112111		
Rhyssomatus lineaticollis (Molytinae1)	1120210111131112111		
Chalcodermus collaris (Molytinae2)	1120210111131112111		
Cossonus sp. (Cossoninae)	1125211111321112111		
Xyleborus sp. (Xyleborini)	1------1113--111111		
Hylurgops planirostris (Hylastini)	1------1113--111111		
Lixus sp. (Lixinae)	1120111011231112111		
Odontocorynus sp. (Baridinae)	1124211111111112111		
Cylindrocopturus adspersus (Conoderinae)	1122111111131112111		
Tyloderma variegatum (Cryptorhynchinae)	1120211111131112111		
Magdalis sp. (Mesoptilinae)	1123211111131112111		
Phytobius sp. (Ceutorhynchinae)	1120112111111112111		
Curculio sp. (Curculioninae1)	1120110111111112111		
Smicronyx squalidus (Curculioninae2)	1120112111111112111		
Gymnaetron sp. (Curculioninae3)	1120110111111112111		
Anthonomus nigrinus (Curculioninae4)	1120110111111112111		

TABLE 2

Taxa examined in this study

In the column labeled "Phylogeny," taxa with an asterisk were specifically included in the phylogenetic analysis.

Superfamily	Family	Subfamily	Tribe	Taxon	Phylogeny
Tenebrionoidea	Salpingidae			*Rhinosimus viridiaeneus* (Randall, 1838)	
Chrysomeloidea	Chrysomelidae			*Diabrotica undecimpunctata* Mannerheim, 1843	
Curculionoidea	Nemonychidae	Cimberidinae	Cimberidini	*Cimberis pilosa* (LeConte, 1876)	*
	Anthribidae		Cratoparini	*Euparius paganus* Gyllenhal, 1833 [in Schönherr 1833]	*
			Ptychoderini	*Ptychoderes* Schönherr, 1823 sp.	*
	Belidae	Pachyurinae	Agnesiotidini	*Dicorydylus* Lacordaire, 1863 sp.	*
		Belinae		*Rhinotia* W. Kirby, 1819 sp.	
	Attelabidae	Attelabinae	Attelabini	*Attelabus* Linnaeus, 1758 sp.	*
		Rhynchitinae	Rhynchitini	*Rhynchites auratus* (Scopoli, 1763)	*
	Caridae			*Caenominurus topali* Voss, 1965	*
	Brentidae	Ithycerinae		*Ithycerus noveboracensis* (Forster, 1771)	*
		Brentinae	Brentini	*Arrenodes minutus* (Drury, 1770)	*
		Apioninae	Apionini	*Apion* Herbst, 1797 sp.	*
			Aplemonini	*Phrissotrichum tubiferum* (Gyllenhal, 1833)	
		Nanophyinae	Nanophyini	*Nanophyes* Schönherr, 1838 sp.	*
	Curculionidae	Brachycerinae	Brachycerini	*Brachycerus* Olivier, 1789 sp.	*
			Erirhinini	*Lissorhoptrus* LeConte, 1876 sp.	*
			Raymondionymini	*Gilbertiola* Osella, 1982 sp. [in O'Brien and Wibmer, 1982]	*
		Dryophthorinae	Sphenophorini	*Sphenophorus* Schönherr, 1838 sp.	*
			Sphenophorini	*Rhodobaenus* LeConte, 1876 sp.	*
			Litosomini	*Sitophilus oryzae* (Linnaeus, 1763)	
		Platypodinae	Platypodini	*Platypus* Herbst, 1793 sp.	*
		Bagoinae		*Bagous restrictus* LeConte, 1876	*
		Hyperinae	Hyperini	*Hypera eximia* (LeConte, 1876)	*
		Entiminae	Cyphicerini	*Cyrtepistomus castaneus* (Roelofs 1873)	*
			Geonemini	*Epicaerus imbricatus* (Say, 1824)	
			Tanyrhynchini	*Tanyrhynchus* Schönherr, 1826 sp.	
		Cyclominae	Rhythirrinini	*Listronotus* Jekel, 1865 sp.	*
		Molytinae	Cleogonini	*Rhyssomatus lineaticollis* (Say, 1824)	*
			Cleogonini	*Conotrachelus* Dejean, 1835 sp.	
			Hylobiini	*Heilipodus polyguttatus* (Hustache, 1938)	
			Sternechini	*Chalcodermus collaris* Horn, 1873	*

Superfamily	Family	Subfamily	Tribe	Taxon	Phylogeny
		Cossoninae	Cossonini	*Cossonus* [Clairville], 1798 sp.	*
		Scolytinae	Hylurgini	*Dendroctonus ponderosae* Hopkins, 1902	
			Xyleborini	*Xyleborus* Eichhoff, 1864 sp.	*
			Ipini	*Ips* DeGeer, 1775 sp.	
			Hylastini	*Hylurgops planirostris* (Chapuis, 1869)	*
		Lixinae	Lixini	*Lixus* Fabricius, 1801 sp.	*
		Baridinae	Madopterini	*Odontocorynus* Schönherr, 1844 sp.	*
		Conoderinae	Zygopini	*Cylindrocopturus adspersus* (LeConte, 1876)	*
		Cryptorhynchinae	Cryptorhynchini	*Tyloderma variegatum* (Horn, 1873)	*
			Cryptorhynchini	*Gerstaeckeria lecontei* O'Brien, 1970	
		Mesoptilinae	Magdalidini	*Magdalis* Germar, 1817 sp.	*
		Ceutorhynchinae	Phytobiini	*Phytobius* Schönherr, 1833 sp.	*
		Curculioninae	Curculionini	*Curculio* Linnaeus, 1758 sp.	*
			Mecinini	*Gymnaetron* Schönherr, 1825 sp.	*
			Anthonomini	*Anthonomus nigrinus* Boheman, 1843 [in Schönherr, 1843]	*
			Smicronychini	*Smicronyx squalidus* Casey, 1892	*

(2014), with the noted exception of a more inclusive Conoderinae that currently seems unwarranted and problematic in the context of some other subfamilies (e.g., Curculioninae).

Anatomical Terminology

Morphological terms follow those used in Davis (2011) and are derived mainly from Lyal (1995), Morimoto and Kojima (2003), and Snodgrass (1935, 1960). While much focus centered on the chitinous and sclerotized features within the rostrum, some other structures and soft tissues (as well as chitinous features) are identified and follow Brack-Egg (1973), Dönges (1954), and Kéler (1963). Other important contributions to head anatomy include Dennell (1942), DuPorte (1960), Stickney (1923), and Ting (1936). Several internal features that were not under investigation during this study, but could be of some phylogenetic significance, including nerves, tracheae, etc., are documented in these latter references.

RESULTS

General and Internal Anatomy of the Adult Weevil Rostrum

Figures 1–11

Before describing variation in the internal structure of the rostrum throughout Curculionoidea, it is critical to briefly outline these features and their characteristics. Beginning at the anterior apex of the rostrum and traversing the mouthparts, a few differences are readily apparent in terms of orientation. As meticulously documented by Morimoto (1962), Morimoto and Kojima (2003), and Morimoto et al. (2006), there are differences in how the mouthparts are angled throughout Curculionoidea. In general, the more basal lineages have mandibles that act in the horizontal plane, whereas in some more derived lineages this plane shifts obliquely and nearly vertically. This rotational shift also is visible in the orientation

of the two mandibular articulations on the head, namely the position of the anterior condyle (precoila) and the posterior acetabulum (postcoila). Along with the change in the positions of these points of articulation, it is largely the size of other features that accompany the fundamental orientation of the mouthparts. For example, most noticeable of these changes is the reduction in the mandibular adductor tendons and the corresponding enlargement of the abductor tendons. This shift in tendon size indicates a different mode of action of the mandibles, from a chewing action to one of a rasping or scraping nature (e.g., *Curculio*).

Plesiomorphically in insects it is possible to divide the subgenal sulcus into two distinct parts (Snodgrass, 1935). The pleurostomal sulcus, comprising the anteriormost section of the subgenal sulcus, runs just behind the mandible. Remnants of this sulcus and the epistomal sulcus are visible (particularly in sections) around or along the margins of the oral cavity, as both connect in the immediate vicinity of the anterior tentorial pits. There is no discernible evidence of the frontal lines delimiting the lateral margins of the frons for most of the rostrum length, although anterior remnants of these lines or sulci appear to be preserved (see char. 13). Delimiting the posterior point of the frons, an abbreviated coronal line often is present and forms a sulcus to which a portion of the mandibular adductor muscles attach by way of an internal phragma. The pleurostomal sulcus connects to the anterior tentorial pits, which are also just posterior to the anterior mandibular articulation, and eventually merges with the occipital sulcus (close to the posterior mandibular articulation). In all weevils, the junction where the pleurostomal and occipital sulci meet has been obliterated, as the pleurostomal sulcus extends laterally and posteriorly for only a short distance. The hypostomal sulcus continues from where the pleurostomal sulcus joins the occipital sulcus, ending at the posterior tentorial pits (from which the gular [postoccipital] sutures continue in Coleoptera). The anterior extension of the hypostomal sulci typically can be observed only in well-macerated dissections and often are internalized in the higher weevils.

In Curculionoidea, the anterior tentorial pits are difficult to locate externally; however, remnants of the anterior tentorial arms (pretentorium sensu Stickney, 1923) usually are visible in sections and are occasionally visible after dissection in the majority of Curculionoidea (fig. 20C, E), though they do not extend very far posteriorly. Proceeding further from the base of the weevil phylogeny, these arms may disappear within some tribal lineages of Curculionidae, though in-depth discussion of such reduction is not possible from this study alone. Although Morimoto and Kojima (2003) mentioned that the anterior tentorial arms seem to be obliterated in all weevils excepting Belidae (which also possess remnant bases of the arms), it has become apparent in this study that at least a small anterior portion of the arms (where they attach adjacent to the dorsal mandibular articulation) are present throughout the superfamily, often being more noticeable in several basal families (e.g., Attelabidae) or in those lineages that mostly lost the rostrum and instead have a large oral cavity (e.g., Scolytinae, Platypodinae). Stickney (1923) also noted this widespread presence in several families, and Brack-Egg (1973) and Dönges (1954) illustrated them with great detail in *Rhynchites* (Attelabidae) and *Cionus* (Curculionidae), respectively. Ting (1936) illustrated the anterior arms in *Ithycerus*, *Rhynchites*, and *Platypus*, but did not discuss their occurrence throughout the superfamily. Near the anterior mandibular articulation, the frontal lines and pleurostomal sulci are readily visible in several basal families as invaginations of the exocuticle (as are all sulci) and are less apparent (at least in sections) beginning in the Dryophthorinae.

An interesting modification of the ventral head sulci arises in Coleoptera that involves the hypostomal sulcus and includes a novel sulcus, the hypostomal-labial sulcus, which appears to separate the hypostoma from the submentum (Lyal, 1995). Its presence within Curculionoidea is substantial, and the pair of sulci may also be prevalent throughout Coleoptera (fig. 15). While the hypostoma reaches the posterior extension of the submentum (and the posterior tentorial pits) in other insects, it shifts anteriad in Coleoptera,

thereby elongating the hypostomal sulcus and essentially extending the postgena to also unite with the submentum (in addition to the posterior extension of the submentum fusing with the gula). Due to the formation of the rostrum in weevils, while remnants of the pleurostomal sulci are visible, the hypostomal sulci often are indistinguishable (except in well-macerated tissues). The separations of the pleurostomal + genal regions and the hypostomal + postgenal regions in weevils, then, become challenging due to the loss of sulci that delimit these regions. Beginning perhaps independently with Belidae, then in Brentidae, and continuing throughout the higher Curculionoidea, the situation becomes further complicated by the apparent merging of the hypostomal and occipital sulci that eliminates some or most of the postgenal region. As seen in higher Curculionoidea (beyond the three groups just mentioned above), this fusion leaves a vague continuity between head sclerites involving a pleural region of the rostrum composed of: the frons (in which the antennae can be found in numerous positions along the rostrum), the pleurostoma + genal regions of the parietals, and the hypostomal + postgenal regions (Davis, 2011). With the apparent loss of most of the hypostomal sulci in the majority of weevils, it is likely that the postgenal region has been greatly reduced in these cases.

The hypostomal-labial sulcus appears to be present in all weevils. Generally, this pair of sulci is nearly indiscernible externally and barely detectable in semithin sections. It is rather short in the basal weevils and greatly abbreviated in the higher weevils, mostly folding inward and internalized distad. Extending into the rostrum internally, it separates the postmentum and hypostoma. Posteriad are two pairs of sulci, the subgenal and occipital sulci. While the plesiomorphic state of separate subgenal and occipital sulci is observed in Nemonychidae (fig. 16), some Anthribidae (fig. 18), and Attelabidae (fig. 22), the remainder of Curculionoidea essentially possess only one pair of ventral sulci. It is possible that, over the course of time, the subgenal sulci became fused with or were subsumed into the occipital sulci, particu-

larly given the extensive apodemes that form from this pair of sulci in the higher weevils. It is also plausible, however, that the subgenal sulci simply were lost as the occipital sulci migrated medioventrally; thus, those that remain are the occipital sulci that support not only the mandibular adductor tendons but also the adductor tendons and those of the maxilla. Support for this latter hypothesis is based on the mandibular adductor and maxillary tendons, where both are supported by the apodemes of the subgenal sulci (at least in Nemonychidae, possibly also in some Anthribidae), whereas the mandibular adductors are supported by the apodemes of the occipital sulci in the remainder of Curculionoidea. The maxillary tendons display a similar trend, though in addition to being supported by the apodemes of the subgenal sulci in Nemonychidae, possibly also in Anthribidae, they clearly remain arranged in this fashion in Attelabidae as well, at least in part. While the additional apodeme emanating mesad from the bifurcate apodeme of the occipital sulcus in weevils that lack the subgenal sulci appears to be a simple fusion of the apodemes of the two sulci, observations (at least in Attelabidae) demonstrate that this additional ramus can form from the occipital sulcus. Therefore, there is no clear evidence yet to favor either hypothesis.

In most extant Curculionoidea, where the rostrum is fairly curved, the mouthpart tendons are situated in cuticular canals that guide and facilitate their sliding action (figs. 1–8). The canals for the larger mandibular tendons, naturally, are quite deep, and constitute apodemes formed by the occipital sulci. In weevils that possess distinct subgenal sulci, separate apodemes are present for supporting the maxillary tendons. In most higher weevils, such as Curculionidae, where only the occipital sulci are present, the apodemes of the sulci have formed a medial bridge (e.g., figs. 34, 39, 44, 45, 47). The tendons of the maxilla rest in canals on this bridge. Nearing attachment to the mouthparts, as was the case at the base of the rostrum, the tendons take a more central position in the rostral cavity, eventually arriving adjacent to and partially enclosed by the pharyn-
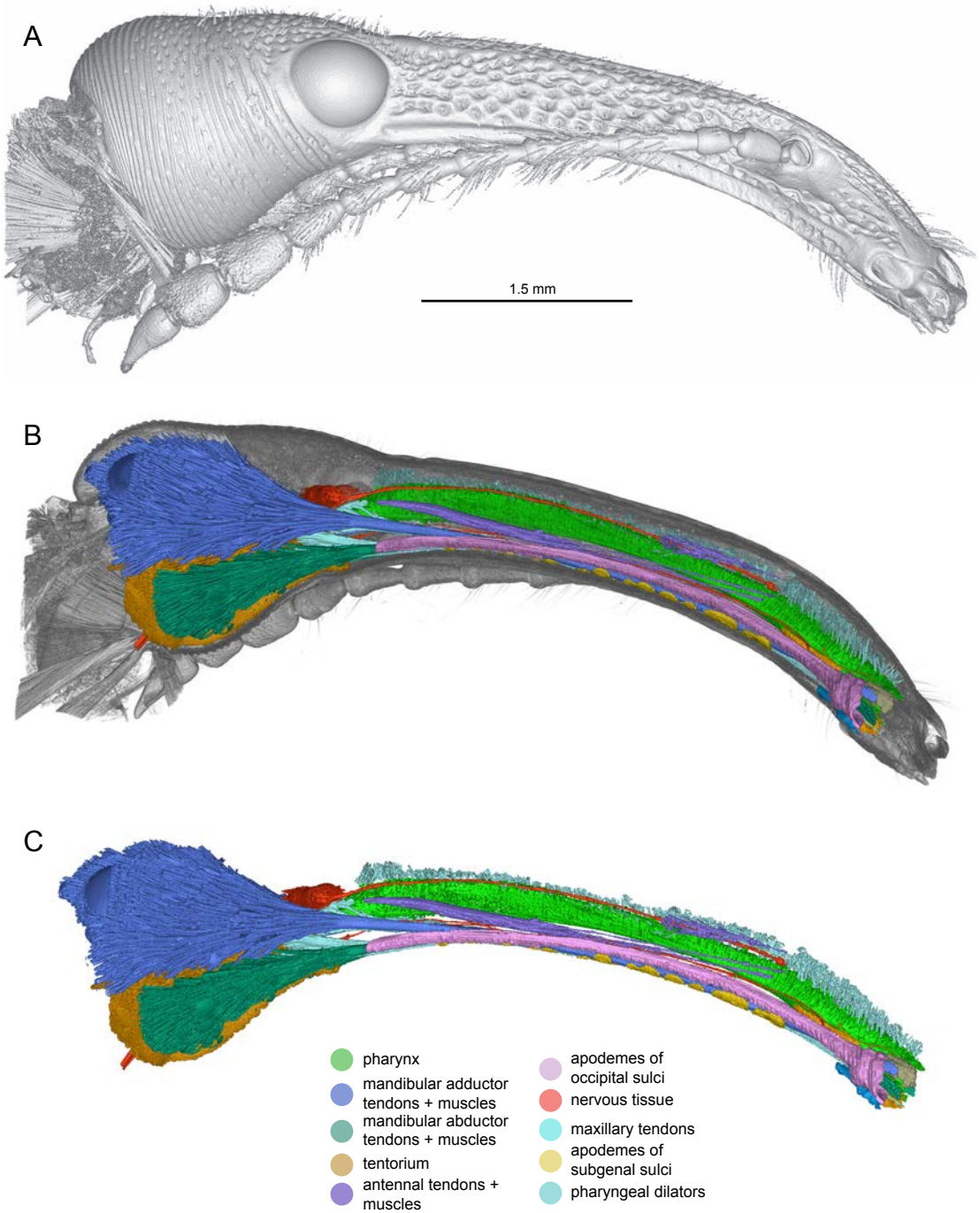
FIGURE 1. µCT scan of *Rhynchites auratus* (Attelabidae), adult head. **A–C,** lateral aspect of head. **A,** scan illustrating unaltered exterior surface of head; **B,** cuticle of right half of head removed, showing internal anatomy; **C,** cuticle of entire head removed, showing internal anatomy. Color legend to highlighted structures presented at bottom.
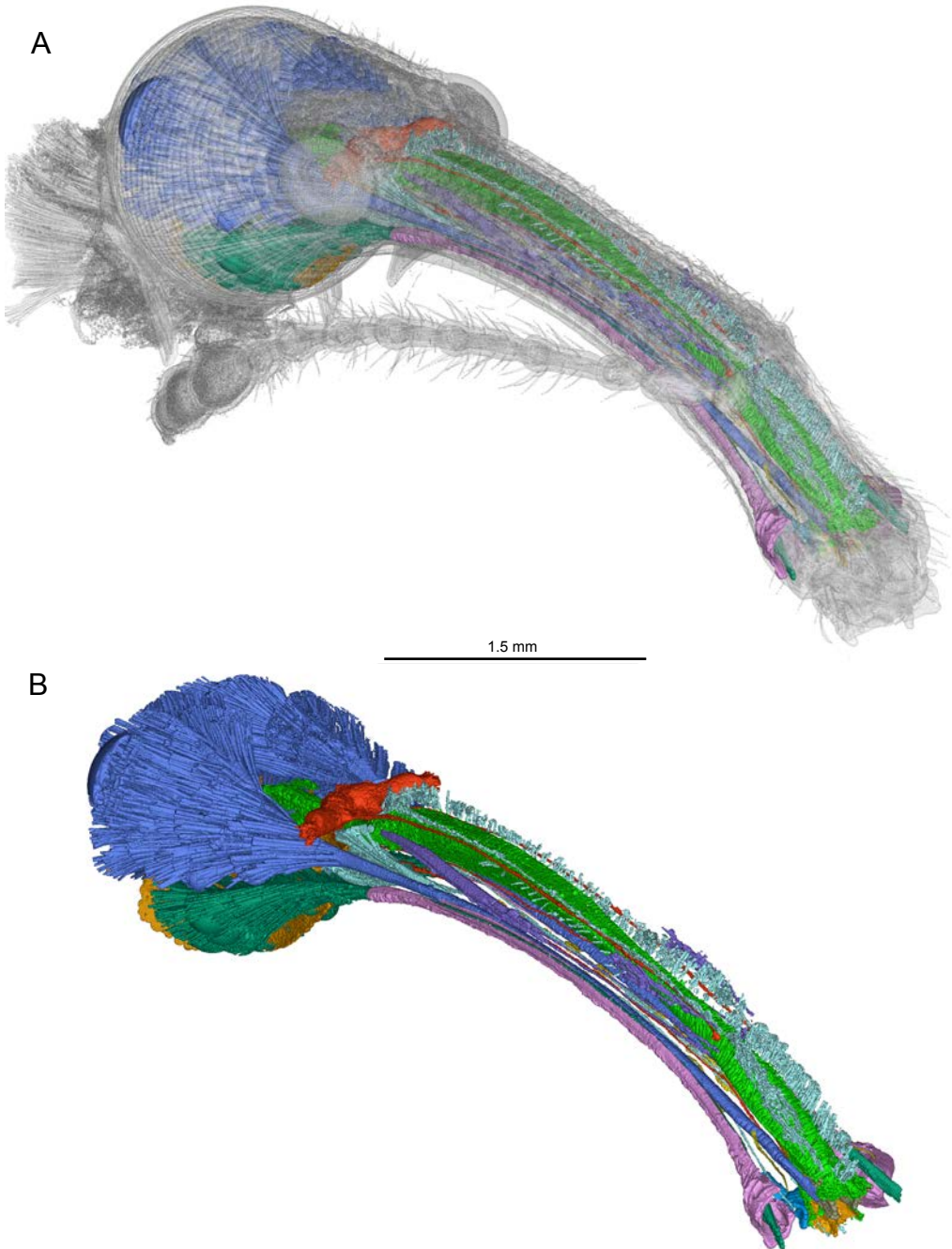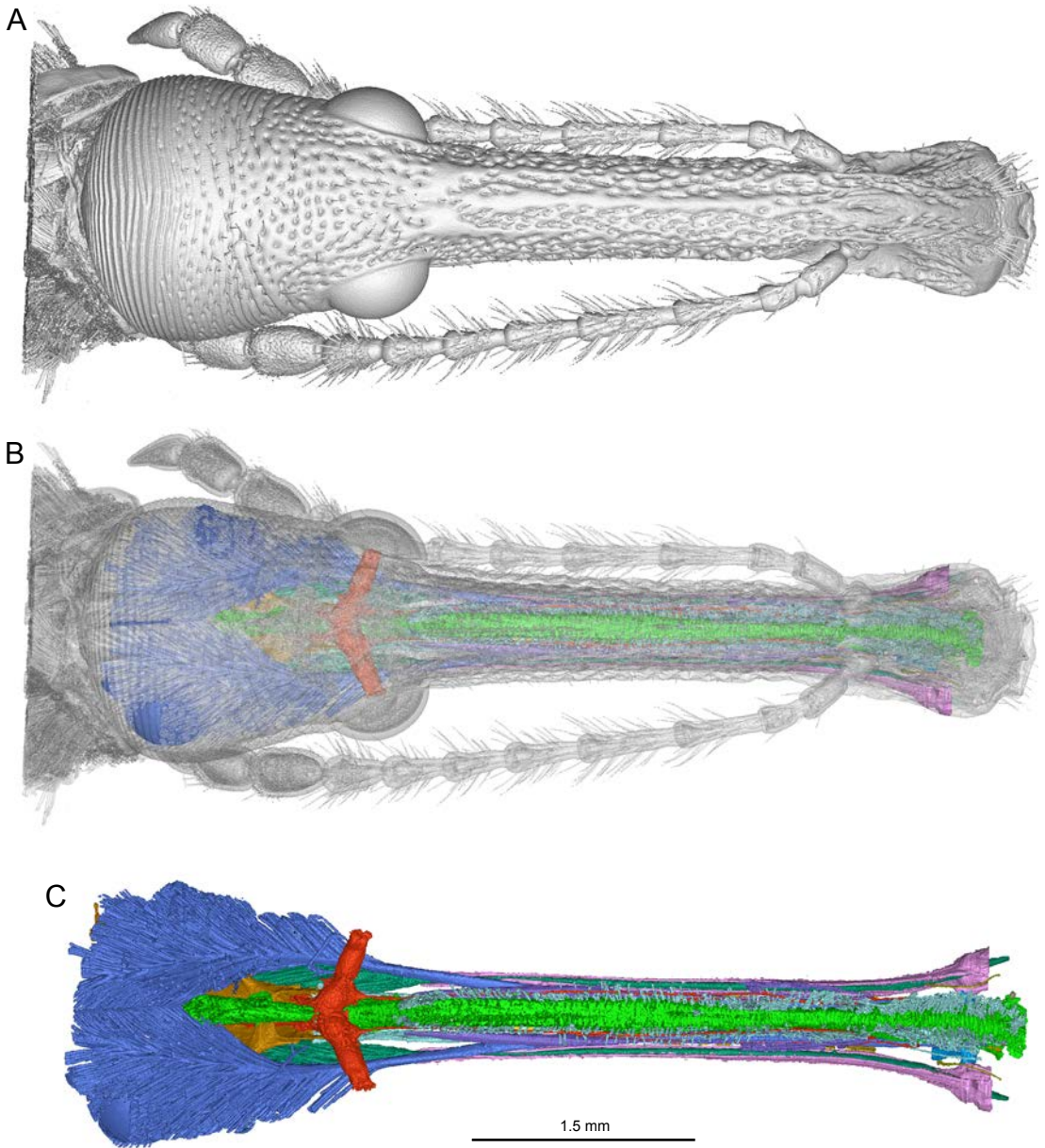
1.5 mm

FIGURE 2. μCT scan of *Rhynchites auratus* (Attelabidae), adult head. **A–B,** anterolateral aspect of head. **A,** cuticle of head rendered semitransparent to reveal internal anatomy; **B,** cuticle of entire head removed, showing internal anatomy.
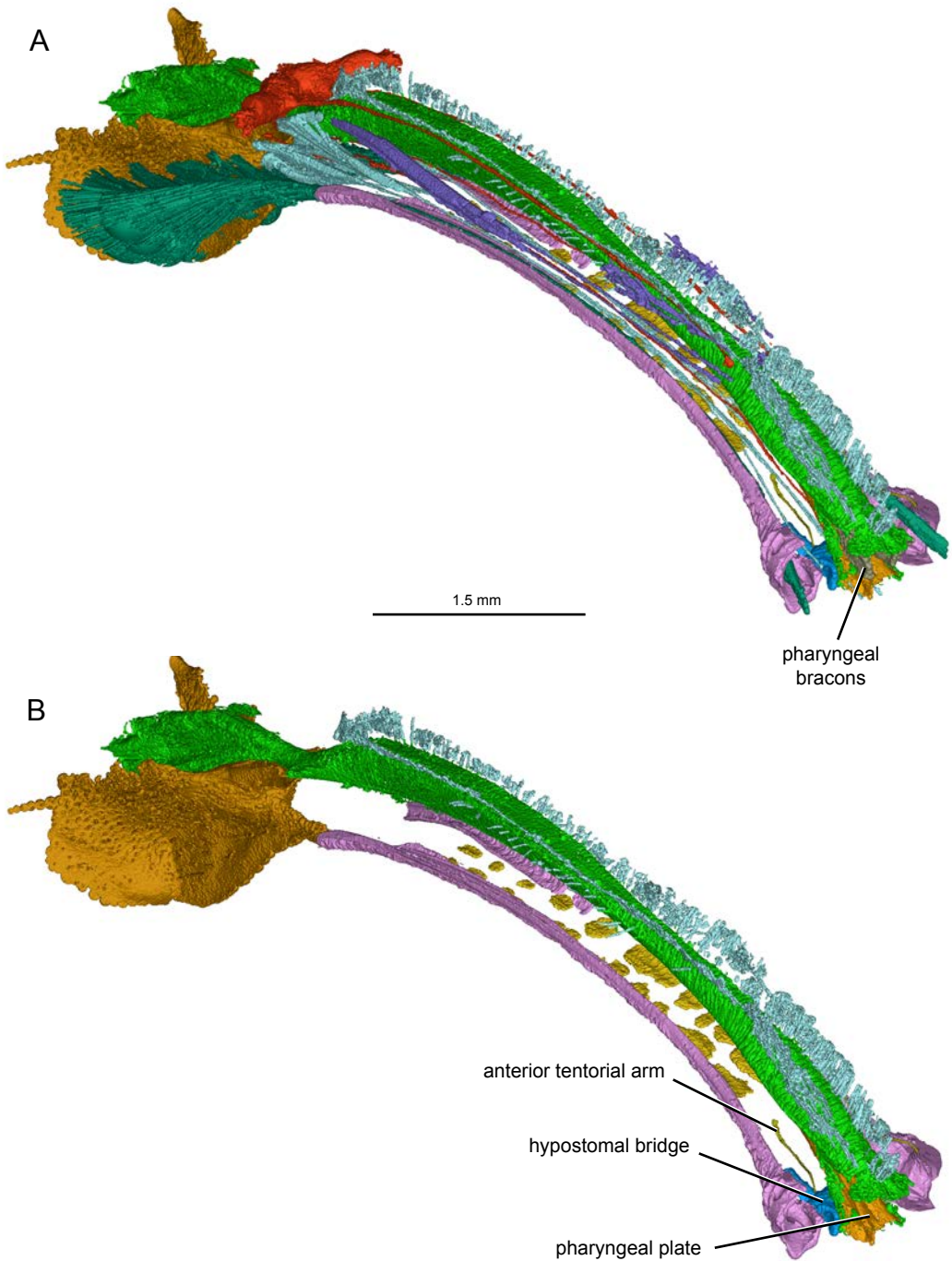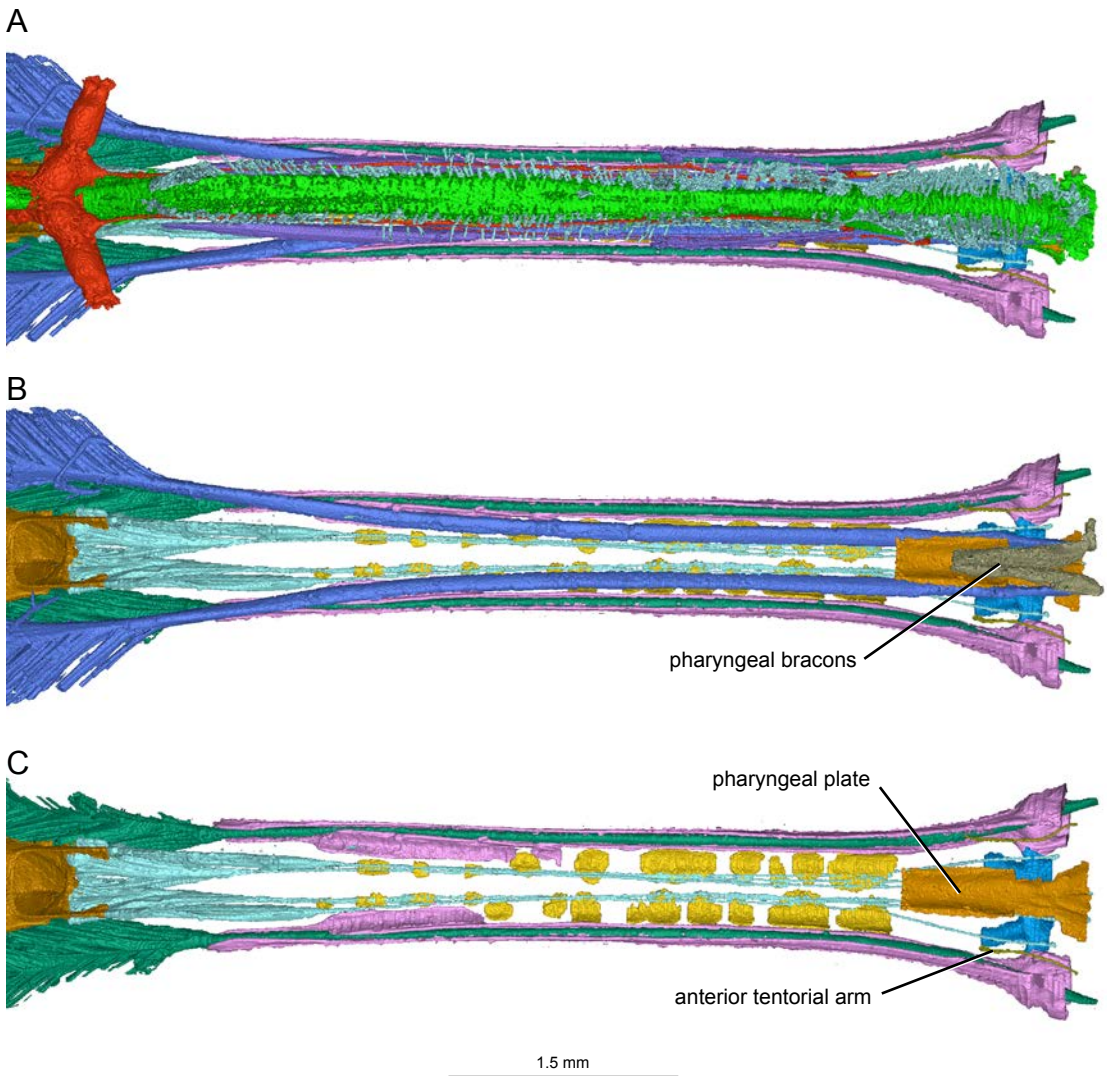
FIGURE 3. μCT scan of *Rhynchites auratus* (Attelabidae), adult head. **A–B,** anterolateral aspect of head with entire cuticle removed. **A,** internal anatomy with mandibular adductor tendons and muscles removed; **B,** internal anatomy with mandibular abductor and adductor tendons and muscles, antennal tendons and muscles, maxillary tendons and muscles, and nervous tissue removed.
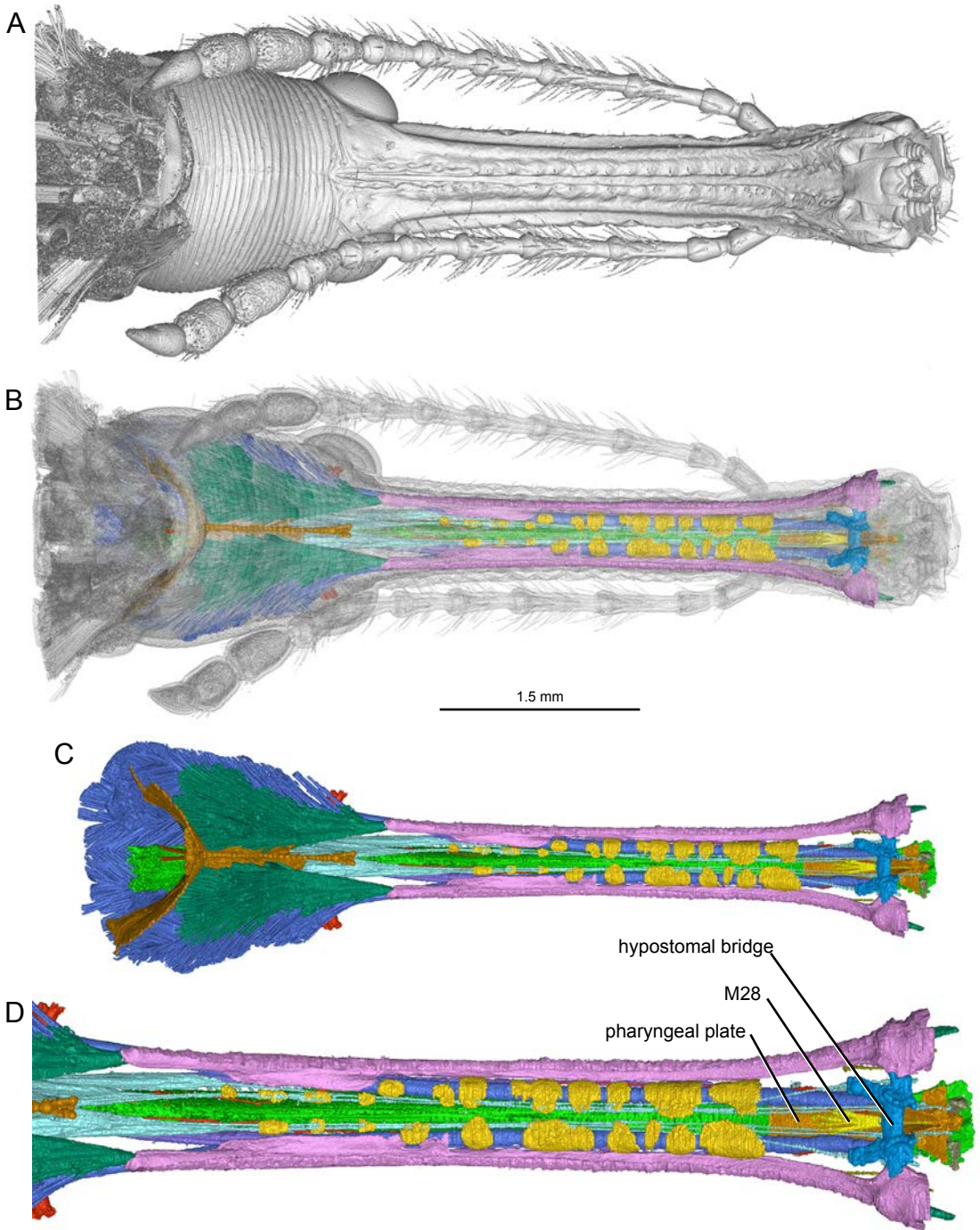
FIGURE 4. μCT scan of *Rhynchites auratus* (Attelabidae), adult head. **A–C,** dorsal aspect of head. **A,** scan illustrating unaltered exterior surface of head; **B,** cuticle of head rendered semitransparent to reveal internal anatomy; **C,** cuticle of entire head removed, showing internal anatomy.

FIGURE 5. μCT scan of *Rhynchites auratus* (Attelabidae), adult head. **A–C,** dorsal aspect of rostrum with entire cuticle removed. **A,** internal anatomy of rostrum; **B,** internal anatomy with nervous tissue, pharynx, and pharyngeal dilator muscles removed; **C,** internal anatomy with nervous tissue, pharynx, pharyngeal dilator muscles, pharyngeal bracons, and mandibular adductor tendons and muscles removed.

FIGURE 6. μCT scan of *Rhynchites auratus* (Attelabidae), adult head. **A–D,** ventral aspect of head. **A,** scan illustrating unaltered exterior surface of head; **B,** cuticle of head rendered semitransparent to reveal internal anatomy; **C,** cuticle of entire head removed, showing internal anatomy; **D,** enlargement of rostrum in C.
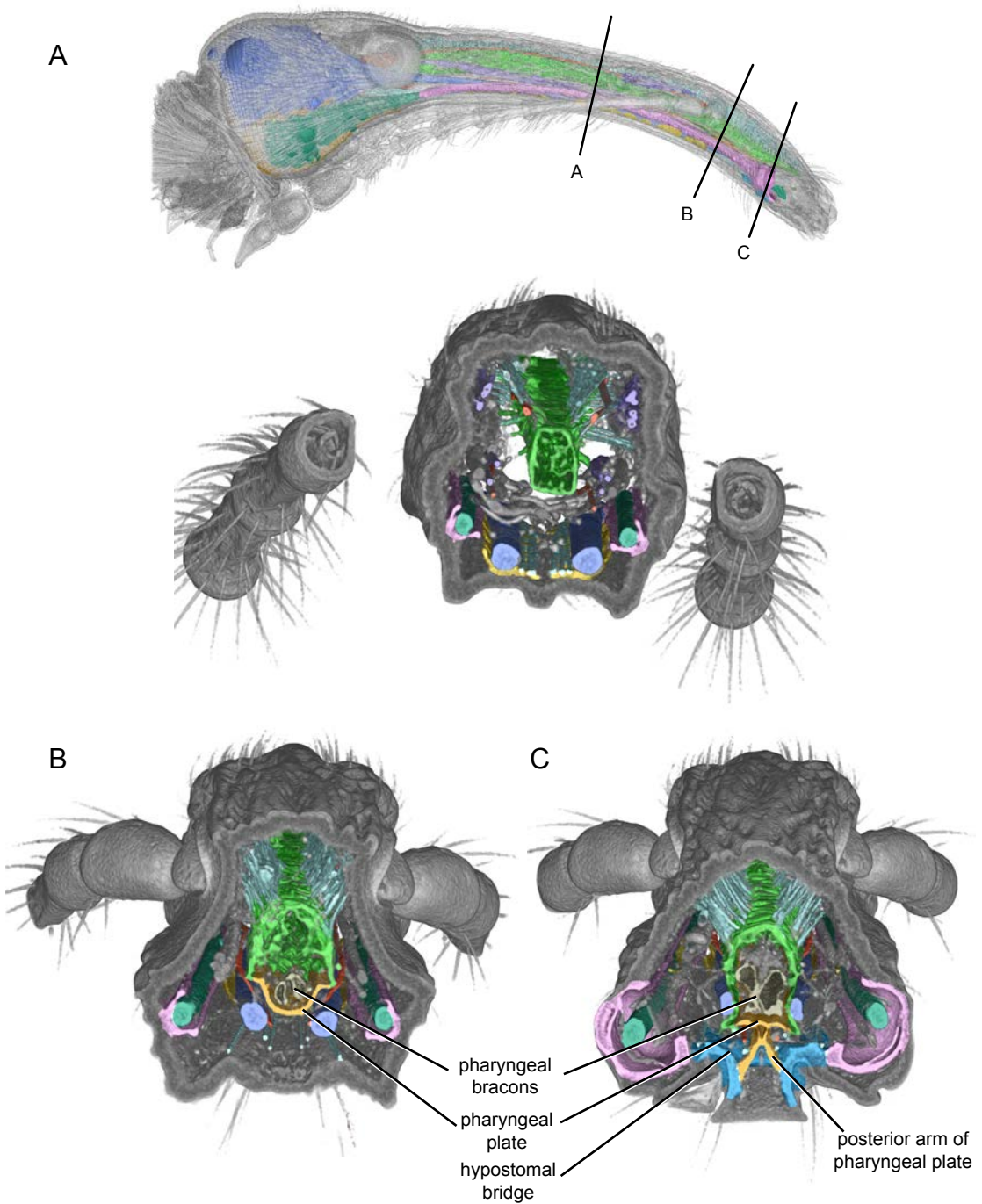
FIGURE 7. µCT scan of *Rhynchites auratus* (Attelabidae), adult head. **A–C,** virtual cross sections through rostrum, revealing internal anatomy at respective areas. **A,** section just posterior to approximate middle of rostrum; **B,** section just anterior to antennal insertion; **C,** section near apex of rostrum, just posterior to pleurostomal sinus. Semitransparent lateral view of head displayed at top, indicating points of cross sections.
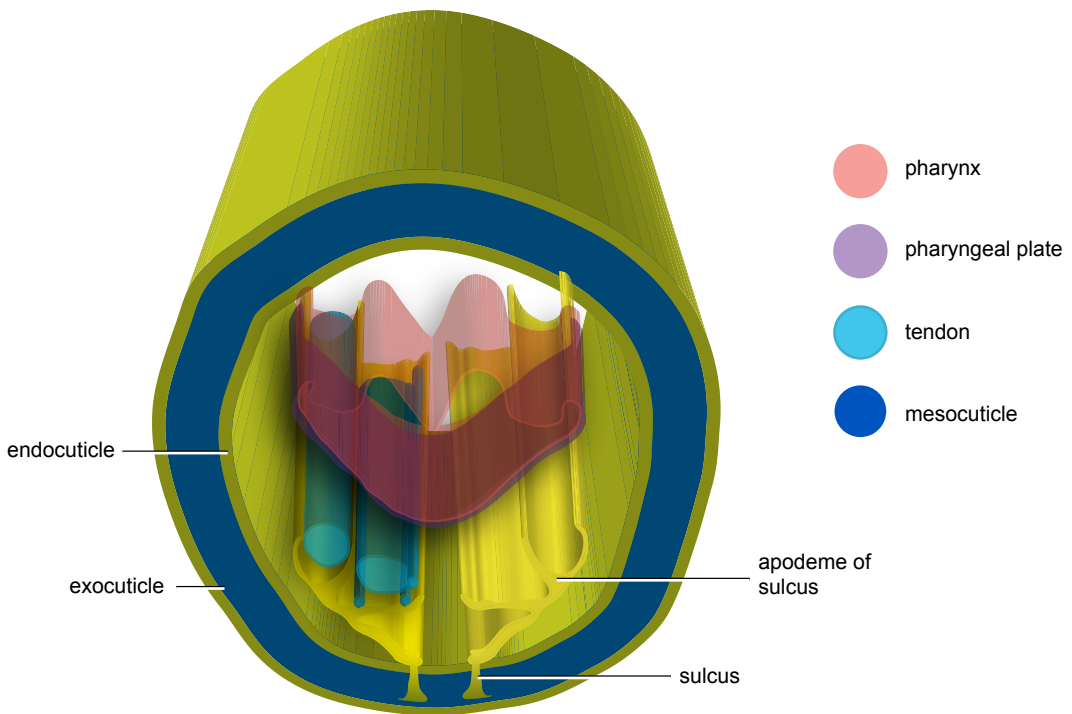
FIGURE 8. General model of a section of the weevil rostrum, illustrating the relative position of key internal structures. Color legend to highlighted structures presented at right.

geal bracons (mandibular processes). Also at the apex, the pharynx widens and the pharyngeal bracons become more visible.

As defined by the position of the hypostomal-labial sulci, the paracoila, or region at which the maxillary cardo articulates with the head, appears to be partially composed of the hypostoma and postmentum. The pharyngeal (cibarial) plate supports the pharynx as well as the anterior extensions of the mandibular adductor tendons (figs. 9–11). This complex likely shares homology with some part of the hypopharyngeal suspensorium or sitophore sclerite in other insects (Snodgrass, 1935), including the hypopharyngeal sclerite and connecting apodemes in other Coleoptera (Weide et al., 2014). It is unlikely that this complex incorporates elements of the premental sclerites, as this set of sclerites appears absent in weevils (at least the vast majority), perhaps lost due to the compression of the labium and reduction of the ligulae. Further observation is necessary in Nemonychidae and

Anthribidae to confirm complete loss in the superfamily. Due to its complexity and prevalence throughout the superfamily, more in-depth documentation and discussion of the pharyngeal plate complex will be covered in a future publication. In Curculionoidea, the pharyngeal plate is variably extended posteriorly, its length typically correlating to the length of the rostrum. The posterior arms of the pharyngeal plate attach to the inner side of the paracoila and thus are from the postmentum. According to sections of this region, it is evident that the hypostomal-labial sulci and, to some degree, the anterior extension of the occipital sulci also contribute to the posterior arms by way of internal apodemes that merge at this area. The anterior arms of the pharyngeal plate attach to the postcoila, immediately above what appears to be the anteriormost reaches of the hypostomal-labial sulcus. From this observation, the anterior arms emanate from the hypostoma and possibly incorporate elements of the hypostomal-labial sulcus. Expound-
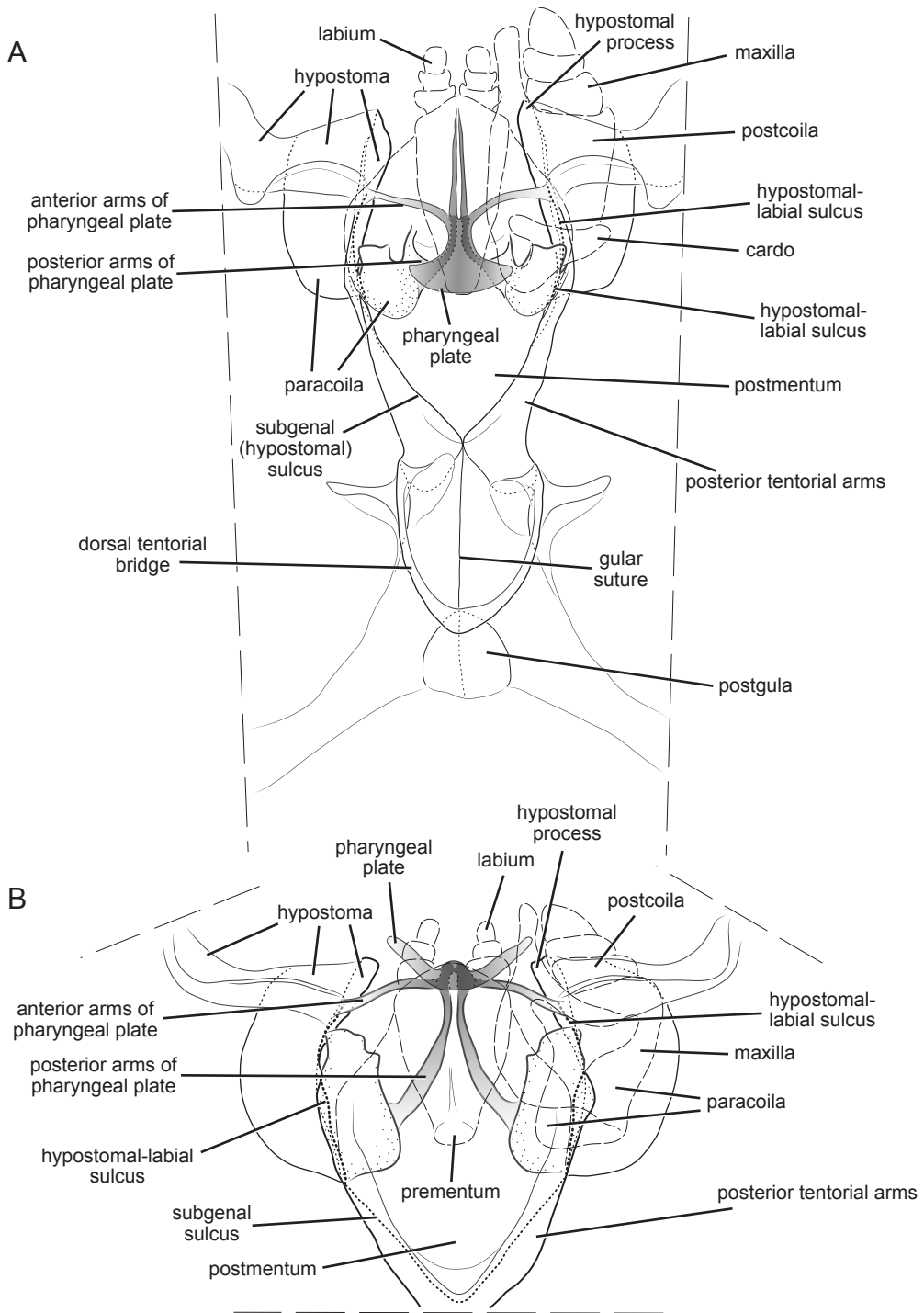
FIGURE 9. Line illustrations of internal head structures in *Platypus* sp. (Curculionidae: Platypodinae), highlighting pharyngeal plate and associated structures. **A,** ventral structures of head in dorsal aspect; **B,** ventral structures of head in posterior aspect.
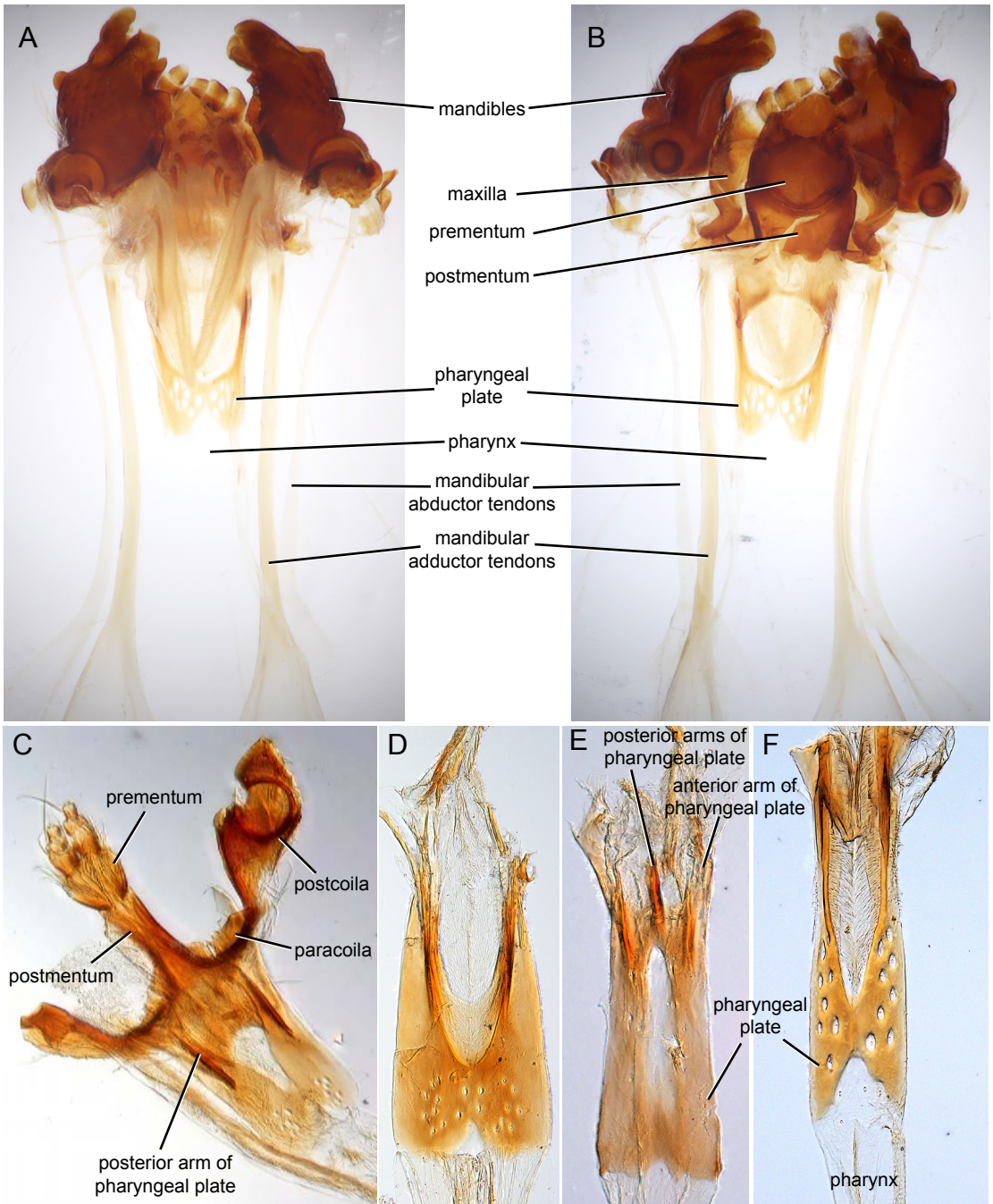
FIGURE 10. Light micrographs illustrating mouthparts, pharyngeal plate, and associated structures. **A–B,** mouthparts and pharyngeal plate of *Listronotus* sp. (Curculionidae: Cyclominae). **A,** dorsal aspect; **B,** ventral aspect; **C,** pharyngeal plate with labium and parts of paracoila and postcoila in *Gerstaeckeria lecontei* (Curculionidae: Cryptorhynchinae); **D,** pharyngeal plate in *Tanyrhynchus* sp. (Curculionidae: Entiminae); **E,** pharyngeal plate in *Phrissotrichum tubiferum* (Brentidae: Apioninae); **F,** pharyngeal plate in *Heilipodus polyguttatus* (Curculionidae: Molytinae).
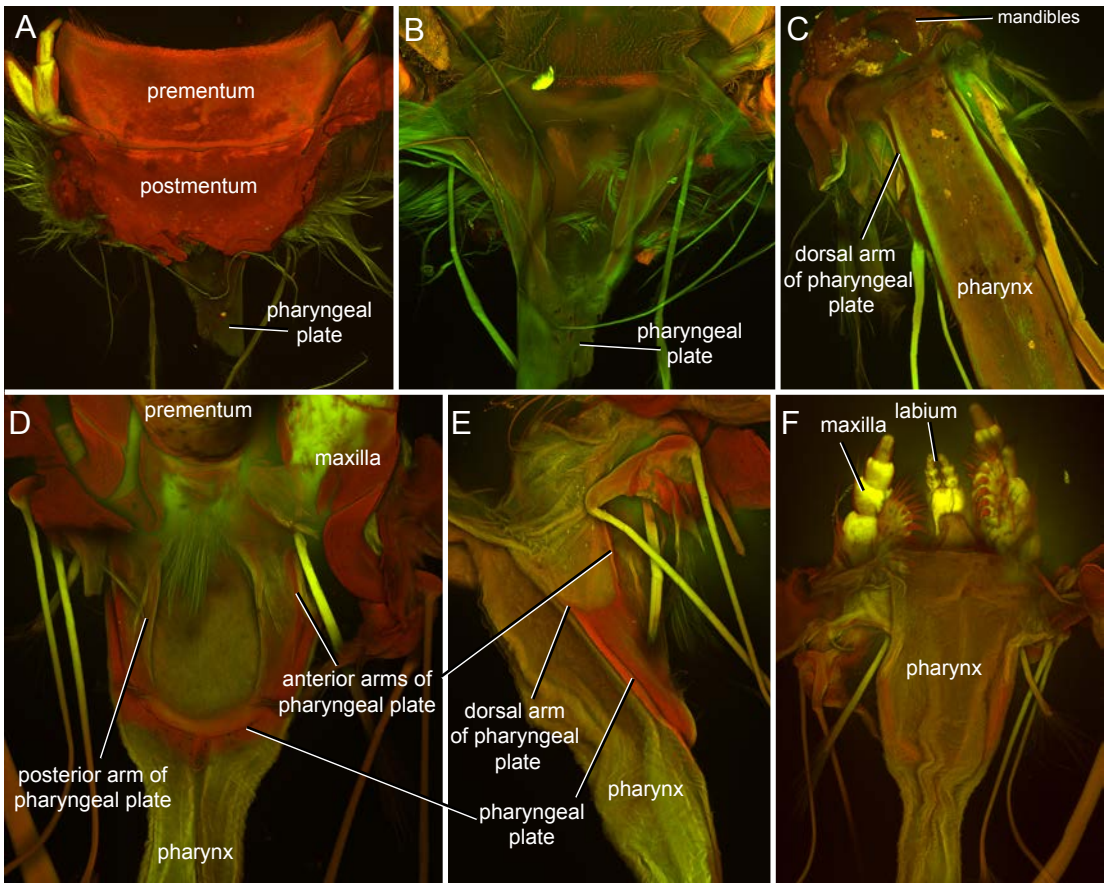
FIGURE 11. Confocal micrographs illustrating pharyngeal plate and associated structures. **A–B,** labium and pharyngeal plate in male *Arrhenodes minutus* (Brentidae: Brentinae). **A,** ventral aspect; **B,** dorsal aspect. **C,** dorsal aspect of pharyngeal plate and mandibles in *Sphenophorus* sp. (Curculionidae: Dryophthorinae). **D–F,** mouthparts and pharyngeal plate in *Epicaerus imbricatus* (Curculionidae: Entiminae). **D,** ventral aspect; **E,** lateral aspect; **F,** dorsal aspect.

ing upon this latter statement, the hypostomal-labial sulci may also form small, distinct apodemes immediately posterior to the posterior arms of the pharyngeal plate, which support the anterior extensions of the maxillary tendons. While the three maxillary tendons are easily recognized in sections, the labial tendon (submentopraementalis muscles [M28]) is not so readily distinguished but can be identified throughout the superfamily (figs. 6, 17, 21–23, 39, 43, 50). As this muscle originates near the basal margin of the mentum, it perhaps is a good landmark for marking division of the postmentum into submentum and mentum, an otherwise vaguely delineated region in Curculionoidea.

Another possible landmark for distinguishing this subdivision is the posteriormost extension of the hypostomal-labial sulci (figs. 6–7, 22). As mentioned above, this pair of sulci is difficult to discern in higher weevils, but usually is visible in lower weevils, particularly when they form distinct internal apodemes or sometimes even bridges (figs. 6–7).

Character List

Morphological characters of this study were largely restricted to the rostrum, specifically to the preocular region, and to features visible in semithin sections. While other features of the

head are certainly of great phylogenetic utility, these have already been well studied, particularly by Morimoto and Kojima (2003) and Morimoto et al. (2006).

Below is a list of the characters scored in this study. Of the morphological variation observed in internal rostrum structure throughout Curculionoidea, the most significant features appear to include the ventral sulci and their associated apodemes, and the tendons of the mouthparts, particularly in the nature by which the mandibular and maxillary tendons are positioned and held by the apodemes. As no suitable outgroup possesses a developed rostrum (which potentially could cause difficulty in character polarization if included), Nemonychidae was used to root the tree. It should be noted that although Nemonychidae appear to display plesiomorphic characters for the weevil clade and sufficiently serve to root the cladogram in this study, outgroup exploration will be needed in future additions to this work as more taxa are examined. This is particularly relevant for the basal families Nemonychidae, Anthribidae, and Belidae, as recent studies (e.g., McKenna et al., 2009) have demonstrated that Nemonychidae may not be basal to Belidae, but perhaps shares a reciprocally monophyletic relationship along with Anthribidae.

1. Apodemes of occipital and subgenal sulci both supporting tendons: **(0)** yes (figs. 5, 22); **(1)** no, only apodemes of occipital sulci supporting tendons (those of the subgenal sulci reduced or absent) (fig. 25).

Both pairs of ventral head sulci (occipital and subgenal) are fairly visible externally and present in basal Curculionoidea. Their associated internal apodemes support the mandibular and maxillary tendons. Toward the higher weevils, the subgenal sulci disappear and the occipital sulci then assume the role of supporting both pairs of tendons. Lyal (1995) speculated that in the higher weevils, where the subgenal sulci are absent, the sulci and their apodemes may have been incorporated into a bridge formed by the medial fusion of the apodemes of the occipital sulci in several lineages. This hypothesis is plausible, as is seen by the relative positions of the maxillary tendons in the lineages bearing these two discernible forms; however, it is also possible that the subgenal sulci, along with their associated apodemes, were simply lost entirely as the occipital sulci migrated ventromedially.

2. Support for mandibular adductor tendons: **(0)** apodemes of subgenal sulci; **(1)** apodemes of occipital sulci.

As mentioned above, both sets of sulci possess apodemes that support the mandibular (and maxillary) tendons. When both sulci are present, apodemes of the occiput support the abductor tendons and those of the subgena support the adductor and maxillary tendons. At least in Attelabidae, the adductor tendons are partially supported by both sets of apodemes (figs. 5, 22).

3. Apodemes of occipital and subgenal sulci near antennal insertion: **(0)** separate (fig. 16, 18); **(1)** fused internally (fig. 5); **(2)** not applicable/subgenal sulcus absent.

Beginning from the oral area and proceeding toward the base of the rostrum, the occipital and subgenal sulci (as determined by the invagination of the exocuticle) are separate and may remain completely separated or fuse to varying degrees. Just as these sulci are separate or possibly have become fused, their invaginated apodemes may also be separate or fuse internally in the rostrum. Separate sulci often denote separate apodemes for supporting the mouthpart tendons (i.e., in Nemonychidae). This is not always the case, as in Attelabidae, in which the sulci are separate, but their apodemes fuse or abut.

4. Apodemes of occipital sulci: **(0)** separate (fig. 4); **(1)** abutting medially, mandibular tendons positioned horizontally (fig. 26); **(2)** abutting medially, mandibular abductor tendons positioned slightly below adductors (figs. 34, 45); **(3)** fused medially forming bridge (fig. 47); **(4)** fused medially and vertically stalked (fig. 44); **(5)** abutting medially, mandibular tendons aligned vertically (fig. 39).

Of the lineages that possess a single pair of ventral rostral (occipital) sulci, a condition that may represent a fusion of the occipital and sub-

genal sulci, the apodemes remain separate or are fused to form a medial bridge. As mentioned above, it has been hypothesized (Lyal, 1995) that this medial bridge represents the fused apodemes of the subgenal sulci, in which case these apodemes would not be lost but merely subsumed into the internal scaffold created by the apodemes. It is also possible that the subgenal sulci and the associated apodemes are lost, in which the medial fusion of these apodemes is purely an extension of the occipital apodemes.

5. Apodeme and tendon orientation: **(0)** apodemes stratified horizontally, mandibular adductor tendons situated outside of abductor tendons (fig. 19); **(1)** apodemes stratified horizontally, mandibular abductor tendons situated outside adductor tendons (figs. 23, 25, 43); **(2)** apodemes stratified vertically, mandibular adductor tendons situated above abductor tendons (figs. 36–39, 46–47); **(3)** apodemes stratified laterally, mandibular adductor tendons situated at a level lower than that of abductor tendons (figs. 24, 28–32, 35).

In all cases where the occipital and subgenal sulci remain separate, the occipital apodemes are situated in the ventrolateral corners of the rostrum and the subgenal apodemes are situated approximately ventromedially in the rostrum. In lineages where the subgenal sulci are absent and only the occipital ones are present, apodeme structure differentiates along two apparent paths. When only the occipital sulci are present their apodemes are located ventromedially and are often stratified horizontally, and an outer canal supports the mandibular abductor tendon while an inner canal or broadly concave surface supports the adductor tendon and maxillary tendons. Another condition has the same general layout of the tendons, but the sulci are located ventrolaterally, causing the apodemes supporting the mandibular abductors to be at a level higher than those supporting the mandibular adductors and maxillary tendons. This condition is defined as having the tendons stratified laterally. It seems to represent a condition similar to that of horizontal stratification, but shows ample consistency to maintain a separate state. According to

the conditions described above, the apodemes may become fused, forming a medial bridge that remains stratified horizontally or that becomes stratified vertically. In the latter condition, the inner arm of the apodeme supporting the abductor tendon extends further to enclose the tendon in a ventral tunnel on the floor of the rostrum, the adductor tendon then assumes a position above the abductor tendon.

6. Position of maxillary tendons near oral orifice (preantenna): **(0)** supported by lateral canals of posterior arms of pharyngeal plate (figs. 20–22); **(1)** not in distinct canals, in angle of posterior arms (figs. 16, 19, 39, 49).

The three tendons that originate from the maxilla are the maxillary remotor, promotor, and lacinial cranial flexor tendons. Generally, three arrangements of these tendons are visible in the area near the oral orifice in which are situated the posterior arms of the pharyngeal plate. In most basal lineages of Curculionoidea, there are small lateral canals stemming from the posterior arms that support the maxillary tendons, though not all are necessarily supported. In most lineages (probably all Curculionidae), the posterior arms form approximate right to subacute angles below the pharynx where at least one tendon is supported in that inner angle.

7. Position of maxillary tendons (of which there are three) on apodemes (at approximately the middle of rostrum): **(0)** 2 central tendons, 1 positioned laterally under adductor tendon (figs. 17–18, 27); **(1)** 3 central tendons (figs. 19, 22, 24); **(2)** 1 central tendon, 2 lateral (1 positioned under and 1 positioned above adductor tendon; figs. 28, 30, 34); **(3)** 2 central tendons, 1 positioned laterally above adductor tendon (fig. 37).

Depending on the orientation of the maxilla and other mouthparts, the tendons of the maxilla may also reflect these different orientations. The following conditions have been observed in cross sections of the rostrum corresponding to the character states above: (1) There may be two central tendons (the maxillary promotor and lacinial cranial flexor tendons) and one lateral tendon (the maxillary remotor) positioned underneath

the mandibular adductor tendon; (2) all three tendons may be positioned centrally; (3) there may be one central tendon (the maxillary promotor) and two lateral tendons, one (the maxillary remotor) positioned underneath the mandibular adductor tendon and the other (lacinial cranial flexor tendon) positioned above the adductor tendon; or (4) there may be two central tendons (the maxillary promotor and remotor tendons) and one lateral tendon (the lacinial cranial flexor tendon) positioned above the mandibular adductor tendon.

8. Posterior arms of pharyngeal plate: **(0)** free/ separated basally (figs. 19, 28–37, 43); **(1)** fused medially (23, 38–42, 44–50); **(2)** fused and stalked medially (figs. 26–27).

The posterior arms of the pharyngeal plate arise from the postmentum to form a scaffold that supports the pharyngeal plate itself, as well as the anterior portions of the pharynx and mandibular adductor tendons. This scaffold of the pharyngeal plate is a complex that is composed of several apodemes and inflexions of the cuticle, namely the posterior arms, which comprise elements of the postmentum and hypostomal-labial sulci, and the anterior arms, which are of hypostomal origin but may also contain elements of the hypostomal-labial sulci. In many lineages, this complex forms a somewhat X-shaped scaffold in cross section, in which the posterior arms are separate (typically when also weakly developed) or fused medially to various degrees. Fusion occurs via a medial bridge joining the two apodemes. This fusion may become greater, forming a short medial stalk before separating again dorsally to form a triangular region below the pharynx, and it may completely fuse, forming a single elongate stalk below the pharyngeal plate (figs. 26–27). Typically, the apodemes are rather weakly developed when separate, often only composed of endocuticle, and become more robust when the apodemes fuse and incorporate more exocuticle.

9. Posterior arms of pharyngeal plate: **(0)** reduced, narrow, thin (figs. 16–33); **(1)** developed, wide, robust (figs. 34–50).

While all Curculionoidea appear to possess both anterior and posterior arms of the pharyngeal plate, basal families have weak, lightly sclerotized, flexible arms that can be difficult to locate. As mentioned below, these and other supporting arms become strengthened and rigid toward the higher Curculionidae.

10. Anterior arms of pharyngeal plate: **(0)** reduced, narrow, thin (fig. 9); **(1)** developed, robust (figs. 11D, E).

Similar to the posterior arms, the anterior arms of the pharyngeal plate undergo a progression in robustness and rigidity toward the higher weevils.

11. Pharyngeal plate, dorsal arms: **(0)** absent; **(1)** present, continuous, connecting to anterior pharyngeal sclerotization (fig. 11C); **(2)** reduced, most of arm absent (not connecting anteriorly), abbreviated to posterior and anterior remnants (figs. 11E, F); **(3)** reduced, abbreviated to lightly sclerotized line.

In basal families of Curculionoidea, the pharyngeal plate complex forms a rather weak scaffold of sclerotized plates and apodemes. This scaffold has become variably strengthened in the lineages leading to Curculionidae, likely as an adaptive response to changes in feeding strategies and functioning in oviposition (Anderson, 1995; Oberprieler et al., 2007). Among other rigidifying features around the oral orifice (Morimoto and Kojima, 2003), those associated with the pharyngeal plate include more robust anterior and posterior arms, as well as the formation of a set of dorsal arms. This set extends from the lateral margins of the plate to the precoila or to an extended sclerotization just posterior to it. In a few curculionid lineages, the dorsal arms have become abbreviated, with narrow posterior and anterior remnants. A further reduction of the dorsal arms (or perhaps independent reduction) results when posterior and anterior remnants have been eliminated and only a faint line or light sclerotization remains in their place.

12. Pharyngeal plate near antennal insertion: **(0)** reduced, short, incompletely sclerotized, exocuti-

cle at most on lateral portions; **(1)** simple, long, completely sclerotized (with exocuticle), modified anteriorly (figs. 11A, B); **(2)** short, incompletely sclerotized, open anteriorly (figs. 10A, B, D; 11D–F); **(3)** long, open medially, closed anteriorly (fig. 10C); **(4)** moderately short, bilobed posteriorly.

All weevils possess a chitinous pharyngeal plate (cibarial plate sensu Brack-Egg, 1973, and Dönges, 1954) that supports the pharynx and ends before the beginning of the esophagus. The anterior extension of the pharyngeal plate near the oral orifice is associated with the anterior arms and hypostomal-labial sulci. In a few basal families, the pharyngeal plate is relatively weakly sclerotized in the dorsal aspect. In this case, the posterior and lateral extensions are sclerotized with exocuticle and the plate is quite short, but at least in Nemonychidae it may possess a less sclerotized median part (composed of endocuticle) and extend quite far toward the rostral base. Progressing from the base toward more Recent families, the pharyngeal plate is found to have mostly exocuticle along the lateral and posterior extensions, producing anterolateral ramifications that form canals to hold or guide the mandibular adductor tendons for a short distance. In a few curculionid subfamilies, this strongly sclerotized posterior extension can be fairly long (e.g., Baridinae, Ceutorhynchinae, Curculioninae). In the lineages with a distinguishable rostrum, the pharyngeal plate appears entire and strongly sclerotized with exocuticle; however, in those possessing a shortened rostrum (though not restricted to these lineages), the plate is shorter, membranous medially, open anteriorly, and may have a posterior modification, such as being bilobed. The plate also can be found with a median membranous area but closed anteriorly.

13. Anterior of pharyngeal plate, lateral canals supporting adductor tendons: **(0)** weakly developed (figs. 16–27); **(1)** strongly developed with exocuticle (figs. 28–39, 43–50).

As noted above, the posterior arms of the pharyngeal plate often are weakly developed when separate and more strongly developed when fused medially. In the former condition, the lateral extensions of the pharyngeal plate support the mandibular adductor tendons near the oral orifice and form a shallowly concave shelf for the tendons. In the strongly developed condition, these lateral extensions form a distinct and sturdy C-shaped canal for the adductor tendons.

14. Anterior of occipital sulcus (adjacent to posterior mandibular articulation [postcoila]): **(0)** elongate and continuous toward eyes, supporting mandibular abductor tendons (figs. 16–23); **(1)** short, abrupt, distant from posterior part of sulcus (figs. 24–50).

The anterior extension of the occipital sulcus joins the subgenal sulcus just posterior to the postcoila. In lineages that retain distinct and separate occipital sulci along the length of the rostrum, the sulcus can be traced as a (mostly) continuous line running from the ventral margin of the compound eyes near the base of the rostrum that gradually extends slightly laterally toward the rostral apex; apodemes of the sulcus support the abductor tendons. In lineages in which the subgenal sulci are absent the anterior extension of the occipital sulcus is still visible, but it is abrupt, quickly disappearing just posterior to the mandibles and toward the rostral base.

15. Hypostomal-labial sulcus: **(0)** fully developed, extended, connecting to subgenal sulci (figs. 16–23); **(1)** partially developed, abbreviated (figs. 24–50).

The pair of sulci that extend from near the base of the hypostomal sinus was termed the hypostomal-labial sulci by Lyal (1995). All weevils appear to possess these sulci in various degrees of development. A fully developed sulcus, which generally is fairly elongate and apparently extends to the subgenal sulcus (hypostomal sulcus), is present in several basal lineages and appears to at least contribute (along with the postmentum) to the posterior arms of the pharyngeal plate (possibly also to the anterior arms). A partial or weakly developed sulcus is present in the more derived weevil lineages. This condition is characterized by a sulcus that is abbreviated and whose posterior extension is distant from the subgenal sulci or often not clearly dis-

cernable externally, often restricted to the inflected paracoila region. In the fully developed condition, the anterior and posterior arms of the pharyngeal plate emanate from similar areas on the plate, as evidenced in cross sections. In the weakly developed condition, the attachment points of the anterior and posterior arms are slightly farther apart on the pharyngeal plate, and the lateral extensions of the plate form a strong C-shaped canal for the mandibular adductor tendons.

16. Anterior extension of frontal lines or sulci at anterior mandibular articulation (precoila): **(0)** present, extending laterally toward middle of acetabulum of mandibular articulation (figs. 16–22); **(1)** present, extending dorsally (figs. 23–30, 34–35, 40–42); **(2)** absent (figs. 31–33, 36–39, 43–50).

In several of the basal weevil lineages the anterodorsal extensions of the frontal sulci are present (although generally not visible externally). Ancestrally, this sulcus extends posteriorly from the anterior tentorial pits near the anterior mandibular articulation (precoila). In several basal families (Nemonychidae, Belidae, Anthribidae, and Attelabidae), the sulcus extends slightly laterally toward the middle of the acetabulum of the precoila. Also in these groups, the anteriormost dorsal extensions of the pleurostomal sulci are visible in sections. In lineages appearing more intermediate in the curculionoid phylogeny (Caridae, Brentidae, Brachycerinae, Erirhininae, Raymondionyminae, Bagoinae, and some Scolytinae), the frontal sulci are still present, but extend directly dorsal. While this latter case seems also present in *Ithycerus*, its form appears rather intermediate and displays some lateral extension of the sulci. In the more derived lineages (essentially in Curculionidae), the frontal sulci appear to have been entirely lost (or nearly so and perhaps appearing only at the anteriormost margin of the rostrum).

17. Gular (postoccipital) sutures: **(0)** separate, paired; **(1)** fused medially.

Only a few groups (i.e., Nemonychidae, Anthribidae, and Belidae) have discernible gular regions delimited by separate gular sutures. In the remainder of the superfamily, the gula has been lost due to the reduction of the gular region by the medial fusion of the gular sutures. It has been reported by Wood (1986) that a gula is present in some scolytines, specifically certain species of *Gnathotrupes*. Personal observation of species within this genus has so far yielded no affirmation of this claim. While it is possible that some Scolytinae (and other higher weevils) possess remnants of a gula, as Lyal (1995) pointed out, these may represent secondary acquisitions. He also hypothesized that the postgula represents a fusion of the cervical sclerites to the margin of the occipital foramen. This observation is interesting, particularly given the bilobed condition of the postgula in a majority of Curculionoidea, with notable exceptions of Nemonychidae, Anthribidae, Belidae, and much of Attelabidae in which there are two separate sclerites. In some cases, a slightly enlarged postgular area may be hypothesized as the remnant of a gula (e.g., Dryophthorinae), but these conditions appear to represent fully fused sclerites (apparent by the closer cervical muscle insertions) that may have become secondarily enlarged.

18. Antennal form: **(0)** orthocerus (straight); **(1)** geniculate (elbowed).

Antennal form, although seemingly straightforward, is somewhat deceptive when the scape elongates or shortens. In the orthocerus form, all joints are arranged linearly. In geniculate forms, the face at which the pedicel articulates with the scape has shifted and become angled. While seemingly geniculate antennae are found outside Curculionidae (e.g., in Caridae and Brentidae), the point of articulation between the scape and pedicel remains of an orthocerus type, in which it is apical on the scape. Consequently, the condyle of the pedicel is angled so as to functionally yield a geniculate form of movement.

This character mostly was added to the dataset to provide greater polarity to the analysis. As few characters are included, any character displaying homoplasy is fairly influential on the resulting

topology, an admitted weakness of this study (particularly for the higher Curculionidae).

19. Labrum: (0) present; (1) absent, fused with clypeal-frons complex.

A distinct, articulating labrum is present only in Nemonychidae and Anthribidae. Wood (1986) mentioned that many lineages within Scolytinae and Platypodinae have an enlarged epistomal lobe (though the same might be said of many Attelabidae as well), and may even be delimited by a rudimentary sulcus. It is unclear whether the absent condition represents complete losses or variable fusions of the labrum and clypeus, and whether the epistomal lobe is a derived modification of the frons or a remnant of the clypeus or labrum. However, given the similarity in chaetotaxy of the episotmal lobe and labrum in some lineages (such as those mentioned above), it is evident that the structure is a reduction and fusion of the labrum that has undergone further modification (including complete loss) in various weevil lineages.

Phylogeny Utilizing Rostral Characters

The strict consensus tree of 3224 most-parsimonious trees, L = 87, CI = 40, RI = 67 (MP trees of L = 59, CI = 59, RI = 85), is presented in figure 12, mapping unambiguous character support. The phylogeny demonstrates that internal characters of the rostrum examined in this study are of great utility at least at the familial level. By examining the 50% majority-rule tree (L = 64, CI = 54, RI = 82; fig. 13), rostral characters also may be informative at the subfamilial level. A broader taxon sampling should augment these findings, particularly with regard to the Curculionidae.

Phylogenetic Analysis
of Rostrum Anatomy

OUTGROUPS (figs. 14–15)

Outside Curculionoidea the ventral head sulci do not invaginate to produce apodemes as they do in weevils. The pharyngeal (cibarial)) plate tends to be more sclerotized (if it is present at all) in lineages with some derivation of a rostrate

head, although this is deserving of further investigation. As weevils display the most-developed and longest rostra, they have developed relatively robust pharyngeal plates to support the pharynx along its extended length, including wide, often elongated arms that support the anterior extensions of the mouthpart tendons. While rostra have developed in the adults of some other coleopteran lineages (e.g., Lycidae, Salpingidae [fig. 14], Staphylinidae), weevils appear to have uniquely derived the apodemes of the ventral head sulci used to support the mouthpart tendons. As such, apodemes and invaginations of the exocuticle or endocuticle are absent in these other families (e.g., Chrysomelidae; fig. 15).

CURCULIONOIDEA (figs. 16–50)

Aside from the aforementioned structures, other consistent features among the weevils include the following: two longitudinal rows of muscles (the pharyngeal dilator muscles) dorsolateral to the pharynx; the pharyngeal circular muscles, which essentially envelop the pharynx, though they are limited to the dorsal and lateral surfaces where the pharyngeal plate is present; salivary glands (mandibular glands sensu Dönges, 1954) and the associated canals located lateral to the pharynx; several pairs of nerves and tracheae, such as the dorsalmost and often largest tracheal pair, t8, which most often are situated dorsolaterally to the pharynx.

The following descriptions highlight the main similarities and differences within the major weevil families and subfamilies (confined to those taxa sampled) concerning internal rostrum morphology. Given the multiple sampling in several higher-level taxa conducted here, these observations may perhaps be extended to include remaining taxa within their respective groupings.

Nemonychidae (fig. 16)

Although Nemonychidae are known to be at the very base of Curculionoidea, the extant fauna (as with all of the extant weevil groups) appears to show a somewhat derived rostral form. As Dönges (1954) and Lyal (1995) clearly illustrated, a hypothesized weevil ancestor or early weevil lineage would probably display all sutures and sulci
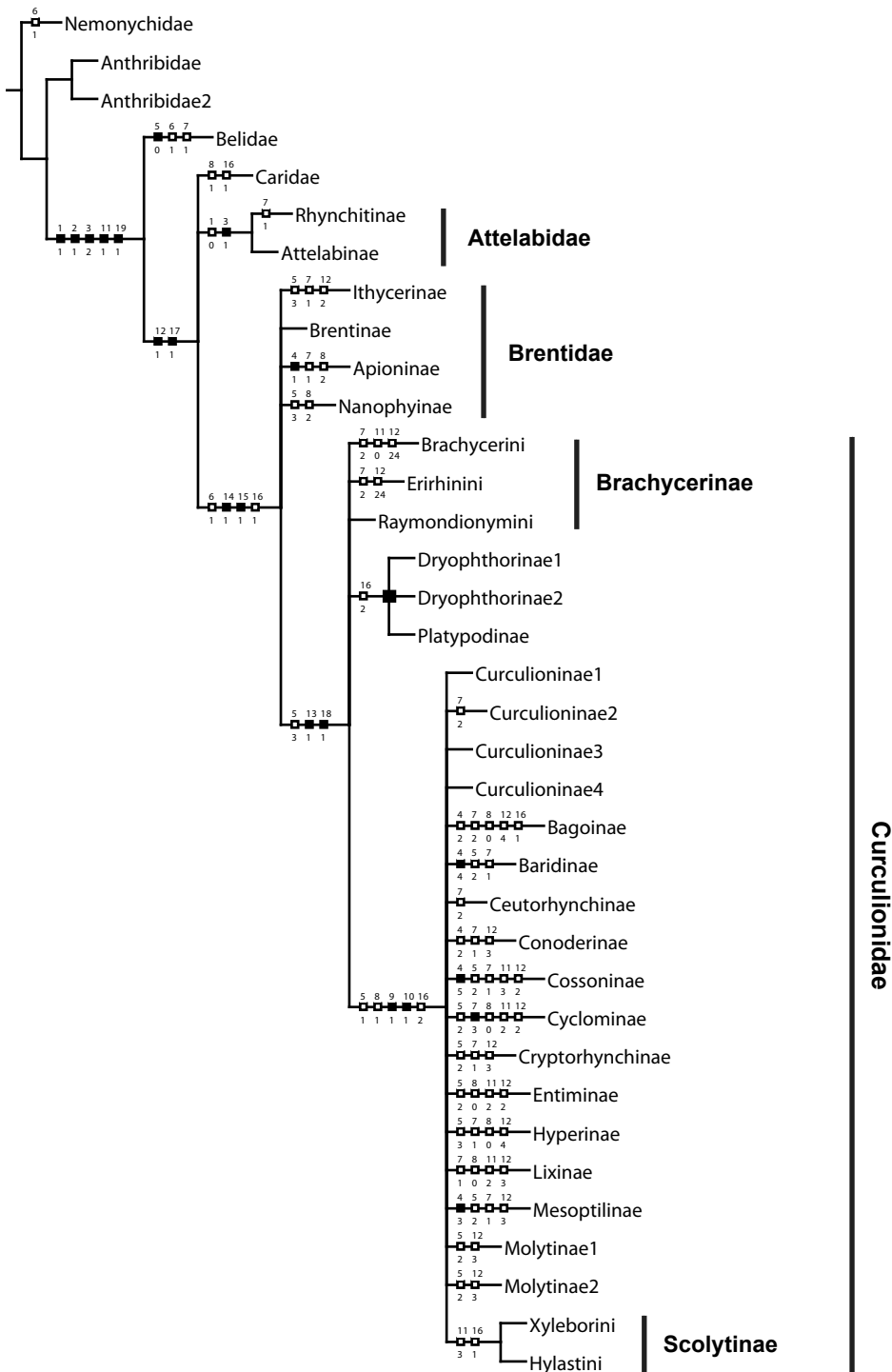
FIGURE 12. Strict consensus tree of an analysis of 36 taxa coded for 19 rostral-associated morphological characters, showing phylogenetic relationships among Curculionidae and other weevil families. Strict consensus of 3224 most-parsimonious trees, L = 87, CI = 40, RI = 67 (MP trees of L = 59, CI = 59, RI = 85). Unambiguous characters mapped.
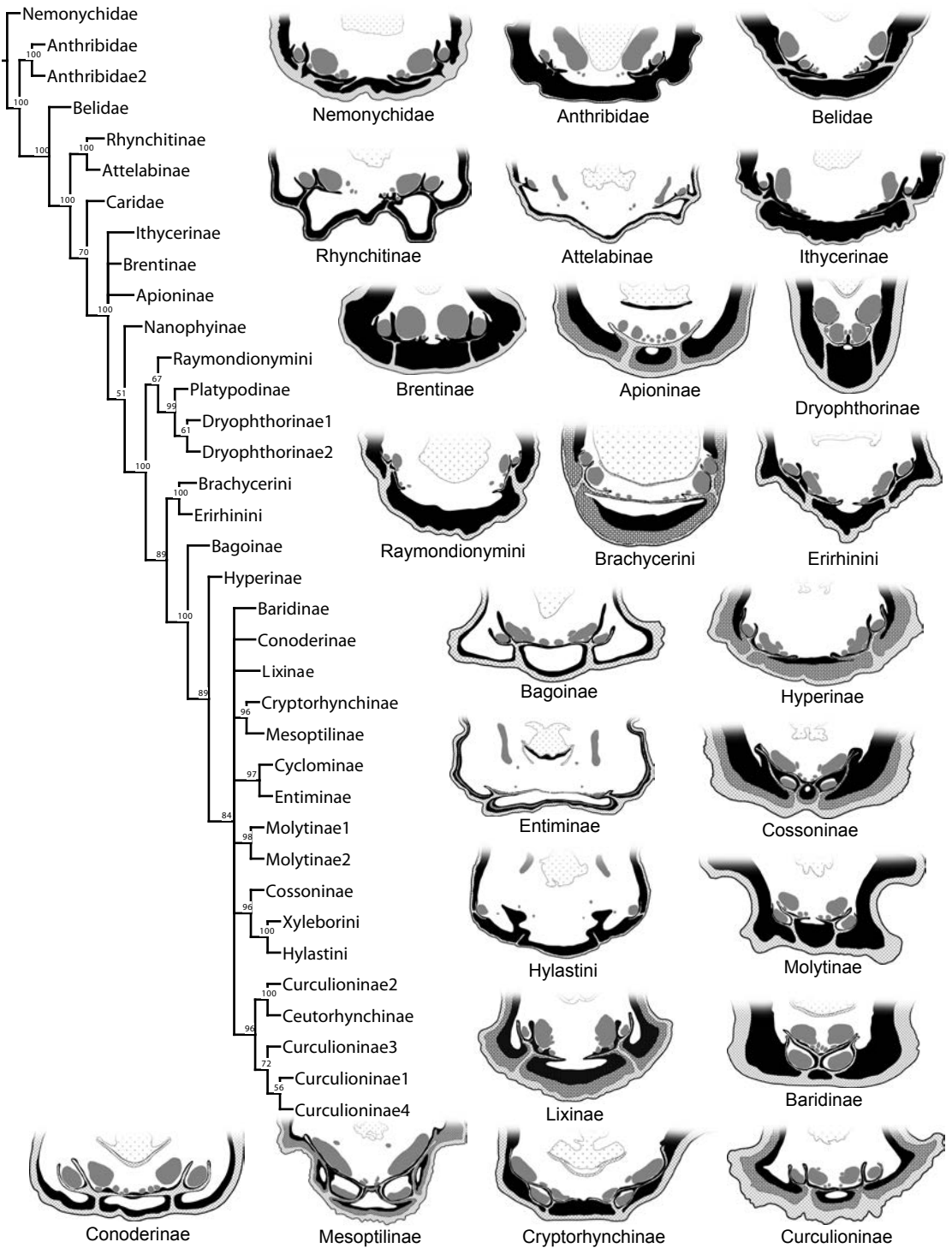
FIGURE 13. 50% majority rules tree of the phylogenetic analysis of 36 taxa coded for 19 rostral-associated morphological characters (MR tree of L = 64, CI = 54, RI = 82). Illustrations on the right side depict diversity of rostral anatomy throughout Curculionoidea as viewed from histological sections.
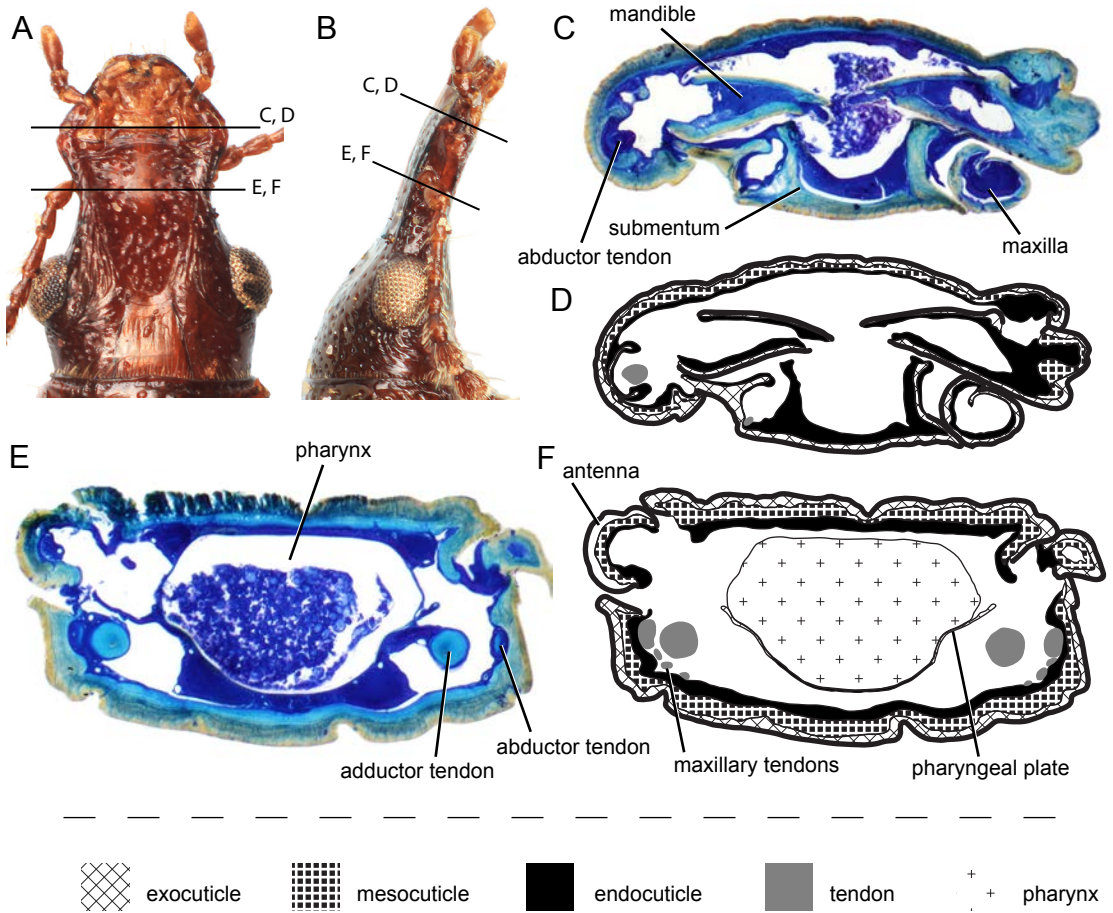
FIGURE 14. Semithin sections of head of *Rhinosimus viridiaeneus* (Salpingidae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–F,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** diagram of C; **E,** section near middle of rostrum; **F,** diagram of E. Section illustration legend presented at bottom.
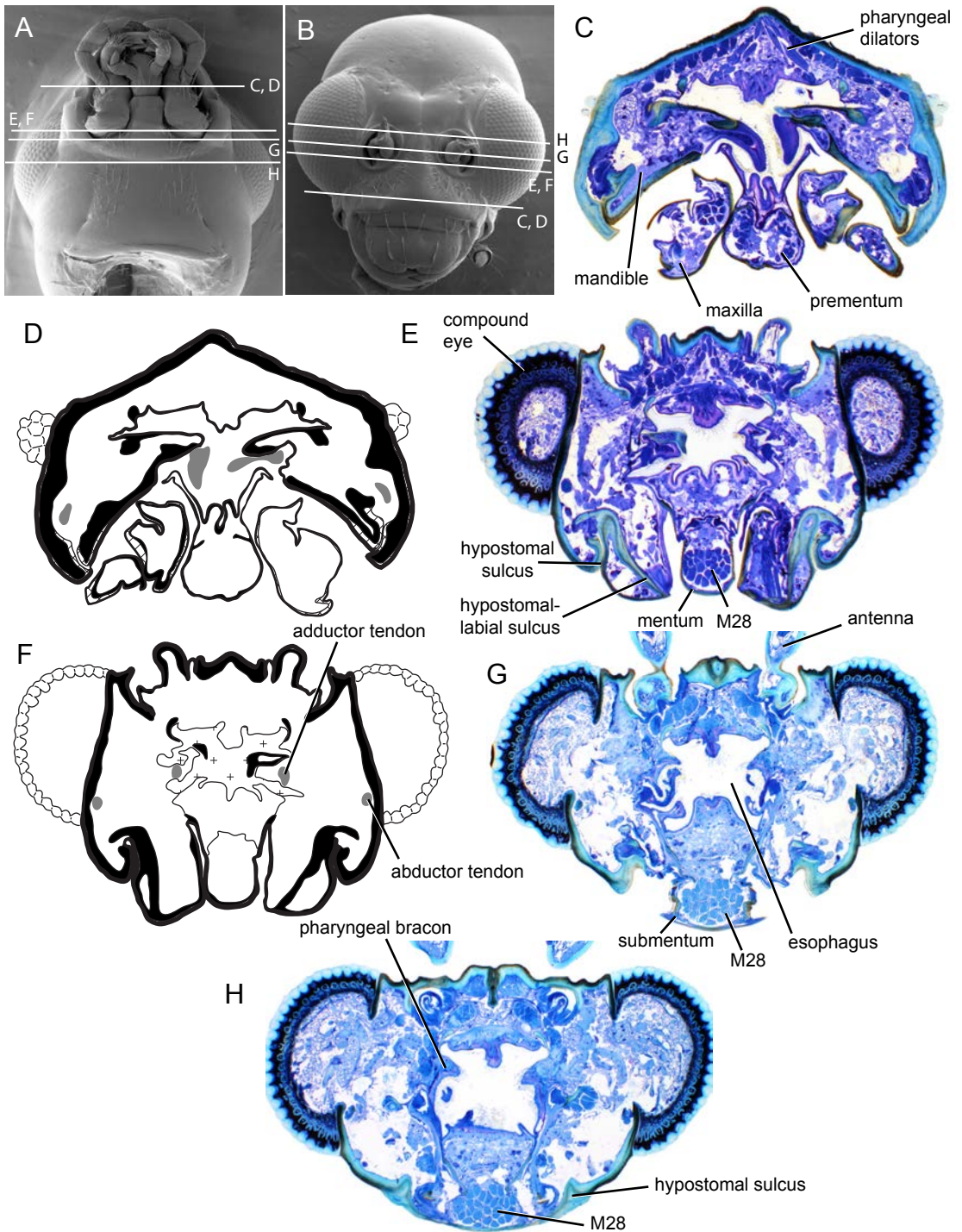
FIGURE 15. Semithin sections of head of *Diabrotica undecimpunctata* (Chrysomelidae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from mouthparts to base of head; **C,** section apex of head and mouthparts; **D,** diagram of C; **E,** section through anterior of eyes and proximal area of mouthparts; **F,** diagram of E; **G,** section just behind mouthparts; **H,** section through middle of eyes and head.
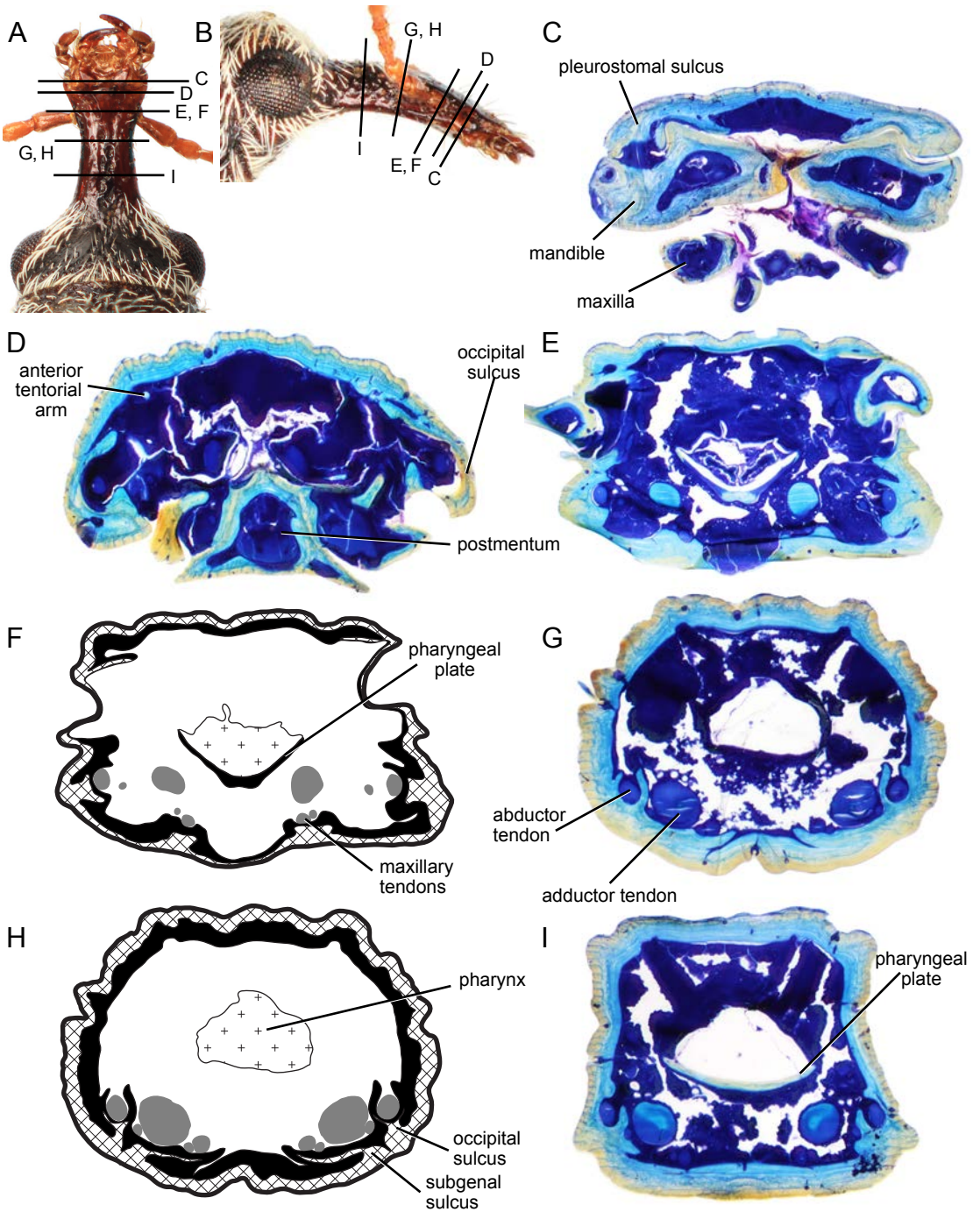
FIGURE 16. Semithin sections of head of *Cimberis pilosa* (Nemonychidae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section at proximal area of mouthparts, anterior to antennal insertion; **E,** section at antennal insertion; **F,** diagram of E; **G,** section approximately at middle of rostrum, posterior to antennal insertion; **H,** diagram of G; **I,** section near base of rostrum.

on the head, including distinctly separate subge-nal and occipital sulci. While the study herein examined only one nemonychid representative (*Cimberis pilosa*), its features do not appear as primitive as had been suspected. If one could clearly visualize the head features of more basal genera or some of the extinct nemonychid line-eages, it is probable that more primitive features showing closer resemblance to the hypothesized weevil ancestor of the aforementioned authors would be found. In extant Nemonychidae, the plurostomal sulcus is visible in cross section as a somewhat lateral line extending from near the anterior mandibular articulation. The frontal lines also remain, but are not observable in the pre-sented sections. Remnants of the anterior tentorial arms are also visible as a pair of small circles of exocuticle near the dorsolateral corners of the ros-trum, just posterior to the mandibles. The subge-nal and occipital sulci are separate, though are situated much closer than one might suspect from examinations of the external rostral surface. The pharyngeal plate is robust and strongly sclerotized along the majority of the rostral length.

Anthribidae (figs. 17–18)

Anthribidae show a form similar to that of Nemonychidae, particularly in reference to the position of the occipital and subgenal sulci, though the subgenal sulci appear more reduced in anthribids. The enlarged, bilobed postmentum is a rather striking feature of this family and con-tributes to the well-developed scaffold formed from the pharyngeal plate and apodemes of the hypostomal-labial sulci, most similar to the con-dition present in Attelabidae in which these apodemes directly support some of the maxillary tendons. The pleurostomal and frontal sulci are distinct, also extending dorsolaterally in opposite directions as in Nemonychidae, and the pharyn-geal plate appears to be rather thin, becoming weakly sclerotized posteriad. The antennae are supported by apodemes located along the dorso-lateral corners of the rostral cavity.

Belidae (fig. 19)

The occipital apodemes are present, sup-porting all the mouthpart tendons, and the

subgenal apodemes appear to have been lost. A peculiar feature of the belid rostrum lies in the arrangement of the mandibular tendons. The adductor tendons nearly always are situated mesally in the rostrum with the abductor ten-dons more lateral, and positioned along the rostrum according to their point of derivation from the mandible. While the positions of these tendons are normal along the anterior portion of the rostrum, they change posterior to the antennae, where the adductor tendons assume a more lateral position in the apodemes of the occipital sulci. The posterior arms of the pharyngeal plate are simple and rather elongate dorsally, more similar to the condition observed in Nemonychidae than in Anthribidae or Attel-abidae. The pleurostomal and frontal sulci also are distinct and extend dorsolaterally. The pha-ryngeal plate appears to be rather thin and weakly sclerotized.

Attelabidae (figs. 1–7, 20–22)

ATTELABINAE (figs. 20–21): This group pos-sesses separate occipital and subgenal sulci, although the latter (and the associated apodemes) may be indistinct and reduced in short-snouted taxa and may not support the maxillary tendons. As in Anthribidae, the posterior arms of the pha-ryngeal plate and apodemes of the hypostomal-labial sulci are fairly elaborate and support some of the maxillary tendons. The pleurostomal and frontal sulci are distinct and extend dorsolater-ally. The pharyngeal plate is thin anteriorly and appears to become diminished posteriorly at least by the middle of the rostrum.

RHYNCHITINAE (figs. 1–7, 22): This group is similar to Attelabinae, although slightly dif-ferent in that the occipital and subgenal sulci are distinctly separate and bear well-developed apodemes. While these pairs of sulci remain separate along the length of the rostrum, the lateral extensions of their internal apodemes fuse on each side and form intermittent bridges. The pleurostomal and frontal sulci are distinct and extend dorsolaterally. The pha-ryngeal plate, similar to its condition in Attela-binae, is short, distinct, and thin anteriorly, becoming weaker posteriorly.
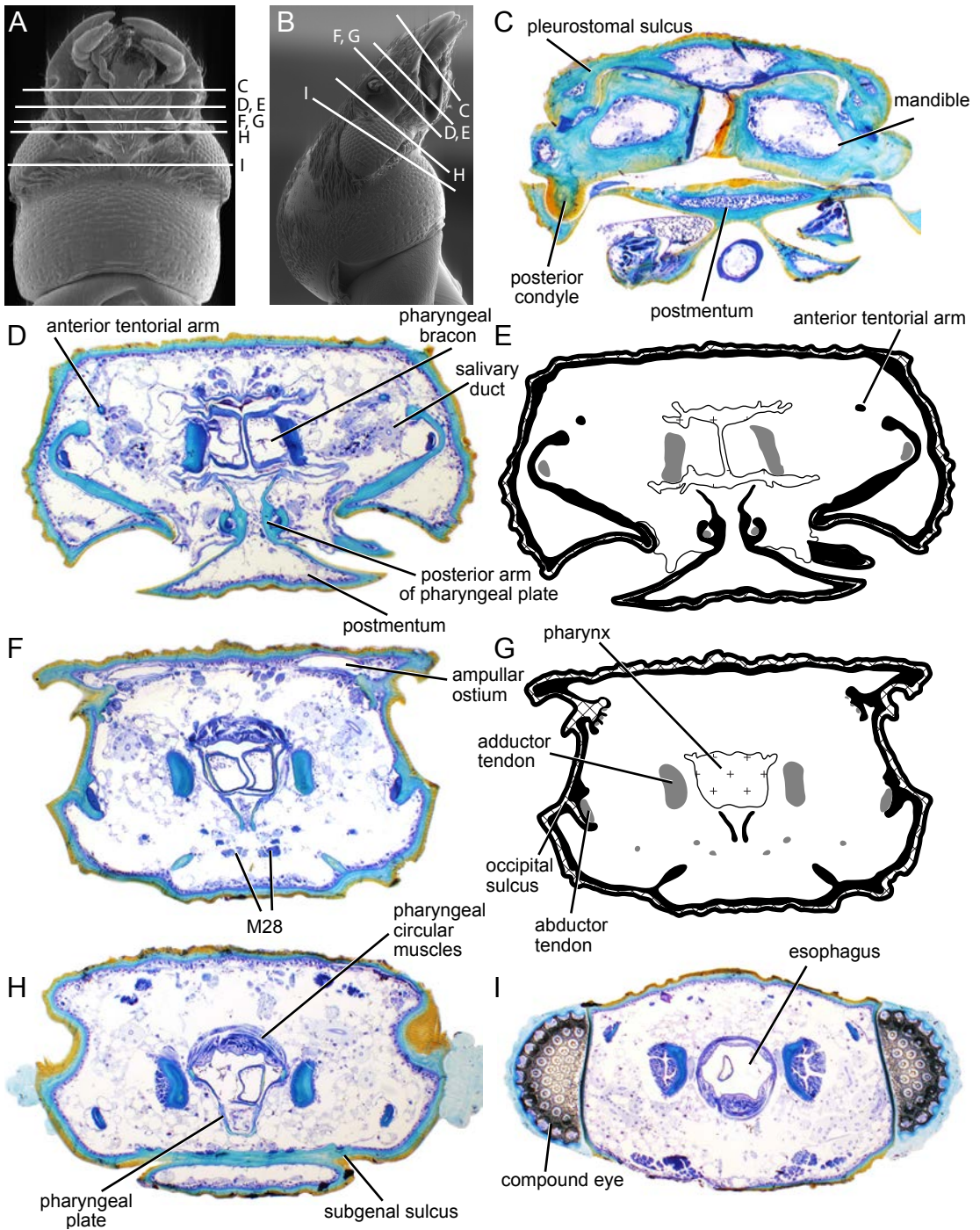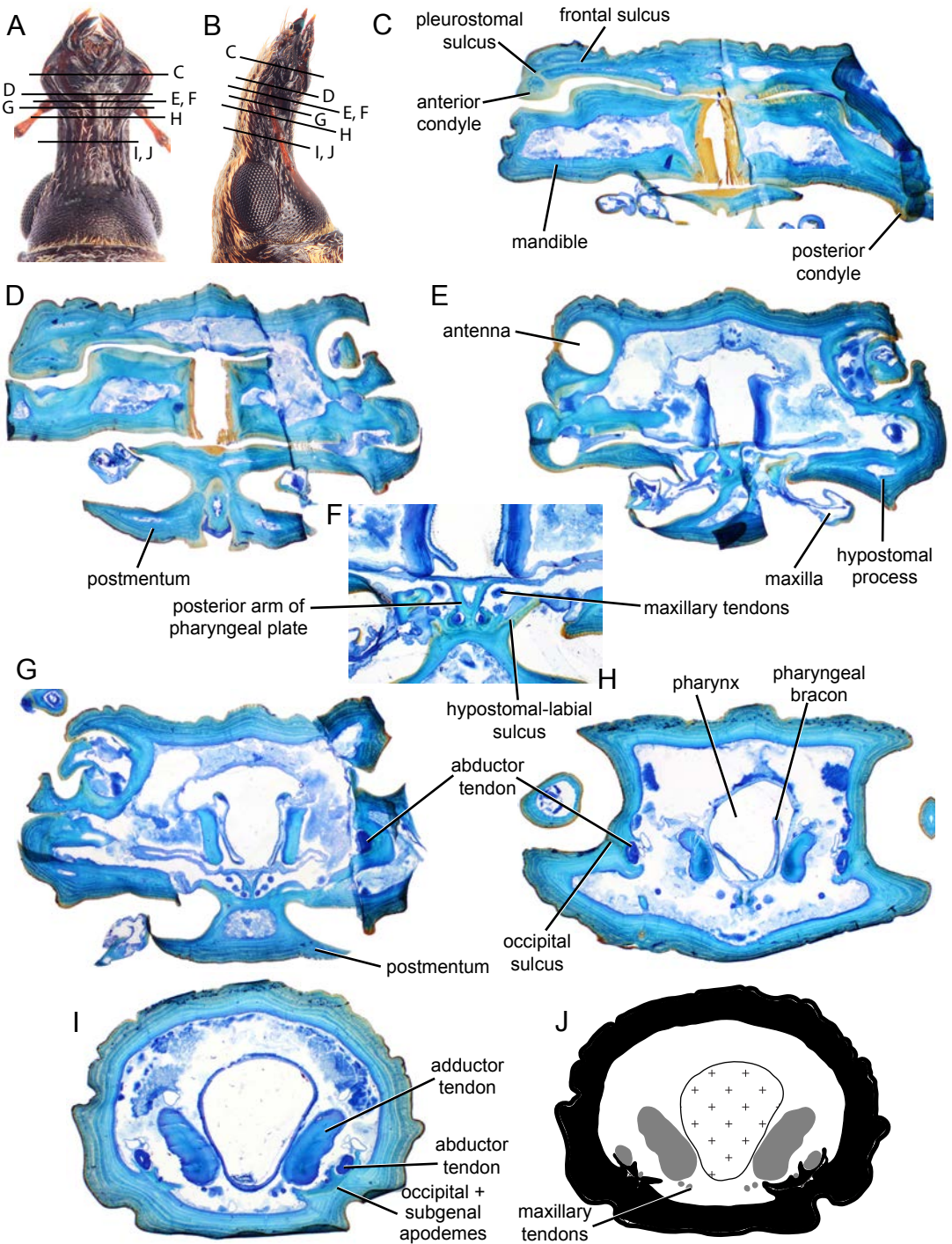
FIGURE 17. Semithin sections of head of *Euparius paganus* (Anthribidae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex of rostrum to base; **C,** section at apex of rostrum through mouthparts; **D,** section at proximal area of mouthparts, anterior to antennal insertion; **E,** diagram of D; **F,** section at base of rostrum, posterior to mouthparts and approximately at antennal insertion; **G,** diagram of F; **H,** section at anterior of eyes, posterior to antennal insertion; **I,** section through middle of eyes and base of head.

FIGURE 18. Semithin sections of head of *Ptychoderes* sp. (Anthribidae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–J,** cross sections proceeding from apex of rostrum toward base; **C–E,** sections from apex of rostrum through mouthparts and proceeding posteriad near proximal area of mouthparts and antennal insertion; **F,** proximal area of mouthparts, showing pharyngeal plate complex; **G,** section near antennal insertion, posterior to mouthparts; **H,** middle of rostrum, posterior to antennal insertion; **I,** section near base of rostrum; **J,** diagram of I.
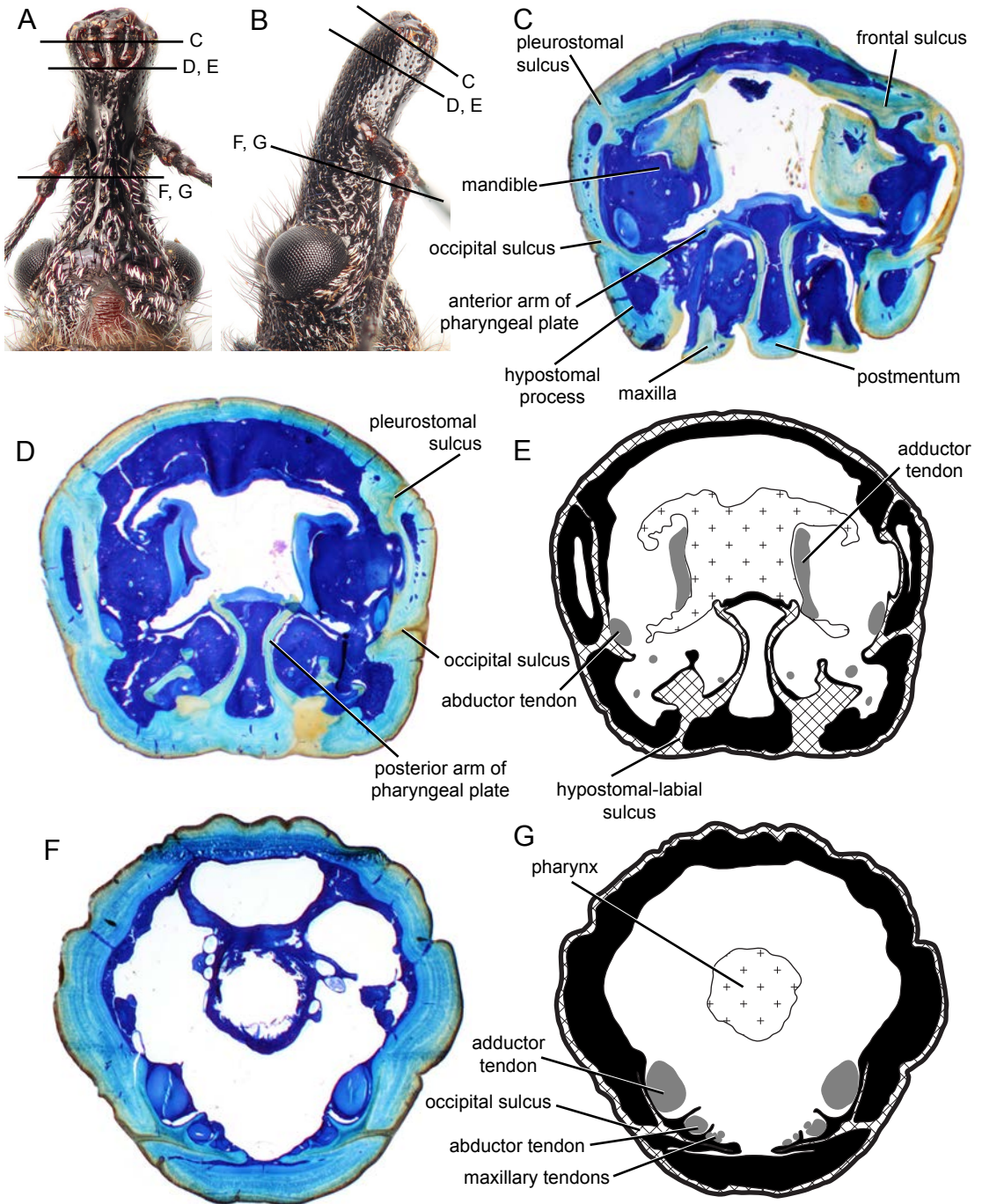
FIGURE 19. Semithin sections of head of *Dicorydylus* sp. (Belidae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–G,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section just posterior to mouthparts, anterior to antennal insertion; **E,** diagram of D; **F,** section posterior to antennal insertion near base of rostrum; **G,** diagram of F.
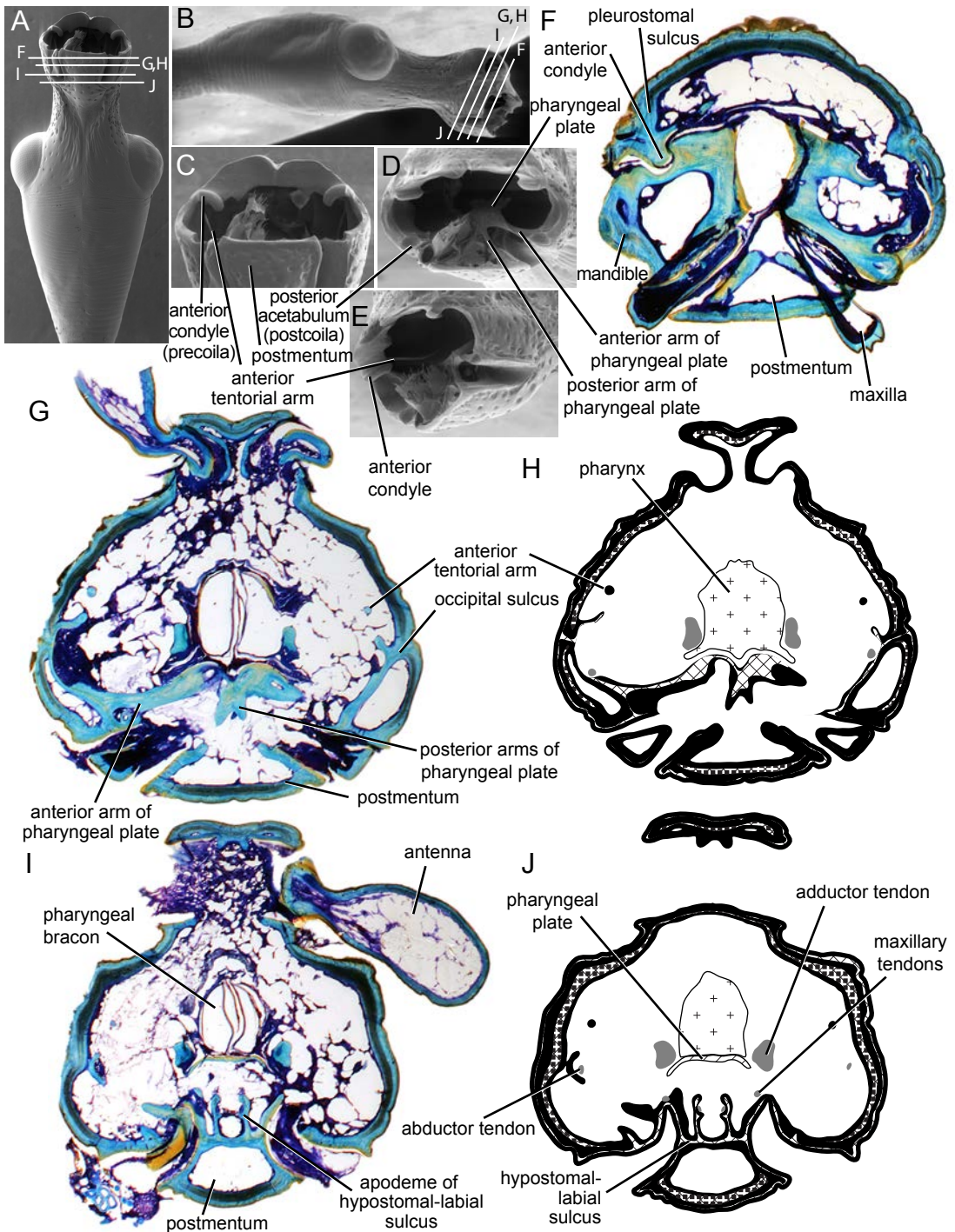
FIGURE 20. Semithin sections of head of male *Attelabus* sp. (Attelabidae: Attelabinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–E,** SEM's of anterior region of oral cavity, showing pharyngeal plate and remnants of anterior tentorial arms; **F–J,** cross sections near apex of rostrum; **F–I,** sections from apex of rostrum through mouthparts and proceeding posteriad to proximal area of mouthparts and antennal insertion; **H,** diagram of G; **J,** diagram of section just posterior to mouthparts and antennal insertion.
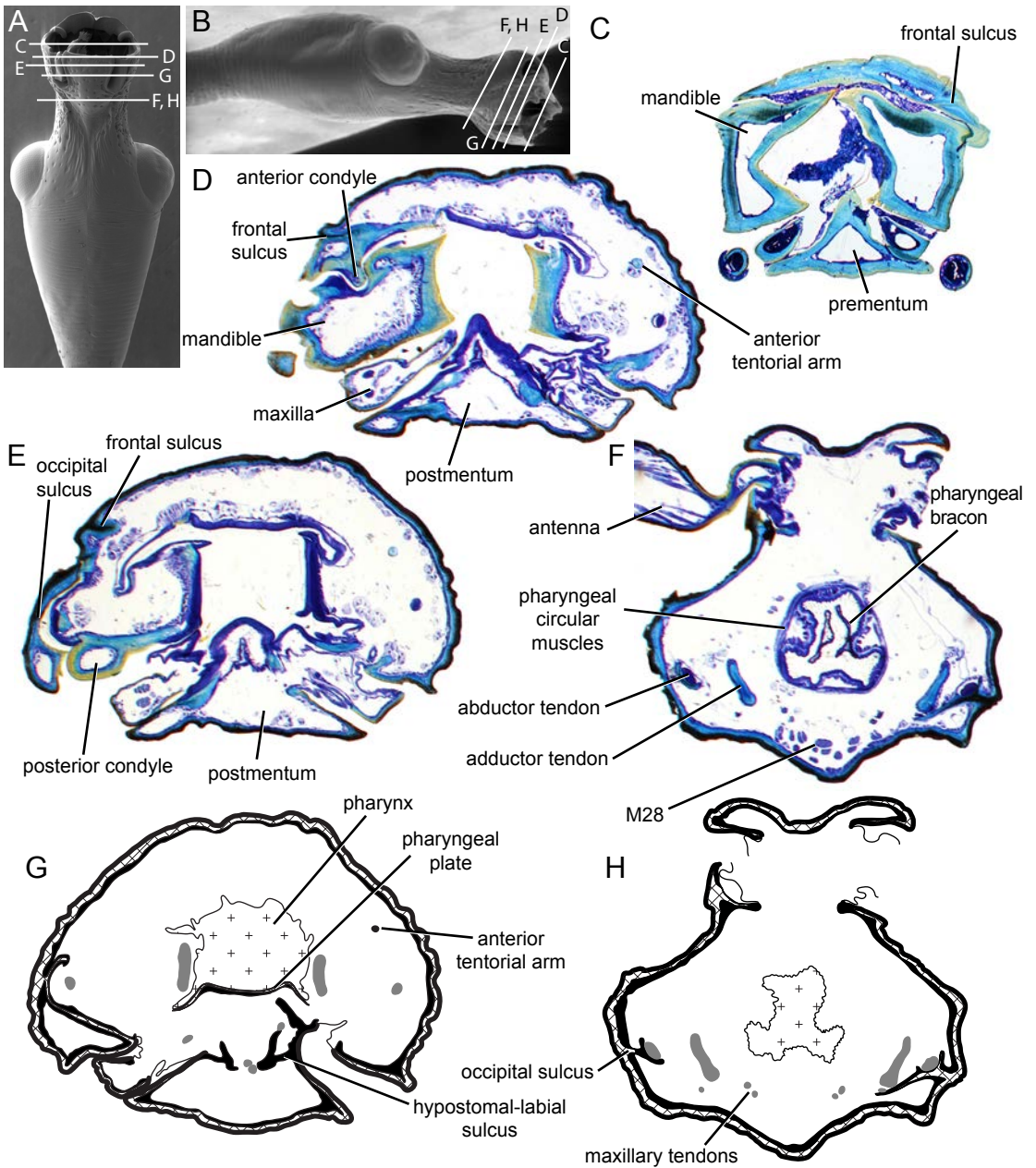
FIGURE 21. Semithin sections of head of female *Attelabus* sp. (Attelabidae: Attelabinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections along apical half of rostrum; **C–E, G,** diagram of section from apex of rostrum through mouthparts and proceeding posteriad to proximal area of mouthparts and antennal insertion; **F,** section near middle of rostrum and antennal insertion; **H,** diagram of F.
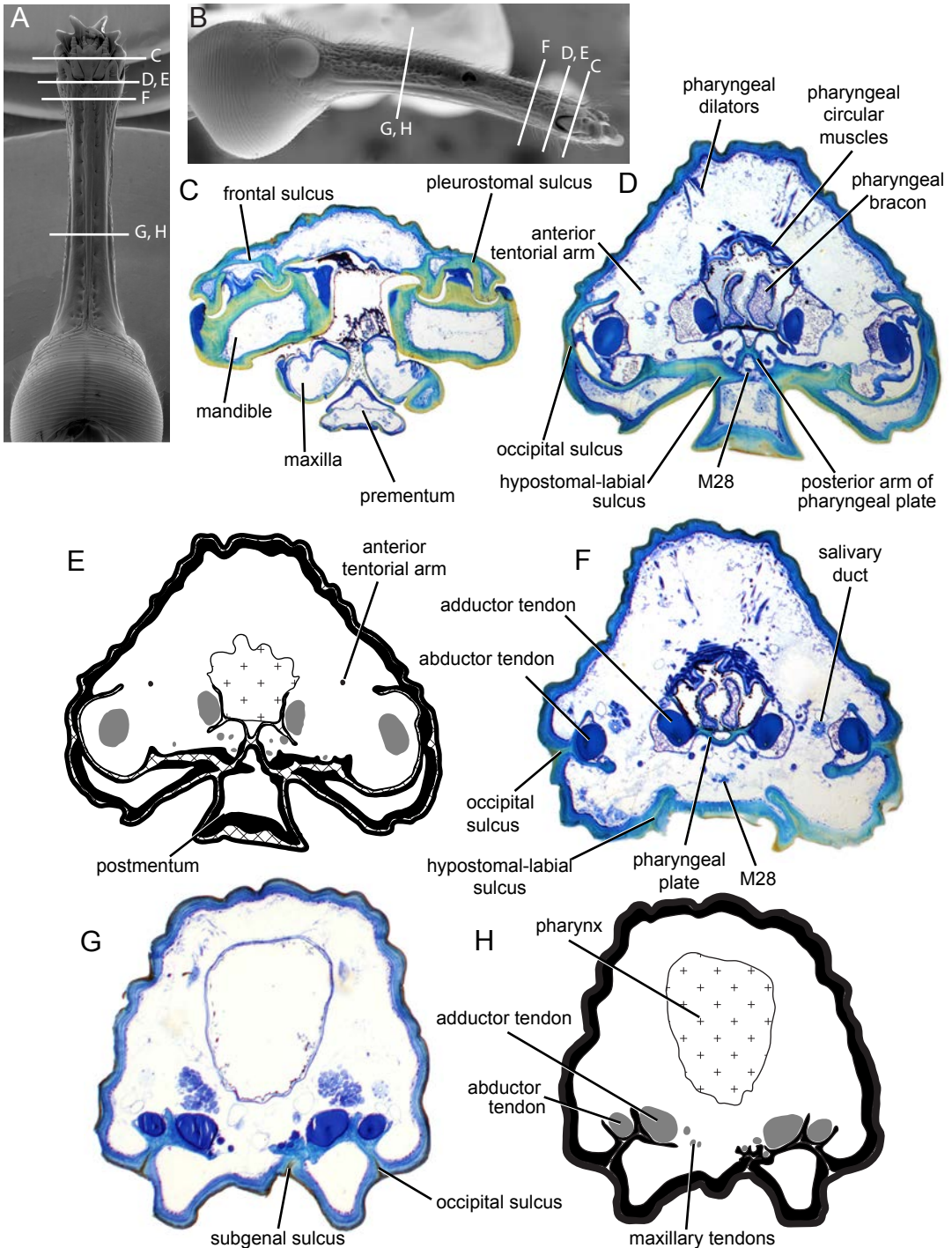
FIGURE 22. Semithin sections of head of *Rhynchites auratus* (Attelabidae: Rhynchitinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section just posterior to mouthparts; **E,** diagram of D; **F,** section posterior to mouthparts and anterior to antennal insertion; **G,** section near base of rostrum, posterior to antennal insertion; **H,** diagram of G.

Caridae (fig. 23)

In Caridae, the pleurostomal region extends more ventral than in all other weevils, a feature noticeable by the near ventral insertion of the antennae. Perhaps only the rostrum in Apioninae approaches a similar condition. Likewise, the occipital sulci have migrated ventrally and nearly touch mesally. This character is visible in sections adjacent to the sulci, and the tendons are located fairly closely as well as a result. The pleurostomal sulci are distinct and the frontal sulci extend dorsally. The pharyngeal plate is fairly robust and sclerotized. The posterior arms of the pharyngeal plate (apodemes of the postmentum) form a broad complex in proximity to the anterior arms, thus appearing to form a bridge with the apodemes of the occipital sulci just posterior to the mandibles (as they do in Nemonychidae, Anthribidae, Belidae, and Attelabidae). Immediately posterior to the postmentum, the apodemes of the hypostomal-labial sulci (essentially extensions of and indistinguishable from those apodemes of the postmentum) are moderately developed, strongly sclerotized, and fused for a short distance at midheight.

Brentidae (figs. 10E, 11A–B, 24–27)

ITHYCERINAE (fig. 24): The middle part of the rostrum in Ithycerinae appears somewhat similar to Nemonychidae in the position of the occipital sulci and mandibular tendons, though it lacks distinct subgenal sulci and the associated apodemes. The pharyngeal plate also does not extend far, ending before midlength of the rostrum. Near the apex, the similarity more resembles the condition in the Brentidae, particularly in the weakly developed posterior arms of the pharyngeal plate. The pleurostomal sulci are distinct and the frontal sulci extend dorsally. A rather unique feature appears to be the position of the occipital sulci and the associated internal apodemes, both situated more dorsally in the rostral cavity than in other weevils.

BRENTINAE (figs. 11A–B, 25): The rostral structure of this group appears quite similar to that in Caridae along the middle portion of the rostrum (largely with respect to apodeme structure and tendon placement), though it differs

substantially near the base (adjacent to the antennal insertion) and at the apex (particularly in form and robustness of the posterior arms of the pharyngeal plate). In relation to its diameter, the rostrum in this group possesses a thick cuticle in comparison to those of most weevils, with perhaps the rostrum of some curculionines approaching a similar form and thickness. Nearer to the rostral base, the mandibular adductor tendons assume a slight dorsal position above the abductors. Near the base of the occipital sulci, as they migrate laterally toward the compound eyes at the rostral base, evidence of their position is retained by the presence of their internal apodemes, even though the invagination of any exocuticle diminishes. Also, while the tendons of the antennae appear to usually move rather freely within the rostrum in most weevils, or at least along the sides of the rostral cavity, small cuticular canals (similar to those in some Anthribidae) are present dorsolaterally in Brentinae to receive these tendons. The pleurostomal sulci are distinct and the frontal sulci extend dorsally. The pharyngeal plate is short and does not extend to midlength of the rostrum.

Other interesting features include the crystalline lens covering the ommatidia (also mentioned by Zimmerman, 1994), apparently a fusion and tremendous thickening of the cuticle of the individual lenses, and the cephalic glands on both sides of the head and immediately anterior to the compound eyes (Zimmerman, 1994). Fresh material unfortunately was not utilized for this taxon, and in the absence of preserved glands, histological detail was not obtained.

APIONINAE (figs. 10E, 26): This group is similar to Brentinae in which the occipital sulci and their apodemes are situated ventrally on the rostrum, though the apodemes are fused medially for nearly the entire length of the rostrum. This fusion of the apodemes is quite distinct and unique near the rostral apex, appearing as a nearly semicircular platform supporting all mandibular and maxillary tendons. Toward the rostral base, the curvature of this apodemal platform lessens. Any modifications for reception of the antennal apodemes do not appear to be present. The pharyngeal plate is larger and more sclero-
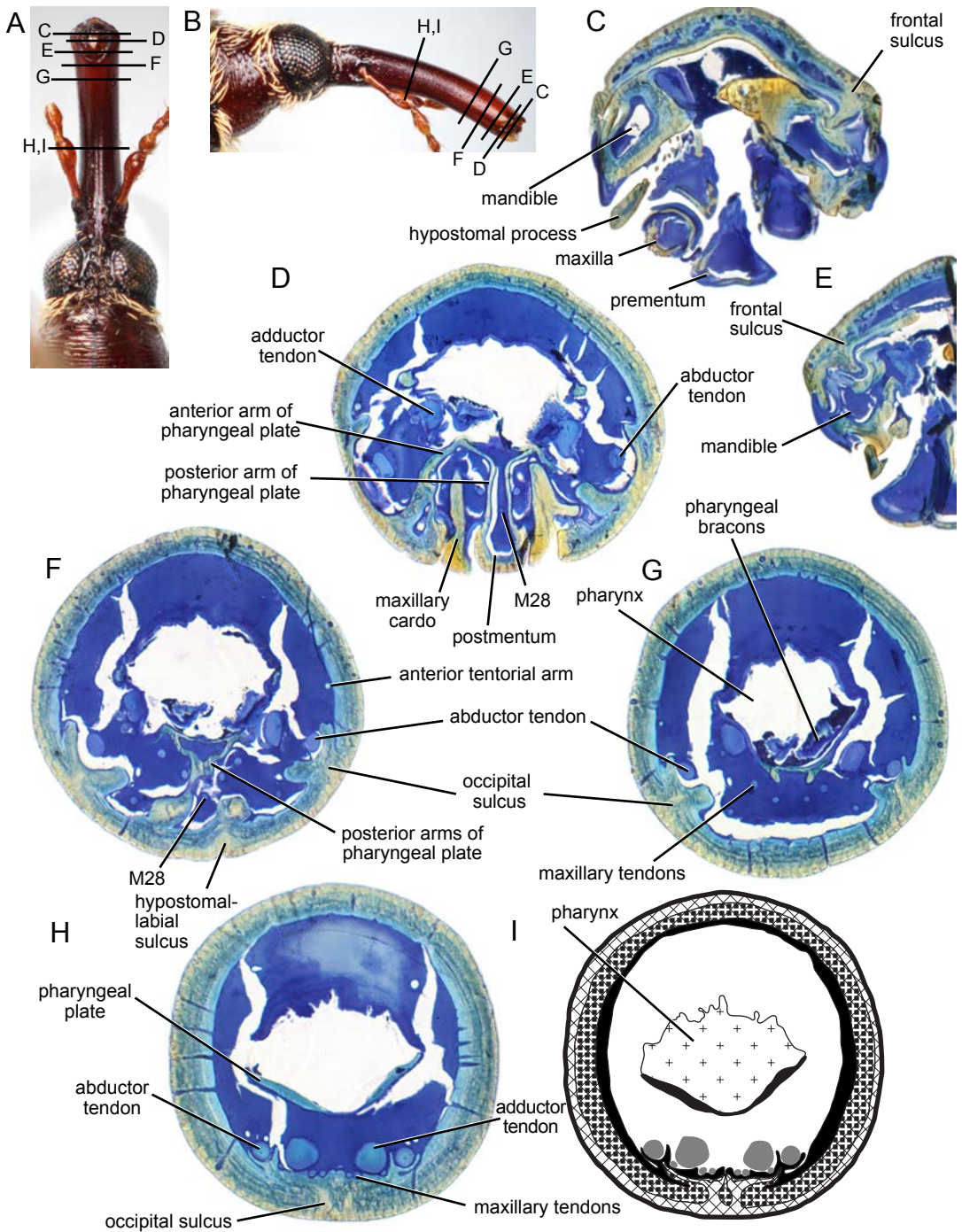
FIGURE 23. Semithin sections of head of *Caenominurus topali* (Caridae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex of rostrum toward base; **C–D,** sections at apex of rostrum through mouthparts; **E,** section at proximal area of mouthparts; **F–G,** sections posterior to mouthparts, anterior to antennal insertion; **H,** section before antennal insertion just posterior to middle of rostrum; **I,** digram of H.
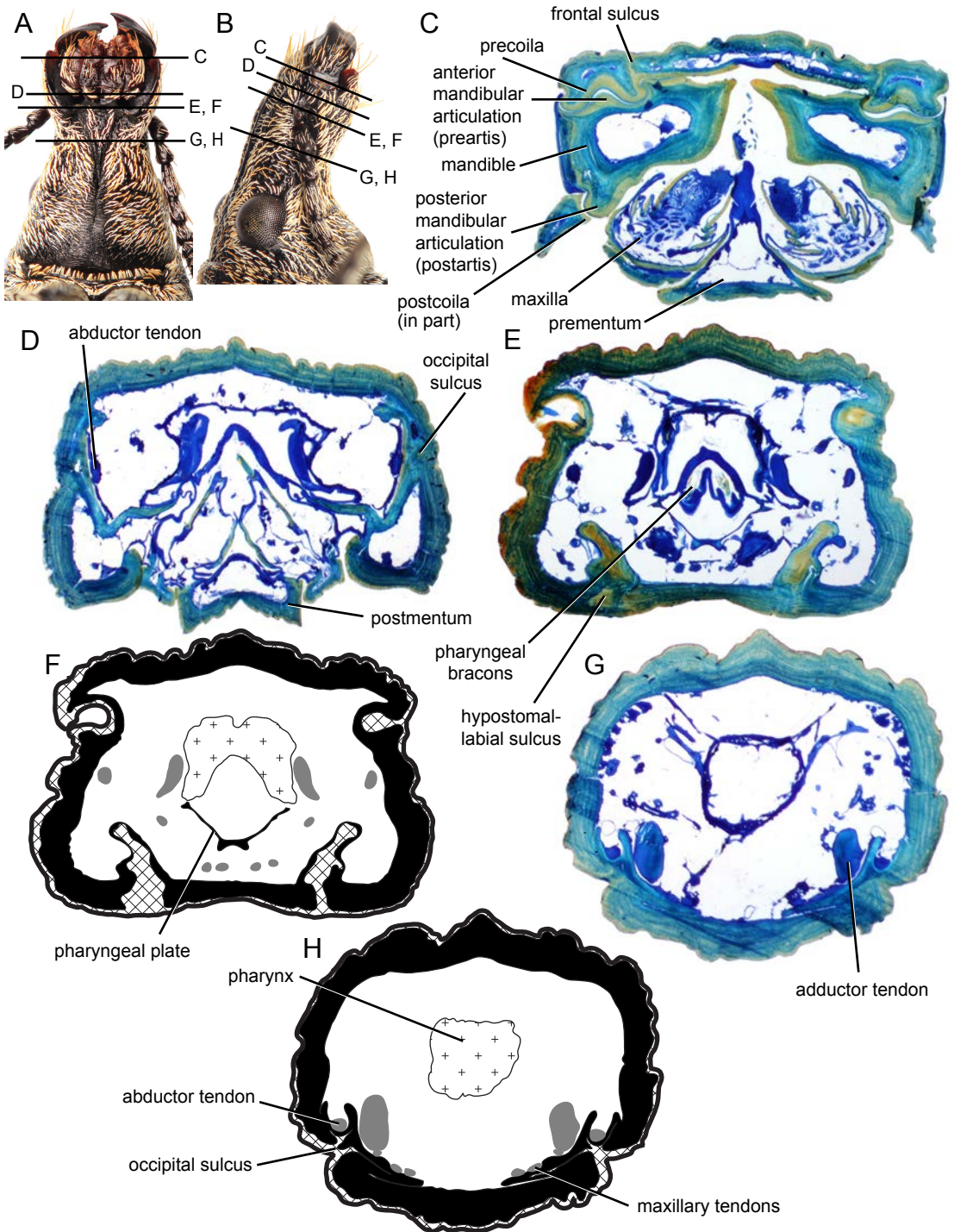
FIGURE 24. Semithin sections of head of *Ithycerus noveboracensis* (Brentidae: Ithycerinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section at proximal area of mouthparts; **E,** section posterior to mouthparts at antennal insertion; **F,** diagram of E; **G,** section posterior to middle of rostrum and antennal insertion; **H,** diagram of G.
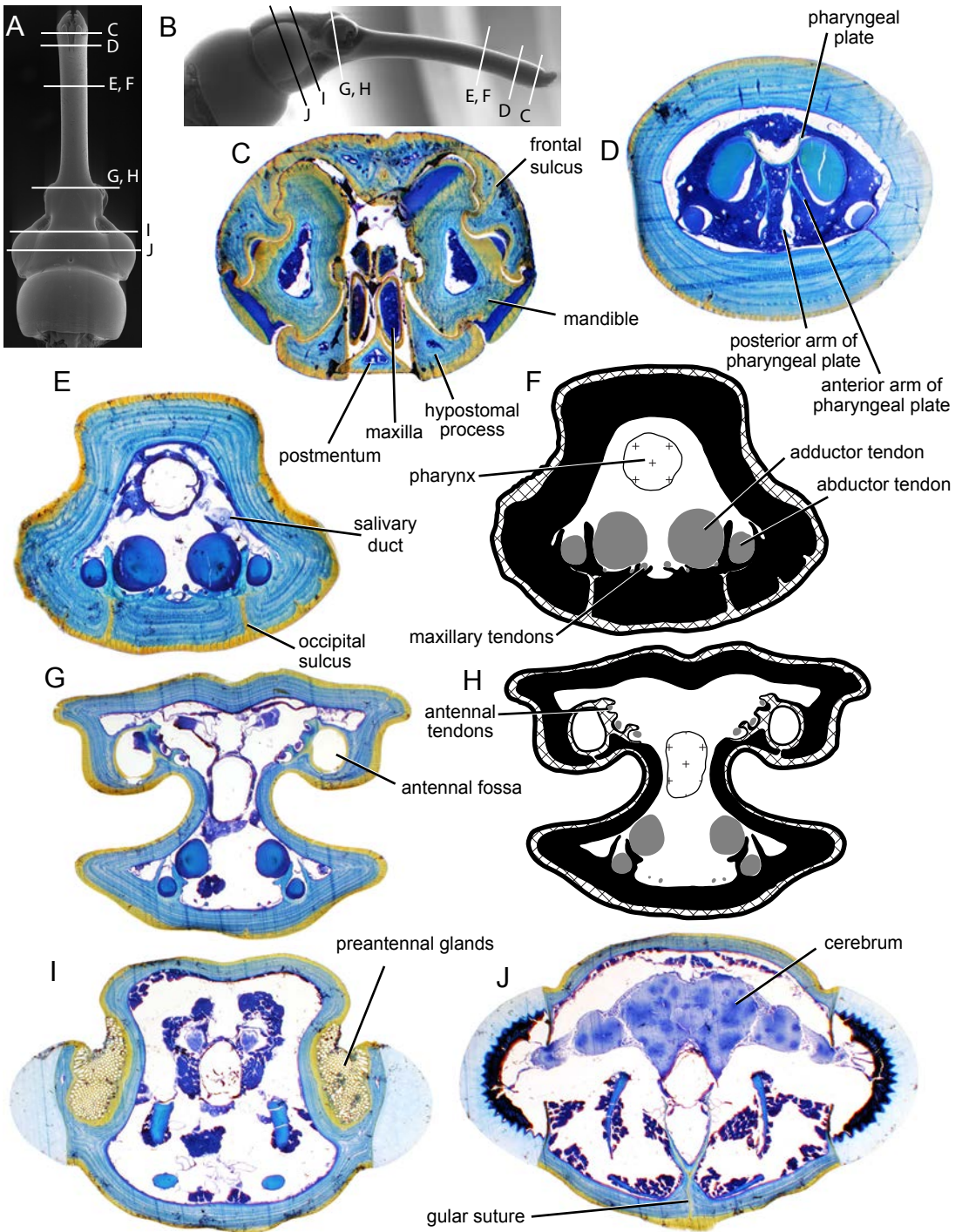
FIGURE 25. Semithin sections of head of female *Arrenodes minutus* (Brentidae: Brentinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–J,** cross sections proceeding from apex of rostrum to base and into head; **C,** section at apex of rostrum through mouthparts; **D,** section posterior to mouthparts; **E,** section anterior to antennal insertion and slightly anterior to middle of rostrum; **F,** diagram of E; **G,** section at base of rostrum and antennal insertion; **H,** diagram of G; **I,** section through anterior part of head and eyes; **J,** section through middle of eyes and head.
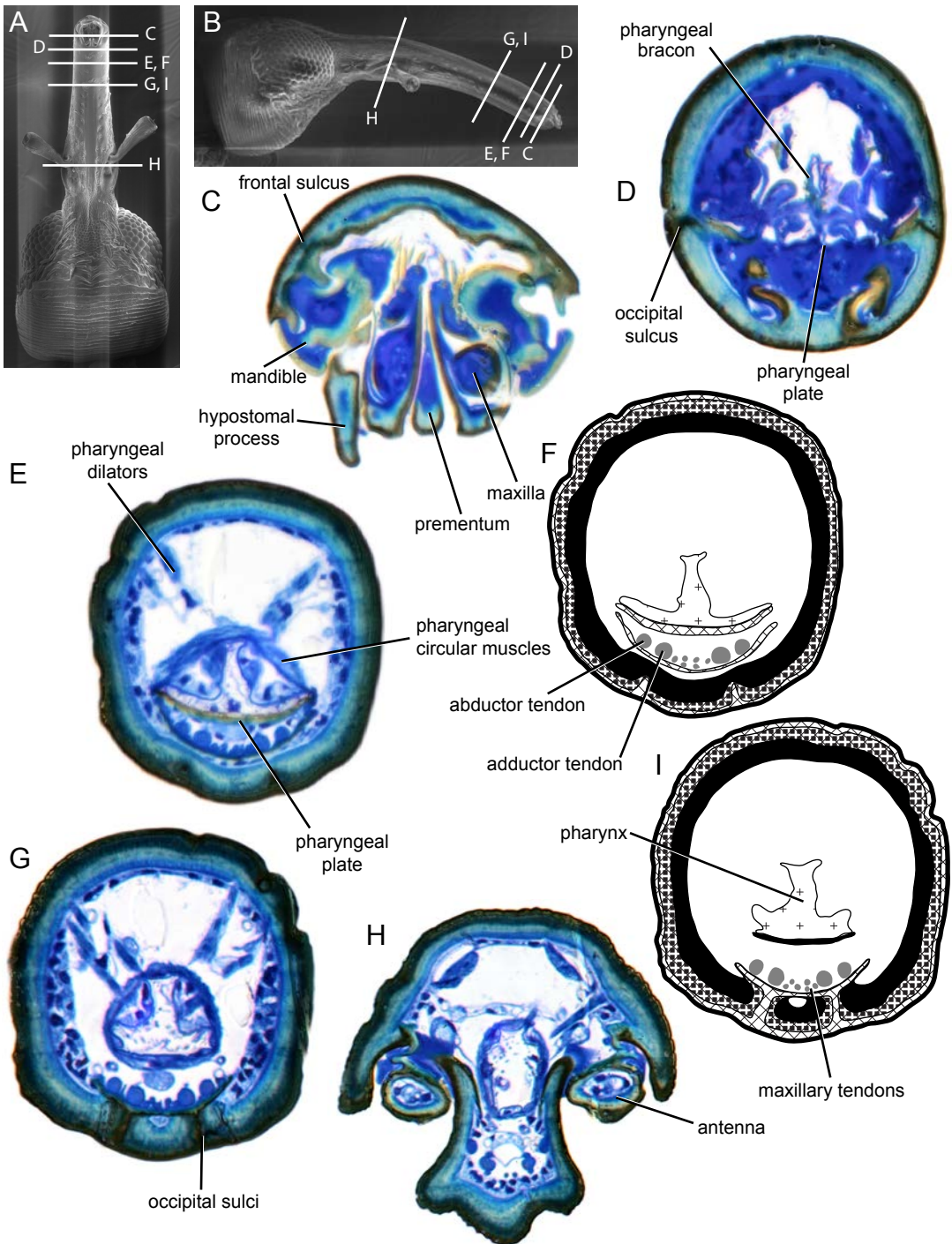
FIGURE 26. Semithin sections of head of *Apion* sp. (Brentidae: Apioninae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section just posterior to mouthparts; **E, G,** sections posterior to mouthparts and anterior to antennal insertion; **F,** diagram of E; **I,** diagram of G; **H,** section near base of rostrum at antennal insertion.
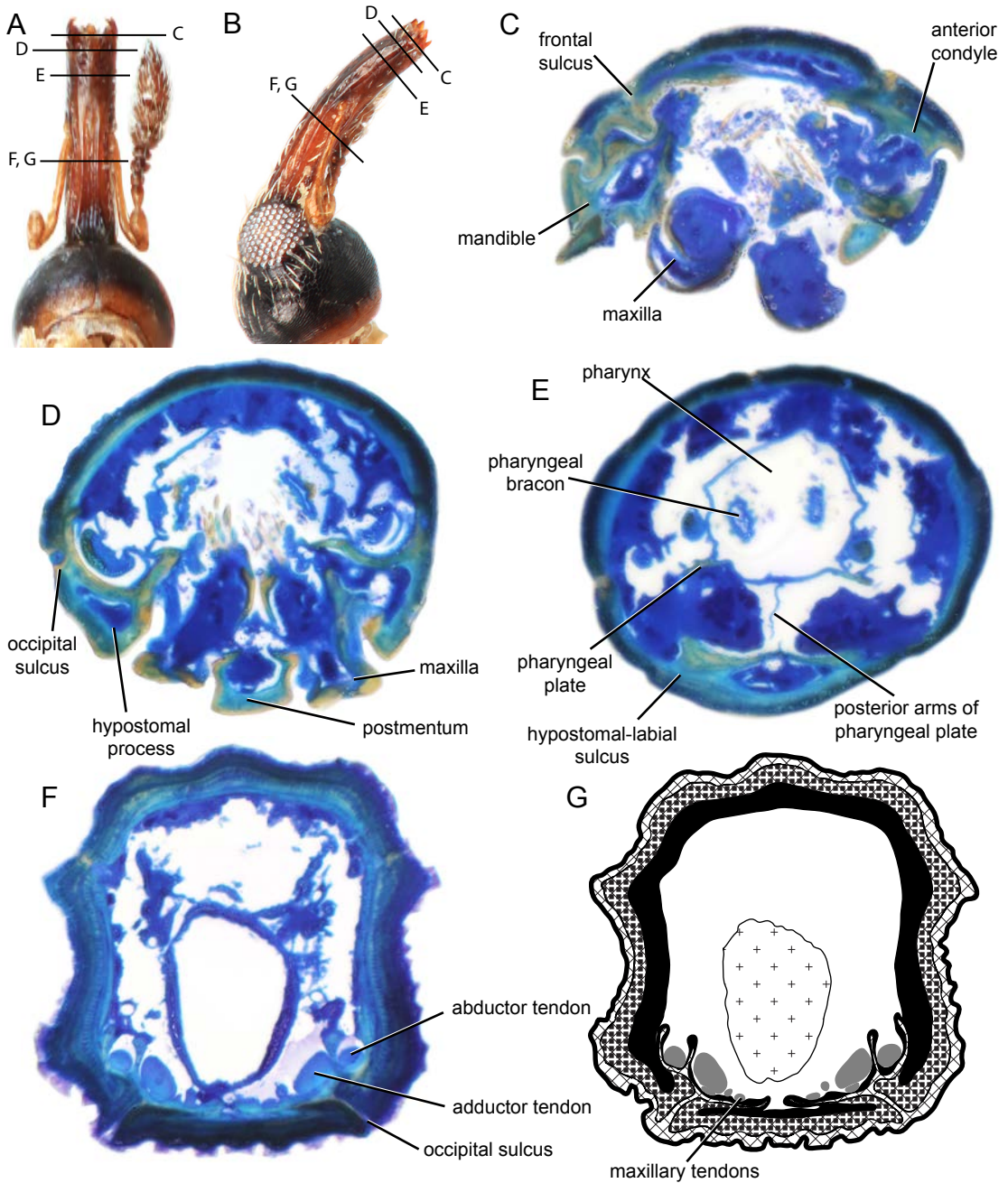
FIGURE 27. Semithin sections of head of *Nanophyes* sp. (Brentidae: Nanophyinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–G,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of head through mouthparts; **D,** section through proximal area of mouthparts; **E,** section posterior to mouthparts, anterior to antennal insertion; **F,** section posterior to middle of rostrum and to antennal insertion; **G,** diagram of F.

tized than in Brentinae. The pleurostomal sulci are distinct and frontal sulci extend dorsally.

NANOPHYINAE (fig. 27): While Nanophyinae also maintains some similarity with Brentinae, the occipital sulci and their apodemes are more distanced from each other and positioned at the ventrolateral corners of the rostrum. These apodemes also do not join medially, but remain separate, their form and sequence of supporting the mandibular and maxillary tendons similar to those of many groups basal to and within Curculionidae. The posterior arms of the pharyngeal plate are similar to those of Brentinae in being quite thin and appearing rather frail, though they are apparently fused to form one medial apodeme in this subfamily. The pleurostomal sulci are distinct and the frontal sulci extend dorsally. The pharyngeal plate is thin near the rostral apex, becoming thicker and more strongly sclerotized posterior to the posterior arms, but does not appear to extend beyond midlength, or it is at least indistinct and weakly sclerotized near this area.

Curculionidae (figs. 28–50)

Although the subgenal sulci and apodemes are absent in this family, it perhaps possesses the most diversity in terms of internal rostral structure. The pleurostomal sulci are absent, possibly present only as remnants in the immediate area of the precoila. The frontal sulci are visible in at least Brachycerinae, Bagoinae, Hyperinae, and some Scolytinae. The occipital sulci seem to be similarly positioned ventrally in all curculionid lineages; however, the form of their apodemes varies rather dramatically between subfamilies and appears to remain fairly stable within subfamilies. The posterior arms of the pharyngeal plate are well developed and sclerotized, forming C-shaped supports (in cross section) at their dorsal extensions for the mandibular adductor tendons near the oral orifice and posterior to the mandibles. Probably due to the stronger curvature of the rostrum and not necessarily dependent upon its length, the pharyngeal plate is well sclerotized and extends along most of the length of the rostrum in several curculionid subfamilies; however, it may weaken and become indistinct in lineages with a shortened rostrum.

BRACHYCERINAE (figs. 28–30). Brachycerini (fig. 28): The occipital sulci and apodemes are positioned more laterally and are somewhat elevated from the ventral floor of the rostrum in the Brachycerini. Somewhat similar to Apioninae, the apodemes of the occipital sulci form a broad platform. However, it is unclear whether the individual apodemes completely merge medially or merely touch. The placement of the apodemes and arrangement of the tendons are most similar to the conditions found in Nanophyinae and Raymondionymini. The pleurostomal sulci are distinct and the frontal sulci extend dorsally. The pharyngeal plate is thin but distinct and well sclerotized, extending to the rostral base. A short, wide cavity was found along the dorsal surface of the rostrum between the two distinct layers of endocuticle. It is possible that the cavity resulted from a distortion through desiccation of the specimen.

Raymondionymini (fig. 29): The occipital sulci, their associated apodemes, and mandibular and maxillary tendons are positioned similarly to those in Brachycerini and Erirhinini, although the apodemes are fairly short and do not approximate one another medially, a condition more similar to that in the latter lineage than the former. The posterior arms of the pharyngeal plate are weakly developed near the rostral apex, similar to those in Nanophyinae in which they fuse medially and form an elongated stalk ventral to the pharynx. Slightly posteriad they become separated by a thin medial bridge, then gradually become thicker and more robust before disappearing. Posterior to the hypostomal-labial sulci and toward the middle of the rostrum, the pharyngeal plate is thin and weakly sclerotized and does not appear to surpass midlength of the rostrum. The pleurostomal sulci are distinct and the frontal sulci extend dorsally.

Erirhinini (fig. 30): This tribe is similar to Raymondionymini, possessing more laterally positioned occipital sulci with short and separated apodemes. The apodemes, however, become slightly more elongated near the rostral base, but they do not merge medially. The arrangement of the maxillary tendons approximates that of Dryophthorinae and Bagoinae. The posterior
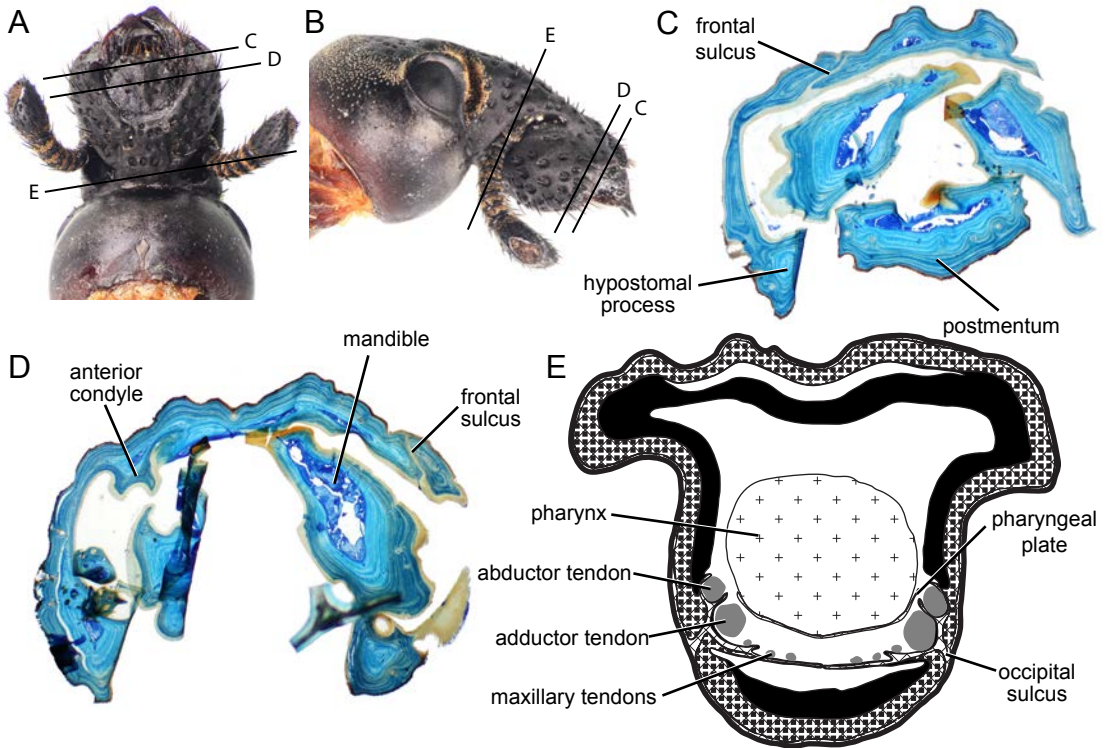
FIGURE 28. Semithin sections of head of *Brachycerus* sp. (Curculionidae: Brachycerinae: Brachycerini). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–E,** cross sections proceeding from apex of rostrum toward base; **C–D,** sections at apex of rostrum through mouthparts; **E,** diagram of section at base of rostrum, posterior to antennal insertion.

arms of the pharyngeal plate are similar to those of Raymondionymini and Bagoinae, although perhaps more like the latter in the more robust form of the apodemes and fusion at the middle. The pleurostomal sulci are distinct and the frontal sulci extend dorsally. The pharyngeal plate is thin but distinct and moderately sclerotized.

Dryophthorinae (figs. 11C, 31–32): Continuing throughout the Curculionidae, the number and position of sulci remain moderately stable, and the pleurostomal and frontal sulci are indistinct (excepting the lineages noted above). In this group, the pharyngeal plate is well sclerotized with exocuticle, wide, distinct, and extends to the rostral base. The posterior arms of the pharyngeal plate are well developed and sclerotized, fused medially and forming a slender stalk. In cross section, these apodemes also form slightly distorted C-shaped supports at their dorsal extensions for the mandibular adductor tendons near the oral

orifice and posterior to the mandibles. As the occipital sulci are positioned more ventrolaterally, the mandibular abductor tendons are held more dorsal to the adductors and maxillary tendons.

Platypodinae (figs. 9, 33): This group superficially appears similar to Scolytinae in internal rostral structure, and to *Ithycerus* in terms of the general structure of the rostral apex in particular. The subgenal sulci are evident both externally and internally, forming moderately long apodemes internally that fuse near the paracoila, though the occipital sulci are rather indistinct. While there seems to be a faint line of exocuticle near the dorsal mandibular articulation, distinct pleurostomal and frontal sulci are not evident. As in Scolytinae, the hypostomal sinus is slightly internalized, though to a lesser degree. The pharyngeal plate is thin and sclerotized and the posterior arms of the pharyngeal plate are thin and closely situated, a condition present in only one
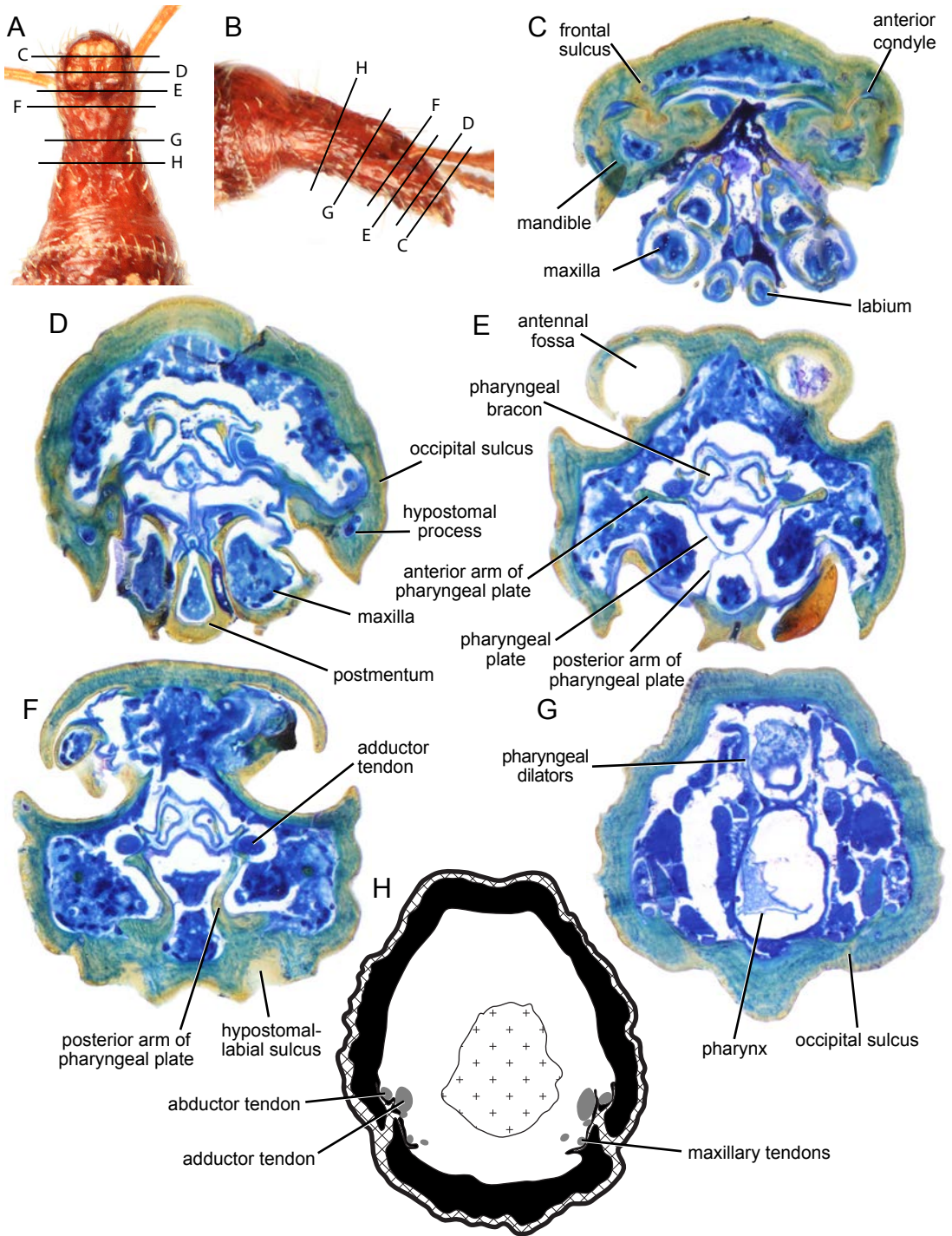
FIGURE 29. Semithin sections of head of *Gilbertiola* sp. (Curculionidae: Brachycerinae: Raymondionymini). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C–D,** sections at apex of rostrum through mouthparts; **E,** section at proximal area of mouthparts, anterior to antennal insertion; **F,** section at antennal insertion, posterior to mouthparts; **G,** section at middle of rostrum; **H,** diagram of section near base of rostrum.
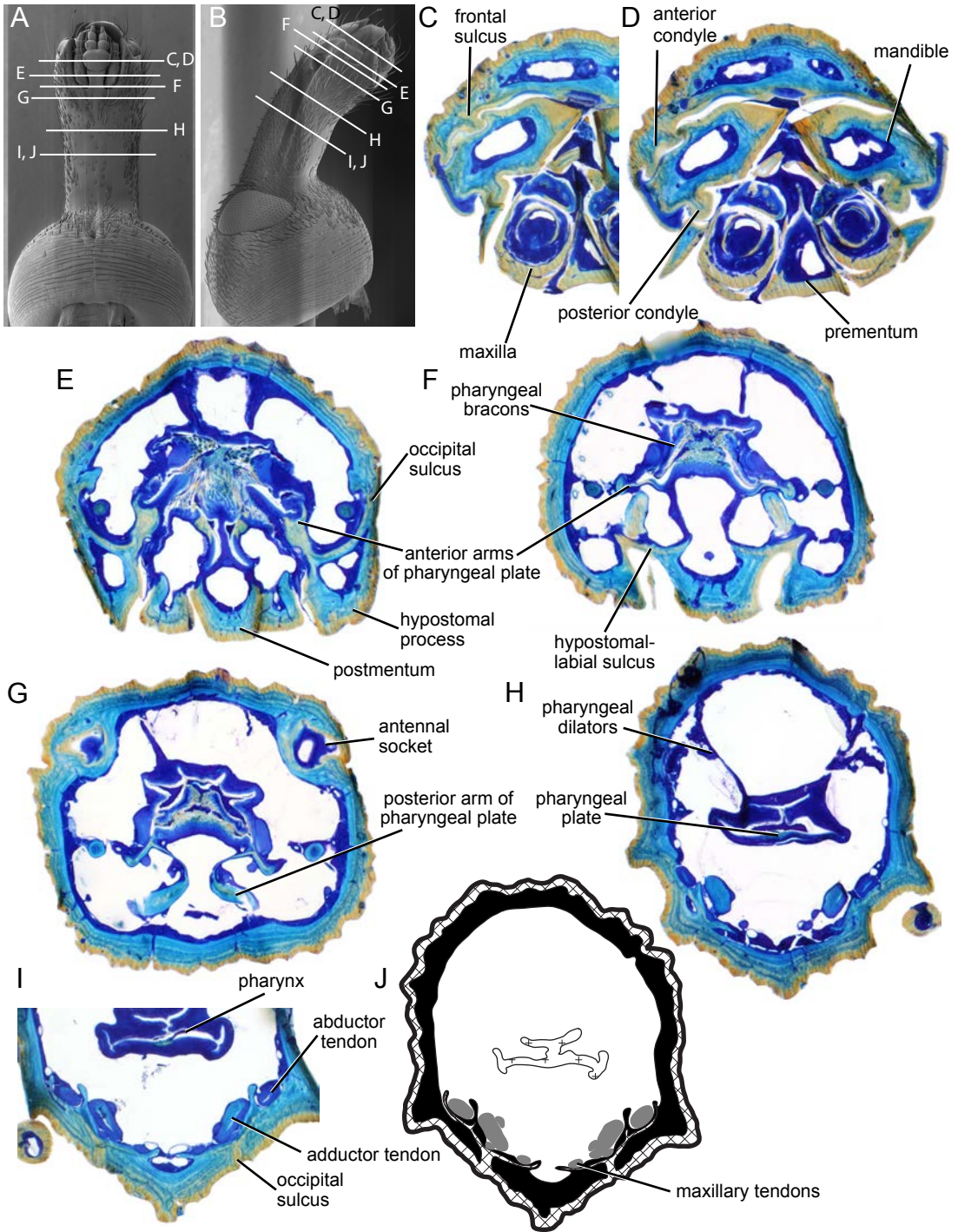
FIGURE 30. Semithin sections of head of *Lissorhoptrus* sp. (Curculionidae: Brachycerinae: Erirhinini): *Lissorhoptrus* sp. **A,** ventral aspect of head; **B,** lateral aspect of head; **C–J,** cross sections proceeding from apex of rostrum toward base; **C–D,** sections at apex of rostrum through mouthparts; **E,** section at proximal area of mouthparts; **F,** section immediately posterior to mouthparts; **G,** section posterior to mouthparts at antennal insertion; **H,** section posterior to antennal insertion at middle of rostrum; **I,** section near base of rostrum; **J,** diagram of section from I.
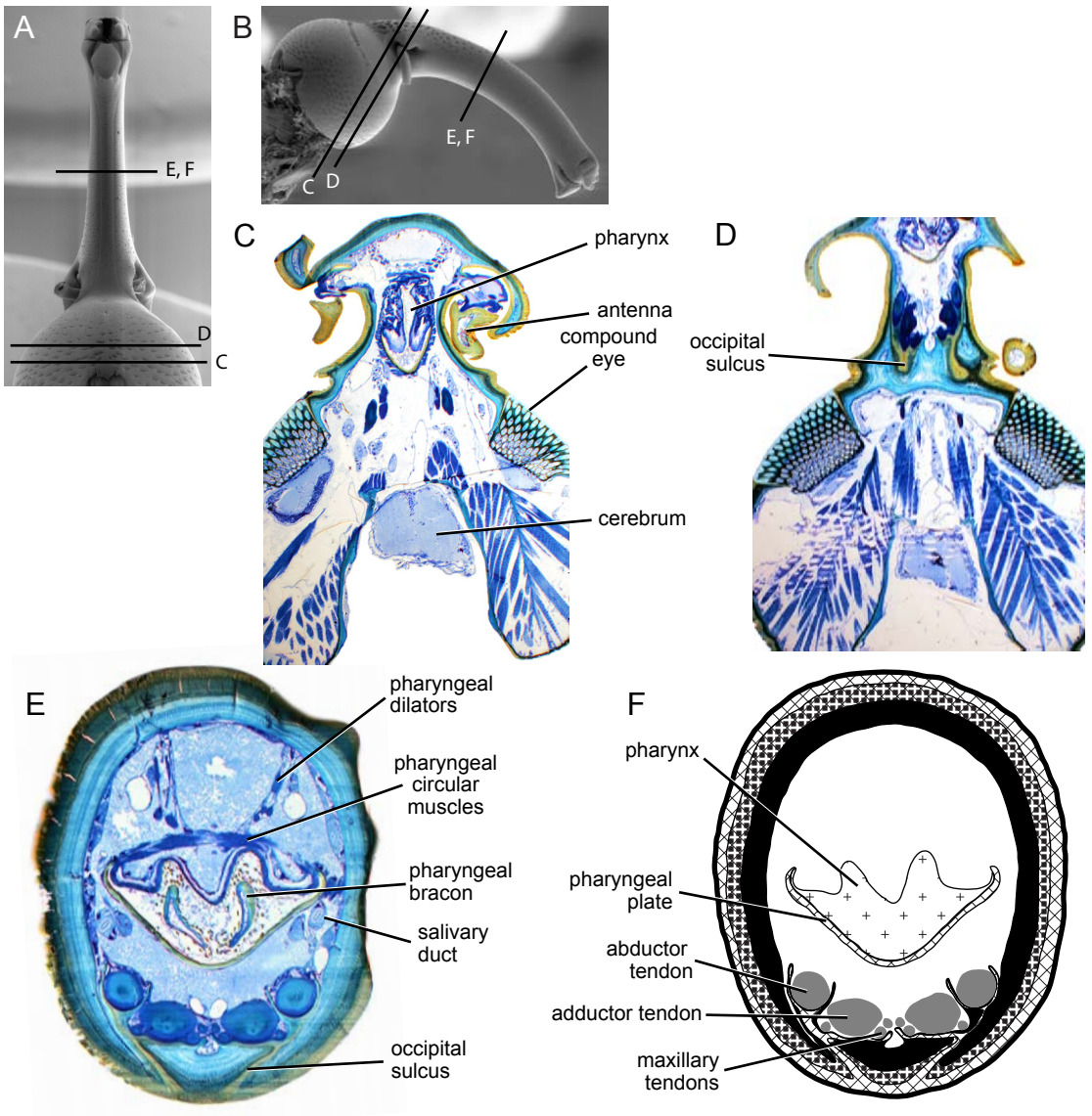
FIGURE 31. Semithin sections of head of *Sphenophorus* sp. (Curculionidae: Dryophthorinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–F,** oblique cross sections along rostrum and head; **C–D,** sections at antennal insertion and base of rostrum and head; **E,** section at middle of rostrum, anterior to antennal insertion; **F,** diagram of E.
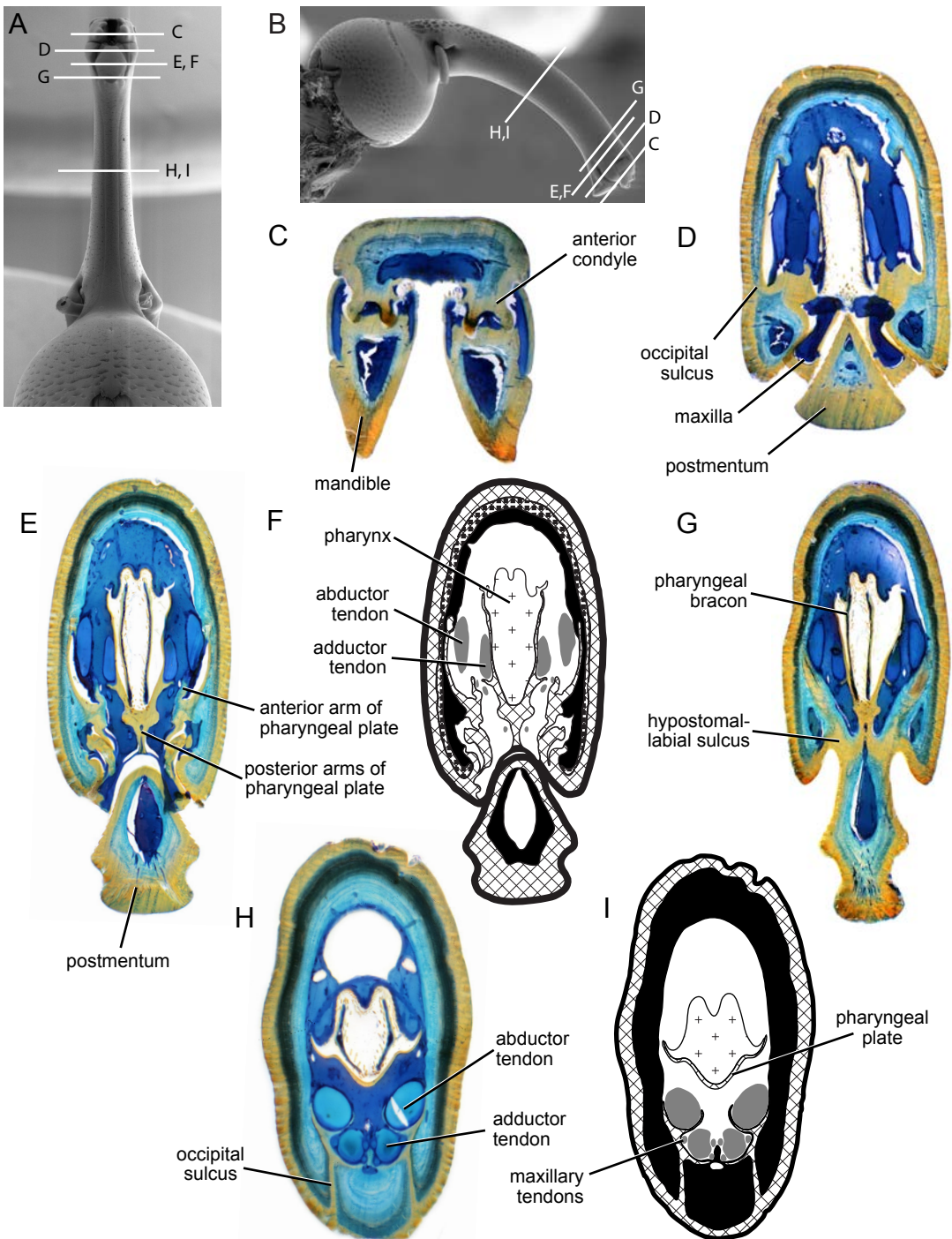
FIGURE 32. Semithin sections of head of *Rhodobaenus* sp. (Curculionidae: Dryophthorinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex to middle of rostrum; **C,** section through apex of rostrum and mandibles; **D,** section through apex of rostrum and mouthparts; **E,** section through proximal area of mouthparts; **F,** diagram of E; **G,** section immediately posterior to mouthparts; **H,** section at middle of rostrum, anterior to antennal insertion; **I,** diagram of H.
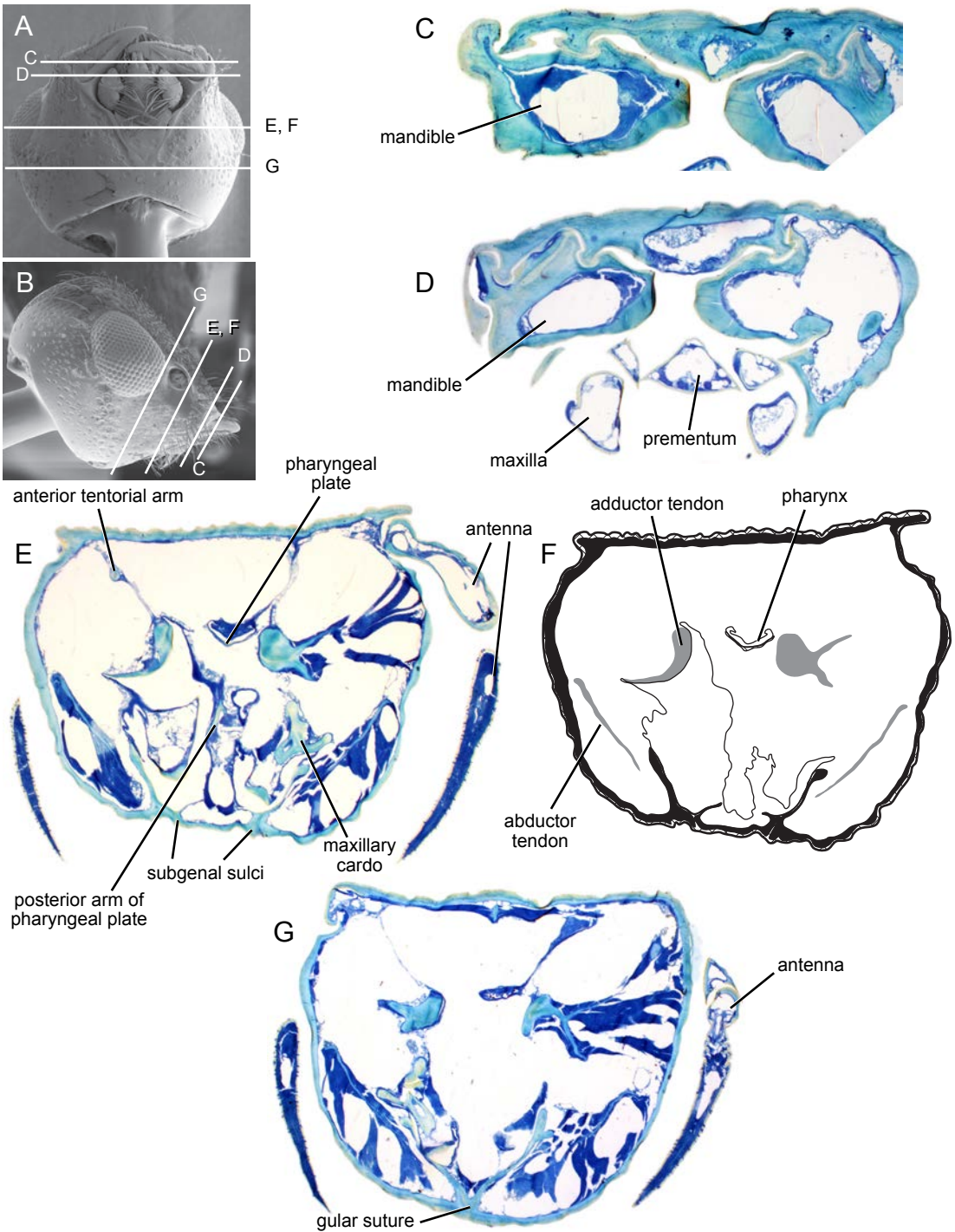
FIGURE 33. Semithin sections of head of *Platypus* sp. (Curculionidae: Platypodinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–G,** cross sections proceeding from anterior to middle of head; **C–D,** sections at anterior of head through mouthparts; **E,** section near antennal insertion, posterior to mouthparts; **F,** diagram of E; **G,** section near middle of head, posterior to antennal insertion and anterior to eyes.
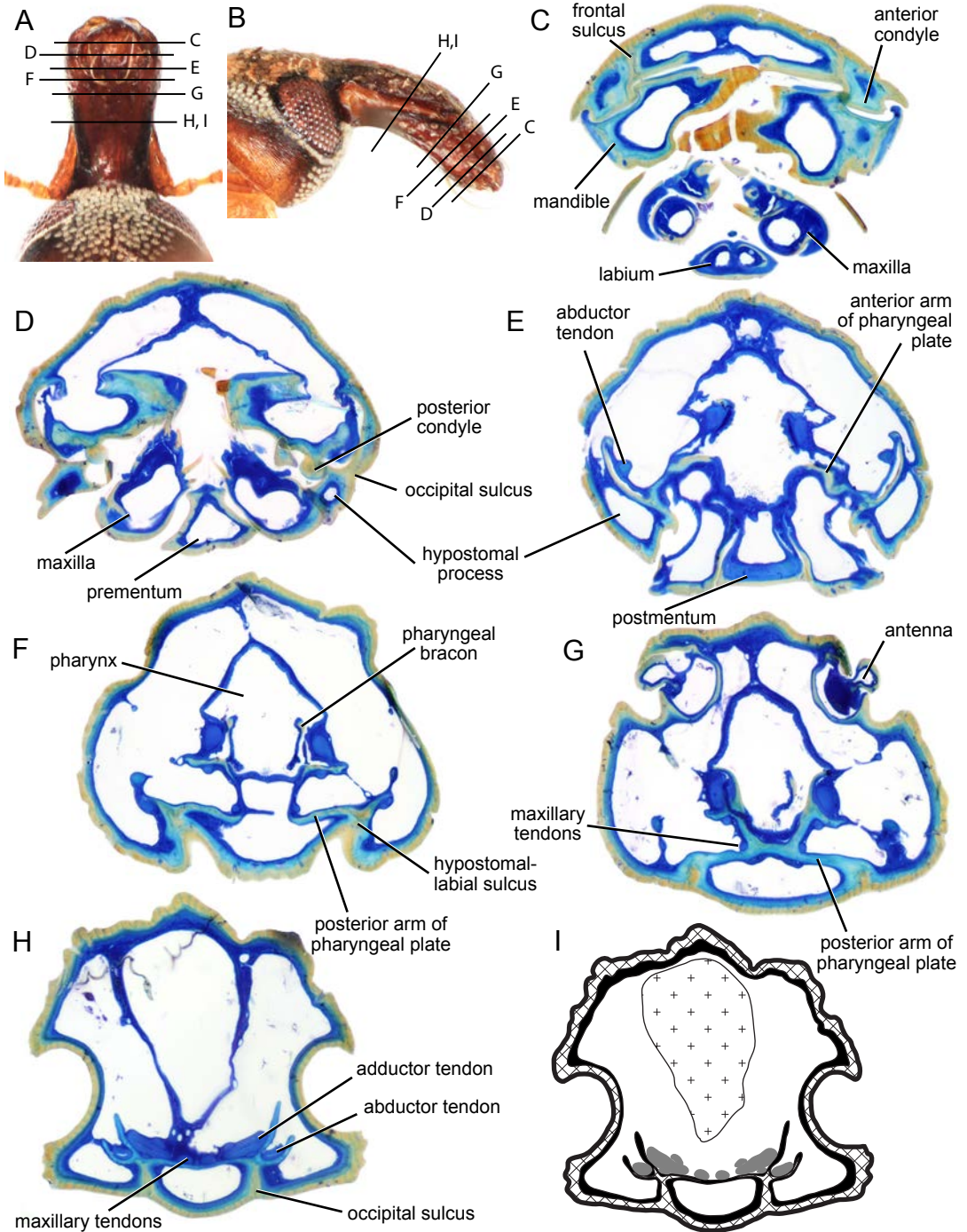
FIGURE 34. Semithin sections of head of *Bagous restrictus* (Curculionidae: Bagoinae): *Bagous restrictus* (Curculionidae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex of rostrum toward base; **C–D,** sections at apex of rostrum through mouthparts; **E,** section at proximal area of mouthparts; **F,** section immediately posterior to mouthparts, anterior to antennal insertion; **G,** section posterior to the mouthparts at antennal insertion; **H,** section posterior to middle of rostrum and antennal insertion; **I,** diagram of H.

other lineage, Dryophthorinae. Different from the condition in Scolytinae, the maxilla extends further into the head and the cardo articulates at the merged junction of the postmentum and apodemes of the subgenal sulci.

Bagoinae (fig. 34): Along with Hyperinae, this group is closest to the remaining Curculionidae (fig. 13), but possesses distinct, dorsally extending frontal sulci. The cuticle is comparatively thin, similar to that in Mesoptilinae, Conoderinae, and many Entiminae. The apodemes of the occipital sulci are fairly elevated above the ventral floor of the rostrum, at least partially due to the relatively thin cuticle, and they merge medially. The posterior arms of the pharyngeal plate are similar to those in many other curculionids, rather robust, fusing and forming a bridge medially, and their dorsal extensions forming distinct C-shaped supports. A peculiar feature is the large size of the pharynx beginning around the middle of the rostrum, in which it extends to the inner dorsal surface of the rostrum, causing the pharyngeal dilator muscles to be greatly shortened.

Hyperinae (fig. 35): Hyperinae is quite similar to Lixinae, as well as to Molytinae, differing mostly from the former in not possessing a strong basal constriction of the rostrum, which causes the apodemes of the occipital sulci to approach one another, such that they become positioned on the ventral floor of the rostrum (not elevated). As in the previous two subfamilies, the pharyngeal plate is short and weakly sclerotized, ending before the antennal insertion. The posterior arms of the pharyngeal plate also are robust, separated at their distal extensions along the rostrum, then fusing medially. Contrasting to Bagoinae, the frontal sulci are indistinct.

Entiminae (figs. 10D, 11D–F, 36): Although members of Entiminae often possess a shortened rostrum, its structure is akin to that of Conoderinae and Bagoinae, in which the apodemes of the occipital sulci are slightly elevated from the ventral floor of the rostrum; in taxa bearing a longer rostrum, the mandibular adductor tendons also rest on these apodemes (fig. 36H). A major difference is that the posterior arms of the pharyngeal plate are separate, similar to those in Cyclominae,

and are less robust. In those taxa with a short rostrum, the apodemes of the occipital sulci appear to stratify horizontally, with the mandibular abductor tendons situated laterally to those of the adductors. In longer rostrate taxa, the apodemal arrangement matches that in Cyclominae, in which they are stratified vertically and the mandibular adductor tendons situated dorsal to the abductors. The pharyngeal plate is short but distinct, appearing to extend at least beyond the antennal insertion and to nearly midlength of the rostrum. Interestingly, apodemes for supporting the antennal tendons are present in Entiminae, located along the dorsolateral corners in the rostral cavity. From this study, it appears that this subfamily is unique in possessing these antennal supports within Curculionidae. This feature was also found to be present in Brentinae (Brentidae) and Anthribidae.

Cyclominae (figs. 10A–B, 37): As the occipital sulci are positioned more ventrolaterally in this group, the apodemes do not merge medially but do approach one another toward the rostral base. The mandibular adductor tendons are held dorsally, while the abductor tendons are immediately ventral, enclosed in a tunnel formed by the apodemes. The pharyngeal plate is distinct and strongly sclerotized, extending a short distance near the rostral apex and ending before the antennal insertion. The posterior arms of the pharyngeal plate are robust and only narrowly attach medially at two points to form the plate (figs. 10A–B). The form of the pharynx may also be noted, becoming large and circular near the rostral base.

Molytinae (figs. 10F, 38): Molytinae display a fairly typical sulcus and tendon orientation, in which the occipital sulci are adjacent to the lateral corners of the rostrum and their apodemes short, separated, and resting on the ventral floor of the rostrum. The mandibular adductor tendons are located mesal and slightly dorsal to the abductor tendons. The pharyngeal plate is distinct and strongly developed, mostly visible near the rostral apex due to the short extension of the medial part of the plate, and is absent posterior to the antennal insertion. The posterior arms of the pharyngeal plate are robust, initially sepa-
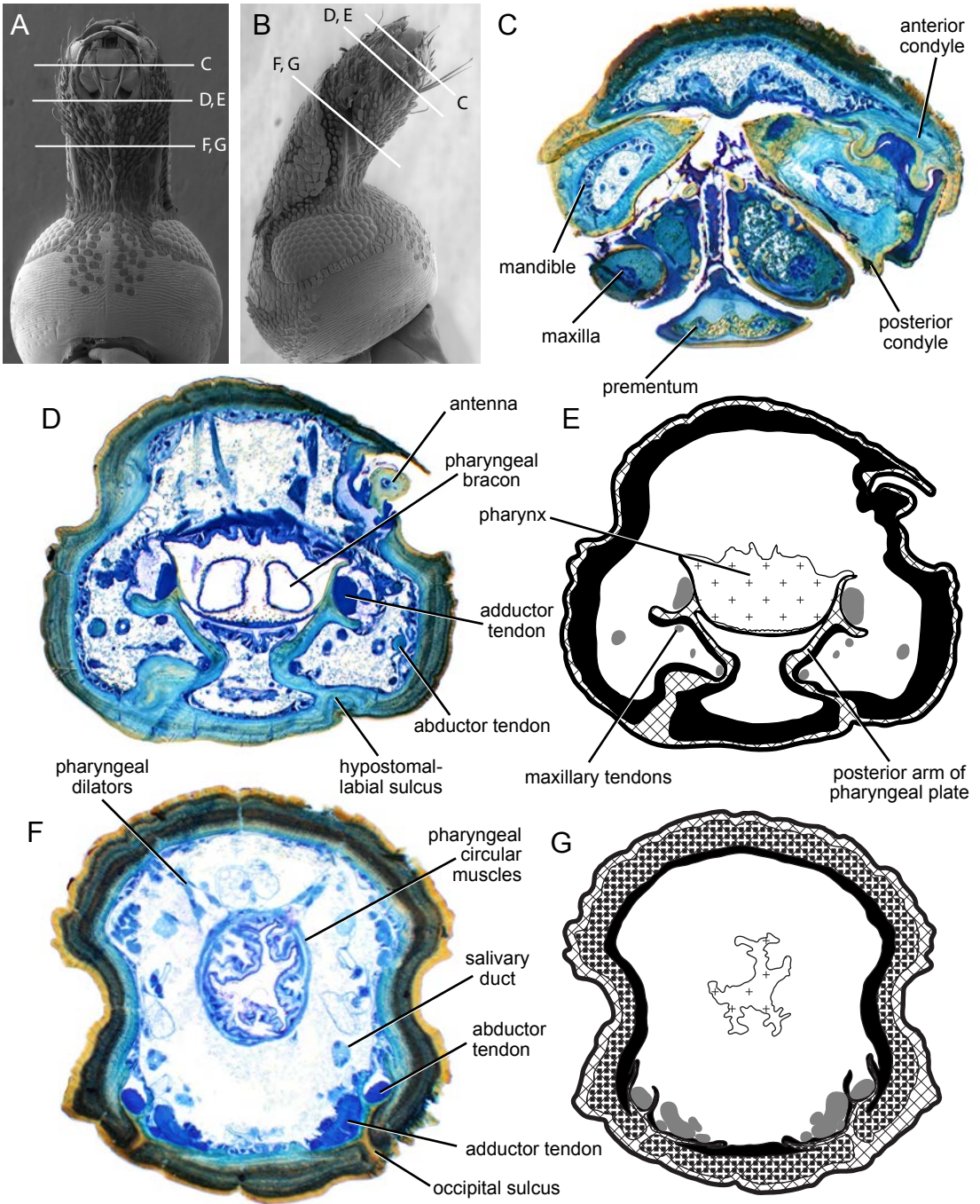
FIGURE 35. Semithin sections of head of *Hypera eximia* (Curculionidae: Hyperinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–G,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section immediately posterior to mouthparts and near antennal insertion; **E,** diagram of D; **F,** section posterior to middle of rostrum and antennal insertion; **G,** diagram of F.
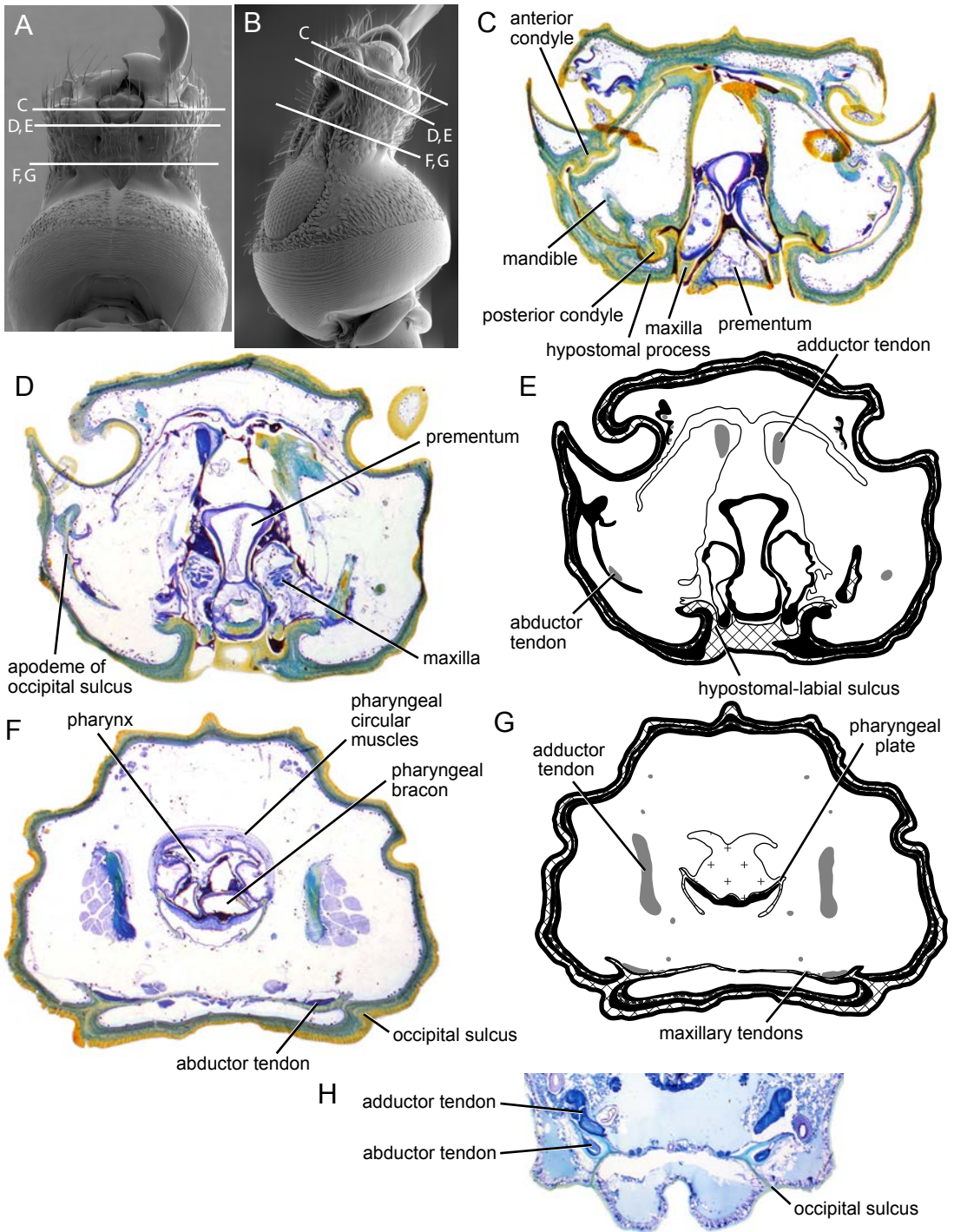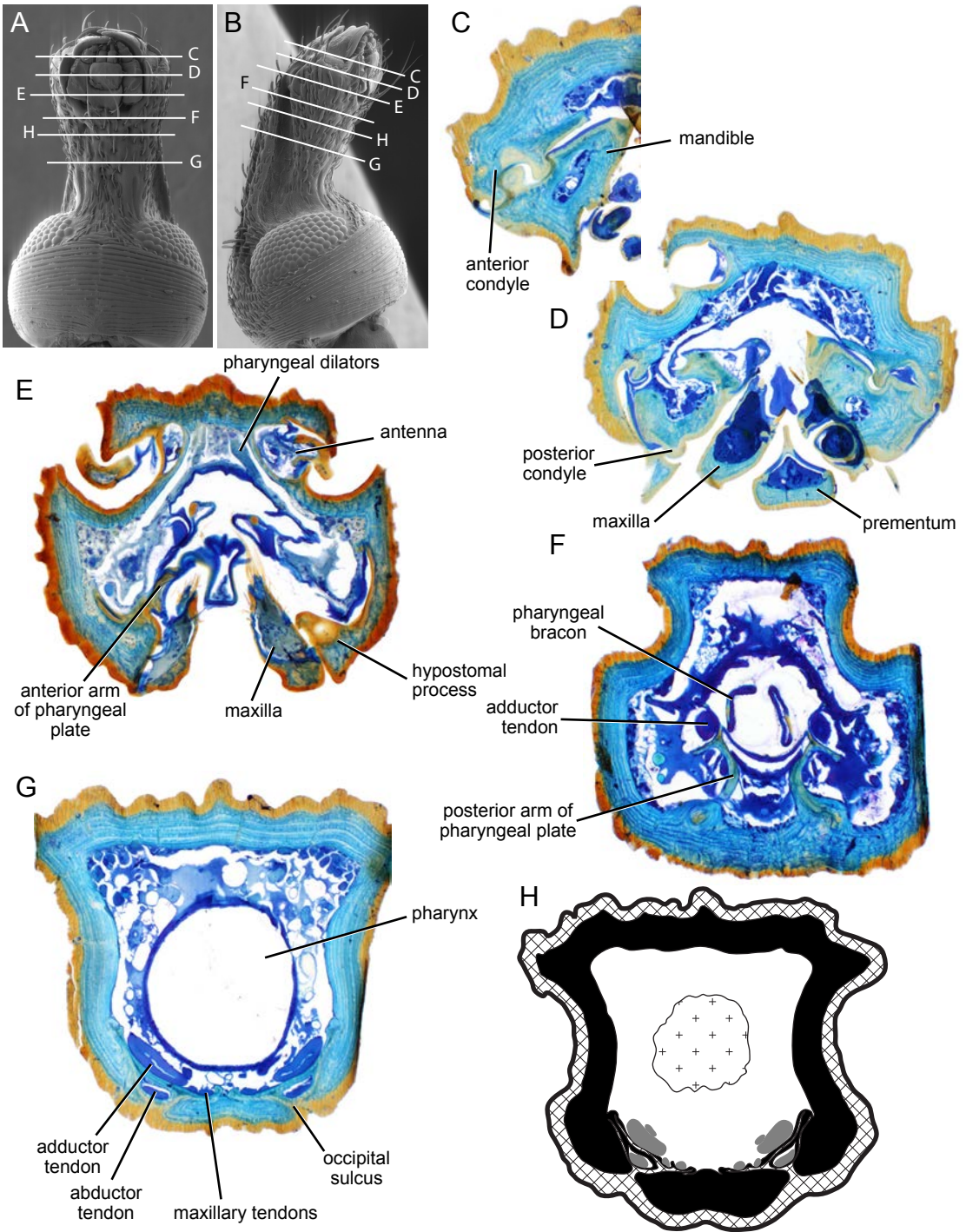
FIGURE 36. Semithin sections of head of *Cyrtepistomus castaneus* (Curculionidae: Entiminae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–G,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum, antennal insertion, and through mouthparts; **D,** section at proximal area of mouthparts, immediately posterior to antennal insertion; **E,** diagram of D; **F,** section at base of rostrum; **G,** diagram of F; **H,** *Diaprepes abbreviatus* (Curculionidae: Entiminae), section at middle of pupal rostrum.

FIGURE 37. Semithin sections of head of *Listronotus* sp. (Curculionidae: Cyclominae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C–D,** sections at apex of rostrum through mouthparts; **E,** section at antennal insertion and proximal area of mouthparts; **F,** section posterior to antennal insertion, anterior to middle of rostrum; **G,** section slightly posterior to middle of rostrum; **H,** diagram of section at middle of rostrum.
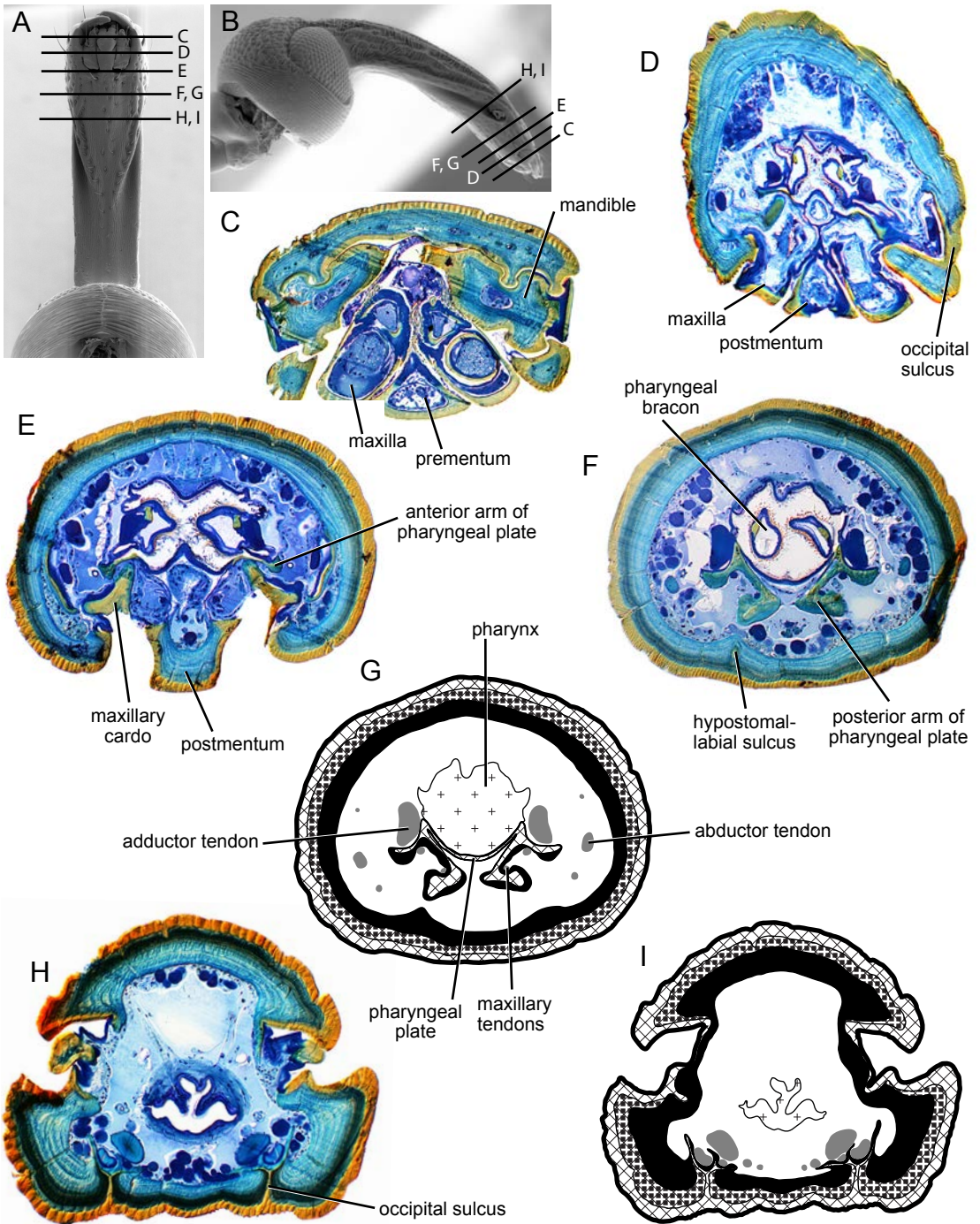
FIGURE 38. Semithin sections of head of *Rhyssomatus lineaticollis* (Curculionidae: Molytinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections along apical half of rostrum; **C–D,** sections at apex of rostrum through mouthparts; **E,** section at proximal area of mouthparts; **F,** section posterior to mouthparts, anterior to antennal insertion; **G,** diagram of F; **H,** section at antennal insertion, anterior to middle of rostrum; **I,** diagram of H.

rated at their distal extensions along the rostrum, then fusing medially and forming a thickened platform at the pharyngeal plate posterior to the endpoint of the hypostomal-labial sulci.

Cossoninae (fig. 39): Cossoninae is fairly similar to Cyclominae and Cryptorhynchinae with vertically stratified apodemes. It is perhaps most alike to Baridinae, however, by the more proximal occipital sulci which allow for the medial fusion of the apodemes. These apodemes also have elongate apical extensions, although they are not so appressed to the inner rostral wall as in Baridinae. The posterior arms of the pharyngeal plate also fuse medially and are robust. The pharyngeal plate is distinct and sclerotized for only a short distance, extending approximately until the antennal insertion.

Scolytinae (figs. 40–42). Xyleborini (figs. 40–41): As the rostrum in the extant members of this group is more or less absent, supposedly diminished from a fully rostrate ancestor with only remnants present in some taxa, much information has been lost in terms of sulci and tendon position, as well as degree of apodeme development. Internally the rostrum appears deceptively simplified and similar to a chrysomelid, in which the tendons no longer require supporting apodemes to facilitate movement and reduce damage. The occipital sulci, therefore, are fairly short (as observed by Lyal, 1995), their apodemes also short and appressed along the rostrum wall. The frontal sulci appear to be faintly present in this subfamily, though are suspected to be largely obliterated in most of the lineage. Due to the compaction of the head and rostrum, the pharyngeal plate appears to have been lost, but there are distinct remnants of the anterior and posterior arms. The postmentum and hypostomal sinus (into which the maxillae are positioned) are reduced and have become more internalized. The apodemes of the postmentum and hypostomal-labial sulci remain, though the internalization of the hypostomal sinus has slightly displaced and changed the typical form of these apodemes as they are seen in other weevils. The pharyngeal plate appears to be absent. The anterior arms are present and the posterior arms reduced, fused to the posterior

articulation of the prementum. The maxillary cardo completely articulates with the postmental apodemes, whereas it jointly articulates at the base of the hypostomal sinus (paracoila) and fusion of the posterior arms of the pharyngeal plate in all other weevils. While not supporting any tendons, the apodemes of the subgenal sulci form a large internal ridge (these internal apodemes are also illustrated in Lyal, 1995).

Hylastini (fig. 42): Hylastini is thought to be more of a basal group within this subfamily and, in accordance with this hypothesis, the sections reveal that indeed has more primitive features . As the subgenal sulci are visible externally and their apodemes developed internally in Xyleborini, they are comparatively more distinct in Hylastini. The apodemes of the occipital sulci are slightly more developed and not as appressed to the rostrum wall. The frontal sulci also are distinct, appearing to extend dorsally as in other families and curculionid subfamilies intermediate in weevil phylogeny. The occipital sulci are fairly distinct and form abbreviated apodemes supporting the mandibular abductor tendons. As in Xyleborini, the pharyngeal plate appears to have been lost or highly reduced and weakly sclerotized.

Lixinae (fig. 43): This group is fairly similar to Molytinae, although the apodemes of the occipital sulci hold the tendons slightly more elevated from the ventral floor of the rostrum. The posterior arms of the pharyngeal plate also are robust, initially separated at their distal extensions along the rostrum, then fusing medially. The occipital sulci are fairly visible externally in Lixinae. Toward the rostral base, the apodemes nearly merge medially due to constriction caused by the antennal scrobe. The pharyngeal plate is weakly developed and appears to end before the antennal insertion.

Baridinae (fig. 44): Baridinae and a few other subfamilies have evolved more derived and elaborate apodemal complexes for holding the mouthpart tendons. The occipital sulci are positioned rather closely and ventrally, while the apodemes have formed a tiered structure caused by the medioventral migration of the mandibular abductor tendons and their associated apodemes under the adductor and maxillary tendons and their
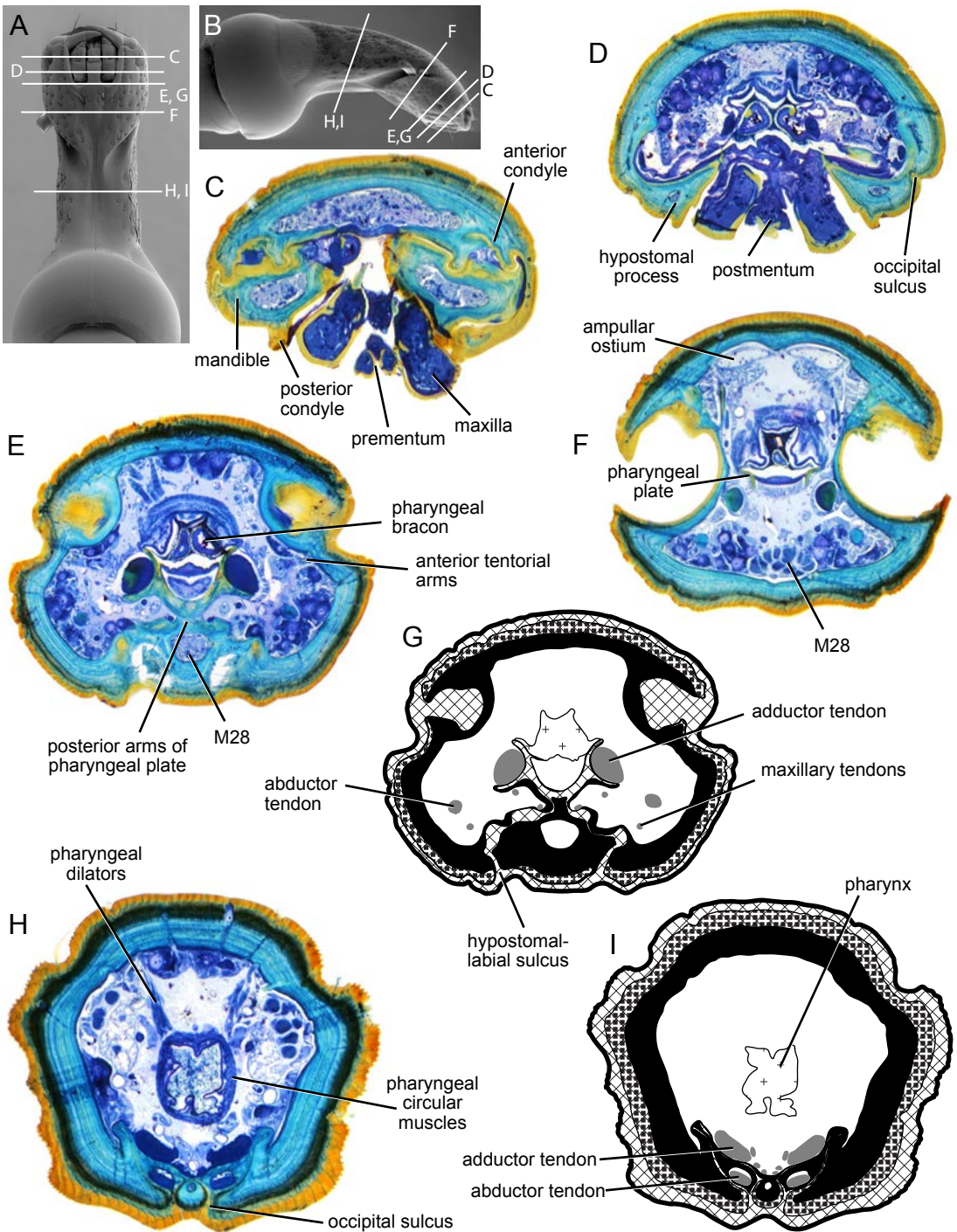
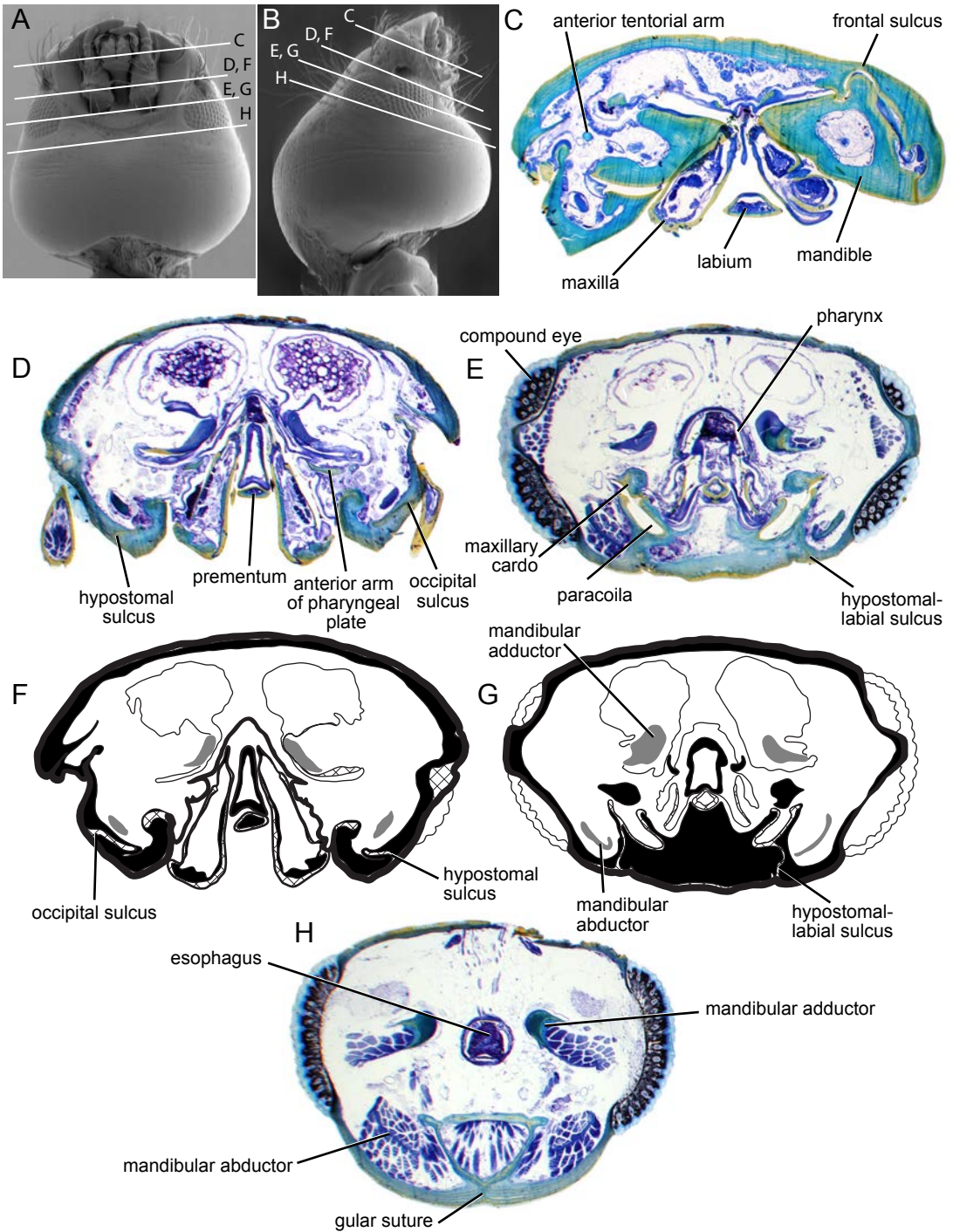FIGURE 39. Semithin sections of head of *Cossonus* sp. (Curculionidae: Cossoninae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section at proximal area of mouthparts; **E,** section immediately posterior to mouthparts, near antennal insertion; **F,** section near middle of rostrum, posterior to antennal insertion; **G,** diagram of E; **H,** section near base of rostrum; **I,** diagram of H.
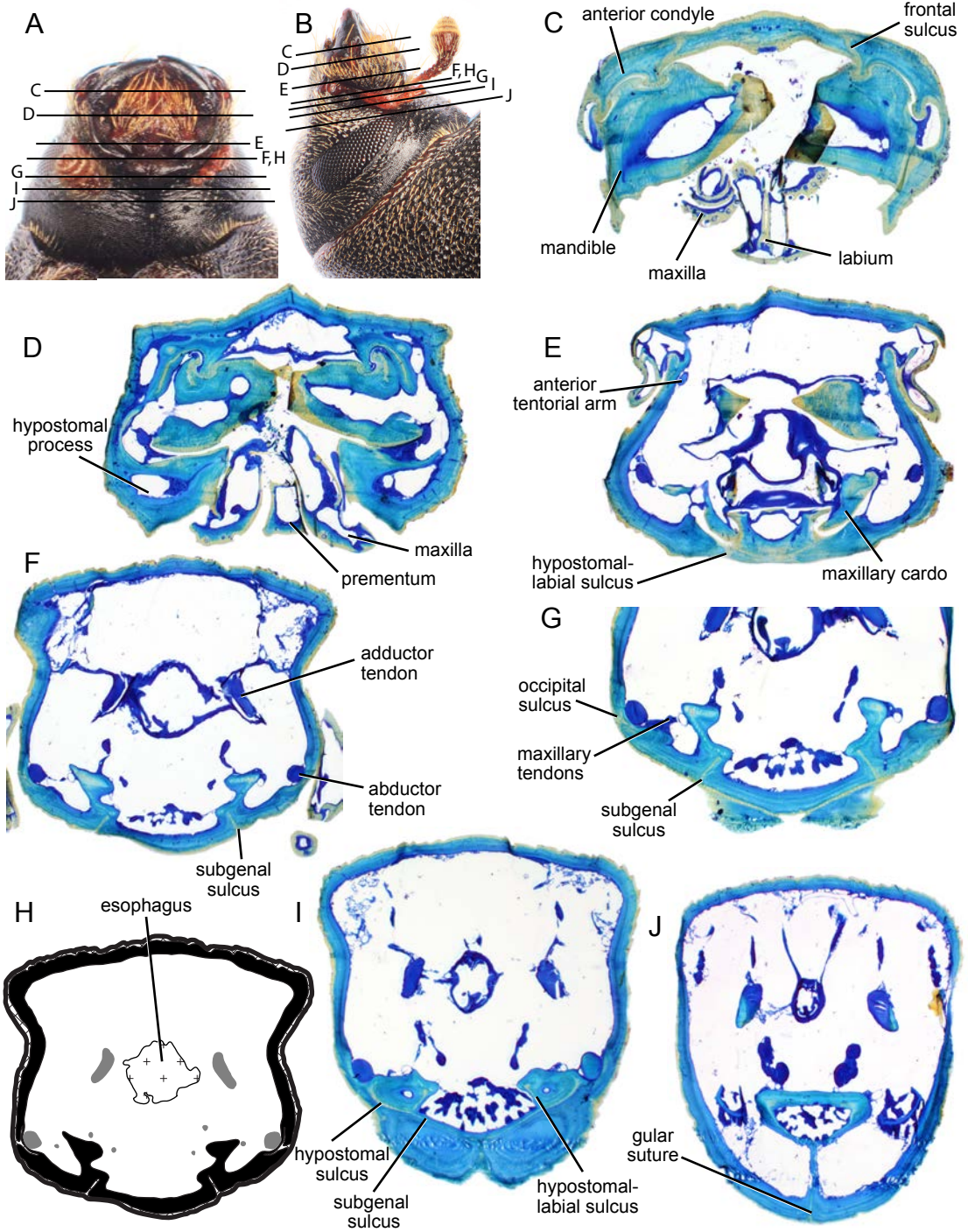
FIGURE 40. Semithin sections of head of *Xyleborus* sp. (Curculionidae: Scolytinae: Xyleborini). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex to middle of head; **C,** section at apex of head through mouthparts, anterior to antennal insertion; **D,** section at proximal area of mouthparts at antennal insertion; **E,** section immediately posterior to mouthparts and through middle of eyes; **F,** diagram of D; **G,** diagram of E; **H,** section through posterior of eyes and near middle of head.
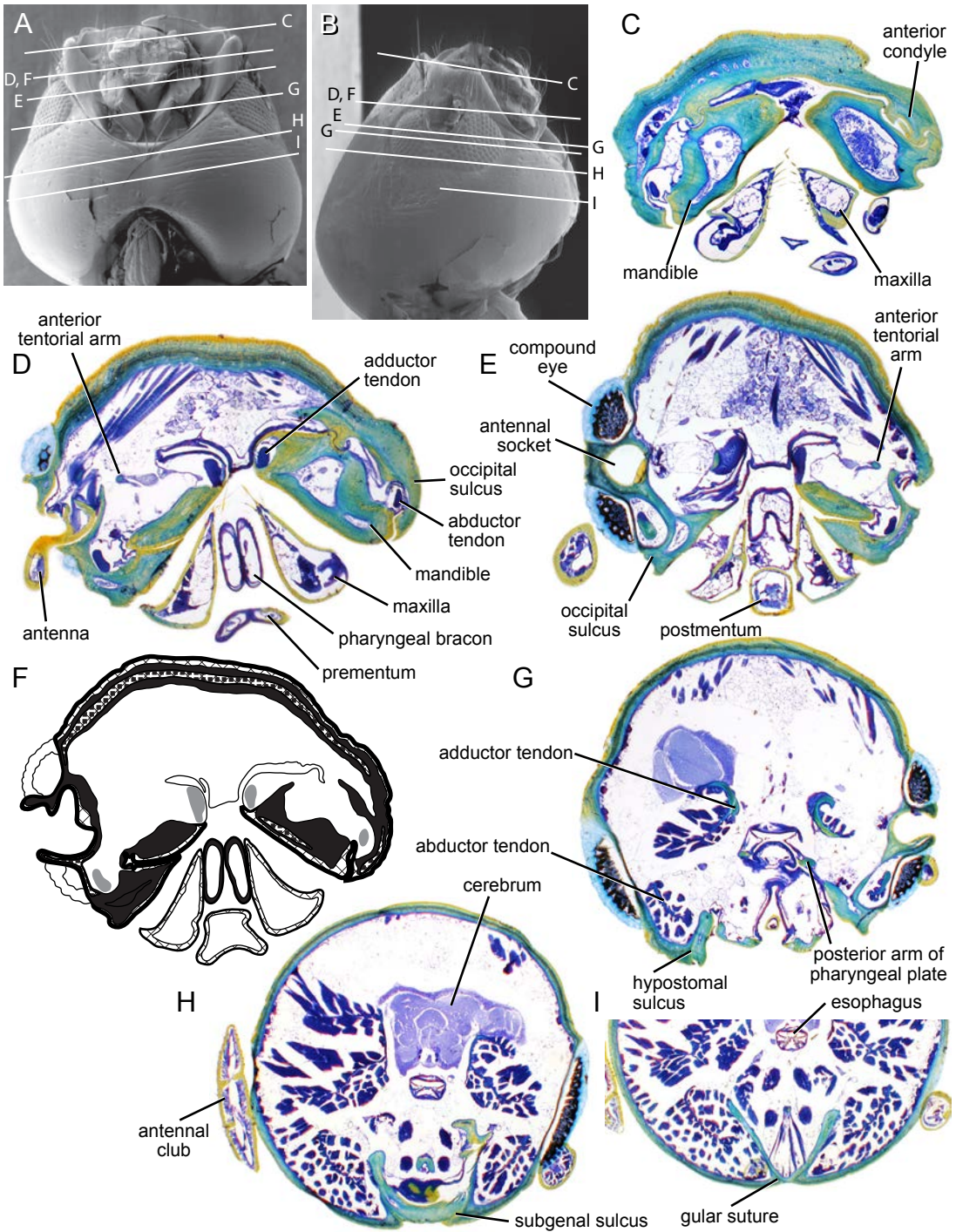
FIGURE 41. Semithin sections of head of *Ips* sp. (Curculionidae: Scolytinae: Ipini). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–I,** cross sections proceeding from apex to middle of head; **C,** section at apex of head through mouthparts; **D–E,** sections at antennal insertion, through mouthparts and anterior of eyes; **F,** diagram of section at antennal insertion, through mouthparts and anterior of eyes; **G,** section at proximal area of mouthparts, posterior to antennal insertion; **H,** section at middle of head and posterior of eyes; **I,** section just posterior to middle of head.

FIGURE 42. Semithin sections of head of *Hylurgops planirostris* (Curculionidae: Scolytinae: Hylastini). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–J,** cross sections proceeding from apex to middle of head; **C–D,** sections at apex of head through mouthparts; **E,** section at antennal insertion and proximal area of mouthparts; **F, G, I,** sections posterior to mouthparts and antennal insertion, anterior to eyes; **H,** diagram of F; **J,** section immediately anterior of eyes.
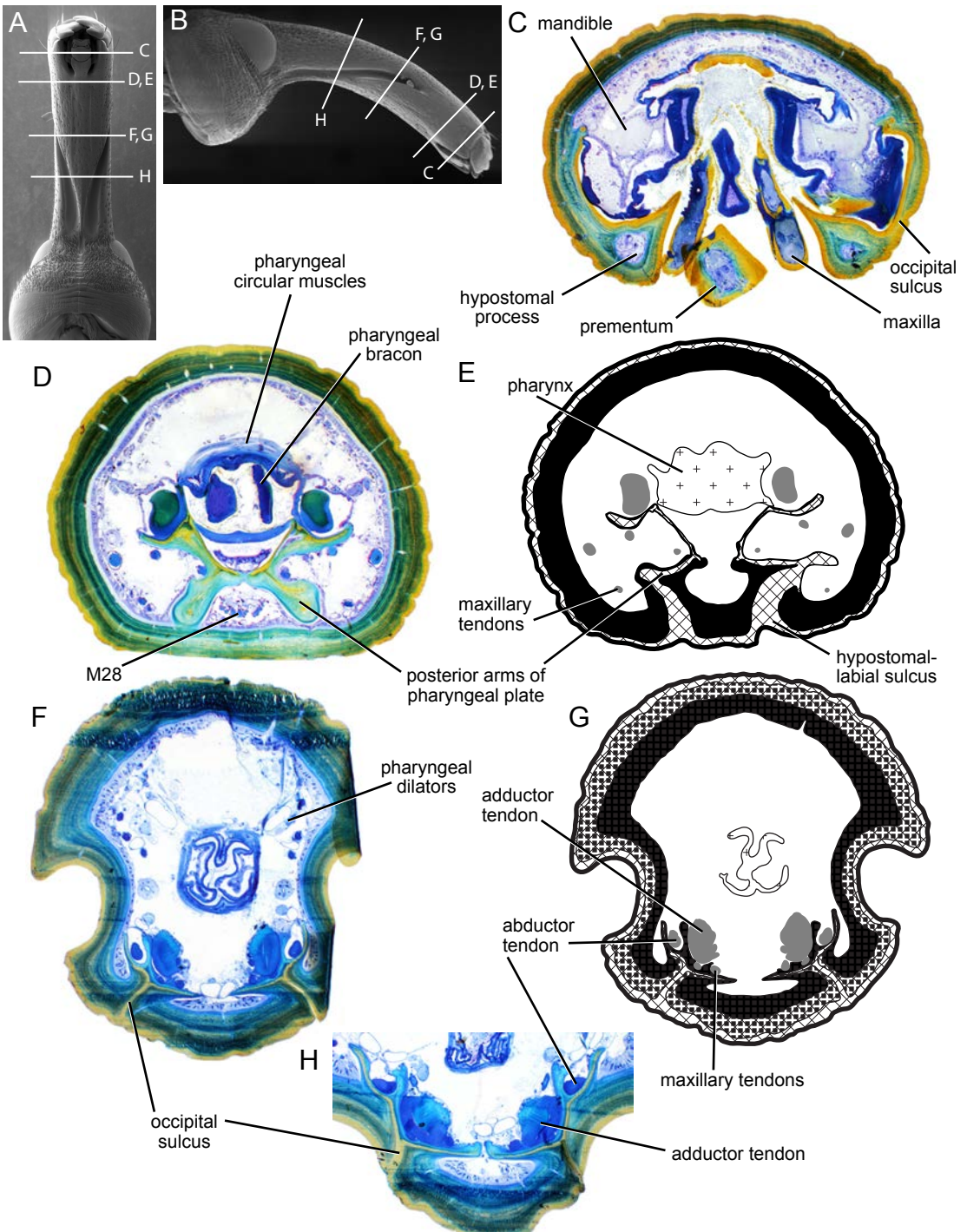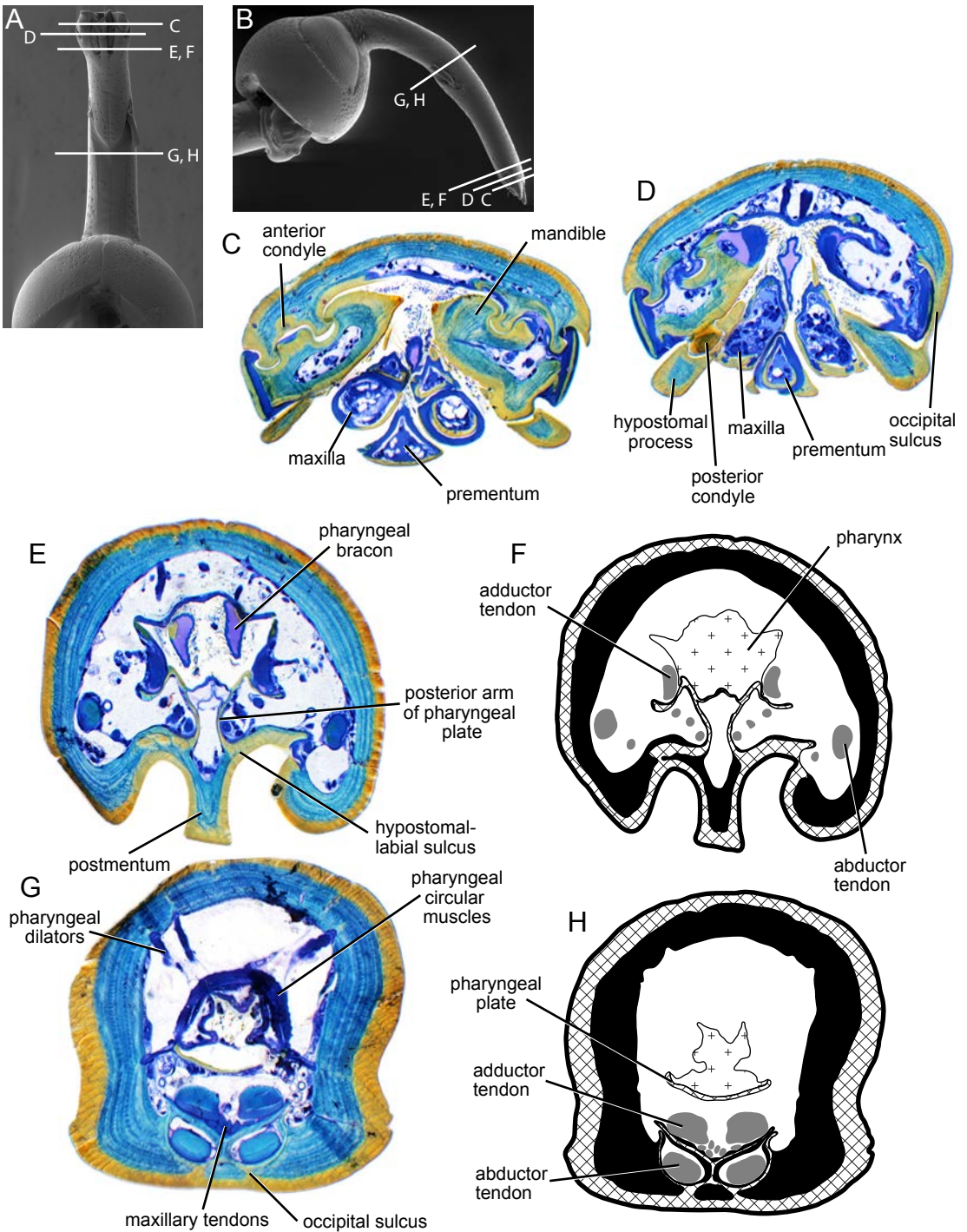
FIGURE 43. Semithin sections of head of *Lixus* sp. (Curculionidae: Lixinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through proximal area of mouthparts; **D,** section posterior to mouthparts, anterior to antennal insertion; **E,** diagram of D; **F,** section at middle of rostrum, posterior to antennal insertion; **G,** diagram of F; **H,** section near base of rostrum, showing ventral portion.

FIGURE 44. Semithin sections of head of *Odontocorynus* sp. (Curculionidae: Baridinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C–D,** sections at apex of rostrum through mouthparts; **E,** section immediately posterior to mouthparts, anterior to antennal insertion; **F,** diagram of E; **G,** section posterior to middle of rostrum and antennal insertion; **H,** diagram of G.

apodemes. The resulting structure is akin to a ventral tunnel through which the mandibular abductor tendons pass, and a dorsal platform supporting the mandibular adductors on the sides and the maxillary tendons in the middle. The posterior arms of the pharyngeal plate are fairly typical, namely moderately robust, separated along their apical extensions in the rostrum at the hypostomal sinus and fusing medially along their posterior extensions. The pharyngeal plate is rather well sclerotized and extends most of the length of the rostrum.

CONODERINAE (fig. 45): The structure of the apodemes and position of the occipital sulci along much of the rostrum in Conoderinae is nearly identical to Bagoinae, in which the apodemes form a platform elevated above the ventral floor of the rostrum (again perhaps at least partially due to the thin rostral cuticle). The major difference lies in a slight alteration in the arrangement of maxillary tendons. Also, as in the former few subfamilies (e.g., Cossoninae, Cryptorhynchinae, Molytinae, Lixinae), the posterior arms of the pharyngeal plate fuse medially. The pharyngeal plate is distinct, sclerotized, and moderately long, ending just before the antennal insertion.

CRYPTORHYNCHINAE (figs. 10C, 46): This subfamily appears nearly identical to Cyclominae, in which the apodemes and tendons are vertically stratified at the lateral corners of the rostrum. Near the rostral apex, however, the posterior arms of the pharyngeal plate fuse medially, forming an X-shaped scaffold as in Molytinae and Lixinae. The pharyngeal plate also is well sclerotized, extending most of the length of the rostrum and ending near the rostral base. Other interesting features include the elongate apical extensions of the apodemes of the occipital sulci, which fuse distally and extend along the inner lateral surface of the rostrum. The maxillary tendons also are particularly enlarged, nearing the size of the mandibular abductor tendon.

MESOPTILINAE (fig. 47): This family displays another distinct vertical stratification of the apodemes of the occipital sulci, similar to that present in Cossoninae, in which there is a short medial bridge linking the apodemes of the two occipital sulci. The apical extensions of these apodemes are fairly elongate, as in Cryptorhynchinae, though

basally divergent and separated from the lateral wall of the rostrum and apically merging with it. The medial fusion of the posterior arms of the pharyngeal plate is also present, though the apodemes are less robust and the C-shaped support for the anterior portions of the mandibular adductor tendons is diminished and weakly sclerotized. The pharyngeal plate is weakly developed and short, ending before the antennal insertion. The mandibular adductor tendons, as well as those of the abductor, are rather enlarged and oblong, a condition similar (though less extreme) to that found in Cyclominae, Cryptorhynchinae, Bagoinae, and perhaps also Cossoninae.

CEUTORHYNCHINAE (fig. 48): The internal rostrum structure in this group is remarkably similar along the entire length to that in Molytinae and Hyperinae. The occipital sulci are positioned ventromedially (as opposed to more ventrolateral as in the former two subfamilies) and are more close together, such as in Baridinae, in which the mandibular adductor tendons are situated mesal to the abductors. The posterior arms of the pharyngeal plate are robust, slightly less so more apically along the rostrum, and appear to remain separate, although the medial portions of the apodemes approach one another quite closely along the hypostomal sinus. The pharyngeal plate is distinct and sclerotized, extending most of the length of the rostrum and ending near the rostral base.

CURCULIONINAE (figs. 49–50): This group perhaps appears most similar to Ceutorhynchinae, particularly in the arrangement of the mandibular and maxillary tendons. The posterior arms of the pharyngeal plate, although distinct, are less robust and slender, fused and stalked medially. The pharyngeal plate appears distinct, well sclerotized, and fairly long, extending just beyond the antennal insertion and ending thereafter. The apodemes of the occipital sulci are ventral, approaching one another medially toward the base of the rostrum, and they seem to at least partially merge medially in some taxa. In *Curculio*, due to the lateral rotation of the mandibular articulations and almost vertical movement of the mandibles, the mandibular abductor tendons are larger and more robust than those of the adductors.
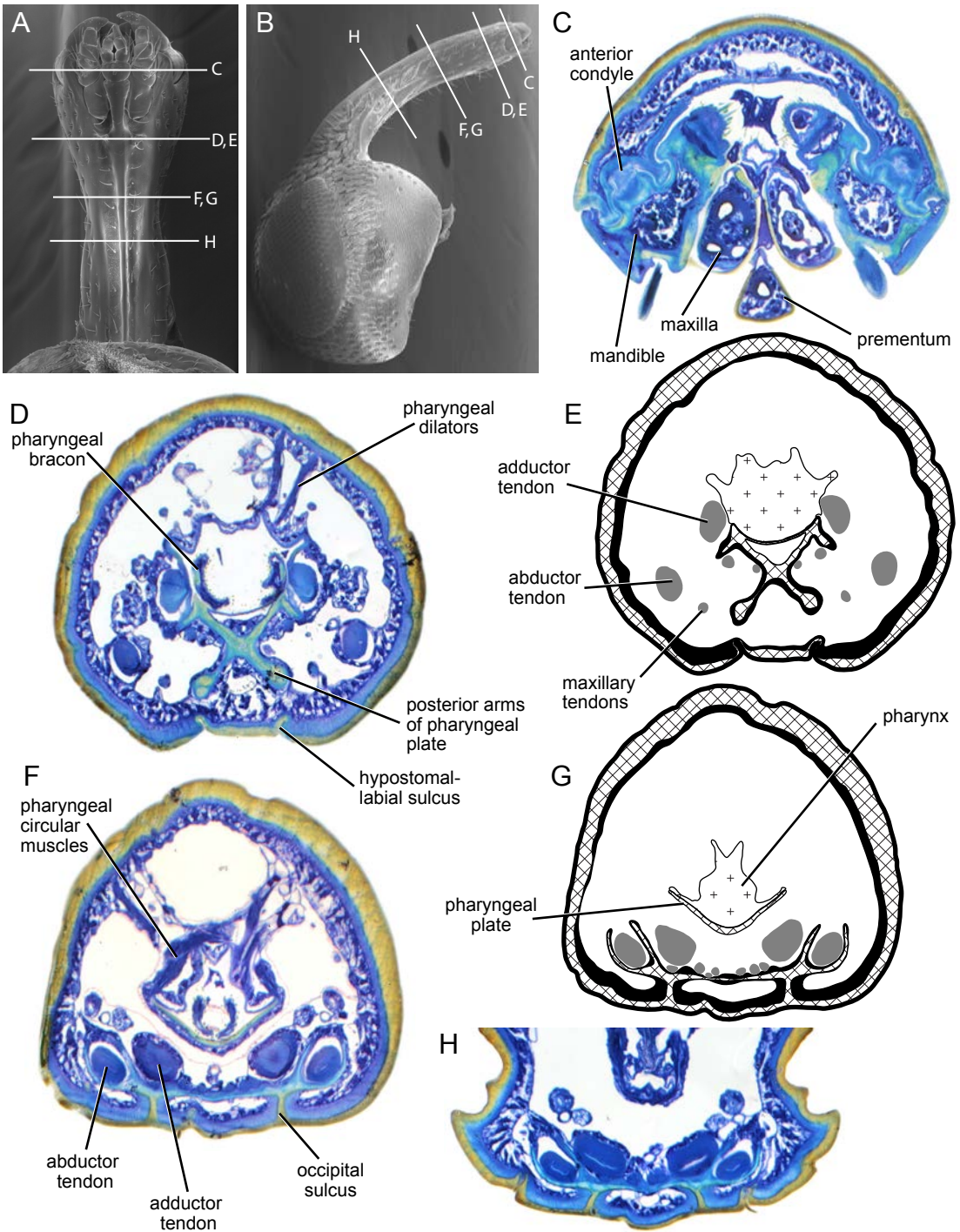
FIGURE 45. Semithin sections of head of *Cylindrocopturus adspersus* (Curculionidae: Conoderinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section immediately posterior to mouthparts; **E,** diagram of D; **F,** section posterior to mouthparts, anterior to antennal insertion; **G,** diagram of F; **H,** section near base of rostrum and antennal insertion, showing ventral portion of section.
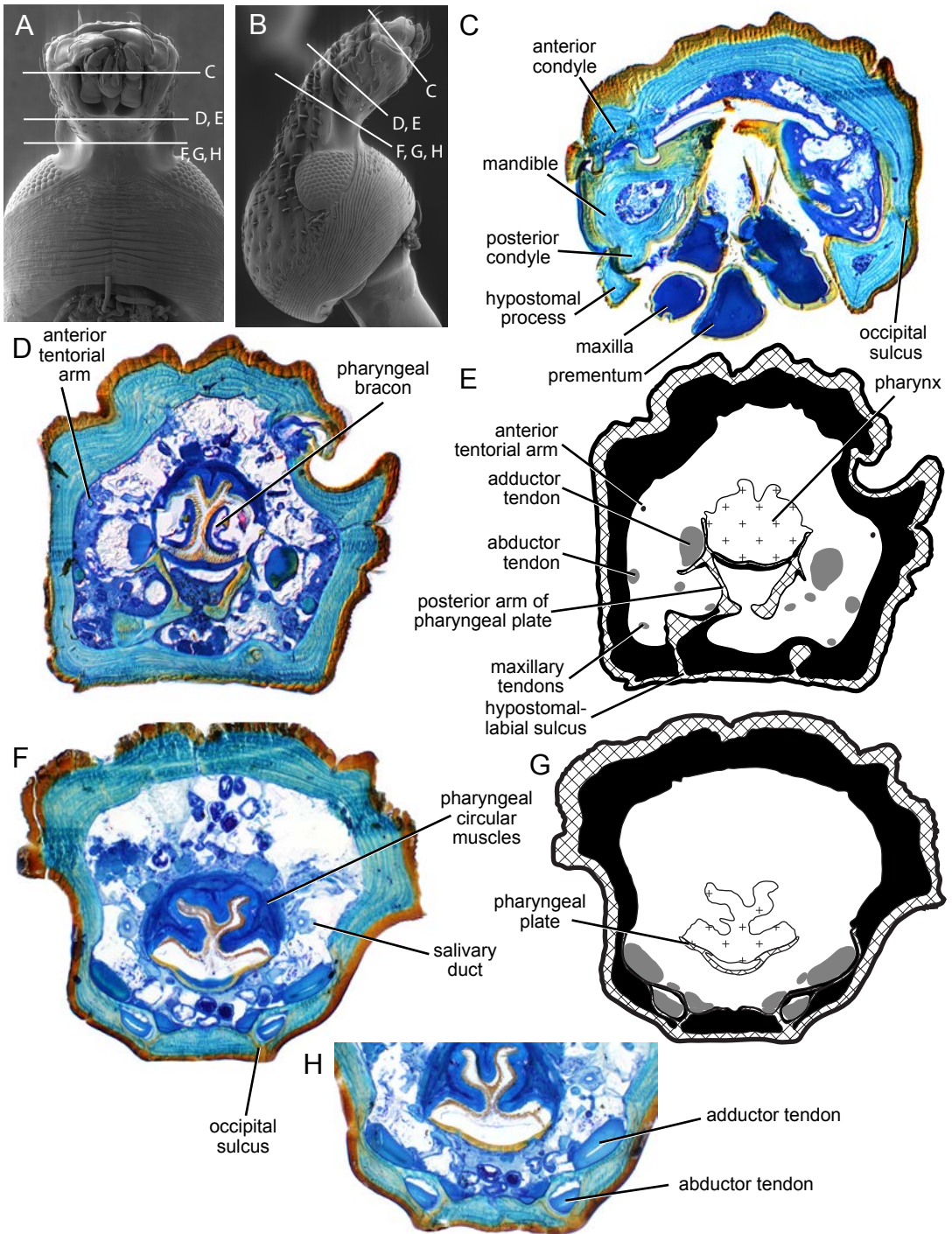
FIGURE 46. Semithin sections of head of *Tyloderma variegatum* (Curculionidae: Cryptorhynchinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section immediately posterior to mouthparts at antennal insertion; **E,** diagram of D; **F,** section at base of rostrum, posterior to antennal insertion; **G,** diagram of F; **H,** section at base of rostrum, showing ventral portion of section.
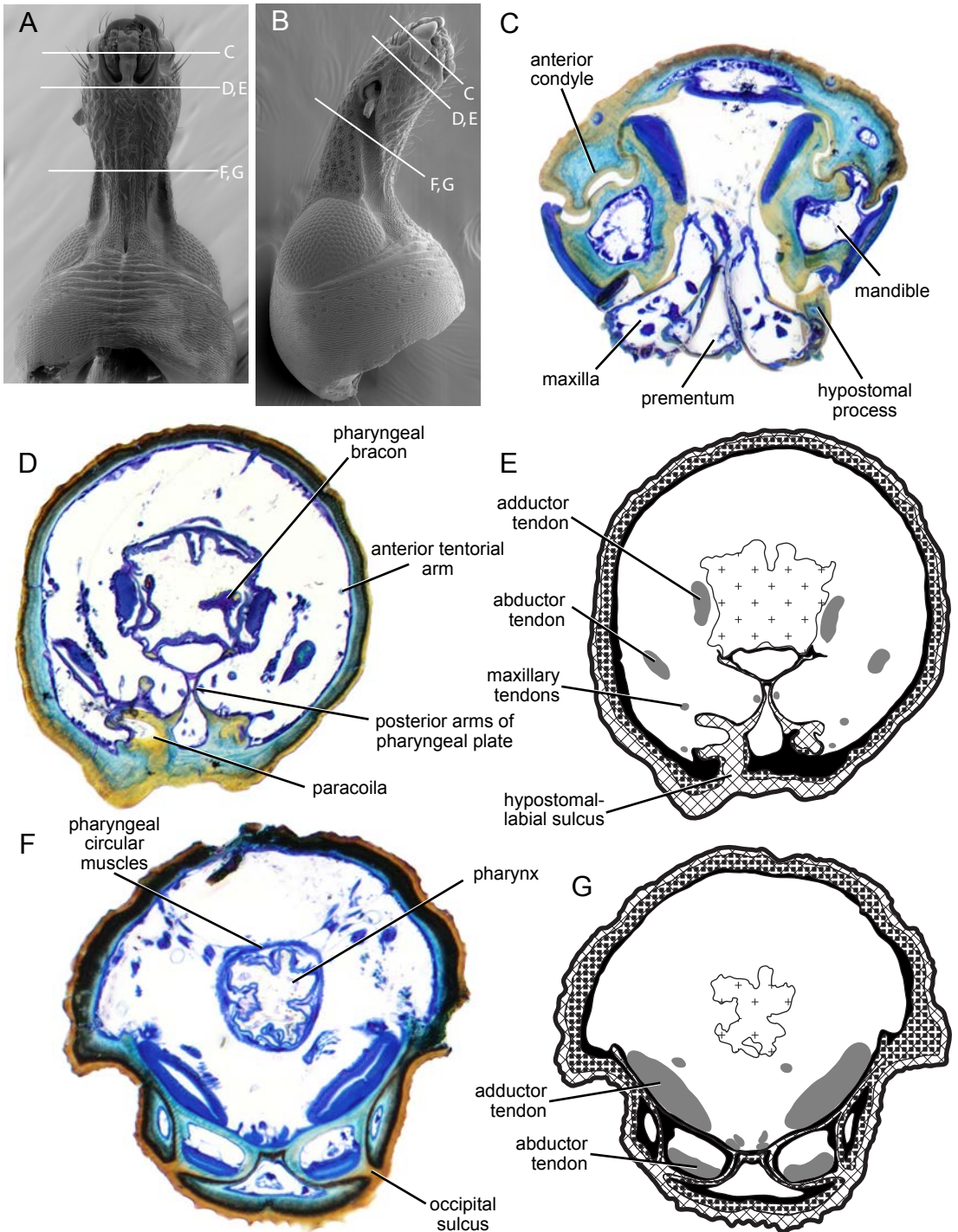
FIGURE 47. Semithin sections of head of *Magdalis* sp. (Curculionidae: Mesoptilinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–G,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section immediately posterior to mouthparts, anterior to antennal insertion; **E,** diagram of D; **F,** section posterior to middle of rostrum and antennal insertion; **G,** diagram of F.
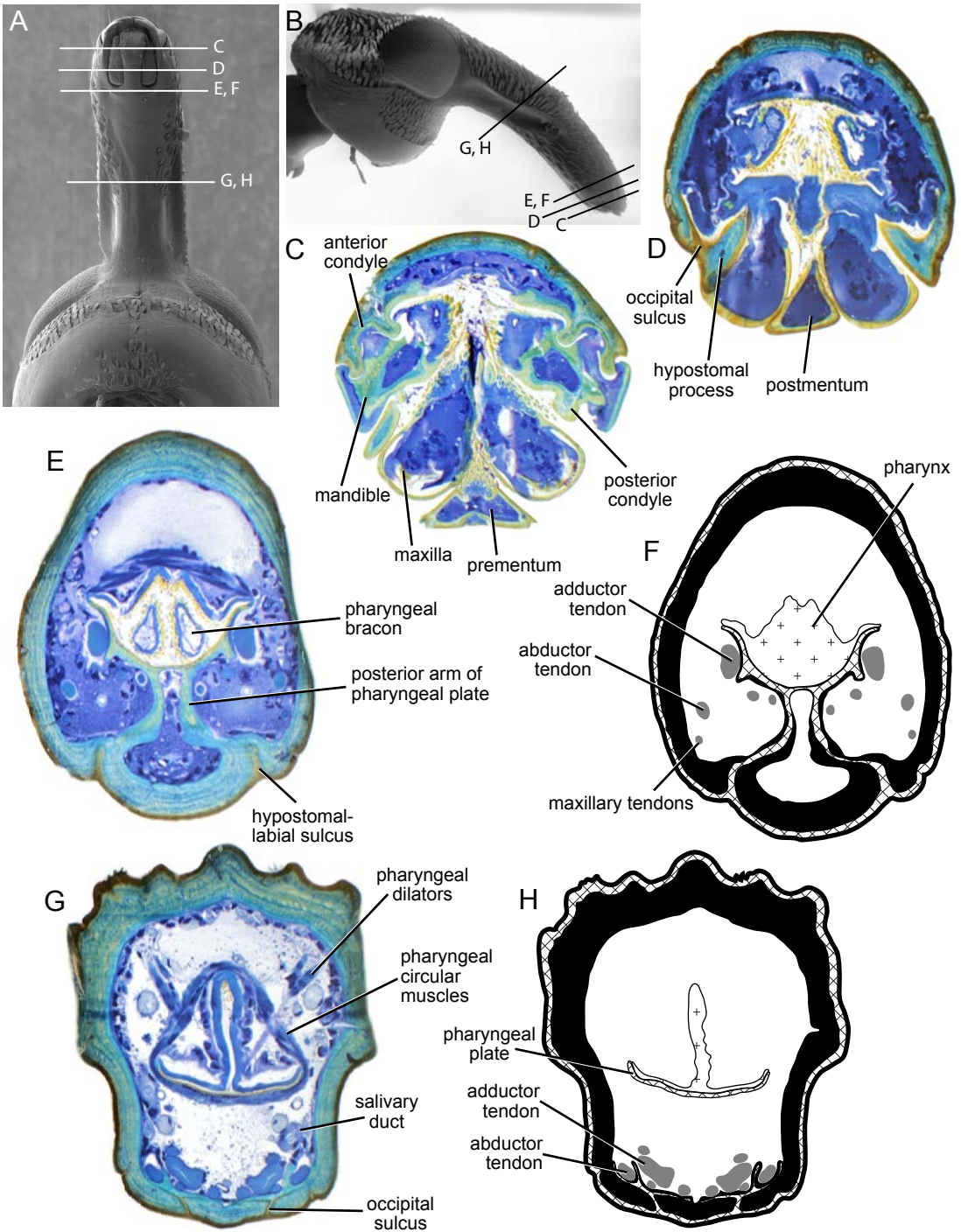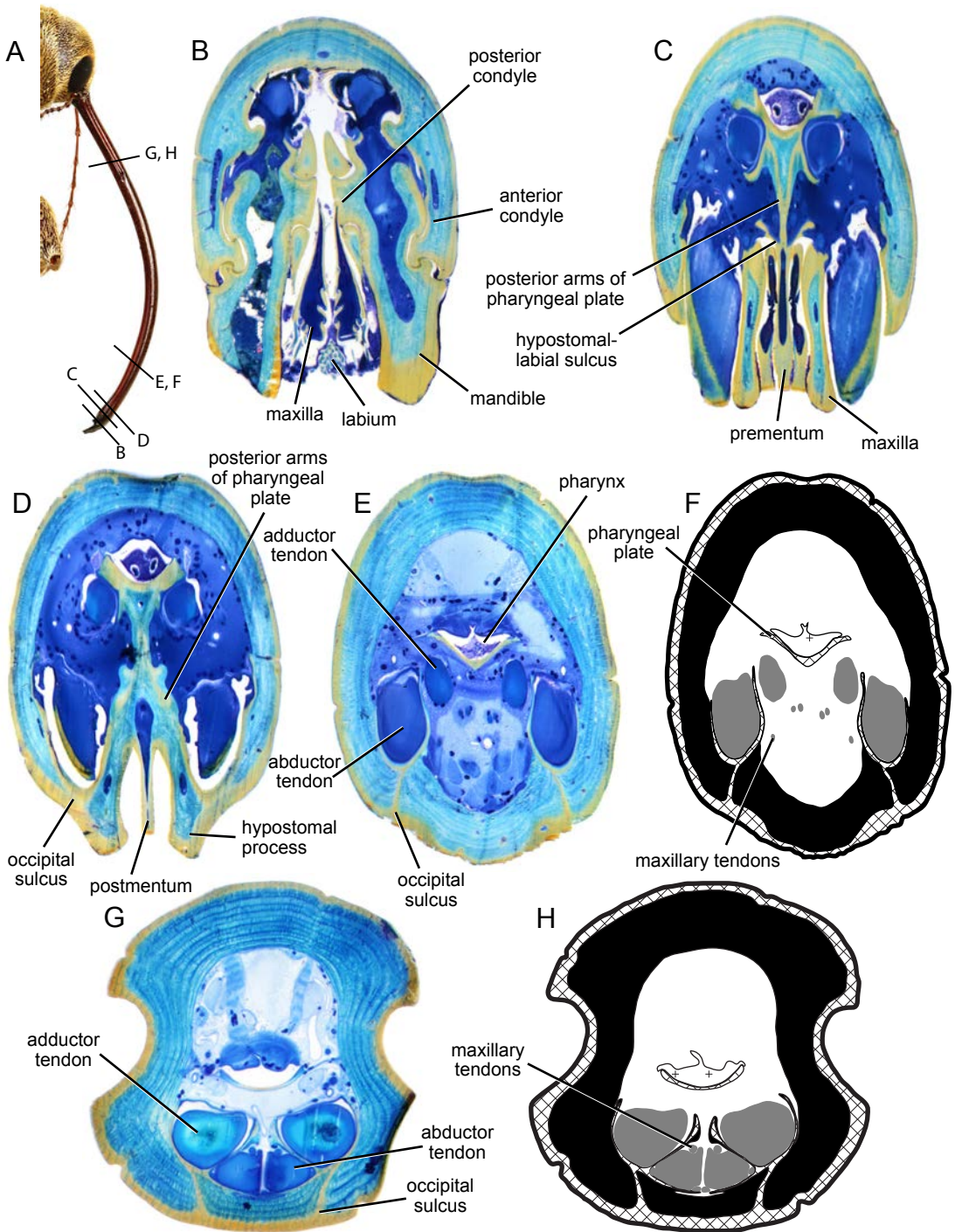
FIGURE 48. Semithin sections of head of *Phytobius* sp. (Curculionidae: Ceutorhychinae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section at proximal area of mouthparts; **E,** section immediately posterior to mouthparts, anterior to antennal insertion; **F,** diagram of E; **G,** section posterior to middle of rostrum and antennal insertion; **H,** diagram of G.

FIGURE 49. Semithin sections of head of *Curculio* sp. (Curculionidae: Curculioninae). **A,** lateral aspect of head; **B–H,** cross sections proceeding from apex of rostrum to base; **B,** section at apex of rostrum through mouthparts; **C,** section at proximal area of mouthparts; **D,** section immediately posterior to mouthparts; **E,** section posterior to mouthparts, anterior to antennal insertion; **F,** diagram of E; **G,** section near base of rostrum, posterior to antennal insertion; **H,** diagram of G.
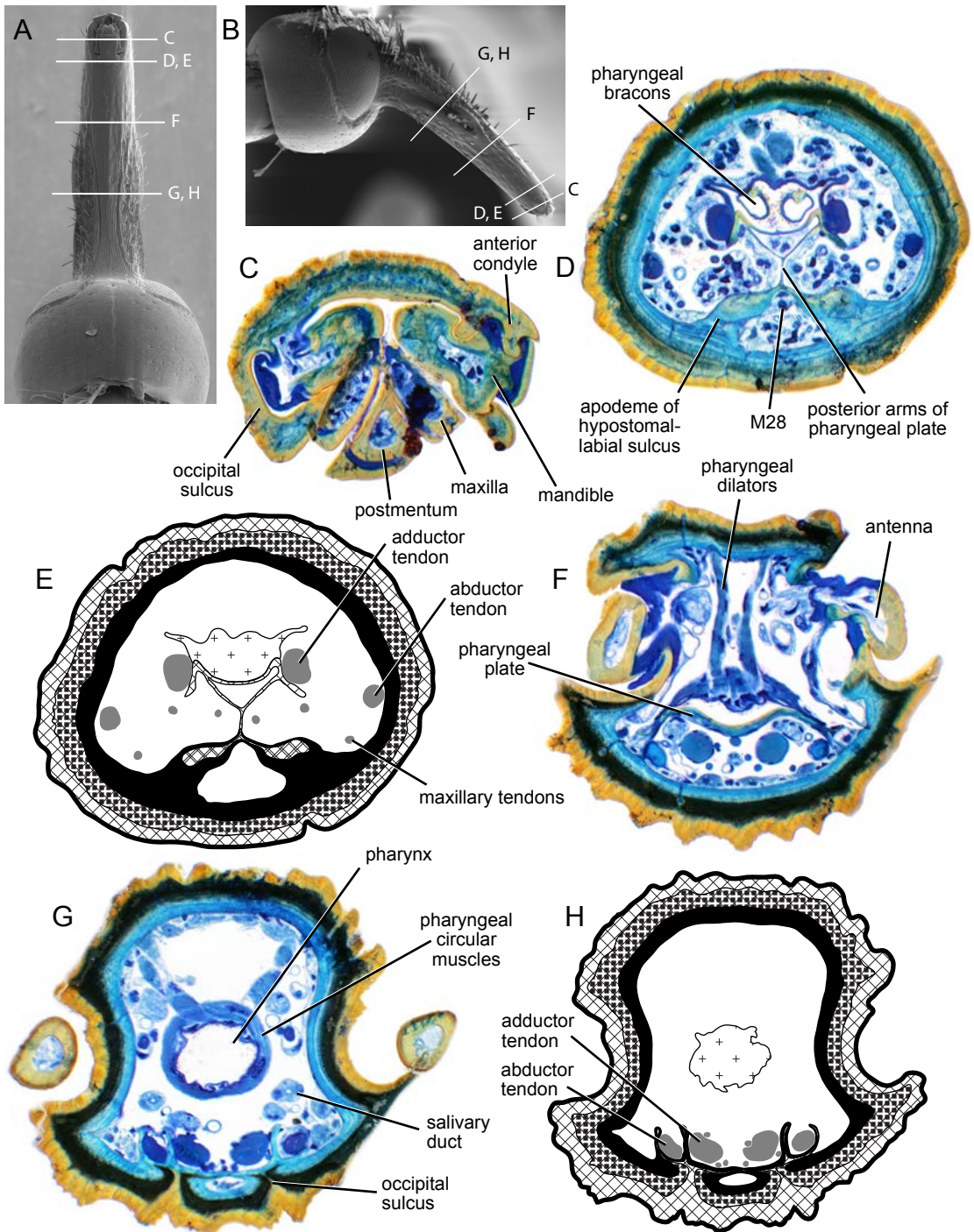
FIGURE 50. Semithin sections of head of *Gymnaetron* sp. (Curculionidae: Curculioninae). **A,** ventral aspect of head; **B,** lateral aspect of head; **C–H,** cross sections proceeding from apex of rostrum toward base; **C,** section at apex of rostrum through mouthparts; **D,** section immediately posterior to mouthparts, anterior to antennal insertion; **E,** diagram of D; **F,** section near middle of rostrum and at antennal insertion; **G,** section near base of rostrum, posterior to antennal insertion; **H,** diagram of G.

DISCUSSION

Rostrum Structure and Evolution

Aside from differences in the basal gular region of the head, the most notable changes in rostrum evolution within Curculionoidea appear to lie in the orientation of the ventral sulci (occipital and subgenal) and in the location and development of the internal apodemes/phragmata that usually are denoted by these sulci (figs. 7–8). At the rostrum apex, all weevils possess a complex internal scaffold (or remnants of it), the pharyngeal plate, which is derived from several adjacent head regions and apodemes extending from the postmentum, hypostomal-labial sulci, and the hypostoma. This X-shape seen in the sections of many groups reflects a form of the pharyngeal plate where both posterior and anterior arms join the plate at similar regions. At least in the families basal to Curculionidae s. str. (excluding Dryophthorinae), this X-shaped complex is contributed to some extent by the anterior extensions of the apodemes of the occipital sulci where they merge with the postcoila and are joined by the anterior arms of the pharyngeal plate. In the basal families of Nemonychidae, Anthribidae, Belidae, and Attelabidae, this merging is fairly robust and distinct. In the phylogenetically intermediate weevil groups, namely Caridae, Brentidae (including Ithycerinae, Apioninae and Nanophyinae), and lower Curculionidae, including Brachycerinae (Brachycerini, Raymondionymini, Erirhinini), Dryophthorinae, Platypodinae, and Bagoinae, the merging of these other sclerotized elements with the X-shaped scaffold is noticeably weaker. In these intermediate groups and the remaining Curculionidae, a feature which becomes augmented and more pronounced are the lateral canals of the pharyngeal plate that hold the anterior extensions of the mandibular adductor tendons. These canals are formed by the strengthening of the plate, as well as lateral extensions of the plate and a broadening of the anterior arms.

In all families except Curculionidae, the occipital sulcus is positioned more laterally on the rostrum, which is apparent from the lateral

apodemes that support the mandibular adductor and abductor tendons. While the subgenal sulci appear to be visible externally in several of these basal families, they do not become internalized. Perhaps it is the case for all major weevil clades that information of substantial value may be obtained by examining these internal rostral features in more primitive members. For example, similar to Nemonychidae, more primitive anthribid and belid lineages may also possess distinct apodemes of the subgenal and occipital sulci. The taxa sampled in this study, however, appear to represent derived lineages in which these features are less distinguishable from more derived states. In the higher Curculionoidea (Curculionidae s. lat.) the occipital sulci have migrated ventrally and the subgenal sulci appear largely internalized and invisible externally, possibly either subsumed into the bridge between the apodemes of the occipital sulci or lost. These hypotheses touch on a contentious area in weevil morphology, that of the homologizing of the head regions and ventral sulci.

Due to the modification of the head into a rostrum in weevils, difficulties have been encountered in understanding the specifics of which regions have been modified and to what extent. The observations presented here are in agreement with the homology statements presented in Lyal's (1995) seminal analysis of weevil ventral head anatomy, and the inclusion of histological sections has allowed for precise recognition of the ventral head sulci, particularly in lineages which have evolved a reduced rostrum. Aside from some uncertainty regarding the identity of the single pair of ventral head sulci (likely the occipital sulci), some additional information can be added to the nature of the hypostomal-labial sulci. As is evident from the sections presented herein, this pair of sulci not only meets the hypostomal sinus, it continues internally as part of the paracoila, thereby dividing the postmentum and hypostoma, and extends at least to the anterior arms of the pharyngeal plate to meet the hypostomal process and postcoila. In a few basal families, e.g., at least Anthribidae and Attelabidae, possibly also Nemonychidae and Belidae, the hypostomal-labial sulci form a distinct pair

of apodemes immediately behind the posterior arms of the pharyngeal plate that support the maxillary tendons for a short distance. Therefore, this pair of sulci is integral to the anterior structures of the rostrum and in supporting the mouthparts, not only forming this novel pair of apodemes from the postmentum, but also integrating into both posterior and anterior arms of the pharyngeal plate.

Because the rostrum is absent in Scolytinae and Platypodinae, any evidence of internal apodemes (aside from those associated with the pharyngeal plate) seems to have also disappeared. Examination of the internal, preocular region of the head in these groups requires further study in different taxa. Despite these problems, internal rostrum structure does provide further support for Curculionidae s. lat. (Oberprieler et al., 2007). Of the taxa studied, Scolytinae + Platypodinae appropriately do not form a monophyletic group, as evidenced by their divergent rostral features. Accordingly, Platypodinae is closely related to Dryophthorinae (see below) and Scolytinae is nested within the higher Curculionidae, possibly close to Cossoninae. Within Curculionidae, in which both the frontal and subgenal sulci have been lost, there appears to be greater differentiation and plasticity of the apodemes of the occipital sulci than in the more basal families. Perhaps possessing both sets of ventral sulci imposes constraints on the degree to which they may be modified.

Phylogenetic Relationships

As few characters were treated in this study, slight alterations have substantial impact in the resulting topology. It is therefore expected that further taxon sampling and observations of internal rostral structure will fortify the findings presented here. Future studies should continue to explore the diversity of the aforementioned structures and patterns in internal rostrum morphology. Following further sampling, the breadth of structural differences seen in the internal rostral apodemes may become more informative of classificatory groupings, particularly in reference to the subdivisions within Curculionidae. That

said, the phylogenetic relationships presented here show strong corroboration of a communal consensus that is emerging with the addition of recent and ongoing studies. The entirety of these relationships will not be discussed here, but rather only a few that are of some contention. These results, while phylogenetically informative at the higher levels, are also not intended to immediately address the current challenges in subfamilial classification, particularly within the Curculionidae. However, provided additional taxon sampling, the morphology discussed herein should be of great utility in delimiting such groupings.

The converging thought of a broader definition of Curculionidae (sensu Oberprieler et al., 2007) is supported in this study, albeit weakly (figs. 12–13). The main feature in support is the condition of the pharyngeal plate complex. Generally speaking, this complex is less developed, in terms of rigidity of the plate and supporting arms, from Nemonychidae to Brentidae. Beginning in Brachycerinae, the pharyngeal plate and associated arms become strengthened through thicker and wider apodemes and form more rigid connections.

Although the analysis presented here shows similar topological rank for Dryophthorinae and Brachycerinae, personal observations and other published studies (e.g., Davis, 2014; Gillett et al., 2014; McKenna et al., 2009) are not necessarily concordant. The absence of anterior remnants of the frontal lines in Dryophthorinae and Platypodinae puts them in agreement, possibly closer to higher Curculionidae than the aforementioned subfamilies, except Hyperinae and Bagoinae. Although not included in this study, the features of the terminalia of Dryophthorinae and Platypodinae (and characters from elsewhere in the body) also agree with such a placement. At least the strict consensus shows support for a more inclusive grouping of Brachycerinae (sensu Oberprieler, 2014b). With regard to grouping Platypodinae with Dryophthorinae, similar comments may be made. Additionally, the form of the pharyngeal plate appears indicative of this relationship as well. The narrow condition of the posterior and anterior arms, including the close association of the

anterior arms ventral to the plate (figs. 9, 32), demonstrates support for shared ancestry.

Regarding Scolytinae, not only are many of the head features and sulci different from Platypodinae (as detailed by Lyal, 1995), such as the postmentum, paracoila, hypostomal sinus, hypostomal sulci, occipital sulci, frontal lines, and tentorium, the form of the pharyngeal plate is different. First, the pharyngeal plate is present in its entirety in Platypodinae, whereas components of it are lost in Scolytinae. Although the scolytine plate is reduced (perhaps not so in more basal taxa), it is in agreement with that of higher Curculionidae, possibly Cossoninae. Specifically, while the plate has been lost, there are remnants of the posterior and anterior arms (figs. 40–41), both of which are robust and wide. The anterior arms also are widely spaced and not closely associated as they uniquely are in Dryophthorinae and Platypodinae.

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REFERENCES

Alonso-Zarazaga, M.A. and C.H.C. Lyal. 1999. A world catalogue of families and genera of Curculionoidea (Insecta: Coleoptera). Barcelona: Entomopraxis.

Anderson, R.S. 1995. An evolutionary perspective on diversity in Curculionoidea. Memoirs of the Entomological Society of Washington 14: 103–114.

Brack-Egg, A. 1973. Der Kopf von *Rhynchites auratus* Scop. (Curculionidae)—Eine konstruktionsmorphologische Untersuchung mit einem Beitrag zum Brutfürsorgeverhalten. Zoologische Jahrbucher, Abteilung fur Anatomie und Ontogenie der Tiere 91: 500–545.

Casey, T.L. 1892. Coleopterological notices. IV. Annals of the New York Academy of Sciences 6 (7–12): 359–712.

Chapuis, F. 1869. Synopsis des scolytides (prodrome d'un travail monographique). Liège Liège: Imprimerie de J. Desoer. 61 pp.

[Clairville, J.P. de]. 1798. Entomologie helvétique ou catalogue des insectes de la Suisse rangés d'après une nouvelle méthode/Helvetische Entomologie oder Verzeichniss der Schweizer Insecten, nach einer neuen Methode geordnet mit Beschreibungen und Abbildungen, vol. 1. Zürich: Orell, Füssli & Co., 149 pp. + 16 pls.

Davis, S.R. 2011. Rostrum structure and development in the rice weevil *Sitophilus oryzae* (Coleoptera: Curculionoidea: Dryophthoridae). Arthropod Structure and Development 40: 549–558.

Davis, S.R. 2014. Morphology, phylogeny, and evolutionary development in the weevils (Insecta: Coleoptera: Curculionoidea). Ph.D. dissertation, Department of Ecology and Evolutionary Biology, University of Kansas, 477 pp.

DeGeer, C. 1775. Mémoires pour servir à l'histoire des insectes, vol. 5. Stockholm: L.L. Grefing, 5 + 448 pp., 16 pls.

Dejean, P.F.M.A. 1835. Catalogue de la collection de coléoptères de M. le Baron Dejean. 2nd ed. Part 4: 257–360. Paris: Méquignon-Marvis.

Dennell, R. 1942. The structure and function of the mouth-parts, rostrum and foregut of the weevil *Calandra granaria* L. Philosophical Transactions of the Royal Society of London Series B, Biological Sciences 231: 247–291.

Dönges, J. 1954. Der Kopf von *Cionus scrophulariae* L. (Curculionidae). Zoologische Jahrbucher. Abteilung fur Anatomie und Ontogenie der Tiere 74: 1–188.

Drury, D. 1770. Illustrations of natural history, wherein are exhibited upwards of 240 figures of exotic insects, according to their different genera: very few of which have hitherto been figured by any author,

being engraved and coloured from nature, with the greatest accuracy and under the author's own inspection, on fifty copper-plates. With a particular description of each insect: interspersed with remarks and reflections on the nature of properties of many of them, vol. 1. London: Printed for the author, XXVII + 130 pp. + 50 pls.

DuPorte, E.M. 1960. Evolution of cranial structure in adult Coleoptera. Canadian Journal of Zoology 38: 655–675.

Eichhoff, W.J. 1864. Ueber die Mundtheile und die Fühlerbildung der europäischen Xylophagi sens. strict. Berliner Entomologische Zeitschrift 8 (1–2): 17–46.

Fabricius, J.C. 1801. Systema eleutheratorum secundum ordines, genera, species: adiectis synonimis, locis, observationibus, descriptionibus, vol. 2. Kiliae [Kiel, Germany]: Impensis Bibliopolii Academici Novi, 687 pp.

Forster, J.R. 1771. Novae species insectorum, Centuria I. London: White, viii + 100 pp.

Germar, E.F. 1817. Miscellen und Correspondenz-Nachrichten. Magazin der Entomologie 2: 339–341.

Gillett, C.P.D.T., et al. 2014. Bulk de novo mitogenome assembly from pooled total DNA elucidates the phylogeny of weevils (Coleoptera: Curculionoidea). Molecular Biology and Evolution 31 (8): 2223–2237.

Goloboff, P.A. 1999. NONA (No Name) ver. 2. Tucumán, Argentina: Published by the author.

Herbst, J.F.W. 1793. Natursystem aller bekannten in- und auslandischen Insekten, als eine Fortsetzung der von Büffonschen Naturgeschichte. Der Käfer, vol. 5. Berlin: Pauli, xvi + 392 pp. + pls. XLIV–LIX.

Herbst, J.F.W. 1797. Natursystem aller bekannten in- und auslandischen Insekten, als eine Fortsetzung der von Büffonschen Naturgeschichte. Der Käfer, vol. 7. Berlin: Pauli, xi + 346 pp. + pls. XCVI–CXVI.

Hopkins, A.D. 1902. A new genus of scolytids from Florida. Proceedings of the Entomological Society of Washington 5 (1): 34–38.

Horn, G.H. 1873. Contributions to a knowledge of the Curculionidae of the United States. Proceedings of the American Philosophical Society 13 (91): 407–469.

Hustache, A. 1938. Curculionides nouveaux de l'Amérique méridionale, qui se trouvent dans le Deutsches Entomologisches Institut. 3ème note. Arbeiten uber morphologische und taxonomische Entomologie aus Berlin-Dahlem 5 (4): 334–349.

Jekel, H. 1865. Recherches sur la classification naturelle des Curculionides. Ire partie. Annales de la Société Entomologique de France 4 (3): 537–566.

Kéler, S.V. 1963. Entomologisches Wörterbuch. Akademie-Verlag, Berlin, 744 pp.

Kirby, W. 1819. A century of insects, including several new genera described from his cabinet. Transac-

tions of the Linnean Society of London 12 (2): 375–453.

Lacordaire, T. 1863. Histoire naturelle des insectes. Genera des coléoptres ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes, vol. 6. Paris: Roret. 637 pp.

LeConte, J.L. and G.H. Horn. 1876. The Rhynchophora of America north of Mexico. Proceedings of the American Philosophical Society 15 (96): 1–442.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum caracteribus, differentiis, synonymis, locis. 10th ed., tomus 1. Holmiae [Stockholm]: Laurentii Salvii, 824 pp.

Linnaeus, C. 1763. Amoenitates academicae, vol. 6. Holmiae [Stockholm]: Laurentii Salvii.

Lyal, C.H.C. 1995. The ventral structures of the weevil head (Coleoptera: Curculionoidea). In R.S. Anderson and C.H.C. Lyal (editors), Biology and phylogeny of Curculionoidea. Memoirs of the Entomological Society of Washington 14: 35–51.

Mannerheim, G.C.G. 1843. Beitrag zur Kaefer-Fauna der Aleutischen Inseln, der Insel Sitkha und Neu-Californiens. Bulletin de la Société impériale des naturalistes de Moscou 16 (2): 175-3125.

McKenna, D.D., A.S. Sequeira, A.E. Marvaldi, and B.D. Farrell. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. Proceedings of the National Academy of Sciences of the United States of America 106 (17): 7083–7088.

Morimoto, K. 1962. Comparative morphology and phylogeny of the superfamily Curculionoidea of Japan (Comparative morphology, phylogeny and systematics of the superfamily Curculionoidea of Japan. I). Journal of the Faculty of Agriculture, Kyushu University 11 (4): 331-373.

Morimoto, K., and H. Kojima. 2003. Morphological characters of the weevil head and phylogenetic implications (Coleoptera, Curculionoidea). Esakia 43: 133–169.

Morimoto, K., H. Kojima, and S. Miyakawa. 2006. The insects of Japan, vol. 3. Curculionoidea: general introduction and Curculionidae: Entiminae (part 1). Phyllobiini, Polydrusini and Cyphicerini (Coleoptera). Fukuoka: Touka Shobo Co., Ltd., 406 pp.

Nixon, K.C. 1999a. The parsimony ratchet, a new method for rapid parsimony analysis. Cladistics 15: 407–414.

Nixon, K.C. 1999b. WINCLADA, (beta) version 0.9. Ithaca, NY: Published by the author.

Oberprieler, R.G. 2014a. 3.7. Curculionidae Latreille, 1802. In R.G. Beutel and R.A.B. Leschen (editors). Handbook of zoology, vol. 4. Arthropoda: Insecta. Part 38. Coleoptera, beetles, vol. 3: morphology and

systematics (Phytophaga): 423–424. Berlin: Walter de Gruyter, 2014.

Oberprieler, R.G. 2014b. 3.7.1. Brachycerinae Billberg, 1820. *In* R.G. Beutel and R.A.B. Leschen (editors). Handbook of zoology, vol. 4. Arthropoda: Insecta. Part 38. Coleoptera, beetles, vol. 3: morphology and systematics (Phytophaga): 424–451. Berlin: Walter de Gruyter, 2014.

Oberprieler, R.G., A.E. Marvaldi, and R.S. Anderson. 2007. Weevils, weevils, weevils everywhere. Zootaxa 1668: 491–520.

Oberprieler, R.G., R.S. Anderson, and A.E. Marvaldi. 2014. 3. Curculionoidea Latreille, 1802: Introduction, phylogeny. *In* R.G. Beutel and R.A.B. Leschen (editors). Handbook of zoology, vol. 4. Arthropoda: Insecta. Part 38. Coleoptera, beetles, vol. 3: morphology and systematics (Phytophaga): 285–300. Berlin: Walter de Gruyter, 2014.

O'Brien, C.W. 1970. A taxonomic revision of the genus Gerstaeckeria north of Mexico (Coleoptera: Curculionidae). Annals of the Entomological Society of America 63 (1): 255–272.

O'Brien, C.W. and G.J. Wibmer. 1982. Annotated checklist of the weevils (Curculionidae sensu lato) of North America, Central America, and the West Indies (Coleoptera: Curculionoidea). Memoirs of the American Entomological Institute 34: i-ix + 1–382.

Olivier, A.G. 1789. Encyclopédie méthodique. Histoire naturelle, vol. 4. Insectes. Paris: Panckoucke, ccclxxii + 331 pp.

Randall, J.W. 1838. Description of new species of coleopterous insects inhabiting the state of Maine. Boston Journal of Natural History 2: 1–33.

Roelofs, W. 1873. Curculionides recueillis au Japon par M.G. Lewis. Première partie. Annales de la Société Entomologique de Belgique 16: 154–193 + pls. II, III.

Say, T. 1824. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. Journal of the Academy of Natural Sciences of Philadelphia 3 (2): 298–331.

Schönherr, C.J. 1823. Curculionides [Tabula synoptica familiae Curculionidum]. Isis von Oken 1823 (10): vols. 1132–1146.

Schönherr, C.J. 1825. Continuatio tabulae synopticae familiae Curculionidum. Isis von Oken 1825 (5): 581–588.

Schönherr, C.J. 1826. Curculionidum despositio

methodica cum generum characteribus, descriptionibus atque observationibus variis seu Prodromus ad synonymiae snsectorum, partem IV. Lipsiae: Fleischer. X + 338 pp.

Schönherr, C.J. 1833. Genera et species curculionidum, cum synonymia hujus familiae. Species novae aut hactenus minus cognitae, descriptionibus a Dom. Leonardo Gyllenhal, C.H. Boheman, et entomologis aliis illustratae, vol. 1 (1): I–XV + 1–381. Paris: Roret.

Schönherr, C.J. 1838. Genera et species curculionidum, cum synonymia hujus familiae. Species novae aut hactenus minus cognitae, descriptionibus a Dom. Leonardo Gyllenhal, C.H. Boheman, et entomologis aliis illustratae, vol. 4 (2): 601–1121. Paris: Roret.

Schönherr, C.J. 1843. Genera et species curculionidum, cum synonymia hujus familiae. Species novae aut hactenus minus cognitae, descriptionibus a Dom. Leonardo Gyllenhal, C.H. Boheman, et entomologis aliis illustratae, col. 7 (2): 1–461. Paris, Roret.

Schönherr, C.J. 1844. Genera et species curculionidum, cum synonymia hujus familiae. Species novae aut hactenus minus cognitae, descriptionibus a Dom. Leonardo Gyllenhal, C.H. Boheman, et entomologis aliis illustratae, vol. 8 (1): 1–442. Paris: Roret.

Scopoli, J.A. 1763. Entomologia carniolica exhibens insecta carnioliae indigena et distributa in ordines, genera, species, varietates: methodo Linnaeana (1763): 1–420. Vindobonae [Vienna]: Trattner.

Snodgrass, R.E. 1935. Principles of insect morphology. New York: McGraw-Hill Book Co., Inc., 667 pp.

Snodgrass, R.E. 1960. Facts and theories concerning the insect head. Smithsonian Miscellaneous Collections 142 (1): 1–61.

Stickney, F.S. 1923. The head-capsule of Coleoptera. Illinois Biological Monographs 8 (1): 1–105.

Ting, P.C. 1936. The mouth parts of the coleopterous group Rhynchophora. Microentomology 1: 93–114.

Voss, E. 1965. The zoological results of Gy. Topál's collectings in south Argentina. 17. Attelabidae (Coleoptera). Annales Historico-Naturales Musei Nationalis Hungarici, Pars zoologica 57: 329–332.

Weide, D., M. Thayer, and O. Betz. 2014. Comparative morphology of the tentorium and hypopharyneal-premental sclerites in sporophagous and non-sporophagous adult Aleocharinae (Coleoptera: Staphylinidae). Acta Zoologica 59: 84–110.

Wood, S.L. 1986. A reclassification of the genera of Scolytidae (Coleoptera). Great Basin Naturalist Memoirs 10: 1–126.

ON THE COVER: MICRO-CT SCAN OF THE HEAD OF *RHYNCHITES AURATUS* (ATTELABIDAE), HIGHLIGHTING IN COLOR THE INTERNAL ANATOMY.