Introduction to the Skeleton of Hummingbirds (Aves: Apodiformes, Trochilidae) in Functional and Phylogenetic Contexts

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INTRODUCTION TO THE SKELETON OF HUMMINGBIRDS (AVES: APODIFORMES, TROCHILIDAE) IN FUNCTIONAL AND PHYLOGENETIC CONTEXTS

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Abstract.—Historically, comparative study of the skeleton of hummingbirds has focused on systematics, emphasizing differences between hummingbirds and other birds and only rarely addressing differences within Trochilidae. This monograph covers both approaches, and comparisons within Trochilidae are framed within recently published, plausible phylogenetic hypotheses. The data are derived mainly from museum collections of anatomical specimens, covering ~256 species of 102 genera of hummingbirds, and 11 genera of other Apodiformes. Although the syringeal skeleton is included, emphasis is on the axial and appendicular skeletons.

The first section deals with the syrinx and with skeletal features mainly associated with nectarivory and hovering, emphasizing characters that are unique to hummingbirds within Apodiformes. The syrinx of hummingbirds lies in the neck rather than the thorax and displays a unique bony knob on the surface of the tympanic membrane. During posthatching development, the upper jaw of hummingbirds undergoes metamorphic changes that produce a morphology uniquely adapted for nectarivory within Aves. The ventral bars of the upper jaw lengthen and rotate to become lateral walls of an incompletely tubular bill that is completed by the closed mandibula, and lateral bowing (streptognathism) of the mandibula helps to seal the tube while a bird drinks nectar. Streptognathism of the opened jaw is used in display by some Hermits. The lamellar tip of the tongue required for nectar uptake also develops after fledging, while young are still fed by the parent. In Trochilines the nasal region changes from its configuration by bone resorption during posthatching development. Cranial kinesis in hummingbirds is poorly documented, but structural differences in the upper jaw of Hermits and Trochilines imply differences in cranial kinesis. The palatum of hummingbirds is distinguished from that of other apodiforms by extreme reduction of the lateral part of the palatinum, greater width of the ventral choanal region, and by a median spine on the vomer. Otherwise the vomer is variable in shape and not compatible with aegithognathism. Among cranial features, the basipterygoid process, lacrimale, and jugale are absent, and the interorbital septum is complete. The hyobranchial apparatus differs from that of other apodiforms in having an epibranchiale that is longer than the ceratobranchiale, and variably elongate in relation to body size. I hypothesize two modes of hyobranchial function—one applicable to moderate protrusion of the tongue (typical nectar eating), and another to extreme protrusion. The pelvis is less strongly supported by the synsacrum, and the proximal portion of the hind limb is more reduced than in other Apodiformes. By contrast, the tarsometatarsus and flexor muscles of the toes are well developed in association with perching and clinging. In the flight mechanism, features uniquely pertinent to hovering are distinguished from those that support stiff-winged flight—the latter common to both swifts and hummingbirds. Hovering is especially dependent on adaptations for axial rotation of the wing at all major joints, and on extreme development in hummingbirds of the unusual wing proportions (short humerus and forearm, and long hand) and enlarged breast muscles found in swifts. Osteological characters of the Oligocene fossil *Eurotrochilus* that can be compared with modern hummingbirds do not indicate nectarivory or sustained hovering in that taxon.

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In the second section, variations within Trochilidae are described and their distributions within the major clades (Hermits, Topazes, Mangoes, Brilliants, Coquettes, Patagona, Mountain Gems, Bees, and Emeralds) are specified. Most diverse are the jaw mechanism, nasal region and conchae, hyobranchial apparatus, cranial proportions, crests, and pneumatic inflation, structure of the ribcage based on number of ribs attached to the sternum, pectoral girdle, and various humeral characters. Other noteworthy but largely unexplained variation characterizes the hyobranchial apparatus of *Heliodoxa*, the humerus of the "*Pygmornis* group" of *Phaethornis*, sexual dimorphism in numbers of thoracic ribs, and synostosis of phalanges of the foot. Although Hermits display distinctive characters, their subfamily status is uncertain for lack of informative outgroups. Major trochilid clades are either weakly supported or unsupported by uniquely derived characters, but apomorphic variation within Mangoes suggests recognition of an *Anthracothorax* group of genera, and within Emeralds, a large *Amazilia* group. Each of the major trochilid clades displays considerable diversity in body size and skeletal characters, and numerous characters show parallel evolution within the family. Intraspecific variation is widespread, and selected examples are highlighted. Patterns of skeletal variations at multiple levels of phylogeny suggest that some variations characterizing higher levels had their origins at the intraspecific level.

A list of unsolved problems of functional morphology of the skeleton in hummingbirds is offered. Especially intriguing are the many posthatching changes in development of the feeding mechanism and the challenge of incorporating morphological data and their implications into models of evolution of hummingbird communities. *Received 17 September 2012, accepted 8 February 2013.*

Key words: Trochilidae, Apodiformes, comparative osteology, myology, inter- and intraspecific variation, nectarivory, hovering, *Eurotrochilus*.

Introducción al Esqueleto de los Colibríes (Aves: Apodiformes: Trochilidae) en Contextos Funcionales y Filogenéticos

Resumen.—El estudio comparativo del esqueleto de los colibríes históricamente se ha enfocado en la sistemática, enfatizando las diferencias entre los colibríes y otras aves, y rara vez se han evaluado las diferencias dentro de Trochilidae. Esta monografía cubre ambas aproximaciones y las comparaciones dentro de Trochilidae se enmarcan en hipótesis filogenéticas plausibles y publicadas recientemente. Los datos se derivan principalmente de colecciones de museo de especímenes anatómicos, abarcando ~256 especies de 102 géneros de colibríes y 11 géneros de otros Apodiformes. Aunque se considera el esqueleto de la siringe, se hace énfasis en el esqueleto axial y el apendicular.

La primera sección trata de la siringe y de las características del esqueleto asociadas principalmente con la nectarivoría y el revoloteo, con énfasis en caracteres que son únicos de los colibríes al interior de Apodiformes. La siringe de los colibríes se ubica en el cuello en vez de en el tórax y muestra una protuberancia ósea en la superficie de la membrana timpánica. Durante el desarrollo posterior a la eclosión, la maxila de los colibríes pasa por una metamorfosis que resulta en una morfología adaptada para la nectarivoría que es única entre las aves. Las barras ventrales de la maxila se elongan y rotan para convertirse en las paredes laterales de un pico tubular incompleto que se completa por la mandíbula cerrada, y el arqueo lateral de la mandíbula (estreptognatismo) ayuda a sellar el tubo mientras el ave toma néctar. El estreptognatismo de la mandíbula abierta es usado en despliegues por algunos colibríes ermitaños. La punta lamelar de la lengua que se requiere para recoger el néctar también se desarrolla después del emplumamiento, mientras los pichones aún son alimentados por sus padres. En los Trochilinae, la región nasal cambia su configuración por reabsorción del hueso durante el desarrollo posterior a la eclosión. La quinesis craneal en los colibríes ha sido pobremente documentada, pero las diferencias estructurales en la maxila de los ermitaños y los troquilinos implican diferencias en la quinesis craneal. El paladar de los colibríes se distingue de el de otros Apodiformes por la reducción extrema de la parte lateral del palatino, una región ventral coanal más ancha y una espina medial en el vómer. Por lo demás, el vómer es variable en forma y no es compatible con el aegitognatismo. Entre las características del cráneo, el proceso basipterigoides, el lacrimal y el yugal están ausentes, y el septo interorbital está completo. El aparato hiobranquial difiere de el de otros Apodiformes en que presenta un epibranquial más largo que el ceratobranquial y elongado de manera variable en relación con el tamaño corporal. Yo propongo dos hipótesis sobre la función del hiobranquial – una aplicable a la protrusión moderada de la lengua (consumo típico de néctar) y otra a la protrusión extrema. La pelvis está menos fuertemente soportada por el sinsacro y la porción proximal de la extremidad posterior está más reducida que en otros Apodiformes. En contraste, el tarsometatarso y los músculos flexores de los dedos están bien desarrollados en asociación con las actividades de percharse y aferrarse. En el mecanismo del vuelo, las características que son pertinentes únicamente para el revoloteo se distinguen de aquellas que soportan el vuelo con alas rígidas, el cual es común a vencejos y colibríes. El revoloteo es especialmente dependiente de las adaptaciones para la rotación axial del ala en todas las articulaciones importantes, y del desarrollo extremo en los colibríes de las proporciones inusuales de las alas (húmero y antebrazo corto, y mano larga) y de los músculos pectorales agrandados que se encuentran en los vencejos. Los caracteres osteológicos del fósil del Oligoceno *Eurotrochilus* que pueden ser comparados con los colibríes modernos no indican nectarivoría o revoloteo sostenido en ese taxón.

En la segunda sección, se describen las variaciones que existen dentro de Trochilidae y se especifica su distribución en los clados principales (Ermitaños - *Hermits,* Topacios - *Topazes,* Mangos - *Mangoes,* Brillantes - *Brilliants, Patagona,* Gemas de Montaña - *Mountain Gems,* Abejas - *Bees* y Esmeraldas - *Emeralds*). Los más diversos son los mecanismos de la mandíbula, la región nasal y los cornetes, el aparato hiobranquial, las proporciones del cráneo, las crestas, la inflación neumática, la estructura de la caja torácica basada en el número de costillas unidas al esternón, la cintura pectoral y varios caracteres del húmero. Otra variación notable pero no explicada en gran medida caracteriza el aparato hiobranquial de *Heliodoxa,* el húmero del "grupo *Pygmornis*" de *Phaethornis,* el dimorfismo sexual en el número de costillas del tórax, y la sinostosis de las falanges de la pata. Aunque los ermitaños muestran caracteres particulares, su estatus como subfamilia es incierto debido a la falta de grupos externos informativos. Los clados principales de colibríes están pobremente apoyados o no están apoyados por caracteres únicos derivados, pero la variación apomórfica dentro de los Mangos sugiere el reconocimiento de un grupo genérico *Anthracothorax,* y, dentro de las Esmeraldas, de un gran grupo del género *Amazilia.* Cada uno de los principales clados de colibríes muestra una diversidad considerable en el tamaño corporal y en los caracteres del esqueleto, y muchos caracteres presentan evolución en paralelo en la familia. La variación intraespecífica está ampliamente difundida y se resaltan algunos ejemplos. Los patrones de variación en el esqueleto en múltiples niveles de la filogenia sugieren que algunas de las variaciones que caracterizan los niveles profundos tienen sus orígenes en el nivel intraespecífico.

Se ofrece una lista de problemas sin resolver sobre la morfología funcional del esqueleto de los colibríes. Resultan especialmente intrigantes los muchos cambios posteriores al nacimiento en el desarrollo de los mecanismos de alimentación y el desafío de incorporar los datos morfológicos y sus implicaciones en modelos sobre la evolución de las comunidades de colibríes.

> The skeletal system is composed of bone, cartilage, and ligaments. (Campbell and Lack 1985:543)
>
> Frequently a distinction is made between the Axial and the Appendicular Skeleton—the former being restricted to the Vertebral Column and the Cranium proper, while the latter comprises the Ribs, Breastbone ... Limbs and their arches, the Hyoid apparatus and the Jaws. (Newton and Gadow 1893–1896:848)
>
> Syrinx.... The essential features...are, first, membranes stretched between the several parts of a cartilaginous or bony framework, and next, special muscles which by their action vary and regulate the tension of the membranes. (Newton and Gadow 1893–1896:937)

INTRODUCTION

Prologue.—This monograph summarizes data from private and institutional collections housed in museums of natural history—the ultimate sources for comparative anatomical studies. In particular, it is based on specimens prepared as skeletons and spirit specimens, preparations that, traditionally, were neglected in favor of the study skin. With few exceptions, the specimens studied here were not obtained for this study, but were accumulated in museums over the years as an archive of the diversity of birds. The number of individuals of each species in anatomical collections usually is low, sometimes only one or zero, and data on older specimen labels are often minimal. These deficiencies are balanced by the taxonomic richness now available in collections. Because the skeleton consists of more than bones, spirit specimens are important adjuncts to the exposition of major skeletal variation. The syringeal skeleton is included here with the more commonly studied axial and appendicular skeletons.

Hummingbirds comprise some 330 extant species restricted to the Western Hemisphere and are the most speciose of non-passeriform families (Bock and Farrand 1980). Linnaeus (1758) described 18 species, but by the late 1800s ninety percent of the species now recognized had been described (Graves 1993). However, monographic treatments of the family based on variations in the integument produced little agreement on the composition of genera and higher categories, and major classifications lacked higher-level groupings (Cory 1918, Peters 1945, Morony et al. 1975). Striking elaborations of plumage associated with sexual selection rendered generic allocation difficult and resulted in a proliferation of genera. Nevertheless, the rapid development of hummingbird taxonomy has provided a basis for meaningful, anatomical comparisons.

Within this monograph, "variation" includes differences between individuals of a species, species of a genus, genera within higher categories, higher categories up to subfamily, and families of an order. Some characters that show little variation within Trochilidae but that differ from other Apodiformes are discussed as variation within Apodiformes rather than within Trochilidae. The variation in morphological states presented here is essentially qualitative, involving differences in shape, presence or absence, and relations to other characters, and a few characters are meristic (e.g., counts of vertebrae). Proportions, based on small samples, are usually expressed in words rather than numbers, and, as a result, this monograph is only an introduction. Most of the data on osteological variation within Trochilidae presented here were originally amassed for phylogenetic analysis.

Comparative anatomy.—Most early anatomical work on hummingbirds comprised interordinal surveys of selected anatomical structures (e.g., sternum and shoulder girdle, L'Herminier 1827; pterylosis, Sclater 1867; syrinx, Müller 1878; palate, Huxley 1867, Parker 1878; pelvic musculature, Garrod 1873a). The growing data base of comparative anatomy, as enlarged and analyzed by Fürbringer (1888), Gadow and Selenka (1891), Beddard (1898), and others, supported a general consensus on the monophyly of Trochilidae and a close relationship of swifts and hummingbirds. Nevertheless, additional studies, largely of comparative osteology in which higher-level grouping was inferred from enumeration of similarities or differences, produced a heated and colorful controversy concerning the relationships of hummingbirds to swifts and of swifts to swallows (reviewed by Sibley and Ahlquist 1972). In the late 19th century, Robert W. Shufeldt and William K. Parker maintained their convictions that swifts and swallows were closely allied and that hummingbirds had no special relationship with swifts.

Until recently, most anatomical studies were minimally comparative *within* Trochilidae; in the late 19th century, Shufeldt stated that the U.S. National Museum's (USNM) anatomical collections included no Apodiformes (Shufeldt 1885). The monographic works on avian anatomy and systematics by Huxley (1867), Fürbringer (1888), and Gadow and Selenka (1891) included only one or a few species of hummingbird represented by few, sometimes damaged, specimens. Even the most detailed treatment of the hummingbird skeleton (Shufeldt 1885) described only a single species. A survey of myology of the avian hindlimb by Hudson (1937) did not include a hummingbird, and Zusi and Bentz (1984) covered only six species in their description of hummingbird myology. Major anatomical collections have greatly increased their taxonomic coverage of hummingbirds in recent years (Zusi et al. 1982, Livezey 2003). Thus, analysis of variation in a single wing muscle by Zusi and Bentz (1982) covered 19 species of swift, 88 species of hummingbird, and many non-apodiform species, whereas the present monograph includes almost 75% of the extant species and 92% of extant genera of hummingbirds (Appendix 1).

To summarize, within 200 years, anatomists had identified ostensibly unique aspects of hummingbird anatomy and fostered a majority view of the close relationship between hummingbirds and swifts, but had left the subject of comparative osteology within the Trochilidae largely unexplored. More recently, interest has shifted to many other aspects of hummingbird biology and ecology, and phylogenetic inference has been based largely on molecular data.

Uniqueness, parallelism, and convergence.—Most purportedly unique skeletal characters of hummingbirds have pertained to the shoulder girdle, sternum, and forelimb. Demonstration of uniqueness in the hummingbird skeleton is complicated by the uniquely specialized structure of the flight mechanism found in both swifts and hummingbirds, reflecting their commonality of stiff-winged flight and a strongly powered upstroke of the wing (Savile 1950). Similarities in the flight mechanisms of the two families have been interpreted either as derivations from a common ancestor or as convergent evolution. Probably both processes were involved, and separate, parallel morphoclines of specialization in the wings also occur within both modern swifts and hummingbirds (Zusi and Bentz 1982, Bleiweiss 2002). Given this high level of parallel evolution, gross anatomical features of the flight apparatus that are unique to hummingbirds and significant for hovering are often subtle. No such parallelism exists in the feeding mechanisms of swifts and hummingbirds. However, functional comparison of hummingbirds with long-billed, nectar-eating passeriforms reveals convergence related to nectarivory (Paton and Collins 1989).

Functional osteology.—In contrast to static, anatomical description of the skeleton, a functional approach may involve structural complexes and kinematics of movable parts. The role of ligaments in osteological kinematics (e.g., Sy 1936, Bock 1964, Zusi 1967) is critical, but often neglected. Papers by Moller (1930, 1931), Scharnke (1930, 1931b), Steinbacher (1935a), Weymouth et al. (1964), Wolf and Hainsworth (1977), Ewald and Williams (1982), Kingsolver and Daniel (1983), Montgomerie (1984), Paton and Collins (1989), Rico-Guevara and Rubega (2011), and others explored the functional basis of nectar eating. Similarly, Lorenz (1933), Stolpe and Zimmer (1939), Cohn (1968), Karhu (1992, 1999), and others clarified the mechanism of stiff-winged flight in swifts and hummingbirds, and of hovering in hummingbirds. In addition, many more recent studies on muscle physiology (electromyography) in relation to wing stroke, aerodynamics of the wing, energetics of hovering, physiological limits of hovering in different environments (hypoxic, hypodense), mechanics of nectar uptake, coevolution of bill and flower structure, and other topics have provided a new understanding of the functional, ecological, and evolutionary aspects of hovering and nectarivory. Several explanations for hovering, rather than perching, when feeding at flowers were offered by Pyke (1981), Miller (1985), Hainsworth (1986, 1991), and Gill (1985), and each explanation may be relevant in a particular context. Currently predominant are physiological studies of hummingbird flight in both laboratory and field, but insights concerning other anatomical complexes (nasal region, hyoid apparatus, syrinx) are essentially lacking.

Phylogenetic contexts.—Recent evidence from morphological data (Livezey and Zusi 2007) and molecular data (McGuire et al. 2007) supports monophyly of Apodiformes—Hemiprocnidae, Apodidae, and Trochilidae. Molecular studies of phylogeny have employed increasing taxonomic representation of Trochilidae (Gill and Gerwin 1989, Sibley and Ahlquist 1990, Bleiweiss et al. 1997, Gerwin and Zink 1998, Altshuler et al. 2004, McGuire et al. 2007). These studies present plausible hypotheses concerning the phylogeny of major clades within Trochilidae as shown in Figure 1. The results from molecular analysis were broadly supported by exploratory cladistic analyses of morphological data (R. L. Zusi unpubl. data). Nevertheless, basal polarities of various anatomical character-state variations within Trochilidae are uncertain because closely related sister taxa of Trochilidae are unrepresented by living species or fossils. The most intriguing fossil, *Eurotrochilus*, is too distant (Oligocene) to serve that purpose. Therefore, questions about modern hummingbirds persist: for example, are the Hermits a sister clade to all other hummingbirds (Trochilines) or are they a specialized clade within the Trochilines?

Objectives of this monograph.—This study supplements current, experimental approaches by presenting species-rich description of variation in the skeleton of adult hummingbirds. In Section I, I emphasize the uniqueness of the syrinx and of feeding and flight anatomy by comparison with a sample of other Apodiformes and with *Aegotheles*, thus highlighting characters of low variability within Trochilidae that may represent anatomical correlates of hovering and nectarivory. In addition, comparison of modern hummingbirds with fossils assigned to *Eurotrochilus* (Mayr 2004) prompted reevaluation of levels of behavioral specialization in the Oligocene taxa. In Section II, I present major variation within Trochilidae and indicate distribution of such variation within and among the major clades of hummingbirds. Examples of intraspecific variation are presented, and patterns of diversity and possible adaptation at various phylogenetic levels are identified. Throughout this study, and especially under headings in all-capital italics, I offer speculations on function that could be profitably tested by other methods.

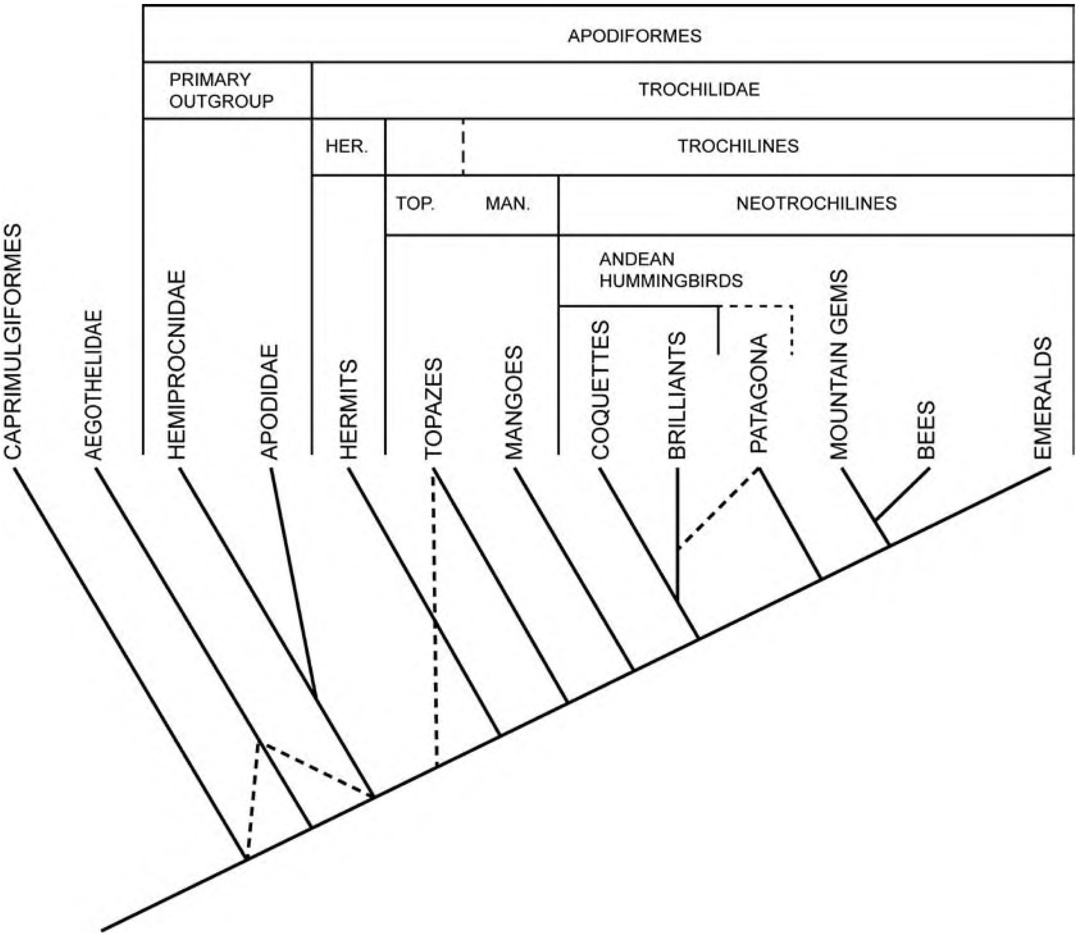

Fig. 1. Branching diagram of a higher-level phylogenetic framework of hummingbirds and outgroups followed in this monograph. Branch lengths are arbitrary. Dashed lines show other plausible arrangements (see text). If Topazes are considered sister to all other hummingbirds, one could recognize Topazinae for Topazes, Phaethornthinae for Hermits, and Trochilinae for all other hummingbirds (see Chesser et al. 2012). This diagram is modified from McGuire et al. (2007), not based on a new phylogenetic analysis. Abbreviations: HER. = Hermits, MAN. = Mangoes, TOP. = Topazes.

Methods and Materials

Taxonomic nomenclature.—I follow the American Ornithologists' Union (1998) *Check-list of North American Birds*, seventh edition, and Remsen et al. (2007) for nomenclature of generic and specific level taxa of South American birds. For Old World birds, I follow Dickinson (2003), and names of fossils are from Mayr (2004). I use Hemiprocnidae (crested swifts) and Apodidae (swifts) as primary outgroups, and Aegothelidae (owlet frogmouths) as a more distant outgroup to Trochilidae (hummingbirds). I use the scientific names of outgroup families if the character in question is thought to be similar throughout the family, and English names when referring to a subset of species in the family. Bleiweiss et al. (1997) and McGuire et al. (2007) proposed informal names for major clades within Trochilidae. I employ the vernacular names "Hermits," "Topazes," "Mangoes," "Brilliants," "Coquettes," "Patagona," "Mountain Gems," "Bees," and "Emeralds" used for the major clades by McGuire et al. (2007), but for convenience in summarizing distribution of anatomical characters I place Topazes next to Mangoes within Trochilines (Fig. 1). I follow the placement of *Patagona* as sister to Mountain Gems, Bees, and Emeralds, although some anatomical characters support its inclusion in Brilliants.

Scientific names for the nine major clades informally named above are presented by McGuire et al. (2009), but formal names to represent a hierarchy of those clades were not proposed. If Topazes are considered as sister to all other hummingbirds, one could recognize Topazinae, Phaethornithinae, and Trochilinae (Chesser et al. 2012). Throughout, I use the capitalized informal terms "Hermit" and "Trochiline" (i.e., non-Hermit) without necessarily accepting the validity of the traditional subfamilies Phaethornithinae and Trochilinae. Within Trochilines, I separate Mangoes and Topazes from a clade that contains all other non-Hermits, and term the latter, unnamed clade "Neotrochilines." Names are needed to represent the Brilliants and Coquettes (sometimes called "Andean Hummingbirds"), the clade comprising Mountain Gems plus Bees, and the clade that includes Mountain Gems, Bees, and Emeralds (Fig. 1). Within Apodidae, I include species representing major clades hypothesized by Price et al. (2005).

Anatomical nomenclature.—With few exceptions, anatomical nomenclature follows Baumel et al. (1993)—specifically Clark (1993), Baumel and Witmer (1993), Baumel and Raikow (1993), Vanden Berge and Zweers (1993), and King (1993). Additional names follow Zusi and Livezey (2006) and Livezey and Zusi (2006). Terms of orientation are those proposed and explained by Clark (1993). Nevertheless, difficulties persist. For example, the upper jaw of vertebrates includes not only the primary tooth-bearing bones but also those of the palate, linked by the quadrates to the lower jaw. In external topography of birds, the mandibles covered by rhamphotheca constitute the beak or bill and are termed "rostrum maxillare" and "rostrum mandibulare" by Clark (1993:1–2). However, under "Osteologia" (Baumel and Witmer 1993), the term "rostrum maxillae" refers only to the symphysial portion of the paired premaxillary bones, which forms the anterior tip of the upper jaw, and "rostrum mandibulae" refers only to the symphysial portion of the paired dentary bones, which form the anterior tip of the lower jaw. No term is offered to represent the entire bony portion of the upper jaw that excludes the palate. Livezey and Zusi (2006) used the term "rostrum maxillae" not only for this portion of the bony upper jaw but also for the entire maxilla. Here, I propose the term "prepalatal upper jaw" for the osseous portion of the upper jaw that is covered by ramphotheca in modern birds.

Within the palatum, the maxillary process of the palatinum fuses with the palatine process of the maxillare in adult birds. I refer to the resulting structure as the "rostral bar," connecting the palatum with the prepalatal upper jaw.

In Sections I and II, I use English anatomical terms in text and figures, with the singular form of Latin equivalents in parentheses at first use (e.g., "dorsal bars (pila supranasalis)"). When English and Latin names are identical or nearly so, I use only the Latin name (e.g., mandibula for mandible). Latin names of bones that include "os," as in "os palatinum," are Anglicized in many other works by the single adjectival form, for example "palatine." Here, I omit "os" and use the Latin noun (e.g., palatinum) in place of the English name (palatine bone). Conventionally, Latin names of muscles are preceded by "m." or "musculus" but are otherwise identical to English names. For this reason, I use either English or Latin names for muscles.

Taxonomic coverage and sample sizes.—Species studied as skeletons and spirit specimens and the museum collections consulted for each are listed in Appendix 1. Of 330 extant species, 256 (about 75%) were studied. Of 111 extant genera, 102 (92%) were examined. The frequency matrix in Appendix 2 contains 33% of extant species and 90% of extant genera. In the matrix, I usually recorded data from four specimens of each species, but for some anatomical characters fewer specimens were available, and for others more than four specimens were coded. Unossified structures (nasal cartilage, muscles, and ligaments) usually were scored from a single spirit specimen per species and were thus unavailable for discussion of intraspecific variation. Species listed in Appendix 1 but not included in the matrix were examined for selected characters in the course of the study.

Sources of error and missing data.—A potential source of error in skeletal specimens of hummingbirds is the misidentification of some specimens (especially females or immatures) before preparation. In general, I found that most skeletons were identifiable to genus from skeletal characters alone. I believe that few uncorrected errors of species identification occurred in the present study and that any such errors would have pertained to congeners. A more prevalent problem was over-cleaned skeletal specimens that were damaged or incomplete, and under-cleaned specimens in which parts of the skeleton were not visible. The number of fully useful, skeletal specimens in museums was thus less than the totals listed in skeleton inventories (Wood and Schnell 1986). In addition, incorrect sexing of specimens that were ultimately prepared as skeletons occurred at rates that probably differed among species. Skeletal specimens of juveniles young enough to retain sutures of the cranium were not found, and all specimens discussed here were of adult size with the exception of one nestling of *Chlorostilbon swainsonii*—a spirit specimen that was cleared and stained.

Each skeletal specimen in museums is routinely identified before preparation and labeled with the prevailing scientific name. Especially during historical periods of taxonomic lumping, two or more subsequently recognized species may have received the same name on skeleton boxes. This problem probably was most troublesome for me with regard to skeletal variation among specimens commonly labeled "*Phaethornis longuemareus*," now thought to represent at least three species (see Section II under "Humerus").

Anatomical specimens.—Description of most individual skeletal elements of hummingbirds required magnification with a dissecting microscope, thus limiting simultaneous comparisons to a few species. Using a camera lucida, I made line drawings of the cranium, palatum, humerus, and sternum of many species to permit broad, synoptic comparisons for the initial discovery of major variations. Skeletons with articulated vertebrae, trunks, and digits of the foot were indispensible for counts of vertebrae, ribs, and phalanges.

Spirit specimens listed in Appendix 1 were used for determining gross morphology of the (cartilaginous) nasal region, conformation and asymmetry of the epibranchiales, and variation in muscles and ligaments. Although not central to the present study, data that supplement the widely cited information on the tendons of m. tensor propatagialis brevis (Zusi and Bentz 1982) are presented in Appendix 3.

Selected specimens of 44 species (35 genera) from the USNM spirit collection were cleared and stained for bone, or cartilage and bone. These specimens were especially useful for (1) determining the nature of cartilaginous structures in the nasal region and patterns of ossification, (2) verifying delicate ossifications in the prepalatal upper jaw, (3) verifying presence of bones often lost in skeleton preparation (e.g., sesamoids of the tail, free ribs, phalanges), and (4) clarifying syringeal structure. A juvenile specimen (nestling) and an adult specimen of *C. swainsonii*, both cleared and stained, provided the only direct contrast between juvenile and adult features and served as a basis for discussion of ontological metamorphosis of the jaws, a phenomenon that I have assumed to be widely applicable within Trochilidae.

Functional anatomy and adaptation.—Functional properties of osteological entities include resistance to and propagation of forces, and contributions to kinetic systems that usually involve joints, ligaments, and muscles. Here, I inferred such properties from examination and manipulation of specimens rather than from measurements on live birds. For example, to obtain qualitative information on flexibility within the upper jaw during cranial kinesis, I manipulated freshly dead individuals of three species of Hermits and three of Trochilines. Rostrodorsal pressure on the articular–quadrate region simulated contraction of m. depressor mandibulae and m. protractor quadrati et pterygoidei during cranial kinesis. The same tactic was employed on hydrated skeletons of additional species. Manipulation of cleared and stained specimens clarified motion at some articulations, and actions of several muscles of the forelimb were noted while tensing their tendons. I inferred interrelations of bones and muscles during extension and retraction of the tongue from superficial dissection of spirit specimens that had been fixed with the tongue conveniently positioned in randomly different stages of protrusion.

When structures or functions are associated with behaviors such as foraging, locomotion, or social interactions, their biological role may become evident. A structural complex can serve more than one biological role within or between species. Structural adaptation requires a phylogenetic perspective and demonstration of a change from the ancestral condition (inferred from outgroups); the change may increase efficiency of the structure in the same biological role or may enable its use in a new biological role.

The bulk of this monograph concerns descriptive anatomy, thus filling gaps in the record of hummingbird osteology and raising new questions. Functions and biological roles are inferred throughout, and evidence is presented for adaptations related to nectarivory or sustained hovering in all hummingbirds. Still unexplored, however, are the biological roles, ecological significance, and adaptation of many variations of the skeleton within Trochilidae.

Histology.—Histological transverse sections of the prepalatal upper jaw of *Glaucis hirsutus* and *Heliodoxa xanthogonys*, nasal region of *Eulampis jugularis* and *Phaethornis malaris*, and syrinx of *G. hirsutus* and *E. holocericeus* provided information on tissue structure and details of anatomical relationships not evident under low magnification. These specimens were decalcified, sectioned at 8 microns, and stained with haematoxylin and eosin or Masson trichrome stain.

Fossils.—Fossils of Cypseli from Early Eocene to Middle Oligocene—predominantly isolated humeri and coracoids—include a few partially articulated skeletons of swift-like birds, several of which have well-preserved feather impressions. Three fossil families have been proposed (Mayr 2003b). The most interesting find for the present study is *Eurotrochilus inexpectatus* from the Oligocene of Germany (Mayr 2004, 2007) and other fossils referred to that genus (Louchart et al. 2007, Bochenski and Bochenski 2008). My knowledge of the osteology of these fossils is based solely on published illustrations and descriptions.

Intraspecific variation.—The anatomical variations discussed under Section II represent phenotypes that differed qualitatively or meristically and were coded originally as two or more states of each morphological character. Coded states that applied to each species were either constant (monomorphic) or variable (polymorphic) within the sample of specimens, as detailed in the frequency matrix (Appendix 2). For interspecific comparison, each species was characterized by its modal (majority) state, or if two character states were equally represented in a sample, I chose the state that was typical of congeners; in monotypic genera, I used the state that appeared to be derived. Sample sizes (1 to 4, sometimes more) were mostly too small to permit a comprehensive representation of intraspecific variation here. Nevertheless, I describe selected examples of such variation. With the exception of sexual dimorphism in numbers of ribs attached to the sternum, I did not undertake analysis of sexual dimorphism in the skeleton.

Behavioral data.—I observed nectar-drinking behavior of Ruby-throated Hummingbirds (*Archilochus colubris*) on 20 May 1986, at the Carnegie Museum of Natural History's banding station at Powdermill, Pennsylvania. Birds captured in mist nets for banding were retained briefly in restraining tubes and allowed to feed on sugar water from an inverted tube feeder. A dissecting microscope was oriented to allow observation at 6× magnification of the bill and tongue in either ventral or lateral view during feeding. Additional species (*Eulampis jugularis, Orthorhynchus cristatus*, and *Cyanophaia bicolor*) were netted inadvertently in the course of other studies in Dominica (Lesser Antilles), March 1990. These birds were held briefly in the field and observed in ventral view with the aid of a flashlight and mirror while they fed on sugar water from a vial. Other details of bill movement and hovering were obtained from videos and published photographs or descriptions.

Size comparisons.—I relied on data in Dunning (2008) for broad comparisons of body weight within Apodiformes. Within Trochilidae, coracoid length is highly correlated with cube root of body weight, and the two measures vary isometrically (R. L. Zusi unpubl. data). Within a single species (*Trochilus citulus*), Graves (2009) found sternal length to be most highly correlated with body weight. Whether this result applies within all interspecific comparisons is unknown. In the text, I made some comparisons between species of similar body size (based on body weight or on coracoideum length) to highlight proportional differences or similarities; in the figures, scale bars are not included, but individual skeletal elements are sometimes scaled to a similar length or width to emphasize proportional differences.

Phylogeny.—Phylogenetic hypotheses derived from morphological or molecular evidence (Sibley and Ahlquist 1990; Bleiweiss et al. 1994; Johansson et al. 2001; Mayr 2002, 2003a; Chubb 2004; Cracraft et al. 2004; Livezey and Zusi 2006, 2007; Hackett et al. 2008) agree on the monophyly of Apodiformes (Hemiprocnidae, Apodidae, and Trochilidae), but differ in the proposed sister-group relationship of Apodidae (i.e., to Trochilidae or to Hemiprocnidae). Here, I accept the monophyly of Apodiformes and the sister-group relationship of Hemiprocnidae and Apodidae. Aegothelidae provides a more distant outgroup, either as an early branch of Apodiformes (Mayr 2002) or as a basal branch of the sister order Caprimulgiformes (Livezey and Zusi 2007). The phylogenetic context is presented in Figure 1.

The two most comprehensive molecular studies (Bleiweiss et al. 1997, McGuire et al. 2007) largely agree on the constitution and sister relationships of major clades within Trochilidae. Other studies have addressed relationships at various levels using molecular or morphological data—groups of clades (Zusi and Bentz 1982), *Heliodoxa* (Gerwin and Zink 1989), Hermits (Gill and Gerwin 1989), and some Brilliants and Coquettes (Roy et al. 1998).

Section I. The Uniqueness of Hummingbirds

Except for the syrinx, this section is based on intensive taxonomic sampling within Trochilidae and limited sampling of outgroups represented by one or a few species each of Apodidae, Hemiprocnidae, and Aegothelidae (Appendix 1). I describe the syrinx, on the basis of limited taxonomic sampling that included both Hermits and Trochilines, to characterize probable synapomorphies of Trochilidae. With respect to the tongue and hyobranchial apparatus (apparatus hyobranchialis), I make some comparisons also with long-billed, nectariverous Passeriformes (Nectariniidae). The data in this section are organized topographically to emphasize structural complexes that may support functional capabilities unique to hummingbirds.

Syrinx

The larynx, trachea, syrinx, and bronchi of birds incorporate cartilaginous or osseus skeletal elements of the respiratory system. Skeletal muscles interconnect the larynx with the hyobranchial apparatus, and the trachea with the sternum. Both interconnections are present in Hemiprocnidae and Apodidae but absent in Trochilidae. Independent movement of the hyobranchial apparatus, decoupled from the larynx, allows extreme protrusion of the tongue in hummingbirds. Intrinsic muscles, associated only with the syrinx, are present in hummingbirds and lacking in outgroups.

The structure of the syrinx of many birds (but not hummingbirds) has been reviewed by King (1989). In *Aegotheles* and Apodiformes, the membranous trachea and bronchi are supported by cartilaginous rings. The syrinx of *Aegotheles* consists of bilateral, medial tympanic membranes (membrana tympanica medialis) that interconnect the third and fourth, and fourth and fifth bronchial rings (cartilago bronchialis) caudal to the last tracheal ring (cartilago trachealis) (Beddard 1886). In swifts and hummingbirds the medial tympanic membranes are associated with incomplete bronchial rings, and an ossified drum (tympanum) is formed from modified tracheal and bronchial rings.

Location.—In all birds except hummingbirds (and one species of spoonbill, Plataleinae: *Ajaia ajaja*; Garrod 1875) the syrinx and bronchi lie within the thoracic cavity (cavitas thoracica) caudal to the furcula and interclavicular membrane (saccus clavicularis; hereafter ICM). The syrinx and a major portion of each bronchus of hummingbirds are situated in the neck rostral to the level of the furcula (Müller 1878, Cannell 1986). However, the ICM includes an evagination rostral to the furcula that encloses the syrinx and the rostral portion of each bronchus (Fig. 2). Between

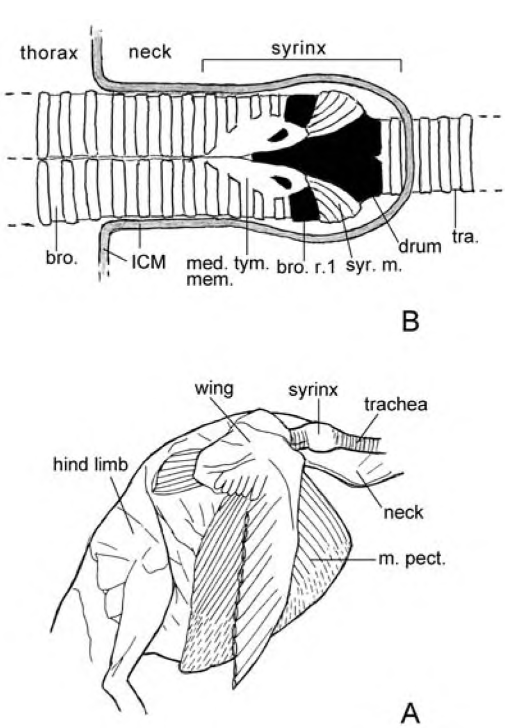

FIG. 2. Location of the syrinx in the neck in hummingbirds. (A) Skinned trunk of a hummingbird in right, lateral view, with primary feathers clipped. (B) Enlarged, semidiagrammatic, dorsal view of syrinx, trachea, and bronchi. Although the bronchi and syrinx extend rostrally into the neck within a pouch of the interclavicular membrane, the pouch represents an extension of the thoracic cavity. Abbreviations: bro. = bronchus, bro. r. 1 = first bronchial ring, med. tym. mem. = medial tympanic membrane, m. pect. = pectoralis muscle, ICM = interclavicular membrane, syr. m. = syringeal muscles, tra. = trachea.

the larynx and syrinx, a trachea of *Florisuga mellivora* comprised 39 rings; and between the syrinx and lung (pulmo), the complete bronchial rings of each bronchus numbered 35; correspondingly, a *Campylopterus* sp. had 40 tracheal and 41 bronchial rings. In hummingbirds, the bronchi, both rostral and caudal to the clavicles, lie side by side, diverging only as they approach the lung. The tubular evagination of the ICM binds the bronchi together by contact with their lateral walls and rostrally forms a globular expansion within which the syrinx is freely suspended. The expansion terminates rostral to the syrinx and is penetrated by the trachea. The limited space between the ICM evagination and the bronchi and syrinx is occupied by the bilaterally merged cervical air sacs (saccus cervicalis), which originate from the caudal extremity of the primary bronchus in the lung (Stanislaus 1937).

Structure.—Extrinsic muscles originate outside of the syrinx and insert upon it. The only extrinsic muscle in hummingbirds is the paired m. tracheolateralis, which is represented by flat bands along opposite sides of the trachea. At the intersection of the ICM and the trachea, this muscle divides into two branches: one spreads over the rostral surface of the membrane and inserts on it; the other passes through the membrane, curves ventrally, and inserts on the caudoventral surface of the drum. M. sternotrachealis is absent. In swifts the sternotrachealis and tracheolateralis muscles may represent an antagonistic pair (Fig. 3A), controlling rostrocaudal movement of the syrinx; both muscles have superfast muscle fibers in some Columbidae that are among the fastest muscle fibers known (Elemans et al. 2004), which suggests a role in vocalization. In hummingbirds the evagination of the ICM surrounding the syrinx may act as a ligament (functionally replacing the sternotrachealis muscle) that limits rostral movement of the syrinx initiated by m. tracheolateralis. In *Apus* an interbronchial ligament (ligamentum interbronchiale) from each bronchus attaches separately on the adjacent, dorsally situated esophagus. This ligament is lacking in hummingbirds.

Here, I offer a description of the syrinx, based mainly on *G. hirsutus*, *Threnetes leucurus*, *Eulampis holosericeus*, and *Coeligena coeligena*, that expands on those by Müller (1878) and Cannell (1986). In *Aegotheles* and Apodiformes the free tracheal and bronchial rings are cartilaginous, and the syrinx (rings or drum) is ossified. The free tracheal rings and all bronchial rings except the rostral three or four pairs are complete in hummingbirds. Unlike passeriform birds described by Ames (1971), they are not differentiated into flattened and thickened rings. Instead, the cartilage of each ring is thickened, becoming flatter only in its medial portion. A medial tympaniform membrane closes the gap in the bronchial tubes left by incomplete rings. The drum in *Apus* is shorter than that of hummingbirds (Fig. 3A, B).

At its rostralmost extremity, the ossified drum equals the shape and diameter of the trachea, but the drum abruptly widens caudally (Fig. 3B). The wide portion represents a merging of adjacent bronchi, as demonstrated by the syrinx of *Mellisuga minima* (USNM 318954) in which there are six, partly cartilaginous, median partitions (remains of bronchial rings) within the lumen of the drum. Some portions of the bony drum are thin and single-layered, whereas others are expanded into crests or ridges by addition of a second, external layer of bone that encloses a fatty marrow cavity and is reinforced by trabeculae. These ridges are typically on the caudal portion of the drum midventrally and dorsolaterally, but in a few species they extend dorsolaterally along the full length of the drum. The ridges and crests expand the origins of intrinsic muscles. A pillar separates the bronchial openings of the drum caudally (Fig. 3B). This ossified, medial pillar (pessulus) is roughly triangular in transverse section, enclosing a fatty marrow. Its caudolateral edges support the two, medial tympaniform membranes.

Between the caudolateral rim of the drum and the first free bronchial ring is a partly membranous, lateral lamella (lamella lateralis) that projects into the air passage of the drum (Fig. 3C) and extends from the base of the pessulus to the upper limit of the first, free bronchial ring. Müller (1878:37) described it as an "excessively small" first bronchial ring. The lamella is strengthened by an internal cartilage in some species or is ossified in others (e.g., *P. superciliosus* USNM 511312). The osseous portion, somewhat irregular in shape, may be limited to the midsection of the lamella.

In hummingbirds the first free bronchial ring is larger than the others. It is incomplete in its medial portion, as in other bronchial rings associated with the medial tympaniform membrane. Its C-shaped cartilage is roughly circular in transverse section except at the dorsal end, where it is expanded and flattened. The dorsal portion or head (caput) is ossified, as is the

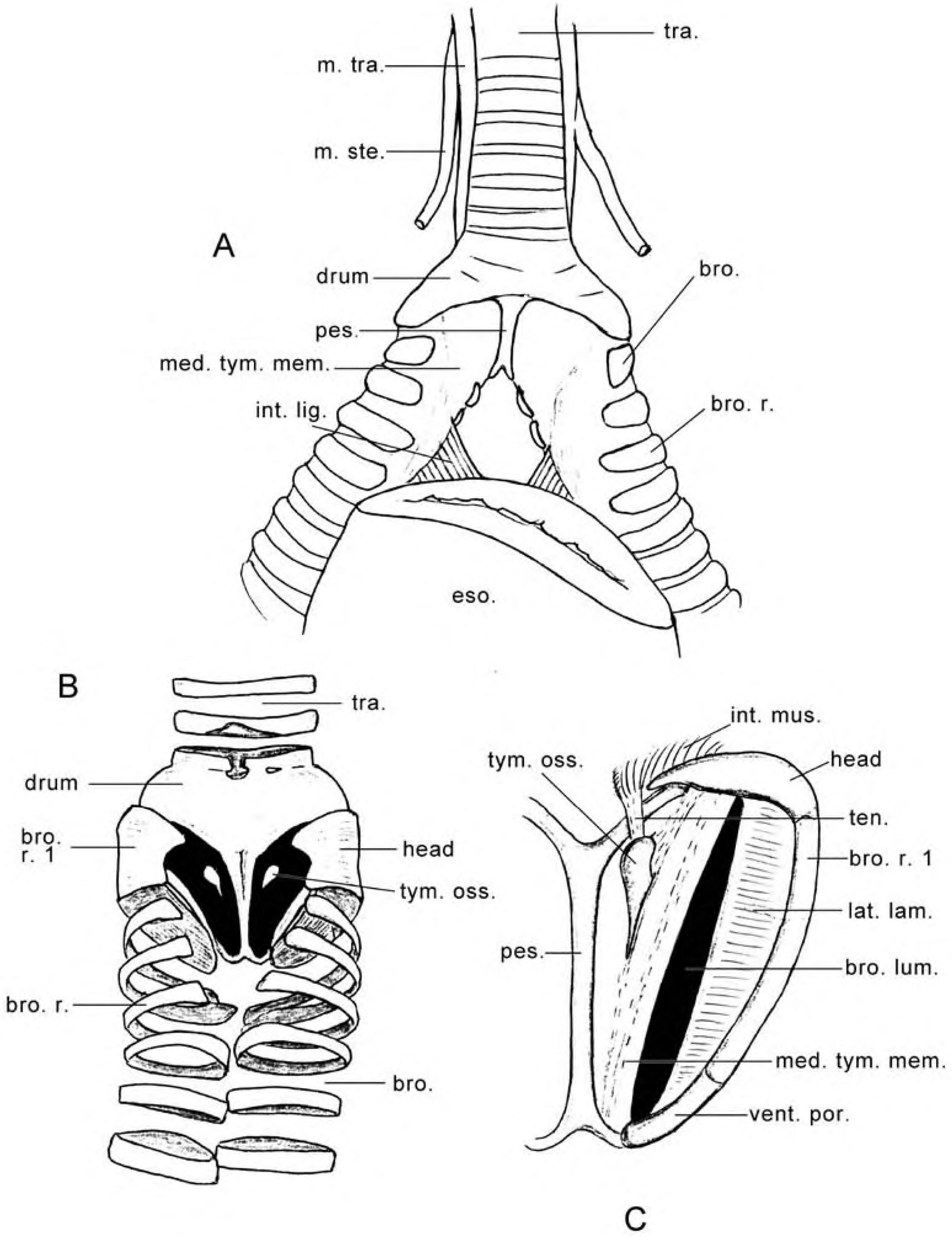

FIG. 3. The syrinx of a swift and hummingbird. (A) Swift (*Apus affinis*), drawn from spirit specimen; dorsal view. (B) Hummingbird (*Threnetes leucurus*) drawn from a cleared and stained specimen in which only cartilage, bone, and ligaments remain; dorsal view. (C) Semidiagrammatic composite of section through a hummingbird bronchus with view into the interior of the drum. (B, C) Lumen of drum shown in solid black. Adjacent bronchi, intrinsic muscles, modified head of first bronchial ring, tympanic ossicle, and lateral lamella are unique to hummingbirds within Apodiformes. Hummingbirds lack the sternotrachealis muscle and interbronchial ligament. Abbreviations: bro. = bronchus, bro. lum. = lumen of bronchus, bro. r. = bronchial ring, bro. r. 1 = first bronchial ring, eso. = esophagus, int. lig. = interbronchial ligament, int. mus. = intrinsic syringeal muscles, lat. lam. = lateral lamella, med. tym. mem. = medial tympanic membrane, m. ste. = sternotrachealis muscle, m. tra. = tracheolateralis muscle, pes. = pessulus, ten. = tendon of intrinsic syringeal muscles, tra. = trachea, tym. oss. = tympanic ossicle, vent. por. = ventral portion.

ventral portion to a varying degree (Fig. 3C). The ring's cranial margin is separated from the caudal edge of the drum by the lateral margin of the lateral lamella, and the ventral end is attached by connective tissue to the apex of the pessulus. The head of this ring projects rostrad over the caudolateral portion of the drum, producing a translation articulation.

Attached to the medial surface of each tympanic membrane is a partially ossified, cartilaginous, tympanic ossicle (ossicula tympanica). The ossicle (Fig. 3C) varies in size and shape among species, but in all cases it projects into the extra-syringeal space bounded by the medial tympaniform membrane and the ICM. In single specimens of *E. holosericeus* and *G. hirsutus* sectioned histologically, the ossicle was solid cartilage with a thin, ossified layer on all surfaces except at the basal contact with the medial tympaniform membrane. The ossicle rests on a ligament that passes along the membrane from the ossified head of the first bronchial ring to its ossified ventral portion. Medial fibers of the main intrinsic muscle insert by a short tendon on the base of the tympanic ossicle. The presence of an ossicle on the external surface of each medial tympaniform membrane of hummingbirds is apparently unique among birds (Müller 1878). The ossicle is not homologous with internal cartilages of certain passerines such as Tyrannidae (Ames 1971) or Pipridae (Prum 1990) because it is not a flat, cartilaginous extension of a bronchial or tracheal ring.

Müller (1878) and Cannell (1986) described two pairs of intrinsic muscles in unspecified species of *Campylopterus, Phaethornis, Lampornis, Orthorhynchus,* and *"Ornismyia"* and in *Hylocharis cyanus.* My superficial dissection of muscles in *G. hirsutus* confirmed two major pairs, but observations on *Pterophanes cyanoptera* revealed additional differentiation of muscle slips originating midventrally from the ossified drum, the rostral bronchial rings, and the caudal tracheal rings. The insertions of three slips were on the ossified head of the first bronchial ring, whereas other portions inserted more broadly along the first bronchial ring. Naming of hummingbird muscles must await further study.

Differences between the syrinx of a swift and the species of hummingbirds studied (Fig. 3) are summarized in Table 1. I tentatively assume that the character states listed for hummingbirds are constant for Trochilidae, and that the states listed for a swift are characteristic of Apodidae. If so, the states of hummingbirds are probably synapomorphic within Apodiformes.

In a sample of seven species, bilateral syringeal nerve branches (ramus syringealis) were interconnected rostral to the syrinx along the cranial edge of the ventral, intrinsic muscle mass (*Eutoxeres aquila, Anthracothorax nigricollis, Coeligena bonapartei, Heliodoxa xanthogonys, Campylopterus falcatus, C. duidae,* and *Chalybura buffonii*); in three others the nerves entered the muscle mass without external interconnection (*Amazilia fimbriata, A. viridigaster,* and *Leucippus fallax*).

Functional considerations.—Little is known about functional anatomy in the hummingbird's syrinx, or about its specific adaptations. In the first free bronchial ring the cartilaginous portion probably allows for some change in its shape. Muscle

TABLE 1. Morphological comparisons of the syrinx in swifts and hummingbirds.

Character	Swift (*Apus affinis, Chaetura pelagica*)	Hummingbird (*Glaucis hirsutus, Coeligena coeligena*)
Location of syrinx	Thorax	Neck
Sternotrachealis muscle	Present	Absent
Intrinsic syringeal muscles	Absent	Present
Interbronchial ligament	Present	Absent
Bronchi	Diverge caudal to drum	Parallel and adjacent caudal to drum
First bronchial ring	Unmodified	Enlarged, ossified head
First bronchial ring	Separate from drum	Head articulates with drum
Lateral lamella	Absent	Present
Tympanic ossicle	Absent	Present
Tendon from intrinsic muscles to tympanic ossicle	Absent	Present

fibers that originate on the drum and insert on the enlarged, ossified head of the first bronchial ring serve to move its head rostrally, laterally, or caudally on its translational articulation with the drum. A tendon from the medial fibers to the tympanic ossicle may represent a unique instance in birds of direct muscle action on the medial tympanic membrane. All intrinsic muscles apparently effect changes in tension of the medial tympanic membrane by moving the first bronchial ring or the tympanic ossicle (Fig. 3D). The tympanic ossicle may serve as a focal point for attachment of ligaments of the medial tympanic membrane oriented in different directions. Motion of the first bronchial ring probably also causes positional changes of the lateral lamella.

THE FEEDING MECHANISM

The feeding mechanism embodies many aspects of the skull (Fig. 4). Emphasis here is on the upper jaw (maxilla) and lower jaw (mandibula), the tongue, and the hyobranchial apparatus (apparatus hyobranchialis). Functions of these structures, including cranial kinesis of the upper jaw, streptognathism of the lower jaw, and motions of the

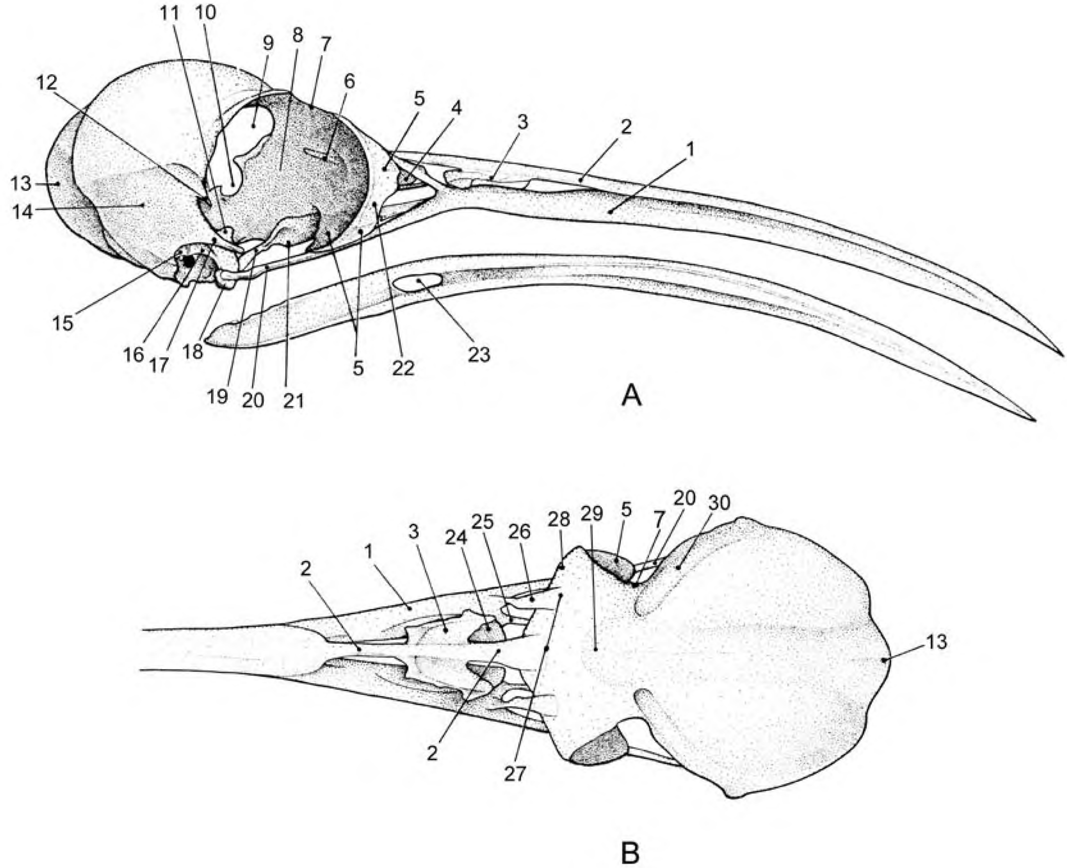

FIG. 4. Topography and nomenclature of the skull of *Eulampis jugularis*. (A) Skull with lower jaw separated; lateral view. (B) Skull with mandible and part of prepalatal upper jaw missing; dorsal view. 1 = ventral bar, 2 = dorsal bar, 3 = nasal roof, 4 = mesethmoidale, 5 = ectethmoidale, 6 = olfactory sulcus, 7 = supraorbital margin, 8 = interorbital septum, 9 = orbitocranial fonticulus, 10 = optic foramen, 11 = orbital process of quadratum, 12 = postorbital process, 13 = cerebellar prominence, 14 = temporal fossa, 15 = otic pillar, 16 = otic process of quadrate, 17 = zygomatic process, 18 = lateral condyle of quadrate, 19 = pterygoideum, 20 = jugal arch, 21 = palatinum, 22 = nasolacrimal sulcus, 23 = rostral mandibular fenestra, 24 = rostral concha, 25 = rostral bar of palatinum, 26 = maxillary process of nasale, 27 = craniofacial hinge, 28 = ectethmoidale, 29 = insertion area of stylohyoideus muscle, 30 = sulcus for cucullaris capitis muscle.

tongue driven by muscles of the hyobranchial apparatus, are applicable not only to the mechanism of nectar eating and arthropod eating but also to some social displays.

Prepalatal Upper Jaw

Technically, the upper jaw of birds includes a rostral portion, the prepalatal upper jaw (maxilla prepalata), and a caudal portion, the palatal upper jaw (palatum), whereas the lower jaw consists of the mandibula. Both jaws articulate with the quadratum, which, in turn, suspends them from the cranium. The prepalatal upper jaw of outgroups and passeriform nectarivores is composed of two parts—symphysial (pars symphysialis) and nasal (pars nasalis). By contrast, the prepalatal upper jaw of hummingbirds includes three parts, regardless of bill length or shape—symphysial, intermediate (pars intermedialis), and nasal (Fig. 5). In most birds the prepalatal upper jaw forms a craniofacial hinge (zona flexoria craniofacialis) with the cranium, and the palatum articulates with the cranium at the parasphenoidal rostrum (rostrum parasphenoidale) and/or the basipterygoid processes (processus basipterygoideus). Features unique to Trochilidae are emphasized in this section.

The prepalatal upper jaw is basically one of open construction—that is, the bony nasal opening (apertura nasi ossea) occupies most of its length (Cracraft 1988). Although open construction is exemplified also in long-billed Chardrii and Gruiformes, the open construction in hummingbirds becomes obscured during development as explained below.

All outgroups differ from hummingbirds in having bills that are short, broad at the base, and roughly uniform in shape. However, the symphysial part is short in relation to the nasal part throughout Apodiformes (Cracraft 1988). In hummingbirds a ventrally concave conformation characterizes both the intermediate part (see below) and the symphysial part, but it becomes progressively less deep anteriorly and is essentially absent at the bill tip. Passerine nectarivores (Nectariniidae) differ from hummingbirds in that

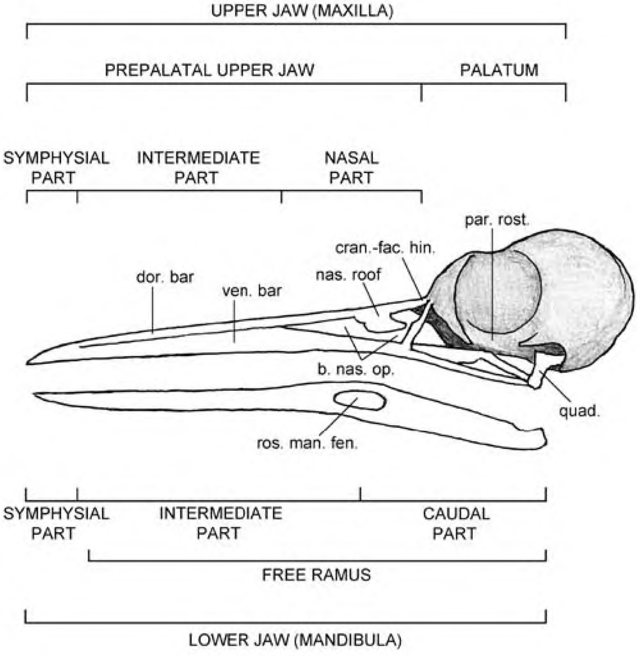

Fig. 5. Topography and nomenclature of the jaws in hummingbirds. Lower jaw removed from quadrate. Semidiagrammatic, with cranium shaded. Presence of an intermediate part of the prepalatal upper jaw in adult hummingbirds is unique within Apodiformes. Abbreviations: b. nas. op. = bony nasal opening, cran.-fac. hin. = craniofacial hinge, dor. bar = dorsal bar, nas. roof = nasal roof, par. rost. = parasphedoidal rostrum, quad. = quadratum, ros. man. fen. = rostral mandibular fenestra, ven. bar = ventral bar.

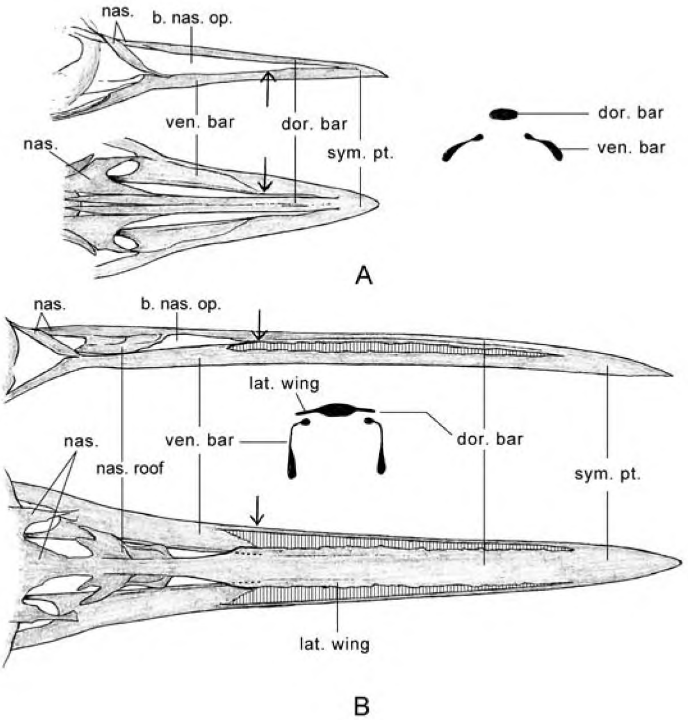

FIG. 6. Prepalatal upper jaw of a hummingbird, showing developmental change in *Chlorostilbon swainsonii*. (A) Nestling. (B) Adult. Shaded drawings are of cleared and stained specimens in lateral (upper) and dorsal (lower) views, drawn to same scale. Solid black figures are diagrammatic transverse sections of the intermediate part of the prepalatal upper jaw. Note the change in orientation of the ventral bars and their association with the dorsal bar from nestling to adult. Arrows show approximate rostral limit of the nasal part. Vertical hatching represents a thin portion of the ventral bar that is often missing in skeletal specimens. Abbreviations: b. nas. op. = bony nasal opening, dor. bar = dorsal bar, lat. wing = lateral wing, nas. = nasale, nas. roof = nasal roof, sym. pt. = symphysial part, ven. bar = ventral bar.

the symphysial portion is relatively long, the intermediate part is essentially absent, and the internal concavity is extensively developed within the symphysial part.

Intermediate part.—In the juvenile hummingbird (exemplified here in Fig. 6A by *Chlorostilbon swainsonii*) the entire prepalatal upper jaw more closely resembles the adult bills of outgroup taxa and is both proportionally and actually shorter than that of the adult. The nasal part is relatively long and the intermediate part relatively short. In the juvenile the dorsal bar (pila supranasalis) is moderately long, the symphysial part short, and the bony nares extensive. The dorsal bar consists of the paired frontal process (processus frontalis) of the premaxillare and is oval in transverse section. The ventral bars (pila subnasalis), formed by the premaxillary process (processus premaxillaris) of the maxillare and maxillary process (processus maxillaris) of the premaxillare, are dorsoventrally compressed and somewhat concave ventrally. The planes of the flattened ventral bars are approximately parallel to the frontal plane, although each tilts upward medially (Fig. 6A).

Compared with the juvenile, the adult *C. swainsonii* (Fig. 6B) exhibits a more dorsoventrally flattened dorsal bar. During ontogenetic, posthatching metamorphosis the intermediate part elongates disproportionately toward adult length. At this time the ventral bars rotate in opposite directions and the medial edge of each moves dorsolaterally to occupy a position ventral to the lateral margin of the dorsal bar. Thus, each ventral bar becomes an approximately vertical and medially concave lamina (Fig. 6B). Together, the single dorsal and paired ventral bars produce an inverted U-shaped trough that houses the tongue and most of the closed mandibula. The medial (now dorsal) portion of the ventral bar is well ossified, as is the lateral (now ventral) portion. However, between these well-ossified portions, the ventral bar may be thinly or incompletely ossified (Fig. 6B). The result in an adult skeleton is often that the middle portion of the lateral wall of the prepalatal upper jaw may be artifactually missing after preparation and may therefore comprise two bars rather than one. This may account for an apparent extra bar in the prepalatal upper jaw of hummingbirds described by Bühler (1981) as the "palatine bar (rostral part)." Probably all juvenile hummingbirds undergo a posthatching metamorphosis to produce the unique adult structure. The effect of axial rotation of the ventral bar is that the original nasal opening is closed rostrally and is relatively short caudally in adult hummingbirds, regardless of bill length (Fig. 6B).

A histological transverse section through the prepalatal upper jaw of *G. hirsutus* (Fig. 7) shows that the dorsal bar has a central rod of cancellous bone flanked on either side by a thin, lateral wing (ala lateralis). The dorsal margin of the vertical portion of the ventral bar is sharply inclined medially and lies ventral and parallel to the lateral wing of the dorsal bar, where the bars are separated by a venous sinus (sinus venosus) and fibrous connective tissue. It is not known whether rostrocaudal translational movement of the ventral bar in relation to the dorsal bar is possible.

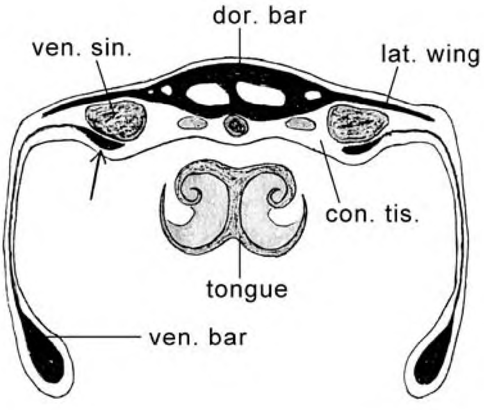

Fig. 7. A histological section through the tongue and intermediate part of the prepalatal upper jaw of an adult hummingbird (*Glaucis hirsutus*). Semidiagrammatic. Bone is solid black. The arrow shows the dorsal portion of the ventral bar, narrowly separated from the lateral wing of the dorsal bar by connective tissue and a venous sinus. Rostrocaudal motion of the ventral bar in relation to the dorsal bar (not yet demonstrated in hummingbirds) is required for independent raising and lowering of the tip of the upper jaw (demonstrated in some hummingbirds). Abbreviations: con. tis. = connective tissue, dor. bar = dorsal bar, lat. wing = lateral wing, ven. bar = ventral bar, ven. sin. = venous sinus.

Nasal part.—The maxillary process of the nasale (processus maxillaris nasale) in adult hummingbirds is flattened and appears to have undergone torsion along its length (Fig. 8), a conformation apparently unique to hummingbirds (Moller 1930, Livezey and Zusi 2006). This configuration probably results from restructuring of bone during development to accommodate passage of an adjacent artery (probably arteria ethmoidalis, ramus lateralis). The nasal part of the upper jaw includes the nasal cavity (cavitas nasale) and its associated rostral conchae (concha rostralis), the latter unossified in outgroups but ossified in many hummingbirds. (Variation in the cavity and conchae is described for hummingbirds in Section II.) Caudally, the nasal part is defined largely by the morphology of the nasale and its relation to the bony nasal opening and the craniofacial hinge (Fig. 8A). Partial ossification of the roof of the nasal part (tectum nasi) occurs rostral to the nasale in Trochilines, but in Hermits the ossified nasal roof abuts the nasale, and both ossifications influence the posterior contour of the bony nasal opening. The latter configuration occurs also in some swifts (e.g., *Streptoprocne semicollaris*). *Eutoxeres* differs from other Hermits in that the notch medial to the maxillary process of the nasale extends caudally almost to the craniofacial hinge. Although Hermits and Trochilines differ from each other in the structure of the nasal part, both differ from the simple structure of Hemiprocnidae and most Apodidae (Fig. 8B), in which a nasal roof is absent or very small.

CRANIOFACIAL HINGE

The base of the prepalatal upper jaw and the craniofacial hinge (or bending zone) of birds have been characterized as either holorhinal or schizorhinal (Garrod 1873b). "Holorhinal" indicates a caudal border of the bony nasal opening that terminates rostral to the craniofacial hinge and usually is more or less rounded. "Schizorhinal" typically indicates a bony nasal opening that extends caudally beyond the craniofacial hinge (Garrod 1873b, Bock 1964, Zusi 1984) in a narrow or slit-like (less commonly rounded) contour. In Trochilines, the bony nasal

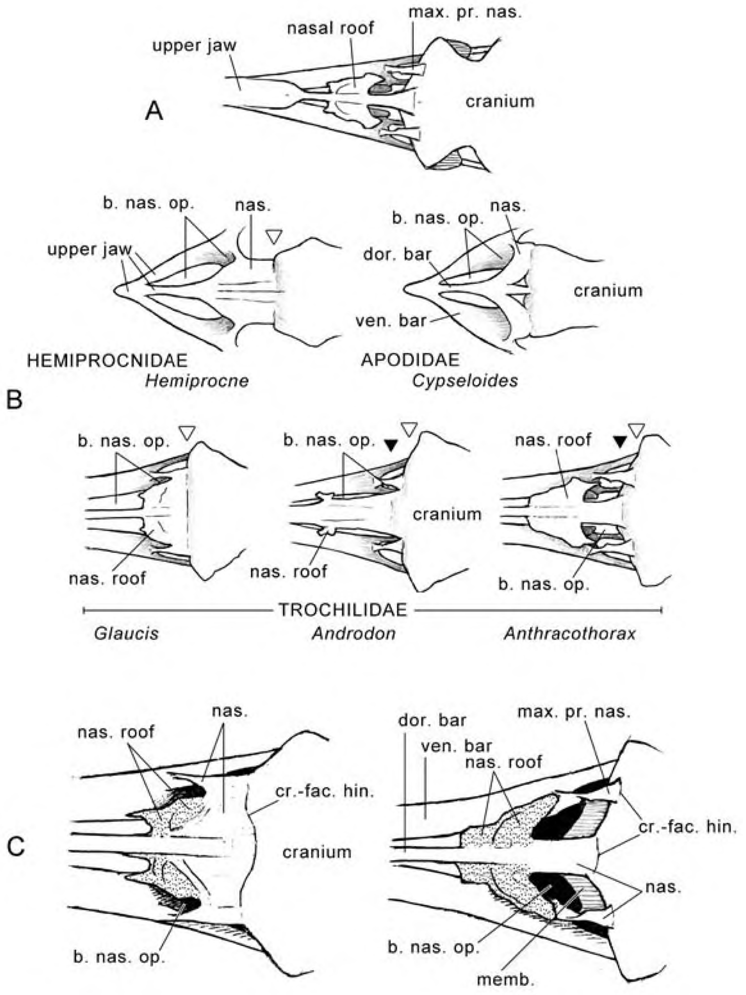

FIG. 8. Variation in the craniofacial hinge and bony nasal openings of hummingbirds compared to other Apodiformes. Dorsal views, with most of the prepalatal upper jaw missing in the hummingbirds. (A) Partial hummingbird skull for orientation of detailed drawings in B and C. (B) Triangles point to the transverse axis or axes of the craniofacial hinge, showing the continuous, single axis in the Hermit (*Glaucis*) and the transected, double axes in the Trochilines (*Androdon and Anthracothorax*). Black triangles show the medial portion of the double hinge. A nasal roof, prominent in most Trochilines, is absent or small in Hemiprocnidae and Apodidae. (C) Comparison of a Hermit (left) and a Trochiline (right). Stipple represents the nasal roof. The hatched membrane in adult Trochilines (ossified in nestlings) is visible in spirit specimens but lost in skeletons. Its widespread occurrence is inferred from the angled medial margin of the maxillary process of the nasale in skeletons of adult Trochilines. See text. Abbreviations: b. nas. op. = bony nasal opening, cr.-fac. hin. = craniofacial hinge, dor. bar = dorsal bar, max. pr. nas. = maxillary process of nasale, memb. = membrane, nas. = nasale, nas. roof = nasal roof, ven. bar = ventral bar.

opening extends caudally almost to, or usually beyond, the craniofacial hinge, and therefore they are essentially schizorhinal. Aegothelidae, Hemiprocnidae, Apodidae, and Hermits are holorhinal.

In many schizorhinal birds the craniofacial hinge has two axes of bending (diaxial), one through the lateral portion of the nasale and the other through the medial portion of the nasale and the frontal process of the premaxillare (Fig. 8A). If the two axes are sufficiently separated, cranial kinesis produces forces that require bending not only at the craniofacial hinge but also *within* the prepalatal upper jaw (rhynchokinesis) (Zusi 1962, 1984). Close apposition of the two bending axes in Trochilines probably reduces the conflicting forces, and rhynchokinesis may be minimal. Hermits have only a single axis (monaxial).

Conformation of the nasale and bony nares is complicated in Hermits by partial ossification of the nasal roof, and in Trochilines by bone resorption during development. An understanding of the nasale in adult Trochilines is best gained by revisiting the juvenile and adult specimens of *C. swainsonii* discussed above. The nestling is holorhinal, with bony nasal openings ending in a rounded contour rostral to the craniofacial hinge (Fig. 6A). During development the calcified rostrodorsal portion of the nasale evidently becomes decalcified and the unossified portion of the nasal opening is correspondingly expanded caudally beyond the craniofacial hinge; however, the originally calcified portion of the nasale is still discernable as a thickened portion of the membranous roof of the nasal cavity, and the angular projection on the medial rim of the maxillary process of the nasale in most adult Trochilines indicates the rostral location of the thickened membrane (see Fig. 8C). Thus, *C. swainsonii* changes from monaxial and holorhinal in the nestling to diaxial and schizorhinal in the adult, a transformation that may be typical of Trochiline hummingbirds.

PALATUM

The palatal upper jaw or palatum, as defined here, consists of the membrane bones forming the roof of the pharynx. Specifically, it includes the jugal arch (arcus jugalis), quadratum, pterygoideum, palatinum, vomer, and portions of the maxillare (Fig. 9). Whether or not hummingbirds and swifts have an aegithognathous palate has been debated (Huxley 1867, Parker 1878, Lowe 1939), but this question is less important than comparison of the individual constituents of the palatum (Zusi and Livezey 2006).

Maxillare.— In all outgroups the palatal process of the maxillare (processus palatus maxillaris, often referred to as "maxillopalatine") passes dorsal to the rostral portion of the palatine, or rostral bar (pila palatini; synonym of "processus rostralis palatini" of Zusi and Livezey 2006), with limited or no direct contact between them. In Aegothelidae the palatal process passes medial to the rostral bar of the palatinum and becomes truncate or angled slightly caudad (Fig. 9A). By contrast, in Hemiprocnidae and Apodidae a marked caudal extension of the tip of the palatal process occurs as a flattened blade between the rostral bar and rostromedial process (processus rostromedialis) of the palatinum (Fig. 9B, C). The rostral bar is dorsoventrally compressed rostrally, forming a palatine hinge (zona flexoria palatini). In hummingbirds the palatal process of the maxillare is broad at its base and narrow medially, and it is fused with the dorsal margin of the rostral bar (Fig. 9D). The resulting T-bar structure resists lateromedial and dorsoventral bending and forms a firm pterygopalatine arch (arcus pterygopalatinus) between the palatum and prepalatal upper jaw. In some apodids the medial portion of the palatal processus has limted synostosis with the medial edge of the rostral bar, but both processes are dorsoventrally flattened, and dorsoventral flexibility exists as a palatine hinge.

Vomer.—The avian vomer is derived from bilaterally paired elements and consists of a body (corpus vomeri) and paired pterygoid processes (processus pterygoideus). The vomer of *Aegotheles* is markedly pneumatic and inflated (Fig. 9A). Its body is rod-like and truncate rostrally, and it abuts the palatal process of the maxillare just medial to the palatinum. At that juncture the palatal process terminates or extends slightly caudad, but it lacks the prominent caudal extension seen in Hemiprocnidae and Apodidae. The pterygoid processes are variously fused rostrally. In Hemiprocnidae and Apodidae the vomer is less pneumatic and the pterygoid processes less fused; the body is blunt rostrally but flared rostrolaterally to form processes that closely approach or abut the medial base of the palatal process as a syndesmosis (Fig. 9B, C).

The vomer in hummingbirds (Fig. 9D) makes no direct contact with any part of the maxillare, and the anterolateral margin of the vomeral body is only distantly connected by membrane to the palatal process of the maxillare and the caudal tip of the rostral concha (concha rostralis). Lowe (1939) stated that the pterygoid process of the vomer abuts the anterior tip of the pterygoideum, but my interpretation of a cleared and stained specimen of a juvenile *C. swainsonii* is that the caudal portion of the palatinum separates these bones. In any case, Lowe's contention that hummingbirds display a "palaeognathous condition" is unjustified (Zusi and Livezey 2006).

Unlike all outgroups, almost all hummingbirds exhibit a bony, vomeral spine (spina vomeris) directed rostrally from the vomeral body (Fig. 9D). The spine lies ventrally within the nasal septum

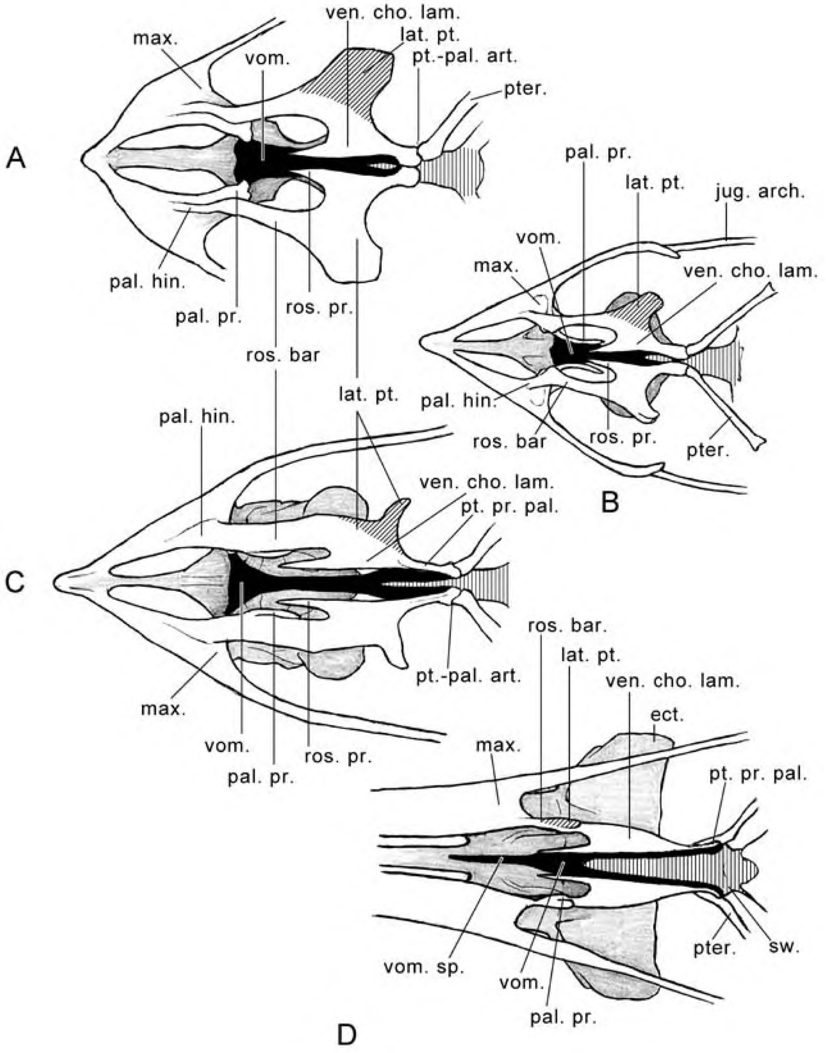

FIG. 9. Palatum of Aegothelidae and Apodiformes. Ventral view. The parasphenoidal rostrum is vertically hatched, the lateral part of the palatinum is obliquely hatched, and the vomer is solid black. Abrupt, caudal broadening of the parasphenoidal rostrum, extreme reduction of the lateral part of the palatinum, lateral displacement of the pterygoid process of the palatinum, and presence of a vomeral spine characterize Trochilidae. (A) Aegothelidae (*Aegotheles*). (B) Hemiprocnidae (*Hemiprocne*). (C) Apodidae (*Hirundapus*). (D) Trochilidae (*Threnetes*). Abbreviations: ect. = ectethmoidale, jug. arch = jugal arch, lat. pt. = lateral part of palatinum, max. = maxillare, pal. hin. = palatine hinge, pal. pr. = palatal process of maxillare, pter. = pterygoideum, pt.-pal. art. = pterygopalatine articulation, pt. pr. pal = pterygoid process of palatinum, ros. bar = rostral bar of palatinum, ros. pr. = rostromedial process of palatinum, sw. = swelling of parasphenoidal rostrum, ven. cho. lam. = ventral choanal lamella of palatinum, vom. = vomer, vom. sp. = vomeral spine.

(septum nasi), and it may be strong and linear or more slender and sometimes angled dorsally. As an artifact, the entire spine may become displaced toward the dorsal bar of the upper jaw in cleaned skeletons.

Palatinum.—In most birds, including hummingbirds as described above, the pterygopalatine arch transmits compression and tension forces during cranial kinesis (Zusi and Livezey 2006). In outgroups of this monograph, the rostral bar of the palatinum is dorsoventrally flattened, forming a palatine hinge just caudal to its association with the maxillare. The palatine hinge is associated with prokinesis. By contrast, in hummingbirds the rostral bar has a T-bar form and lacks a palatine hinge, thus providing a stronger arch that is compatible with rhynchokinesis. Therefore, I disagree with the conclusion of Moller (1930) that the palatinum of hummingbirds is too thin anteriorly to be useful for transmitting forces during kinesis.

Caudal to the rostral bar, the palatinum of hummingbirds consists largely of a choanal part, which delimits a portion of the respiratory passage. Although the dorsal choanal lamella (lamella choanalis dorsalis) is poorly developed in hummingbirds, the ventral lamella (lamella choanalis ventralis) is prominent and broad caudally, with wide bilateral separation of the pterygoid processes of the palatinum (Fig. 9). The choanal region in outgroups is less expanded, and the pterygoid processes (processus pterygoideus) of the palatines abut or closely converge toward the midline.

The lateral part of the palatinum (pars lateralis palatini) is well developed in *Aegotheles*, and in Hemiprocnidae and Apodidae typically forms as a prominent, caudolaterally directed process (Fig. 9). By contrast, the lateral part of the palatinum in hummingbirds is restricted to a small tubercle or short hook (hamulus). As noted by Lowe (1939), development of the lateral part of the palatinum is correlated with width of the mouth—it is wide in outgroups and narrow in hummingbirds. From the tip of the lateral part of the palatinum, m. pterygoideus passes caudally to the tip of the medial process of the mandible (processus medialis mandibulae; Morioka 1974, Zusi and Bentz 1984). This portion of m. pterygoideus is thus oriented roughly parallel to the midsagittal plane of the skull throughout Apodiformes, maximizing its efficiency in lowering the prepalatal upper jaw (kinesis) and in rotating the caudal part the mandiblar ramus laterally (streptognathism).

Pterygoideum and basipterygoid process.—A functional basipterygoid process is absent from *Aegotheles* and Apodiformes. The pterygoparasphenoidal articulation (articulatio pterygoparasphenoidalis) in swifts is denoted on the parasphenoidal rostrum by a faint swelling. In hummingbirds this articulation occurs on the anterior, medially inclined surface of a marked swelling near the base of the parasphenoidal rostrum (Fig. 9D). The swelling is more pronounced caudally and ends abruptly. This structure in hummingbirds has been interpreted as fused basipterygoid processes by some authors. For example, Parker (1879) and Lowe (1939) each stated that the "basipterygoid process" in hummingbirds was shifted farther forward than in any other bird. In swifts and crested swifts a few adult specimens retain nonfunctional vestiges or spicules of basipterygoid processes caudal to the pterygoidal articulation on the parasphenoidal rostrum (*Hemiprocne mystacea* USNM 560827, 560829; *Streptoprocne niger* USNM 290999, 555770; *S. phelpsi* USNM 622775, 622774; *S. rutilus* USNM 614122). Similar vestiges, and corresponding spicules on the pterygoideum, also occur rarely in Podargidae (*Batrachostomus javensis* AMNH 9189), indicating their loss in most Apodidae, Hemiprocnidae, and Podargidae. I found no such vestiges in hummingbirds.

The pterygoideum of outgroups has a uniform, rod-like shape and lacks a dorsal process (processus dorsalis). Anteriorly the pterygoideum articulates with the parasphenoidal rostrum and with the palatinum. Caudally, the articulation in *Aegotheles*, Hemiprocnidae, and Apodidae is a ball-and-socket structure located ventral to the orbital process (processus orbitalis) on the body of the quadratum (corpus quadratum), with additional linear contact dorsally on the quadrate body. The linear contact is reduced or lost in hummingbirds, leaving only the ball-and-socket joint.

The palatine part of the pterygoideum (pars palatina pterygoidei)—"mesopterygoid" of Parker (1879)—in juvenile swifts becomes fused with the palatinum in adults. Thus, the articulation that appears to be between pterygoideum and palatinum in adult swifts is actually between the palatine part of the pterygoideum and the main body of the pterygoideum (pars proprius pterygoidei) and represents an intrapterygoid articulation (articulatio intrapterygoidea). The same is true of hummingbirds, as seen in juvenile and adult *C. swainsonii* (see also Parker 1879). However, the intrapterygoid articulation may be present or absent in adult hummingbirds, and localized flexibility of the bone probably exists even in its absence (see Zusi and Livezey 2006). A pterygopalatine articulation (articulatio pterygopalatina) is present in *Aegotheles* and Apodiformes.

Quadratum.—The orbital process of the quadratum is extremely reduced in Aegothelidae, and is short, blunt, and narrow in Hemiprocnidae and Apodidae. In Trochilidae the process is better developed and often manifested as an acute angle of the rostral margin of the quadratum in lateral view (Fig. 4A: 11). As noted by Shufeldt (1885) for *Archilochus alexandri*, the long axis of the otic process (processus oticus) of the quadratum in lateral view is oriented more horizontally in many hummingbirds than in outgroups. I did not measure variation in this character throughout hummingbirds, but it may play a significant role in kinesis and nectar eating (see below under *CRANIAL KINESIS*). The quadratum of hummingbirds and all outgroups is similar in having pneumatic foramena (foramen pneumaticum) on the caudal surface of its otic process and in lacking a caudal condyle (condylus caudalis).

The jugal arch articulates with the quadratum at a deep cotyla in the anterolateral surface of the lateral condyle (condylus lateralis) of the quadratum in hummingbirds (Fig. 4A: 18), but it rests on top of the condyle as a weak syndesmosis in outgroups. The lateral condyle of hummingbirds is located more distally on the body of the quadrate than in outgroups.

MANDIBULA

The avian mandibula may be divided into (1) a symphysial part with a more-or-less protrusive tip where the rami (ramus) abut rostrally and become fused, and (2) the diverging free rami (Fig. 5). The latter are subdivided into two parts; the intermediate part (pars intermedia) and the caudal part (pars caudalis), often separated by the rostral mandibular fenestra (fenestra rostralis mandibulae). The caudal part of the ramus receives insertions of jaw muscles and the facets and condyles of the quadratomandibular articulation (articulatio quadratomandibularis). The mandibular symphysis approximately equals the symphysis of the prepalatal upper jaw in length in *Aegotheles* and Apodiformes.

Lateromedial flexibility is present in the rami of *Aegotheles* and Apodiformes, particularly at two intramandibular hinges of the ramus—an anterior one (zona flexoria intramandibularis rostralis) caudal to the symphysial part and a caudal one (zona flexoria intramandibularis caudalis) between the intermediate and caudal parts. Only in Aegothelidae does a narrowing of the rami mark the anterior hinge, and the caudal hinge is poorly demarked or absent in Apodiformes. Lateromedial flexibility of the free ramus in hummingbirds is possible at or just caudal to the rostral mandibular fenestra and throughout the intermediate part of the ramus. Their mandibula differs from that of passerine nectarivores in greater length of the free rami in relation to the symphysial part (Fig. 10A, D).

Unlike outgroups, all bones of the adult mandible of hummingbirds are fused.

JAW ARTICULATION

The quadratum of Apodidae and Hemiprocnidae has a prominent, ridge-like medial condyle (condylus medialis) of the quadratomandibular articulation oriented caudolaterally to rostromedially. The articular fossa (fossa articularis) of the mandible in outgroups contains a moderately developed lateral cotyla (cotyla lateralis) and well-developed medial cotyla (cotyla medialis), both trough-like, oriented rostromedially, and bordered by prominent ridges. The pneumatic foramen (foramen pneumaticum) of the articulare opens just medial to the medial cotyla, and there is no pronounced medial process medial to the foramen. By contrast, hummingbirds (Fig. 10B) have a poorly defined lateral cotyla and a shallower, more caudo-rostrally oriented medial cotyla, neither of which is bordered by a prominent ridge. The pneumatic foramen lies between the caudal end of the medial cotyla and a well-defined, medial process of the mandible.

A medial portion of the postorbital ligament (ligamentum postorbitale) attaches on the jugal arch in some hummingbirds. The main, lateral portion of the ligament makes no separate connection with the mandibula. Instead it merges with the lateral jugomandibular ligament (ligamentum jugumandibulare laterale), which extends rostroventrally from the caudal end of the jugal arch or adjacent quadratum to the lateral surface of the mandibula (Fig. 10C).

CRANIAL KINESIS

Despite the name, "cranial kinesis" in modern birds does not refer to mobility of parts of the cranium, but rather to movement of the upper jaw on the cranium, or mobility within the prepalatal upper jaw.

Apodiformes.—The configuration of the jaw in *Aegotheles*, Hemiprocnidae, Apodidae, and Hermits is holorhinal, and the jaw motion is prokinetic around a single craniofacial hinge axis, as confirmed by manipulation of hydrated

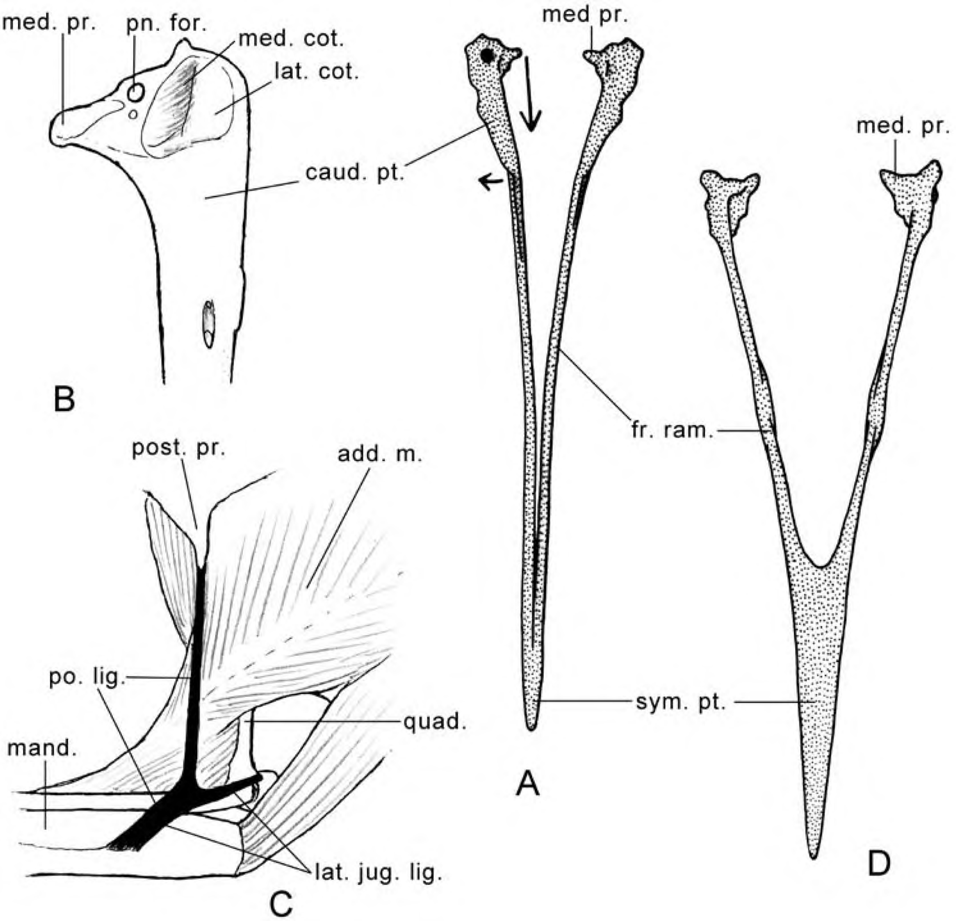

FIG. 10. Mandibula and associated ligaments typical of hummingbirds, and a mandibula typical of nectarivorous passerines. (A) Mandibula of hummingbird in ventral view. Long arrow shows force vector of pterygoideus muscle on the medial process of the mandibula, associated with lateral motion (short arrow) at the caudal bending zone of the free mandibular ramus around the rotational axis (black dot) of the jaw articulation. (B) Detail of articular fossa of a hummingbird mandibula in dorsal view of the left ramus. Most notable is the presence of a process (med. pr.) that is lacking in other Apodiformes. (C) Jaw articulation of hummingbird; jaw muscles shaded, and mandibular ligaments shown in black; left, lateral view. Unlike other Apodiformes, the postorbital ligament has no separate attachment on the mandibula; instead it joins the lateral jugomandibular ligament in a common attachment. (D) Mandibula typical of nectarivorous passerines, showing much enlarged symphysial part; there is little or no lateral motion of the free ramus. Abbreviations: add. m. = adductor mandibulae externus muscle, caud. pt. = caudal part of mandibular ramus, fr. ram. = free mandibular ramus, lat. cot. = lateral cotyla, lat. jug. lig. = lateral jugomandibular ligament, mand. = mandibula, med. cot. = medial cotyla, med. pr. = medial process of mandibula, pn. for. = pneumatic foramen, po. lig. = postorbital ligament, post. pr. = postorbital process, quad. = quadrate, sym. pt. = symphysial part of mandibula.

skeletons. Some Trochiline hummingbirds and non-apodiforms, notably many charadriiforms and gruiforms, pigeons, and ibises, have an upper jaw that is flexible at one or more hinges rostral to the craniofacial bending zone. The bony nares extend backward, sometimes as a slit, to transect the portion of the craniofacial hinge formed by the nasale, and two hinge axes are usually present. This configuration of the jaw is schizorhinal and the jaw motion, which usually entails dorsoventral bending of the bill tip, is rhynchokinetic (Zusi 1984). Several early studies indicated presence of independent bill-tip movement in hummingbirds (Nitzsch 1816, 1817; Moller 1930; Simonetta 1967).

Prokinesis maintains static relations between the dorsal and ventral bars of the prepalatal upper jaw during jaw movement because the two bars are firmly connected proximally by the nasale. Rhynchokinesis includes rostrocaudal translational motions of the ventral bar in relation to the dorsal bar, made possible by separation of the nasale into two independent parts. Thus, fusion of the nasal capsule or conchae with both bars of the upper jaw are possible only in prokinetic birds. Despite extensive ossification in the nasal region of many hummingbirds, the lack of synostosis with the ventral bar in any hummingbird is compatible with rhynchokinesis.

These morphologies are reflected by developmental changes in *C. swainsonii*. During post-hatching development, that species (and all other Trochilines?) transforms a holorhinal and potentially prokinetic, prepalatal upper jaw into a schizorhinal and presumably rhynchokinetic one, while also, curiously, reducing the probability of independent motion of the ventral and dorsal bars required for rhynchokinesis. Such motion would depend on the elasticity of the connective tissue connecting the ventral and dorsal bars (Fig. 7). It is also possible that the midsection of the ventral bar is less mineralized and more flexible than its dorsal and ventral portions (Meyers and Meyers 2005), allowing the bar's ventral portion to move forward and backward, parallel to its more stabilized dorsal portion—a movement analogous to that in rhynchokinetic shorebirds. Unfortunately, precise measurements of cranial kinesis of live hummingbirds and knowledge of the physical properties of the structural components of the prepalatal upper jaw are lacking. The following observations are related to kinesis, first in nearly closed mandibles and second in widely opened ones.

In 1986, I observed captive birds (*Archilochus colubris*) drinking sugar water from an inverted tube feeder (see below under *STREPTOGNATHISM*). At rest, the tomia of the bill tips met precisely when closed. While feeding, the tips of the upper and lower mandibles separated enough to permit the tongue to flick in and out. In lateral view the bill tips vibrated dorsoventrally without actually closing, as the tongue flicked in and out. During feeding, the tongue protruded a third or less the length of the bill whether the bill tips were submerged in or just beyond the fluid. The tip appeared to be the only portion of the upper jaw in motion. Slight bending of the tip of the upper jaw is shown by Rico-Guevara and Rubega (2011; compare frames A and C of fig. 4) in high-speed video frames of a captive *Amazilia cyanifrons*. These data suggest that distal rhynchokinesis facilitates nectar eating in at least two Trochiline species, and probably many others. Kinetic motion at the tip of the upper jaw occurs while the rest of the bill maintains a nearly closed tube for nectar transport.

My manipulation of fresh specimens of hummingbirds, causing wide opening of the jaws, produced marked bending at the craniofacial hinge in *G. hirsutus* and *P. guy*, and moderate bending in *Anthracothorax nigricollis* and *Amazilia tobaci*. If these examples reflect differences in both form and magnitude of cranial kinesis between Hermits and Trochilines, they supplant the tentative conclusions about hummingbird kinesis by Zusi (1984). There are no data on kinesis for Hermits during nectar eating, but with the bill opened widely they appear to exhibit prokinesis.

Bending within the upper jaw of highly rhynchokinetic Scolopacidae occurs usually at flattened regions (hinges) of the dorsal and ventral bars, and the axes of bending are circumscribed (Zusi 1984). Free rostrocaudal movement of the ventral bars in relation to the dorsal bar causes the bill tip to rotate about the distal hinge on the dorsal bar. Even the longest-billed shorebirds (e.g., Long-billed Curlew) maintain the integrity of their bill shape under the forces of probing by a strongly configured dorsal bar (caudal to its anterior hinge), and by immobility of the medial portion of the craniofacial hinge by fusion with the underlying mesethmoid. Some long-billed hummingbirds (e.g., *Ensifera* and *Coeligena*) have similarly lost mobility of the medial portion of the craniofacial hinge, leaving distal (bill tip) rhynchokinesis as their only option.

Cranial kinesis always is driven by muscles that rotate the quadratum about its squamoso-otic articulation (articulatio quadrato-squamoso-otica). The anteroposterior component of this motion is transmitted through the palatum to the ventral bars of the prepalatal upper jaw. In prokinetic birds this produces rotation of the entire prepalatal upper jaw around the craniofacial hinge axis. In rhynchokinetic species, palatal motion is passed directly to the ventral base of the symphysial part through the ventral bar, causing upward tilt of the tip of the jaw around the anterior hinge of the dorsal bar. Even a slight anteroposterior motion of the ventral bar in a slender upper jaw would cause significant rotation of the symphysial part (Zusi 1984). A more horizontal orientation of the body of the quadratum in hummingbirds mentioned earlier would limit the forward component of the quadrate's rotation and maximize the mechanical advantage of m. protractor quadrati et pterygoidei muscle on the quadrate—actions that would raise the symphysial part of the upper jaw forcefully through a limited angle. The symphysial part is lowered when m. pseudotemporalis profundus rotates the quadratum ventrolaterally. Antagonistic actions of these two muscles could be significant for safely maintaining rapid but limited motions of the bill tip during nectar eating.

By contrast, arthropod eating often employs wide opening and rapid closing of the jaws. Maximum opening is effected by m. protractor quadrati et pterygoidei (raising the prepalatal upper jaw) and m. depressor mandibulae (depressing the lower jaw). Maximum power for closing the jaws is found in m. pterygoideus (prepalatal upper jaw) and m. adductor mandibulae externus and m. pseudotemporalis superficialis (mandibula). Lack of extensibility in the postorbital ligament of many birds may play a role in coordinating opening of both jaws (Bock 1964, Zusi 1967). This role may pertain in *Chaetura* and *Hemiprocne* because the postorbital ligament makes direct contact with the mandibula. In hummingbirds the postorbital ligament merges at an obtuse angle with the lateral jugomandibular ligament (Fig. 10C). Tension in the postorbital ligament would not occur until the rostral section of the lateral jugomandibular ligament became collinear with the main portion of the postorbital ligament in the widely opened mandible, as confirmed by my manipulation of the jaws in cleared and stained specimens. The postorbital ligament therefore has no coupling effect on the nearly closed jaws during nectar eating.

Passeriformes.—Long-billed nectarivores occur in only two avian orders within Aves—Apodiformes (Trochilidea) and Passeriformes (Meliphagidae, Zosteropidae, Nectariniidae, Drepanidini, Thraupini, and Mohoidae; see Fleischer et al. 2008). All of these birds also eat arthropods. The upper jaw of passerine nectarivores is holorhinal and has a monolithic structure that bends only at a single craniofacial bending zone (prokinesis). Housing of the tongue and transportation of nectar are accommodated by a deep, internal concavity of the symphysial part and of the adjacent portion of the nasal part. In the most highly specialized species the ventral bar and adjacent wall of the symphysial part are oriented dorsomedially, and superficially resemble that of hummingbirds. The lateral walls of the passerine upper jaw, however, are less vertical than in hummingbirds, and they are largely associated with the symphysial part (Fig. 10). Except at the tomia, the lower jaw does not fit within the upper jaw as it does in hummingbirds.

STREPTOGNATHISM

Many birds have (at least limited) lateromedial flexibility of the mandibular rami associated with lateromedial rotation at the quadratomandibular articulation (Zusi 1967, Zusi and Warheit 1992). Streptognathism is the capability of pronounced lateral bowing within the rami of the mandibula in the living bird (Bühler 1981). This capability is indicated by the presence of two ramal bending zones (hinges), a rostral one near the symphysial part and a caudal one between the rostral and caudal parts of the rami. The caudal intraramal hinge is not vertically oriented on the horizontal ramus; rather, its axis slopes caudoventrally from the dorsal margin in lateral view. As a result, when lateral bowing occurs at the hinge, the portion of the bill anterior to the hinge also bends downward in relation to the rest of the mandibula (Zusi and Warheit 1992). Streptognathism allows some aerial insect-eaters (Caprimulgidae) to broaden the opened mouth as a funnel (Bühler 1970); the mechanism for similar broadening of the mouth in Apodidae has not been studied (but see photograph of *Apus* in Tidman 2007:489). Pelicans and some hummingbirds are unusual in their capability of strong streptognathism, despite the absence of an anatomically defined caudal intraramal hinge. The degree of flexibility in bone of the pelican's mandibula is inversely related to its mineral content (Meyers and Meyers 2005), a relation that may also pertain to flexibility in hummingbirds.

Activation of m. pterygoideus at its attachment on the medial process of the mandible causes lateral rotation of the caudal portion of the ramus around the quadratomandibular articulation (Fig. 10A) and maximum widening between the bilateral, caudal intraramal hinges. Stored energy within the bent mandible probably reverses bowing upon relaxation of the muscle, perhaps aided by contraction of m. intermandibularis. In hummingbirds the lateral contour of a relaxed ramus of the closed mandible is somewhat concave in dorsal or ventral view, such that the entire rostral portion of the mandible is markedly narrower than the caudal portion.

I have observed a limited form of streptognathism of the *fully closed* jaw in captive hummingbirds (*Archilochus colubris*) while they drank nectar. Observations with a dissecting microscope were made on an adult male, two females, and an immature male. From ventral view of birds that were not feeding, I saw a gap between the lateral walls of the lower and upper mandibles from the symphysial part to the rictus, and the intermandibular, gular region (regio gularis) was concave. When feeding began, the mandibular rami spread laterally and made contact with the ventral bars of the upper mandible and the gular region became stretched and flattened (Fig. 11A, B). These relations were maintained throughout feeding, and no nectar leaked from the jaws except for several drops at the rictus. In other species (*Eulampis jugularis*, *Orthorhynchus cristatus*, and *Cyanophaia bicolor*), observed in the field, the mandibles did not always form a tight seal during drinking, and some liquid escaped along the tomia. Whether this limited streptognathism occurred through muscle contraction (m. pterygoideus) or passively by pressure of nectar within the mandibles is unknown. In either case it apparently expanded the tubular structure of the bill during nectar transport. In passerine nectar-eaters, the mandibular symphysis is long, constant in shape, and suitable for transporting nectar in the closed bill (Fig. 11C). Whether the tube is maintained during nectar uptake is not known.

A well-developed streptognathism of the opened mandible also occurs in some hummingbirds. A few species of *Phaethornis* are known to spread the rami of the opened jaw during display, revealing a brightly colored mouth lining. Reference to spreading is stated explicitly by Snow (1973b) for *P. ruber*, Snow (1974) for *P. guy*, Stiles and Wolf (1979) for *P. guy*, and Schuchmann (1987) for *P. griseogularis*. Snow (1973b:171) observed that "In displaying the gape the rami of the lower mandible were spread wide apart

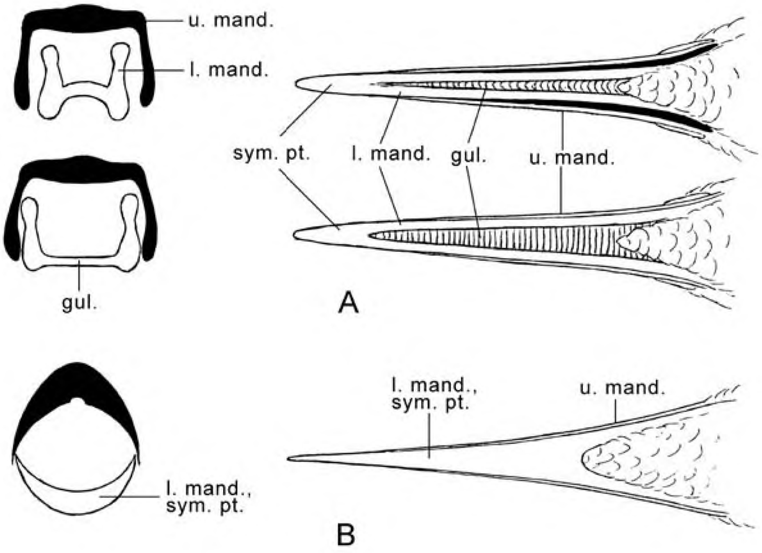

FIG. 11. Structure of the mandibles in relation to nectar eating in hummingbirds and passerines. Semidiagrammatic representation of mandibles in ventral view (right), and transverse section, with upper mandible shown in black (left). (A) Mandibles of a hummingbird while relaxed, showing a lateral gap between the mandibles in solid black (above), and while drinking, with manibular rami spread, the gular region stretched, and the gap between mandibles closed (below). In lower left, note the increased space for nectar transmission in the bill while drinking. (B) In passerines, nectar transmission is largely through the symphysial parts of the mandibles, and there is no capacity for spreading of the mandibular rami. Abbreviations: gul. = gular region, l. mand. = lower mandible, sym. pt. = symphysial part, u. mand. = upper mandible.

so they were about four times further apart than when the beak is closed." Similarly, Snow (1974:285) noted that

> The gape-flash is very spectacular and looks like the sudden flashing of a red light in the dark forest. This effect is produced by the light shining through the red skin of the gape stretched between the rami of the lower mandibles. The two rami are flexible and when the bird opens its beak to make the *tock* they bow apart to a distance of approximately 15mm.

INTEGRITY OF THE BILL

How does the long, slender bill of the Sword-billed Hummingbird (*Ensifera*) maintain its shape against external forces and while performing precise motions of the bill tip when drinking nectar? Motions of the tip of the upper mandible in *Ensifera* and in other Trochilines originate in the quadratum and are transmitted to the ventral bars within the sheath of the ramphotheca. The prepalatal upper jaw of hummingbirds is inherently flexible throughout much of its length because the dorsal and ventral bars are usually long and flattened. In adult birds the upper mandible forms a partial tube. This skeletal morphology and the leathery rhamphotheca resist bending in any plane unless stressed by cranial kinesis or external forces other than gravity. Additionally, in the closed bill, the lower mandible is largely embraced by the upper mandible, completing a tubular conformation that strengthens even extremely long, slender, and lightweight bills. General flexibility, possibly related to reduced mineral content of the bone, would permit bending and protect the bill from fracture if stressed externally. Such forces may be considerable when hummingbirds peck at rivals during territorial fights.

Hyobranchial Apparatus

In outgroups and hummingbirds this complex consists of the fleshy tongue and its supporting hyobranchial apparatus (Fig. 12) and muscles. The tongue is supported basally by a paired paraglossum that articulates with the basihyale. The articulation allows flexion and extension of the paraglossum on the basihyale in the midsagittal plane. Caudally, the basihyale supports a paired, laterally diverging rod, the ceratobranchiale, which can be flexed or extended on the basihyale in both frontal and midsagittal planes. The epibranchiale abuts the caudal end of the ceratobranchiale at a syndesmotic articulation, and together they constitute the hyoid horns. Caudal to the ceratobranchiale articulations, an ossified urohyale is fused with the basihyale in swifts and hummingbirds. The urohyale of swifts supports the larynx, but that of hummingbirds is shorter and there is no support for the larynx by the hyobranchial skeleton. Through its extrinsic and intrinsic muscles, the hyobranchial apparatus supports and moves the tongue and floor of the pharynx. When the bill is closed and the tongue retracted, the tongue and paraglossales occupy the mouth cavity and the ceratobranchiales lie largely below the floor of the mouth; the basihyale represents a link between the tongue and hyoid horns (Fig. 12). With respect to hummingbirds, Weymouth et al. (1964:254–255) wrote that

> Lying immediately deep to M. mylohyoideus is a tough sheet of tissue which forms part of the floor of the oral cavity. Within the oral cavity the basihyal and its musculature are surrounded by a dense tube of fibrous tissue formed by a series of ringlike bands separated by less dense connective tissue. This dense tube is composed of an outer, covering layer of statified squamous epithelium underlain first by a thin layer of loose connective tissue and then by a dense ligament containing large amounts of collagenous and elastic fibers. The tube apparently holds the basihyal in position and permits it to move freely as the tongue is protruded or retracted.

I refer to this tube as "elastic tube" (tuba elastica)—a structure noted over a century ago, but not named, by Lucas (1897). The tongue of outgroups is short, broad, and roughly triangular, whereas that of hummingbirds is long and slender. Neither the elastic tube nor capability for strong protrusion of the tongue is present in the outgroups.

The paraglossales of hummingbirds are short despite their support of a long, partly cartilaginous tongue that occupies most of the bill. In spirit specimens the tongue of *Ensifera ensifera* (USNM 505429) was 104 mm long and the lower jaw (from the rictus (angula oris) 108 mm, whereas the tongue of *Ramphomicron microrhynchum* (USNM 615936) was 12.6 mm long, and the mandible from rictus 12 mm. The basihyale of hummingbirds is laterally compressed and almost completely occupied laterally by m. hypoglossus obliquus, which rotates the paraglossum

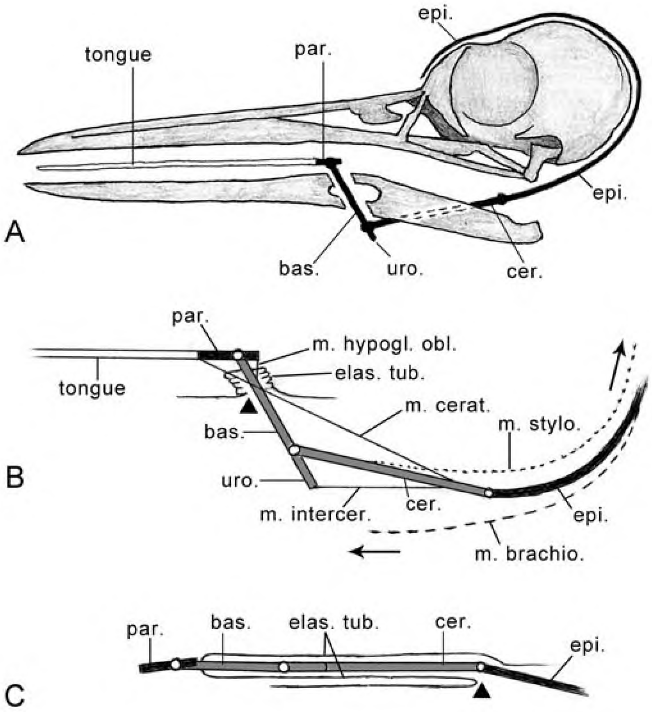

FIG. 12. The hyobranchial apparatus of hummingbirds. (A) Hyobranchial elements in black; skull in gray. Mandibula removed from quadrate and separated at the rostral mandibular fenestra. Semidiagrammatic. (B, C) Diagrammatic representation of hyobranchial elements in relation to the elastic tube and hyobranchial muscles. Paraglossum and epibranchiale in solid black; basihyal and ceratobranchiale in gray; open circles are articulations. Black triangles indicate stable position of base of elastic tube. Arrows show direction of force on hyobranchial apparatus from muscle contraction. (B) Schematic representation with tongue retracted, showing collapsed elastic tube in floor of mouth. Intrinsic muscles are represented by continuous lines, and extrinsic muscles by dashed and dotted lines. With bony elements largely free of the elastic tube, intrinsic muscles could effect flicking of the tongue. (C) With the tongue fully protracted, the basihyale and ceratobranchiale are enclosed in the expanded elastic tube, and only the extrinsic muscles could control tongue flicking. Abbreviations: bas. = basihyale, cer. = ceratobranchiale, elas. tub. = elastic tube, epi. = epibranchiale, m. branchio. = branchiomandibularis muscle, m. cerat. = ceratoglossus muscle, m. hypogl. obl. = hypoglossus oblique muscle, m. intercer. = interceratohyoideus muscle, m. stylo. = stylohyoideus muscle, par. = paraglossum, uro. = urohyale.

and tongue upward around the basihyal. When the tongue is retracted, its base lies just rostral to the larynx and is attached to the compressed, elastic tube from the floor of the mouth. The two ceratobranchiales diverge from their articulation with the basihyale and extend caudally roughly to the jaw articulation. I found that the ceratobranchiales of a swift and hummingbird of equal body size (indexed by coracoideum length) were approximately equal in length. Most variable in hummingbird genera is the epibranchiale, which always exceeds the ceratobranchiale in length; commonly it passes around the occiput and terminates mid-dorsally on the cranium, and exceptionally it extends forward beyond the craniofacial hinge, sometimes into the bony nasal opening. By contrast, the epibranchiale of swifts is shorter than the ceratobranchiale. The ceratobranchiales are slender and cylindrical, but the epibranchiales are dorsoventrally compressed.

Although a woodpecker can actively change the direction of the tip of its tongue, this capability is not present in hummingbirds. In many respects woodpeckers are fundamentally different from hummingbirds in the structure of the tongue and hyobranchiales (Lucas 1891, Scharnke 1931a, Bock 1999). The tongue and paraglossales form a relatively short, stiff unit that can be extruded far beyond the bill tip, where it can be guided in different directions by the hyobranchial muscles. Except for protrusion and retraction, the less protrusable, flexible tip of the hummingbird's tongue is not directly guided by motion of the paraglossales.

MOBILITY OF THE TONGUE

The hyobranchial apparatus of birds serves as a vehicle for movement and stabilization of the tongue, larynx, and floor of the mouth. In most birds the larynx is limited to a position within the pharynx opposite the somewhat elongate opening of the internal nares (choana) as a conduit for breathing, and the tongue has limited rostrocaudal movement. Extension of the tongue far beyond the limit of the bill is a capability of long-billed nectarivores, and coupling of the larynx and hyobranchial apparatus is reduced correspondingly. By manipulation of a cleared and stained specimen (*Threnetes leucurus* USNM 512702), I confirmed that the larynx remained near the base of the elastic tube while the hyobranchial skeleton was greatly protracted and the elastic tube greatly extended. Moller (1930) stated that a tracheal muscle (m. tracheohyoideus) arises from the basihyale in *Eulampis holosericeus*, but neither Weymouth et al. (1964) nor Zusi and Bentz (1984) found any muscle connecting the trachea or larynx to the hyobranchial elements in hummingbirds.

Specimens, photographs, and personal observations indicate that many hummingbirds can extend the tongue almost fully beyond the bill tip (e.g., Grant and Temeles 1992; Schuchmann 1999:478, 507; Temeles et al. 2002). Such extension from nearly closed mandibles may serve to clean the tongue, and the exposed tongue is sometimes used for display (Davis 1958). Extreme extension is accomplished by the paired m. branchiomandibularis, strap-like muscles that originate on the lower jaw and extend back to engulf the epibranchiales along most or all of their length. Contraction draws the base of the epibranchiale forward, and the reduction in muscle length at full contraction must roughly equal the length of the bill. Retraction of the tongue is accomplished by m. stylohyoideus, which originates dorsally on the braincase. This muscle curves around the skull to insert on the basihyale. Motions of the long, slender hyobranchial horns are guided along the braincase by their enclosure in a narrow sheath of connective tissue. By contrast, the stylohyoideus muscle of even the longest-billed passerine nectarivores (e.g., *Arachnothera longirostris*) originates caudal to the orbits; in most hummingbirds the origin is farther forward, almost to or sometimes beyond the craniofacial hinge. Although these two muscles, extrinsic to the hyobranchial apparatus, could power the rapid licking motions of the tongue during nectar eating, another mechanism is postulated below.

Spirit specimens preserved with variously protruded tongues have the basihyale and both ceratobranchiales variously enclosed within the elastic tube. When fully enclosed and the tongue fully protracted, the extended elastic tube occupies almost the full length of the bill (illustrated by Scharnke 1931a: fig. 2). In this state, the enclosed ceratobranchiales and the associated interceratobranchial muscles are pressed together and collinear with the basihyale within the tube. During extreme protraction of the hummingbird tongue, the interceratobranchial muscles probably draw the ceratobranchiales together as they enter the elastic tube. I was surprised to note that in some species, even the rostral portion of the epibranchiale was enclosed by the elastic tube during extreme protraction, and that in those cases the insertion of m. branchiomandibularis began farther caudally on the base of the epibranchiale. (Examples are spirit specimens of *Heliodoxa leadbeateri* [USNM 55623] and *Ensifera ensifera* [USNM 505429], in which the rostral portion of the epibranchiale free of muscle insertion measured 4.9 mm and 22.4 mm, respectively.) All intrinsic muscles of the hyobranchiale apparatus and part of m. stylohyoideus are enclosed in the elastic tube during full extension of the tongue. To reach nectar far beyond the tip of the bill, hummingbirds might fully protract the tongue as described above, and the lapping rate probably would decrease. Ewald and Williams (1982) found the licking rate to be inversely proportional to distance between the bill tip and the sugar solution. However, frequent, full exposure of the tongue when the bird is not feeding indicates that extreme protraction also serves purposes other than nectar uptake.

Here, I propose another mechanism for flicking of the tongue while feeding on nectar. It is possible that the ceratobranchiales and part of the basihyale usually remain caudal to and free from the elastic tube, allowing the two bones to be flexed or extended in both the frontal and sagittal planes, and the basihyale to be flexed or extended against the paraglossum (see Fig. 12). In this configuration, seen in some spirit specimens, the ceratoglossus muscles could cause these flexions simultaneously. Also, extension of the paraglossum on the basihyale by m. hypoglossus obliquus and extension of the basihyale on the ceratobranchials by m. interceratobranchialis could occur. I suggest that alternate contraction of these antagonistic flexor and extensor muscles (see Zusi and Bentz 1984: fig. 4g), when free from the elastic tube, would produce rapid flicking of the tongue tip in and out of the bill as long as the tongue and hyobranchiales were not strongly protracted. During tongue flicking, the amount of tongue protrusion would be roughly proportional to the length of the basihyale and, thus, not highly correlated with bill length. This mechanism could be the norm for nectar drinking. Rapid tongue flicking cannot be observed during normal feeding at flowers, but it is visible at transparent feeders. As proposed by Ewald and Williams (1982), the amount of tongue extension may be similar (adjusted for body size) in both short- and long-billed species, the advantage of long bills mainly being access to nectar in long corollas. Licking rate and its mechanism would remain roughly the same despite differences in bill length.

NECTARIVORY

Detailed discussion of tongue structure and corrections of earlier misrepresentations are found in Weymouth et al. (1964) and are not repeated here. The tongue is capable of taking up nectar in its twin, epidermal tips and of transferring it to the bill and mouth by lapping; nectar is then stripped from the protruding tongue (Paton and Collins 1989) by the nearly closed bill tips (Ewald and Williams 1982). However, the traditional assumption of capillarity of the tongue as a method of initial nectar uptake has been replaced. Rico-Guevara and Rubega (2011) showed that nectar capture involves unfurling and furling of lamellae of the tongue tip that are supported by stiffer rods. Furling of the nectar-filled lamella occurs through Laplace pressure and surface tension forces as the tip leaves the nectar. As noted above, nectar is then stripped from the protruding tongue by the nearly closed bill tip. These authors also point out that the method of nectar transport within the bill leading to swallowing is still unknown.

The lamellae at the tip of the tongue develop gradually in the nestling (Lucas 1891, 1897) and after young birds leave the nest (Scharnke 1931a). Nestlings are fed by regurgitation into their throats by adults, and parental feeding continues after fledging for ~3 weeks (Schuchmann 1999:513). Schuchmann also noted that young learn to feed on flower nectar by watching adults and through trial and error.

The tongue apparently is not involved in the capture of arthropods. However, it was used for licking ashes from the soil by a bird standing on the ground, for licking the wall of a house painted with calcium hydroxide while hovering, and for licking a road surface. In these cases the birds were probably ingesting calcium-rich compounds (Graves 2007, Estades et al. 2008), but whether saliva was used to lubricate the tongue tip in these instances is unknown.

ARTHROPOD CAPTURE

Arthropods (insects and spiders) are an essential part of the diet of hummingbirds and are found in virtually all examined stomachs (Remsen et al. 1986, R. L. Zusi unpubl. data). They are obtained by a variety of foraging techniques (Young 1971, Montgomerie and Redsell 1980, Chavez-Ramirez and Dowd 1992, Stiles 1995). Most prevalent are hover-gleaning from spider webs, leaves, branches, epiphytes, tree buttresses, and other substrates; probing mosses and lichens on branches, while hovering; rapid gleaning between sallying from and returning to a perch; hawking (taking prey from midair) by short dashes and hovering; and hawking after sallying from a perch (Stiles 1995). *Androdon aequatorialis* sometimes probes into curled leaves or cavities for arthropods (Schuchmann 1999:506). Although the sicklebills (*Eutoxeres*) may employ hawking, Hermits specialize in gleaning. The details of capturing and swallowing prey are difficult to observe in the field and are recorded only rarely. Lateral widening of the rami of the mandible apparently is not involved during prey capture when hawking. Instead, while chasing airborne prey (Mobbs 1979) or a spider baling out of its web on a strand of silk (Stiles 1995), the bill is opened wide and the prey is captured in the gape at the back of the mouth. "When a hummer captures an insect in flight, its forward movement forces the prey so far to the rear of the gape that it is readily swallowed. Should for some reason the insect not be taken far enough into the gaping beak, it will be discarded" (Mobbs 1979, captive birds). The role of the neck in insect capture, especially regarding rapid head motions to receive prey into the throat, is unknown.

When gleaning from spider webs or vegetation, hummingbirds take their prey in the tip of the beak, toss it into the air, and fly at it with the bill agape as when hawking. Alternatively, some captive birds may "toss it into the air and then with the beak agape, fly backwards tilting the head so as to enable the prey to fall into the rear of the gape" (Mobbs 1979:28). Similarly, species of high elevations that forage while walking or running on the ground, sometimes hover-assisted, snap at insects and toss them into the air for capture in the gape with the head tilted backwards (Mobbs 1979). Flying insects may be captured also while a bird is perched by lunging with the bill widely open.

Downward bending of the opened mandible in several captive individuals of three species of Trochiline hummingbirds was filmed by Yanega and Rubega (2004). When the bill opened during the act of catching an insect in aerial pursuit, the intermediate parts of the two rami were closely appressed and apparently bent downward. When the insect passed between the opened mandibles and into the wide, posterior mouth opening, the bill snapped shut. In the absence of an anatomically defined, posterior, intramandibular bending zone, no mechanical explanation for ventral bowing of the mandibular rami was proposed.

Rhamphothecal serrations along the tomia of the upper mandible or both mandibles occur in many species of hummingbird (Ornelas 1994). With respect to *Androdon*, Schuchmann (1992) thought the serrations were important in the capture of spiders and nonflying insects. Detailed descriptions of uses of the bill and of the kinds and extent of serrations on the mandibles, their ontogeny, and intraspecific variation throughout hummingbirds are incomplete or lacking. The anatomy of serrations is best studied in live, freshly dead, or alcohol specimens because curling of the rhamphothecae in dried museum skins may prevent observation.

CRANIUM

Ectethmoidale and Lacrimale.—The ectethmoidale extends laterally from the median mesethmoidale. Shufeldt (1885) thought that a lacrimale was fused with the ectethmoidale in hummingbirds, but Parker (1879) and Cracraft (1968) considered it absent. I found vestiges of the lacrimale, each represented by a short caudal spike attached to the caudal margin of the maxillary process of the nasale, in a few specimens (*Hemiprocne comata* USNM 488940; *H. mystacea* USNM 560827, 560828), suggesting absence rather than fusion in Apodiformes. No vestige of a lacrimale was evident in a nestling of *Chlorostilbon swainsonii*. The ectethmoidale of *Aegotheles* is poorly developed, lying entirely medial to the rostral bar of the palatinum. In Hemiprocnidae it is more inflated and extends slightly lateral to the palatinum; that of Apodidae is similar but larger, reaching laterally almost to the jugal arch, and in Trochilidae it extends laterally beyond the jugal arch and supports it; Figs. 4A, B and 9).

Interorbital septum.—In *Aegotheles* and Hemiprocnidae the interorbital septum (septum interorbitale) is complete, but in Apodidae it is thin and usually perforated with one or two interorbital fonticuli (fonticulus interorbitalis). Shufeldt (1885) regarded the interorbital septum of hummingbirds as partially displaced by the orbitocranial fonticulus (fonticulus orbitocranialis), but I found the latter to be restricted to the braincase, and the interorbital septum (Fig. 4A) to be complete in all hummingbirds.

Muscle impressions.—Hummingbirds have long hyoid horns (cornu branchiale), consisting mainly of the epibranchales, that lie in a depression lateral to the cerebellar prominence (prominentia cerebellaris) and rostrally along the mid-dorsum of the cranium (see below). Deep to the epibranchiale is m. stylohyoideus, which usually originates in a shallow depression caudal to the craniofacial hinge (Fig. 4B). Long epibranchiales and the depression for m. stylohyoideus are lacking in all outgroups.

In both Apodidae and Trochilidae, a prominent sulcus on the dorsolateral cranium is occupied by m. cucullaris capitis (Fig. 8B). The sulcus in hummingbirds begins caudolaterally and passes rostromedially along the margin of the orbit (orbita). Although it channels the muscle, insertion occurs only in its rostral portion.

Vascular tube.—In hummingbirds the rostral semicircular canal (canalis semicircularis anterior) is accompanied along a portion of its dorsal and caudal surface by a previously undescribed ossified vascular tube (tuba vascularis) that is absent from all outgroups. Part of the tube is visible through the thin bone of the occiput in skeletons and in cleared and stained specimens of hummingbirds. The content of the tube is unknown.

The Flight Mechanism

Apodiformes were not included in Sy's (1936) excellent description and analysis of the avian flight mechanism covering osteology, arthrology, and myology. Hummingbirds and swifts share many qualitative and proportional attributes of the flight apparatus correlated with stiff-winged flight and a powered upstroke of the wing (Stolpe and Zimmer 1939, Savile 1950, Cohn 1968, Warrick et al. 2005). These include relatively long hand (manus) and distal primaries, and relatively short humerus and forearm that are steadily flexed at the elbow and extended at the wrist. The correspondingly small patagium and the secondary remiges are both of reduced aerodynamic importance. Hummingbirds have developed some of these specializations further than other Apodiformes and evolved new structures related to hovering, as discussed below.

Sternum

The sternum of hummingbirds (Fig. 13) shares several properties with that of swifts: the sternal body (corpus sterni) is long in relation to overall body size, and the carina is deep in relation to sternal length (Fig. 13A); the caudal border of the sternal corpus is entire and markedly broader between the lateral angles (angulus lateralis)

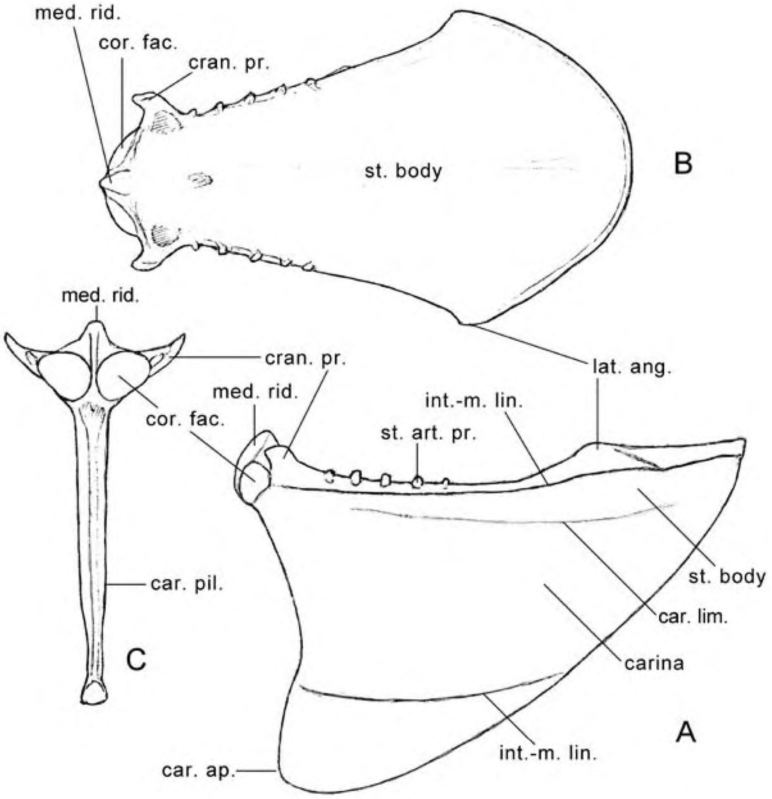

Fig. 13. The sternum of hummingbirds. (A) Left lateral view. (B) Dorsal view. (C) Rostral view. All drawings are to same scale. Rostral narrowing of the sternal body and great depth of the carina in relation to length of the sternal body reflect extreme enlargement of the major breast muscles. Abbreviations: car. ap. = carinal apex, car. lim. = dorsal limit of carina, car. pil. = carinal pillar, cran. pr. = craniolateral process, cor. fac. = coracoidal facet of sternum, int.-m. lin. = intermuscular line, lat. ang . = lateral angle, med. rid. = medial ridge, st. art. pr. = sternocostal articular process, st. body = sternal body.

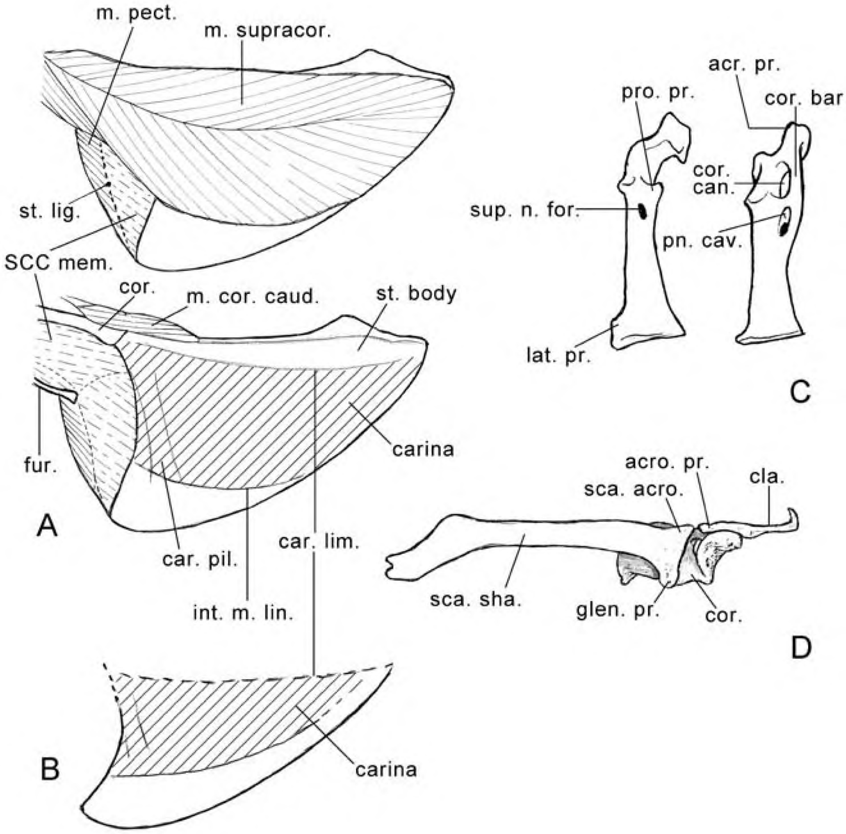

FIG. 14. Muscles of the sternum in modern hummingbirds and *Eurotrochilus*; coracoid of a swift and hummingbird; and shoulder girdle of a hummingbird. (A) Lateral view of hummingbird sternum with left pectoralis muscle removed (above) and left pectoralis plus supracoracoideus muscles removed (below). (B) Carina of the Oligocene fossil, *Eurotrochilus*, in lateral view. (A, B) Oblique hatching indicates origin of m. supracoracoideus on the carina. Compared with modern hummingbirds, *Eurotrochilus* exhibits reduced depth of the carina in relation to sternal body length, and difference in the ventral intermuscular line, both indicating reduced area of origin of m. supracoracoideus (oblique hatching). This configuration is similar to Apodidae. (C) Coracoids of a swift (left) and hummingbird (right); dorsal views, drawn to same length. The hummingbird has a reduced lateral process, larger foramen of the supracoracoidal nerve, and a coracoidal bar. (D) Articulated right clavicle, coracoideum, and scapula of a hummingbird; dorsal view. Both the clavicle and scapula are supported by the coracoidal bar. Abbreviations: acr. pr. = acrocoracoidal process, acro. pr. = acromion process of clavicle, car. lim. = dorsal limit of carina, car. pil. = carinal pillar, cla. = clavicle, cor. = coracoideum, cor. bar = coracoidal bar, cor. can. = coracoidal canal, fur. = furcula, glen. pr. = glenoid process of scapula, int. m. lin. = intermuscular line, lat. pr. = lateral prcess of coracoideum, m. cor. caud. = coracobrachialis caudalis muscle, m. pect. = pectoralis muscle, m. supracor. = supracoracoideus muscle, pn. cav. = pneumatic cavity, pro. pr. = procoracoid process, sca. acro. = scapular acromion, sca. sha. = scapular shaft, SCC memb. = sternocoracoclavicular membrane, st. body = sternal body, st. lig. = sternoclavicular ligament, sup. n. for. = supracoracoidal nerve foramen.

than at the rostral border (Fig. 13B); the coracoidal facets (prominentia articularis) are oval and convex, and nearly meet at the midline (Fig. 13C); and the external spine (spina externa rostri) is lacking. Surfaces of the body and carina are irregular (resembling hammered metal) and in swifts are irregularly perforated. The carina is strengthened anteriorly by a thickening or pillar (pila carina) (Figs. 13A, C and 14A). Although the external spine is absent in apodiforms, short, paired processes are present in *Aegotheles cristatus*, and the spine is replaced in apodiforms by a raised, medial ridge (eminentia medialis) between the coracoidal facets that receives the sternoprocoracoidal ligament (ligamentum sternoprocoracoideum).

On the sternum, the largest pectoral muscles are m. pectoralis and m. supracoracoideus (Buri 1900, Marshall 1906, Hartman 1961, Cohn 1968, Karhu 2001). In hummingbirds, the pectoralis muscle originates from the peripheral portions of the sternal body and keel, and also from the keel ventral to the intermuscular line, from the furcula, and from the sternocoracoclavicular membrane (membrana sternocoracoclavicularis, or SCC membrane). Aponeuroses from the intermuscular lines and ventral margin of the sternal carina are part of the origin. In hummingbirds, the aponeurosis is best developed from the caudal part of the ventral carinal margin and the caudal margin of the sternal body, where the bony sternum is largely occupied by the supracoracoidal muscle. Although the pectoralis muscle overlaps the ventral portion of the rib cage laterally, the muscle is completely independent from the ribs. Sternocostal articular processes (processus sternocostalis articularis) for sternal ribs occur along the lateral margin (margo costalis) of the sternal body and sometimes on the caudal edge of the craniolateral process (processus craniolateralis).

Size of the supracoracoideus muscle is indicated in part by a carinal intermuscular line, which in swifts extends the full length of the carina (Sclater 1865), and a corresponding intermuscular line often is present in Hemiprocnidae. By contrast, the homologous intermuscular line of hummingbirds intersects the carinal margin midventrally (Fig. 14). Swifts and crested swifts also exhibit intermuscular lines that are oriented rostrolaterally on the ventral surfaces of the sternal body. The lines are well developed in hummingbirds along the lateral margins of the sternal body (Figs. 13A and 14A). These differences reflect a more complete occupation of the carina and almost complete occupancy of the sternal body by m. supracoracoideus in hummingbirds. I confirmed that the intermuscular lines circumscribe the limits of the muscle in hummingbirds by dissection of *G. hirsutus*, in which m. supracoracoideus occupies most of the carinal surface except the rosroventral portion, and the entire ventral surface of the sternal body except its caudolateral extremity; by contrast, in *Collocalia esculenta* the muscle narrows caudally and is absent from the ventral and caudal portions of the carina and from a large, caudolateral portion of the sternal body. Buri (1900), Marshall (1906), and Cohn (1968) also showed that m. supracoracoideus of hummingbirds arises from a larger portion of the sternal body than it does in swifts. Thus, osteological features of the sternum that shed light on the size of the supracoracoideus muscles may be preserved in fossils. In all apodiforms, m. supracoracoideus also originates from the shaft of the furcula (scapus claviculae) and the SCC membrane (Fig. 14).

The sternocoracoideus muscle of most birds interconnects the medial surface of the craniolateral process of the sternum and the lateral process of the coracoid (processus lateralis coracoidei). In hummingbirds the craniolateral process is smaller than in outgroups and m. sternocoracoideus is lacking. Nevertheless, m. coracobrachialis caudalis, originating from the lateral surface of the craniolateral process and adjacent portion of the sternal body, is well developed in hummingbirds and represents the third important flight muscle originating from the sternum.

Coracoideum, Clavicula, and Scapula

The coracoideum of hummingbirds differs from that of other Apodiformes in possession of an ossified coracoidal bar (pila coracoidei) that seamlessly interconnects the procoracoidal process (processus procoracoideus) and base of the acrocoracoidal process (processus acrocoracoideus) (Fig. 14B). It encloses the coracoidal canal (canalis coracoidei) and replaces the acrocoraco-procoracoidal ligament (ligamentum acrocoraco-procoracoideum) of other Apodiformes (in one specimen of *A. cristatus* [USNM 620228] the latter ligament was ossified). In addition, hummingbirds have a large pneumatic cavity (cavitas pneumaticum) on the dorsal surface of the coracoid, just proximal to the coracoidal canal (Fig. 14B). The pneumatic cavity, which approximately equals the coracoidal canal in length, receives the supracoracoidal nerve (nervus supracoracoideus) and probably a portion of the interclavicular air sac. Other apomorphic features of the coracoid in hummingbirds represent terminal stages of morphoclines within Apodiformes: (1) the lateral process is well developed in Hemiprocnidae, reduced in Apodidae, and vestigial in Trochilidae; (2) the sternal articular facet (facies articularis sternalis) is ovoid medially, tapering to a narrow trough on the lateral process in Hemiprocnidae, broadly ovoid with a small extension onto the lateral process in Apodidae, and broadly ovoid with no extension or involvement with the lateral process in Trochiidae; and (3) the supracoracoidal nerve foramen is small on the ventral surface of the coracoideum in Hemiprocnidae, larger in Apodidae, and markedly larger in Trochilidae. (Dissection of single specimens of *G. hirsutus* and *C. esculenta*, species of similar body weight, revealed that *Glaucis* has a thick, branching nerve, whereas that of *Collocalia* is a single, thin strand.) The sterno-acrocoracoidal ligament (ligamentum sterno-acrocoracoideum) connects the medial ridge of the sternum (1) with the acrocoracoidal process and medial and dorsal surfaces of the coracoideum in Hemiprocnidae; (2) with the acrocoracoidal process, procoracoidal process, and part of the dorsal surface of the coracoideum in Apodidae; and (3) exclusively with the dorsal surface of the coracoideum medial to the pneumatic cavity in Trochilidae. As one might infer from these morphological differences, manipulation of cleared and stained specimens of a swift (*Chaetura pelagica*) and several species of hummingbird revealed that the sterno-acrocoracoidal ligament restricted ventral, lateral, and dorsal displacement of the cranial portion of the coracoideum in relation to the sternal articulation in the swift, and ventral and lateral displacement in the hummingbird. From the nearly adjacent sternal articulations, the coracoids of hummingbirds diverge anterolaterally such that the shoulder joints are positioned laterally to the same degree as the caudolateral angles of the sternum.

The claviculae are fused medially to form a slender furcula that is U-shaped in rostral view and C-shaped in left lateral view, and the space between the clavicla and coracoideum is occupied by the SCC membrane. The clavicular symphysis (apophysis furculae) of hummingbirds and swifts has no close contact with the sternum, but the furcula is stabilized to the apex of the sternal carina by a sternoclavicular ligament (Fig. 14A). In apodiforms with a shallower carina, the clavicular symphysis is near the carinal apex. The furcula in *Aegotheles* has a blunt, plate-like acromial region (regio acromialis), whereas that of apodiforms is slender and extends beyond the acrocoracoidal tubercle (tuberculum acrocoracoidale). In Hemiprocnidae and Apodidae the clavicular acromion process (processus acromialis) is straight, articulating only with the acrocoracoid process (processus acrocoracoidalis) of the coracoid. By contrast, the clavicular acromion of hummingbirds is down-curved, articulating not only with the acrocoracoid but also with the coracoidal bar (Fig. 14C). As a result, the clavicle has a tight juncture with the coracoid in hummingbirds and provides firm support for the sternocoracoclavicular membrane. The scapular acromion (acromion) also articulates with the base of the coracoidal bar, where, in addition to its usual articulation across the caudal surface of the coracoideum, it abuts the acromion process of the clavicle (Fig. 14C).

SHOULDER JOINT

The shoulder joint (articulatio omalis) is a synovial articulation between the head of the humerus and the glenoid cavity (cavitas glenoidalis), the latter consisting principally of the ligaments supported by the coracoideum and scapula (Baumel and Raikow 1993). The glenoid cavity is somewhat malleable, conforming to, but partially restricting, movements of the humeral head (caput humeri) during flight (Sy 1936). The glenoid cavity and its relation to the humerus in hummingbirds are illustrated by Stolpe and Zimmer (1939) and Karhu (2001).

HUMERUS

In most avian orders the humerus is an elongate bone with well-defined features of its proximal portion that are associated with the shoulder joint and with insertions of muscles powering motions of the upper arm (brachium; Fig. 15A). The morphology of its distal end is associated with the elbow articulations (juncturae cubiti) and with muscles effecting motions of the forearm (antibrachium) and hand, but the elongate shaft is nearly featureless. *Aegotheles* has a typical avian shaft, but that of *Hemiprocne* is relatively shortened. By contrast, hummingbirds and swifts are extreme among birds in the extent to which the shaft has been shortened. As a result, in both taxa, several of the muscles and osteological landmarks usually associated with the distal portion of the humerus intermingle with those of the proximal portion (Fig. 15B). Most notably, swifts and hummingbirds exhibit a well-developed, proximately situated process of m. extensor metacarpi radialis (processus extensor metacarpi radialis; hereafter "EMR process"); this process is synonymous with the "processus supracondylaris dorsalis" of Lowe (1939), Cohn (1968), and Zusi and Bentz (1982). Only in hummingbirds does a crest (crista) interconnect the EMR process with the angle of the tensor propatagialis muscle

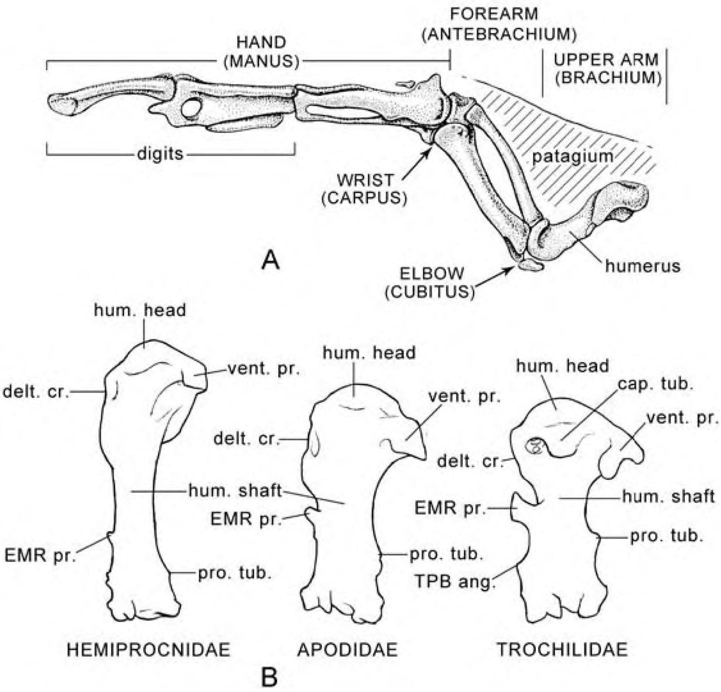

FIG. 15. Configuration of the wing skeleton of a hummingbird as in stiff-winged flight, and comparison of the humerus in Apodiformes. (A) Approximate positions of skeletal elements of a hummingbird's left wing in dorsal view, as in directional or hovering flight (semidiagrammatic). The brachium is caudally adducted toward the body, the antibrachium flexed on the brachium, and the manus extended on the antibrachium. The manus supports the primary remiges and is of greatest aerodynamic importance. The triangle formed by the brachium, antebrachium, and patagium encloses the bulk of the wing muscles that power the manus. (B) Caudal views of the left humeri in Apodiformes, drawn to similar widths of the distal extremities. Length of the humeral shaft (between the EMR process and deltopectoral crest) is reduced almost to zero in Apodidae and Trochilidae. Abbreviations: cap. tub. = capital tuberculum, delt. cr. = deltopectoral crest, EMR pr. = process of extensor metacarpi radius muscle, hum. head = humeral head, hum. shaft = humeral shaft, pro. tub. = pronator tubercle, TPB ang. = angle of tensor propatagialis brevis muscle, ven. pr. = ventral process of humerus.

(TPB angle). In Hemiprocnidae, Apodidae, and Trochilidae the EMR process has shifted proximally on the humerus in relation to the width of the distal portion of the humerus (Fig. 15B).

The humeral head of Apodiformes, as in many other birds, displays a transverse sulcus (sulcus transversus) that receives the acrocoracohumeral ligament (ligamentum acrocoracohumerale). The two-parted ligament spans the acrocoracoidal process of the coracoid and the cranial surface of the humeral head (Sy 1936). Except for hummingbirds, the sulcus of Apodiformes is long and well defined, extending ventrally from the dorsal portion of the head onto the ventral process. The main part of the ligament occupies most of the sulcus, and a weaker portion is confined to its more dorsal portion. In hummingbirds the sulcus is reduced to two scars (Livezey and Zusi 2006: fig. 21F), the ventral one associated with the main portion of the ligament, and the shallower dorsal scar with the weaker part. In all apodiforms, the weaker part of the ligament attaches near the long axis of rotation of the humeral shaft (scapus humeri), and probably serves to maintain the humerus within the glenoid socket. The stronger part of the ligament attaches ventral to the axis of rotation and limits axial pronation of the humerus on the downstroke of the wing (Sy 1936).

In both swifts and hummingbirds the tendon of m. supracoracoideus inserts on the ventral surface of the deltopectoral crest (crista deltopectoralis) directly opposite the dorsal insertion of m. pectoralis (Stolpe and Zimmer 1939, Karhu 1992). I have noticed that symmetrical juxtaposition of insertions of these two major, antagonistic flight muscles is rare in birds, occurring elsewhere in penguins (Spheniscidae) and the Great Auk (*Pinguinus impennis*). That configuration (Fig. 16) appears to equalize the mechanical advantage of the two muscles in relation to a strong, powered upstroke of the wings and to the axial rotation of the humerus.

A well-developed capital tuberculum (tuberculum capitis) on the caudal surface of the humerus extends the articular surface of the humeral head uniquely distad in hummingbirds (Fig. 16). In modern hummingbirds the dorsal portion of this tuberculum is semiglobose, providing an articulation with the glenoid process of the scapula (processus glenoidalis scapulae) during adduction and supination of the humerus (Stolpe and Zimmer 1939, R. L. Zusi unpubl. data). I found a less developed capital tuberculum in one specimen of *Hemiprocne comata* (YPM 7039). As noted by Karhu (2001), a small capital tuberculum is found also in some galliforms and tinamous, probably associated with humeral supination during takeoff. A shallow sulcus between the capital tuberculum and the humeral head channels the tendon of m. supracoracoideus toward its insertion on the humerus in hummingbirds.

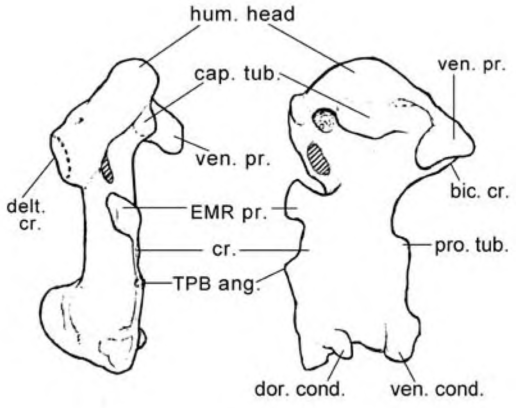

FIG. 16. Insertions of major flight muscles on the humerus of hummingbirds. Left humerus; dorsal view (left); caudal view (right). The dotted line shows the general area of insertion of the pectoralis muscle on the cranial side of the deltopectoral crest; hatching represents insertion of supracoracoideus muscle. The two insertions are roughly opposite on the deltopectoral crest in hummingbirds and swifts, equalizing the mechanical advantage for axial rotation of the humerus during upward (m. supracoracoideus) and downward (m. pectoralis) phases of the wing stroke. Abbreviations: bic. cr. = bicipital crest, cap. tub. = capital tuberculum, cr. = crest, delt. cr. = deltopectoral crest, dor. cond. = dorsal condyle, EMR pr. = process of extensor metacarpi radialis muscle, hum. head = humeral head, pro. tub. = pronator tuberculum, TPB angle = angle of tensor propatagialis brevis muscle, ven. cond. = ventral condyle, ven. pr. = ventral process.

The ventral tubercle (tuberculum ventrale) of the humerus found in most birds has expanded to become a curved process in Apodiformes (Figs. 15 and 16), and for Apodiformes I name it "ventral process" (processus ventralis humeri). It is longer in Apodidae than in *Hemiprocne* and *Aegotheles* and longest in hummingbirds (Karhu 1992: fig. 6). Insertions of muscles from the scapula and coracoid are concentrated distally on the ventral process in hummingbirds. For example, m. scapulohumeralis caudalis inserts on the bicipital crest (crista bicipitalis) in Hemiprocnidae and Apodidae, but on the caudoventral extremity of the ventral process in Trochilidae (Cohn 1968, Zusi and Bentz 1984, Karhu 1992).

I noted but did not measure a progressive increase in the depth and breadth of the olecranon fossa (fossa olecrani; Fig. 15) that houses the insertion tendon of m. triceps brachii within apodiform families (Hemiprocnidae, Apodidae, and Trochilidae). This extensor muscle of the forearm acts with forearm flexors to maintain flexion of the elbow during stiff-winged flight and, especially, during hovering. The angled tendon at the flexed elbow is strengthened by an enlarged sesamoid, as described by Stolpe and Zimmer (1939).

The distal portion of the humeral shaft in swifts and hummingbirds is exceptionally wide (dorsoventrally), and the ventral condyle (condylus ventralis) and dorsal condyle (condylus dorsais) are enlarged (Karhu 1992). The dorsal, or radial, condyle slopes distomedially and the ventral, or ulnar, condyle curves caudomedially to a greater degree in hummingbirds than in swifts—both features enhancing the ability to rotate the ulna about its long axis and supporting the radius during supination of the hand (Stolpe and Zimmer 1939).

RADIUS AND ULNA

Hummingbirds differ from outgroups in having a stout radius that bows away from the ulna (Fig. 17), providing space and increased leverage for

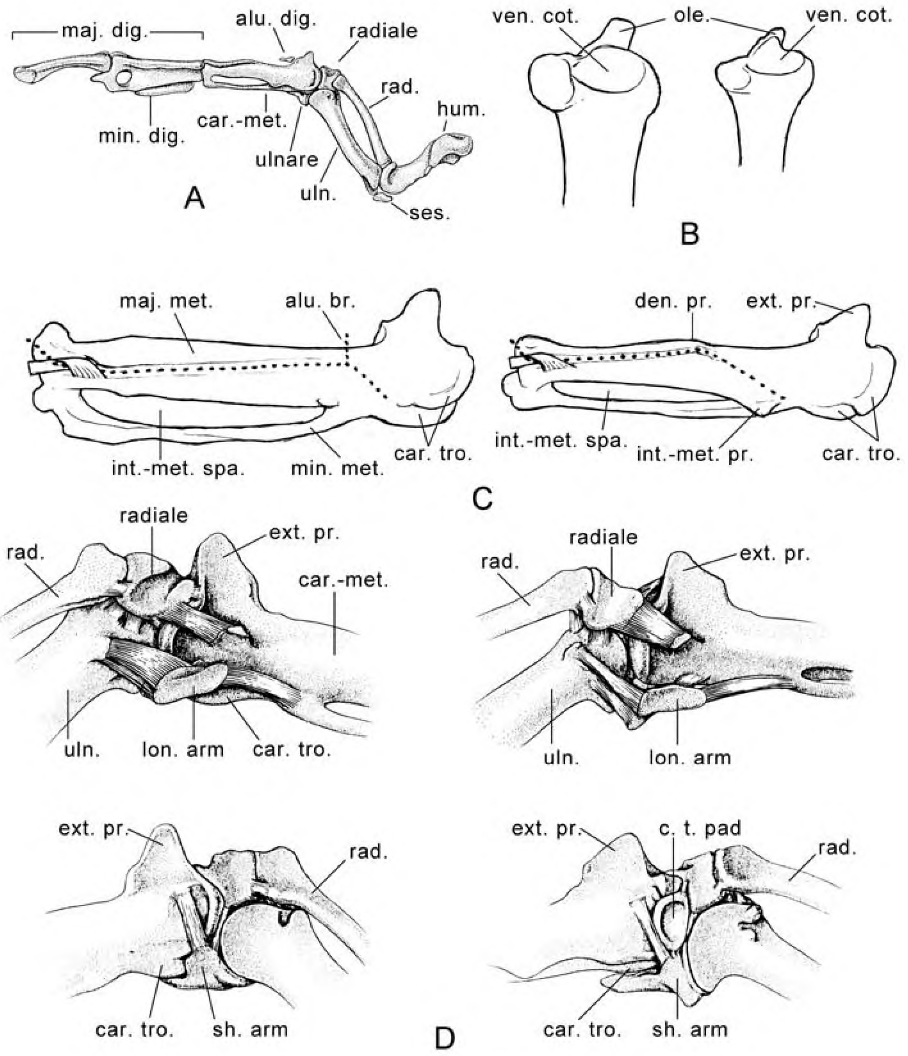

FIG. 17. Wing elements of swifts and hummingbirds. (A) Articulated elements of hummingbird wing (left wing, dorsal view), for orientation of B–D. (B) Proximal end of right ulna in cranial view; *Chaetura* (left), *Eulampis* (right). The notched ventral cotyla is thought to permit axial rotation of the ulna in hummingbirds. (C) Left carpometacarpus in dorsal view; *Cypseloides* (left), *Patagona* (right); alular digit not shown. Dotted lines indicate the courses of insertion tendons of the flexor digitorum profundus muscle; hummingbirds lack the alular branch tendon. (D) Left wrist, showing carpals and ligaments in the extended wing of *Collocalia esculenta* (left) and *Coeligena coeligena* (right); ventral views (upper) and dorsal views (lower). In swifts, but not hummingbirds, the long and short arms of the ulnare clasp the carpal trochlea of the carpometacarpus in the extended manus, limiting supination of the carpometacarpus. Abbreviations: alu. br. = alular branch tendon, alu. dig. = alular digit, car.-met . = carpometacarpale, car. tro. = carpal trochlea, c.-t. pad = connective tissue pad, den. pr. = dentiform process, ext. pr. = extensor process, hum. = humerus, int.-met. pr. = intermetacarpal process, int.-met. spa. = intermetacarpal space, lon. arm = long arm of ulnare, mag. dig. = major digit, maj. met. = major metacarpale, min. dig. = minor digit, min. met. = minor metacarale, ole. = olecranon, rad. = radius, ses. = sesamoid, sh. arm = short arm of ulnare, uln. = ulna, ven. cot. = ventral cotyla.

hypertrophied pronator and supinator muscles (Karhu 1999) and for an enlarged extensor of the major digit (M. extensor longus digiti majoris; Cohn 1968, Zusi and Bentz 1984).

Mayr (2005) indicated that an elongate, narrow, ulnar olecranon in hummingbirds (Fig. 17A) distinguishs them from swifts; however, I found this character to be variable in both hummingbirds and swifts. He also described a deep fossa on the caudal surface of the ulna (Mayr 2007:109) as characteristic of "*Argornis* and crown-group Trochilidae." Karhu (1999) noted that the ventroproximal edge of the ventral cotyla of the ulna (cotyla ventralis ulnae) of hummingbirds is somewhat eroded (Fig. 17B) whereas that of other apodiforms is complete. He thought that the ventral condyle of the humerus in hummingbirds could slide caudoventrally in relation to the ulna during supination of the forearm, and he claimed that the more prominent ventroproximal edge of the ventral cotyla in Apodidae resisted supination of the elbow joint in the spread wing.

Carpales and Carpometacarpus

The carpometacarpus of hummingbirds differs from that of outgroups in its possession of an intermetacarpal process (processus intermetacarpalis), the insertion point of m. extensor metacarpi ulnaris (Fig. 17B). In outgroups, the tendon of insertion of m. extensor digitorum communis (EDC) includes a branch to the alular digit proximal to the intermetacarpal space (spatium intermetacarpale). The main tendon of EDC abruptly changes direction distal to the branch and lies within a groove on the dorsal surface of the major metacarpale (metacarpale majus). Hummingbirds lack the branch tendon to the reduced, largely immobile alular digit, and the tendon of EDC changes direction more gradually distal to the intermetacarpal space to follow a groove in the major metacarpal (Fig. 17B). Ossified connective tissue sometimes encloses part of the groove as a tunnel (see also Cohn 1968). Unlike in outgroups, the distal end of the minor metacarpale (metacarpale minus) of hummingbirds extends beyond that of the major metacarpal. Among apodiforms, only hummingbirds have a dentiform process (protuberantia metacarpalis) on the cranial margin of the major metacarpal. It enlarges the area of origin of m. abductor digiti majoris—an extensor of the major digit (digitus majoris).

From dorsal or ventral view, the carpometacarpus of hummingbirds displays a proximally truncate contour of the cranial part of the carpal trochlea (trochlea carpalis) (Fig. 17C). This cam-like form may help stabilize the carpometacarpus while in the extended position.

As in other birds, the apodiforms have two free carpales. The radiale is essentially a distal extension of the radius that articulates distally with the carpometacarpus, whereas the ulnare is associated with the carpal trochlea of the carpometacarpus. Vazquez (1992) described the structure and interactions of bones of the wrist and contended that flighted birds possessed mechanical restrictions on pronation and supination of the wrist in the extended wing, related in part to channeling of carpometacarpal rotation by the ulnare. He noted that only hummingbirds possessed a significant deviation in this aspect of the wrist, but he did not describe the difference or discuss the functional consequences for hummingbirds.

The long (crus longum) and short (crus breve) arms of the ulnare in swifts (and most birds) embrace the caudal rim of the caudal part of the carpal trochlea in the extended wing (Fig. 17D) and limit pronation and supination of the carpometacarpus as described by Vazquez (1992). The metacarpal incisure of the ulnare of hummingbirds is obtusely angled and poorly defined because its dorsal arm is extremely short. In addition, the caudal part of the carpal trochlea is somewhat reduced (Fig. 17D). As a result, the ulnare does not restrict supination of the carpometacarpus of hummingbirds in the extended wing during the upstroke, and pronation on the downstroke is less strongly restricted than that described for most birds by Vazquez (1992).

Cohn (1968) found that the wrist in swifts displayed strong ventral ligaments that limit supination of the extended hand on the upstroke. These ligaments are superficial on the ventral side of the wrist, fanning out from an attachment on the caudodistal portion of the radius to multiple attachments on the ventroproximal portion of the carpometacarpus (Fig. 18). I found that these ligaments would support the wrist against dorsal forces on the hand during wing strokes, and that the cranial portion of the ligamental fan would specifically restrict supination of the hand in the extended wing. These ligaments are not present in hummingbirds.

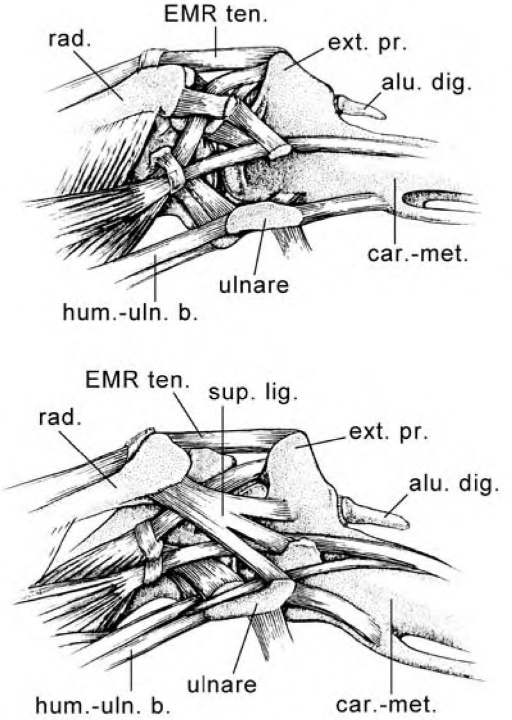

FIG. 18. Comparison of the wrist and superficial ligaments in a hummingbird and swift. Ventral views of left wrist of a hummingbird (above) and a swift (below). Swifts exhibit superficial ligaments of the wrist between the radius and carpometacarpus that limit axial supination of the carpometacarpus and, thus, of the entire hand. Hummingbirds lack these ligaments, allowing supination of the hand during upstroke of the wing. Abbreviations: alu. dig. = alular digit, car.-met. = carpometacarpus, EMR ten. = tendon of extensor metacarpi radialis muscle, ext. pr. = extensor process, hum.-uln. b. = humeroulnar band, rad. = radius, sup. lig. = superficial ligaments.

DIGITS

The major digit of hummingbirds (Fig. 17A), which supports the three outer primary feathers, is the longest in proportion to wing length among Apodiformes. According to Stolpe and Zimmer (1939) and Cohn (1968), axial rotation of the major digit is facilitated by a transversely flattened articular surfaces of both the carpometacarpus and major digit. The enlarged m. extensor longus digiti majoris in hummingbirds probably effects supination of the major digit, whereas the smaller muscle in other apodiforms may serve more as a damper on pronation from air pressure.

The basal phalanx of the major digit is broader in swifts and hummingbirds than in crested swifts and *Aegotheles*, providing greater support for the distal primaries (Sy 1936). In hummingbirds the alular digit is small and bound to the cranial surface of the carpometacarpus.

SESAMOIDS OF THE TAIL

The rectricial bulb (bulbus rectricium) is a bilateral complex of muscle and connective tissue that supports the rectrices and permits coordinated or partially autonomous motions of the rectrices and coverts on either side of the pygostyle (Zusi and Bentz 1984, Zusi and Gill 2009). Here, I highlight a bilaterally paired oval bone unique to hummingbirds within Apodiformes, noted also by Cohn (1968) and Richardson (1972). The bone is a flat, oval-shaped sesamoid embedded in the caudolateral portion of the expanded, cruciate aponeurosis of insertion of m. depressor caudae. The sesamoid supports individual tendons of that muscle that angle abruptly upward to the follicles of the four outer pairs of rectrices. In addition, the tendon of m. caudofemoralis is anchored on the oval bone's caudolateral margin before angling toward the follicle of the lateral rectrix (Zusi and Bentz 1984, Zusi and Gill 2009). Like many sesamoids, it stabilizes a point of abrupt directional change in a tendon (in this case, five paired tendons). All of these tendons transmit forces that depress the rectrices and rectricial bulbs. Repeated, rapid depression of the tail is common in hummingbirds when changing position while hovering at flowers.

STIFF-WINGED FLIGHT

From morphological evidence, Lorenz (1933) proposed that hummingbirds and swifts used a stiff-winged mode of flight that included a strongly powered upstroke (Stolpe and Zimmer 1939, Savile 1950, Cohn 1968). Observational data on wing kinematics of swifts and hummingbirds in free, rapid, forward flight are rare, but larger species have lower wingbeat rates in both families, and those of large swifts are amenable to direct observation of details. Cohn (1968:70–71) watched the White-naped Swift (*Streptoprocne semicollaris*; ~175 g), at close range:

> In rapid forward flight *C. semicollaris* moves the wing from fully extended (up) to fully flexed (down) with no perceptible folding of

> the wrist.... In cruising [slower] flight the hand of the large swifts goes through the same rowing movements so common in other large birds. The hand is extended for the downstroke and partially folded for the upstroke.... That large swifts fly in this manner makes it probable that smaller swifts also move the hand in the same way during relatively slow forward flight. Only in *rapid flight* or during sharp turns would the wing move as a unit.

The wing is "stiff" only in relation to maintenance of flexure of the antebrachium against the brachium, and extension of manus against antebrachium by muscle action during the full wing stroke. In addition, dorsoventral flexion of the manus on the antebrachium is restricted. However, the wing is "mobile" through axial rotation (supination and pronation) of the humerus, ulna, and manus—especially in hummingbirds. High-speed photography of *rapid flight* in a wind tunnel confirmed these propositions in a hummingbird (Tobalske et al. 2007) and a swift (Henningsson et al. 2008). Although both the hummingbird (*Selasphorus rufus*) and the swift (*Apus apus*) flexed the wrist slightly during the upstroke, the wing remained essentially rigid. Nevertheless, the "stiff" wings of *S. rufus* exhibited slight perturbations of various parameters during flight in a wind tunnel (Tobalske et al. 2007). Throughout stiff-winged flight, the flexed antebrachium consolidates the mass of enlarged forearm muscles near the shoulder joint; it also decreases the inertial moment of the moving wing and probably favors intensive flapping flight (Karhu 1992). Most of the aerodynamic role is transferred to the much-enlarged manus and primary feathers. However, flexion of the elbow is not a permanent condition in hummingbirds; during one form of wing stretching, the elbow is extended and the patagium elongated well beyond the position maintained during flight (WNET–Nature 2010).

Cohn (1968) presented preliminary experimental evidence for stiff-winged flight and a powered upstroke in swifts. Features common to swifts and hummingbirds, and probably associated with stiff-winged flight accompanied by a strongly powered upstroke, include (1) extreme reduction in humeral length (Böker 1927); (2) short radius and ulna (Böker 1927) with fewer, shorter secondaries (9–10 in swifts, 6 or 7 in hummingbirds); (3) long hand, in proportion to wing length, supporting long primaries; (4) humerus in which large diameter of the stout shaft provides greater leverage for muscles that effect axial rotation; (5) proximal shift of humeral processes associated with uniquely enlarged extensor muscles of the hand (Cohn 1968, Karhu 1999); (6) elongate ventral process of the humerus, again providing greater leverage for muscles of axial rotation and retraction of the humerus; (7) insertion of m. supracoracoideus opposite that of m. pectoralis, equalizing the leverage for supination and pronation of the humerus by the two largest flight muscles; (8) widening of the articular surfaces of the humerus and forearm in swifts and hummingbirds, accommodating an increased load in the elbow joint (Karhu 1992); (9) enlarged sternum that supports uniquely enlarged pectoralis and supracoracoideus muscles (Buri 1900, Greenewalt 1962); (10) stout coracoid with oval articular facets on the sternum that support the shoulder against multidirectional forces; and (11) humeral head of swifts and hummingbirds angled caudally, apparently increasing support for the humerus in the glenoid socket when the humerus is adducted—the normal position in stiff-winged flight—and during strong supination (Stolpe and Zimmer 1939, Karhu 1992). Axial rotation of the humerus in the stiff-winged position contributes to the aerodynamic motion of the hand and primaries during the wing stroke.

How does free, forward flight of hummingbirds differ from that of swifts? Aerial feeding by swifts entails abrupt changes in direction, speed, and wingbeat rate. Despite the ability to attain high speeds, the long, narrow wings of swifts also favor gliding (Bruderer and Weitnauer 1992). Although bounding flight occurs in hummingbirds, gliding and soaring are more pronounced in the larger species. Wingbeat rates of hummingbirds exceed those of similar-sized swifts (Geenewalt 1962), and they are roughly constant for each species whether in normal forward flight or hovering. Wingbeat rate of hummingbirds is inversely correlated with wing length (Stresemann and Zimmer 1932; Greenewalt 1962, 1975). High wingbeat rates of hummingbirds enhance stability by passive rotational damping (Hedrick et al. 2009).

HOVERING

Asymmetrical hovering.—This weak form of hovering involves an extended wing on the downstroke and folding of the wing on the upstroke

(Norberg 1990). It is used occasionally during short periods of hovering by many species of various orders that lack obvious, anatomical specializations for hovering. Even in swifts, hovering is neither strong nor sustained. Manchi and Sankaran (2010) described a foraging maneuver (flutter) in swiftlets (*Aerodramus fuciphagus* and *Collocalia esculenta*) as "a hover performed with a rapid wing beat and a pause in flight" (p. 260). George (1971:178) saw swifts gleaning insects from outermost branches of deciduous forest. Sometimes a bird would "bank sharply up and flutter briefly" at foliage, or it plummeted more-or-less tail first into canopy openings, braking as when descending into a chimney, and fluttering briefly while gleaning among leaves. Sutton (1927) described entrance to a chimney (in *Chaetura pelagica*) as fluttering over the chimney and settling down, backwards, into it. Cohn (1968:71) saw Chimney Swifts flying straight upward in a chimney with laborious "helicopter" wingbeats. It is not clear whether these swifts were employing asymmetrical hovering. House Finches (*Carpodacus mexicanus*) have been observed hovering (asymmetrically) for ≤5 s below the down-angled spout of a hummingbird feeder and inserting the tip of the bill into the spout (Taylor 1972).

Sustained hovering in hummingbirds requires among the highest mass-specific rates of oxygen consumption in vertebrates (Suarez 1992). Given that hovering is energy-expensive and that it constitutes the signature method of feeding on nectar and non-airborne arthropods, it is reasonable to assume that flight morphologies unique to hummingbirds among apodiform birds are involved with extended symmetrical hovering and rapid forward flight.

Symmetrical hovering.—Only hummingbirds perform sustained and precisely controlled hovering. However, "symmetrical" overstates the case for hummingbirds.

> Given that many birds possess the mass-specific power (using anaerobic metabolism) to hover for short periods, the selective pressure on hummingbird ancestors was probably for increased efficiency (resulting in stiff wings with greatly simplified kinematics), and an upstroke muscle (the supracoracoideus) that makes the recovery stroke rapid, while contributing enough to the hovering power requirements to allow the downstroke muscle (the pectoralis) to operate within its aerobic limits. In other words, this pseudosymmetrical wingbeat cycle is good enough, and although hummingbirds do not exhibit the elegant aerodynamic symmetry of insects, natural selection rewards "good enough" as richly as it does our aesthetic ideals. (Warrick et al. 2005:1096)

While the manus is continuously extended, the wing tips move constantly in a figure-8 pattern with rotational circulation involving pronation at the upper end of the upstroke and supination at the lower end of the downstroke (Stolpe and Zimmer 1939, Warrick et al. 2009). Lift during hovering (*S. rufus* and probably all hummingbirds) is nearly continuous because a leading-edge vortex is maintained throughout the wing stroke during continuous motion of the sharp leading edge of the primaries. Swifts also benefit from a leading-edge vortex when gliding with swept-back wings (Videler et al. 2004).

Anatomical correlates of hovering in hummingbirds include extreme development of most features of stiff-winged flight listed above. For example, hummingbirds have the shortest humerus and ulna and the longest carpometacarpus and major digit in proportion to body size among birds (based on *Thalurania* compared with *Apus* and many other avian taxa in Böker 1927). The inferred positions of the bony wing elements are shown in dorsal views of a captive, hovering hummingbird (*Florisuga fusca*) by Stolpe and Zimmer (1939). Most notable are the general adduction of the humerus and depression of the elbow at the height of the upstroke. During hovering flight, the elbow reaches its maximum forward position at the beginning of the backstroke as supination of the humerus begins (Cohn 1968:74). Nevertheless, details of *skeletal* kinematics, in particular the nature of abduction, adduction, elevation, and depression of the distal end of the humerus in relation to the body axis, the amount of axial rotation (pronation and supination) of the humerus, and the changing areas of humero-glenoid contact during free flight and hovering are lacking. Of special interest is the precise role of tuberculum capitis, which was considered the primary articulating surface in hummingbirds by Stolpe and Zimmer (1939). The role of the ventral process of the humerus and its muscles in fast flight of swifts and hummingbirds and hovering in hummingbirds is also critical but little known (see Cohn 1968).

Axial supination of the humerus within the glenoid fossa is probably minimal when hovering with the body roughly vertical and the wingbeat approximately horizontal (while hovering below a flower to feed at a vertically suspended corolla). Supination would increase when hovering with the body about 45° to horizontal and the wingbeat horizontal at a horizontal corolla, and extreme supination of the humerus would occur when both the body and plane of the wingbeat are approximately horizontal. Among the unique features of hummingbirds are those that facilitate supination of the wing at all of its joints, as summarized and discussed by Karhu (1992).

I found that tensing the aponeurosis of m. supracoracoideus in cleared and stained specimens caused rotation (supination) of the humerus in the partly raised wing. Axial rotation of the humerus is effected not only by m. pectoralis and supracoracoideus but also by muscles inserting on the ventral process of the humerus—m. scapulohumeralis caudalis to pronate the humerus and coracobrachialis caudalis to supinate it (Cohn 1968). Increase in size of pronator muscles that counter supination of the forearm from air pressure during the downstroke is associated with the stout and bowed radius of hummingbirds (Dial 1992). Supination of the hand during the upstroke is facilitated by changes in the carpal structure of hummingbirds and by loss of supination-limiting wrist ligaments present in swifts. According to Cohn (1968), the maximum cumulative axial rotation of the shoulder, elbow, wrist, and digits at outer primaries equals 180°. Thus, at the end of the upstroke the distal primaries are reversed with the ventral side uppermost, and the secondaries roughly vertical with their ventral surfaces facing forward. The alular digit is reduced in size and its aerodynamic function in hummingbirds is not known.

The major pectoral muscles (M. pectoralis major and M. supracoracoideus) that power the upstrokes and downstrokes, respectively, in hummingbirds are the largest in relation to body weight of any apodiform bird (Greenewalt 1962). Given the extreme reduction of the deltoideus muscles in trochilids, the upstroke is powered mainly by the supracoracoideus muscle, which in hummingbirds is also larger in relation to that of m. pectoralis (supracoracoideus/pectoralis ratio 1 to 1.7) than in any other family. The downstroke in *S. rufus* produces 75% of weight support and the upstroke 25% (Warrick et al. 2005). The tendon of insertion of the supracoracoideus muscle is firmly directed toward the humerus through an enclosed passageway, the coracoidal canal, of the coracoid.

In hummingbirds, exceptionally powerful extensor muscles (extensor metacarpi radialis, extensor digitorum profundus, extensor longus digiti majoris, and flexor digitorum profundus) extend the hand. The radius and ulna are separated by a substantial gap that is occupied in part by enlarged extensor muscles. The distal aponeurosis or tendon of m. tensor propatagialis brevis (TPB tendon), unique to hummingbirds, also may contribute to extension of the manus in the extended wing. If so, it shows varying levels of specialization for that function within hummingbirds (Zusi and Bentz 1982; Appendix 3).

The pectoralis muscle of *Sturnus vulgaris* develops force during the final third of the upstroke and sustains it during downstroke, and the supracoracoideus is activated by late-downstroke, which suggests that reduction of wing inertia (damping) is an important function of the major flight muscles (Dial et al. 1991, Biewener et al. 1992). Limited study of *Selasphorus rufus* showed that damping effects of the pectoralis and supracoracideus muscles during a wingbeat applied also to hummingbirds, but that the timing of stimulation was different (Tobalske et al. 2010). M. extensor digitorum communis effects supination of the major digit during the upstroke (traditional function), but probably also damps or limits strong pronation forces from air pressure on the distal primaries during the downstroke (unstated function). It is likely that damping or limiting effects represent a significant function of many muscles.

Hovering limits.—Experiments on hovering limits in gas mixtures at reduced air pressure or reduced oxygen pressure show that hummingbirds demonstrate considerable power reserves for hovering under normal conditions (Chai and Dudley 1996). They compensate for reduced air pressure by increasing wingbeat amplitude but reach an anatomical limit at amplitudes slightly over 180° (Chai and Dudley 1995). In field experiments performed at different altitudes, amplitude increased but limits were not reached (Altshuler and Dudley 2002, 2003; Altshuler et al. 2004). Altshuler et al. (2010) also performed experiments in muscle physiology under conditions of maximum load lifting and found that *Calypte anna* could increase stroke amplitude even at the highest wingbeat rates.

Despite rapid advance in the study of various aspects of hummingbird flight, precise description of the skeletal elements during wing kinematics, as well as detailed functional anatomy of the wing joints and functions of most wing muscles, are still rudimentary.

VERTEBRAL COLUMN

Boas (1929) described taxonomic and functional diversity of the vertebral column (columna vertebralis) in many families of birds, but hummingbirds were excluded. Swifts and hummingbirds have exceptionally large intervertebral openings (foramen intervertebrale) that accommodate the enlarged nerve complexes associated with stiff-winged flight, and the pygostyle is strongly developed in hummingbirds. Variation in the atlas and axis associated with variation in the splenius capitis muscle was documented by Fritsch and Schuchmann (1988). Information on length and mobility of the neck in Apodiformes and within Trochilidea is lacking.

PELVIS (PELVIC ARCH AND SYNSACRUM)

The pelvis of apodiforms differs from that of *Aegotheles* in several respects: (1) the preacetabular ilium (ala preacetabularis ilii) is a nearly horizontal lamina rather than one raised ≥45° to the frontal plane, (2) the dorsal iliac crest (crista iliaca dorsalis) is absent, (3) the medial border of the preacetabular ilium is tightly sutured to transverse processes of the synsacrum rather than elevated above them, (4) the preacetabular ilium lies parallel to or converges rostromedially toward the long axis of the synsacrum rather than diverging laterally from it, and (5) the acetabular ilium (ala acetabularis ilii) receives no support from a rib process as it does in *Aegotheles*. In addition, the obturator foramen (foramen obturatum) is separated from the ischiopubic fenestra (fenestra ischiopubica) rather than partially or wholly subsumed within it; and the caudal spine of the dorsolateral iliac crest (crista iliaca dorsolateralis) is absent. Within apodiformes, hummingbirds (Fig. 19) are unique in having the preacetabular ilium supported rostrally by both the transverse process and rib process of only one or two vertebrae, and in receiving little or no support of the pelvic arch from the synsacrum elsewhere except at the acetabular and postacetabular ilium (ala postacetabularis ilii). In hummingbirds and Hemiprocnidae the synsacrum projects rostrad from the ilium by one or two vertebrae, a morphology mistaken by Rydzewski (1935) for a notarium in hummingbirds. Apodidae have one or no such vertebrae, and *Aegotheles* has none.

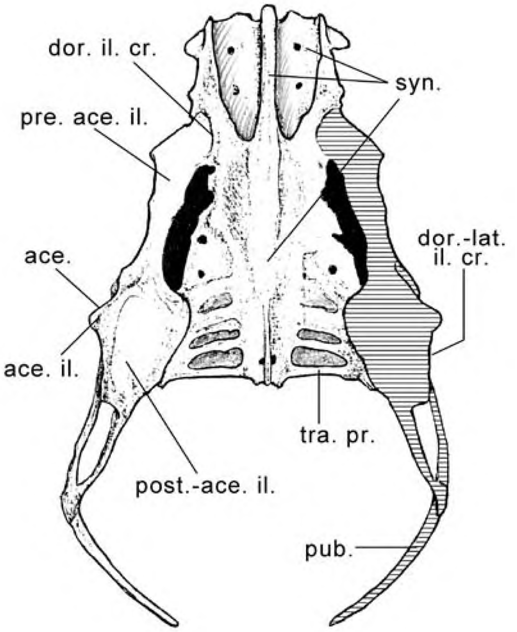

FIG. 19. The pelvis of hummingbirds. Dorsal view of *Eulampis jugularis*. The left pelvic arch is horizontally hatched. A gap between the pelvic arch and synsacrum is shown in solid black. Transverse processes of the synsacrum support the pelvic arch only opposite the hind limb articulation (acetabulum) and at the rostral end of the preacetabular ilum. Abbreviations: ace = acetabulum, ace. il. = acetabular ilium, dor. il. cr. = dorsal iliac crest, dor.-lat. il. cr. = dorsolateral iliac crest, post.-ace. il. = postacetabular ilium, pre.-ace. il. = preacetabular ilium, pub. = pubis, syn. = synsacrum, tra. pr. = transverse process.

TARSOMETATARSUS

In Hemiprocnidae and Apodidae, metatarsal trochlea II and IV (trochlea metatarsus) lie below the plane of I and diverge from the direction of the middle trochlea (III), allowing adduction and abduction of the digits. The trochlea of metatarsus I is modified to allow a variety of motions of the hallux. Steinbacher (1935b) showed that these characteristics are more developed in Apodidae than in Hemiprocnidae and that *Cypsiurus gracilis* could spread digits I and II medially, and III and IV laterally to effect transverse grasping of a vertical, stem-like structure. Collins (1983) described this form of grasping in live *Apus*, and

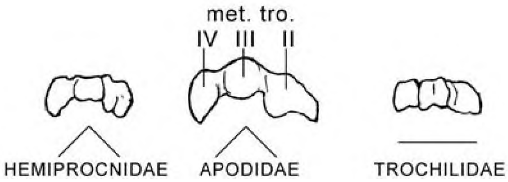

FIG. 20. The metatarsal trochleae of Apodiformes. Proximal view of the articular surfaces for digits 2, 3, and 4 at the distal end of the tarsometatarsus. A section through the plane of the caudal surface of the metatarsals (II, III, and IV) is represented by a line diagram below each tarsometatarsus. Uniformity of orientation of the plane in hummingbirds reflects reduced versatility of lateromedial movement of the digits. Abbreviation: met. tro. = metatarsal trochlea.

saw it also in live individuals of six other genera of Apodinae, but he rarely observed a pamprodactyl arrangement of toes, where all four toes are directed rostrally, in live birds. Nevertheless, pamprodactyly is frequently cited as an adaptation for vertical clinging in swifts.

In hummingbirds, the foot is anisodactyl, with digits II, III, and IV directed rostrally and digit I (hallux) directed caudally. The plantar surfaces of trochleae of metatarsi II, III, and IV lie on a single plane (Fig. 20) and the trochleae are of approximately equal length. Unlike in swifts, the forward toes lack the capability of adduction or abduction, and the foot is best suited for simple grasping.

During their evolution, swifts and hummingbirds have lost more thigh muscles than any other birds (Garrod 1873a, Hudson 1937, Zusi and Bentz 1984), reflecting the limited use of bipedal locomotion. They also lack several abductor muscles of the toes found in Hemiprocnidae and Apodidae (Steinbacher 1935b, Hudson 1937, Zusi and Bentz 1984). The leg muscles of hummingbirds usually represent <1.5% of body weight (Hartman 1961) whereas pectoral muscles represent >20% (Hartman 1954). The legs of hummingbirds provide less boost at take-off than those of other birds. Instead, hummingbirds essentially fly off the perch (Blake 1939, Tobalske et al. 2004). Nevertheless, simple clasping by hummingbirds when perching, clinging vertically, or hanging upside down is supported by strong development of intrinsic, tarsometatarsal flexor and extensor muscles of the digits (Zusi and Bentz 1984).

The hypotarsus of hummingbirds (Fig. 20) resembles that of Hemiprocnidae in having a strong hypotarsal crest (crista medialis hypotarsi) at 90° to the plantar plane of the tarsometatarsus and in osseous enclosure of the canal for m. flexor digitorum longus. *Cypseloides niger* lacks the osseous enclosure, and *Chaetura* and *Apus* exhibit a medial shift of the hypotarsal crest and a deep, caudal concavity (sulcus hypotarsi; Lucas 1895).

DISCUSSION

Synapomorphies of Trochilidae.—Hummingbirds exhibit ≥28 osteological characters of the axial and appendicular skeleton that are synapomorphic in relation to *Aegotheles*, Hemiprocnidae, and Apodidae. Most (~90%) are clearly or potentially associated with either nectarivory or hovering flight. Not included are characters of the sternum and humerus of hummingbirds that are similar to those of Apodidae in relation to their shared behavior of stiff-winged flight with a powerful upstroke of the wing. Probably unique within Aves are the developmental metamorphosis of the ventral bars of the prepalatal upper jaw, extreme reduction of the lateral part of the palatinum, and the globose nature of the capitular tubercle of the humerus. A clasp formed by the carpometacarpal trochlea and ulnare restricts supination of the extended wing in most birds. The clasp is apparently lacking only in hummingbirds (Fig. 17). Although streptognathism of the opened mandible occurs in other birds (especially fish-eaters and aerial insect-eaters), streptognathism of the closed mandible, associated with nectarivory in hummingbirds, has not been reported in other birds. A double sulcus on the head of the humerus at the attachment of the acrocoracohumeral ligament occurs also in Passeriformes, but its functional significance is unclear.

The following lists summarize characters that are unique to Trochilidae within Apodiformes.

Characters of the syrinx of unknown function:

- The syrinx lies within a rostral diverticulum of the interclavicular membrane.
- A tympanic ossicle is present on the medial tympanic membrane.
- The first free bronchial ring has ossified extremities.
- Muscle scars and a bronchial articulation are present on the tympanic drum.

Other characters of unknown function:

- The ventral choanal portion of the palatinum is bilaterally broad.
- The coracoideum has a large, dorsal pneumatic foramen.

- The humerus has a double sulcus for the acrocoracohumeral ligament.

Skeletal characters potentially associated with nectar eating:

- The intermediate portion of the upper jaw is internally, deeply concave.
- The upper jaw undergoes a unique developmental metamorphosis.
- The intermediate portion of the closed mandibula lies within the prepalatal upper jaw.
- All bones of the mandibula are fused.
- The mandibular medial process is well developed.
- The palatal process of the maxillare is fused with the palatinum.
- The lateral part of the palatinum is extremely reduced.
- The parasphenoidal rostrum is abruptly widened at its pterygoid articulation.
- All bones of the jugal arch are fused.
- The epibranchiale is long in relation to the ceratobranchiale (Table 2).
- A sulcus for the origin of m. stylohyoideus is present on the cranium.

Skeletal characters associated with hovering rather than stiff-winged flight:

- The coracoideum has a coracoidal bar between the acromial and procoracoidal processes.
- The supracoracoidal nerve foramen is proportionally large.
- The lateral process of the coracoid is extremely reduced.
- Size-adjusted sternal body length and keel depth are uniquely great.
- An intermuscular line intersects the ventral margin of the sternal keel.
- An intermuscular line follows the lateral margin of the sternal body.
- The articular surface of the capital tuberculum of the humerus is semi-globose.
- The process of m. pronator superficialis is well developed.
- The radius is stout and bowed.
- The ventral cotyla of the ulna has a weakly defined ventroproximal margin.
- The ulnare does not clasp the carpal trochlea in the extended wing.
- The carpometacarpus has a dentiform process.
- The distal articular surface of the carpometacarpus is flattened.
- The proximal articular surface of the major digit is flattened.

Fossils.—The diversity of skeletal characters related to feeding and locomotion that defines modern hummingbirds raises the possibility of inferring functions and biological roles of selected skeletal characters found in fossils. Various exclusively fossil taxa attributed to Cypseli have been described from the Eocene and Oligocene. The most commonly found elements are those of the wing, shoulder girdle, and sternum. When the cranium was preserved, it revealed a swift-like bill and braincase. In the fossils, the shape and proportions of the humeri show a morphocline similar to that of modern taxa (Aegothelidae–Hemiprocnidae–Cypseloidinae–Apodinae; Zusi and Bentz 1982, Mayr and Peters 1999). However, occurrences of highly derived, swift-like, fossil humeri by Middle Eocene and one species (*Scaniacypselus szarskii*) with swift-like feathering (Mayr and Peters 1999) imply an early diversity of aerial insect-eaters with stiff-winged flight. Among those species with swift-like jaws (beak wide and short with pointed tip and large, bony nasal opening) is one (*Paragornis messelensis*) with short, rounded wings and long, broad

TABLE 2. Length of bill and hyobranchiale elements of hummingbirds divided by cube root of body mass.

Species	Cube root body mass	Bill	Basihyale	Ceratobranchiale	Epibranchiale
Doryfera ludovicae	1.82	19.3	1.8	2.6	11.6
Coeligena coeligena	1.89	17.8	2.2	3.0	16.9
Glaucis hirsutus	1.82	17.0	2.3	3.0	14.1
Heliodoxa branickii	1.74	15.3	2.0	2.5	16.0
H. leadbeateri	1.94	14.3	2.3	3.0	22.9
H. xanthogonys	1.91	14.0	1.9	2.9	16.6
H. jacula	2.04	13.2	2.2	2.9	19.8
Chrysolampis mosquitus	1.57	10.2	2.0	2.6	12.8
Florisuga mellivora	1.95	10.8	2.2	2.3	14.1

rectrices, suggesting an adaptive radiation in Cypseli by the Middle Eocene (Mayr 2003a). One taxon (*Jungornis*; Lower Oligocene) displayed a rudimentary tuberculum capitis, a character now best developed in modern Trochilidae. As developed in modern hummingbirds, this structure was claimed to facilitate hovering (Stolpe and Zimmer 1939). More recently, fossils from the early Oligocene of Europe have been interpreted as members of a hummingbird clade and were said to be hummingbirds of "essentially modern appearance," exhibiting morphological specializations toward nectarivory and hovering flight (Mayr 2004). Apparently representing several species of the genus *Eurotrochilus* (Mayr 2004, 2007; Louchart et al. 2007; Bochenski and Bochenski 2008), they reveal many skeletal elements, some in articulation, and skulls with long bills; one specimen shows feathering. In my opinion, the phylogenetic relationships of *Paragornis, Argornis, Jungornis,* and *Eurotrochilus*, shown as a "stem group" to Trochilidae by Mayr (2005), are not convincingly resolved. Here, I comment only on characters claimed by Mayr (2004) to indicate a capacity for hovering and nectivory in *Eurotrochilus*.

The evidence for nectarivory in *Eurotrochilus inexpectatus* was "a greatly elongated beak" (Mayr 2004:863). None of the Apodiformes, modern or fossil, has a long bill other than *Eurotrochilus* and Trochilidae, but the bill of *Jungornis* is unknown. The prepalatal upper jaw of modern hummingbirds usually is long and bilaterally narrowed distal to the nasal region, with lateral margins roughly parallel in dorsal or ventral aspect. Although Mayr (2004) described the beak of *Eurotrochilus* as "narrow," there is no marked narrowing or nearly parallel profile visible in the published figures. According to Louchart et al. (2007), the bill of *Florisuga mellivora* most closely approximates that of *Eurotrochilus* in width. The dorsoventral profile of the bill of *Eurotrochilus* does not preclude nectarivory, but it is not evidence for it. The long bill of another fossil referred to *Eurotrochilus* (Louchart et al. 2007) is exposed in lateral view and differs from modern hummingbirds in its angled gonys, stout dorsal and ventral bars, and long nasal opening. There is no reduction of the nasal opening by vertical orientation of the ventral bars in the intermediate part of the upper jaw. As described previously, the inverted U-shape of the intermediate part of the prepalatal upper jaw in transverse section is not present in the nestling hummingbird, but it develops rapidly with increase in length of the jaws during the first few weeks after fledging. *Eurotrochilus* evidently grew a long bill without acquiring adaptations characteristic of modern hummingbirds.

The same fossil revealed a pair of ceratobranchials associated with the skull, prompting the statement that "As in modern hummingbirds, the new fossil has…very large hyoid bones" (Louchart et al. 2007:173–174). These authors thought that the latter confirm nectarivory because a large hyoid apparatus supports the long protractile tongue used by hummingbirds to lap up nectar. However, I found that the mean ceratobranchial lengths of a swift and two hummingbirds, divided by coracoid length, were as follows ($n = 4$): *Collocalia marginata*, 0.757; *Phaethornis guy*, 0.689; and *Eulampis jugularis*, 0.649. In summary, there is no evidence from the ceratobranchiale or bill structure to support nectarivory.

Tuberculum capitis of the humerus in *Eurotrochilus* is less developed than in modern hummingbirds and apparently lacked a dorsal, globose articular condyle. The globose, ventral surface of the tuberculum capitis of modern hummingbirds articulates with the scapular portion of the glenoid capsule when the humerus is adducted and supinated during hovering (Stolpe and Zimmer 1939, Karhu 2001, R. L. Zusi unpubl. data). A reduced version of the capital tuberculum occurs also in the fossils *Jungornis* and *Eurotrochilus,* rarely in *Hemiprocne,* and in some modern galliforms (Karhu 2001, Mayr 2004), but in view of the small tuberculum in *Eurotrochilus,* a significant role in articulation is questionable.

The carpometacarpus of *Eurotrochilus* has a poorly developed intermetacarpal process and lacks the dentiform process. Illustrations in Mayr (2004, 2007) and Louchart et al. (2007) show that the caudal border of the carpal trochlea of the carpometacarpus was not truncate as it is in modern hummingbirds, which suggests that the ulnare would restrict supination of the carpometacarpus in the extended wing of *Eurotrochilus* as it does in swifts, but not in modern hummingbirds.

The sternum of *E. inexpectatus* clearly shows that linea intermuscularis on the carina has a configuration like that of modern swifts. This implies that m. supracoracoideus is not as enlarged as in modern hummingbirds. Smaller size of the coracoidal foramen (and probably the supracoracoideus nerve) is also consistent with a smaller supracoracoideus muscle. Given the swift-like proportions of the flight apparatus presented by Mayr (2004) and the reduced tuberculum capitis, the combined evidence suggests that *Eurotrochilus* lacked the hovering skills of modern hummingbirds.

Eurotrochilus inexpectatus shares a coracoid length of 7.6 mm with *Hylocharis grayi*, *Cyanophaia bicolor*, *Heliangelus exortis*, and *Chalcostigma stanleyi*. On the basis of published weights of the latter four species (Dunning 2008), *Eurotrochilus* probably had a weight in the range of 4.5–5.8 g. Using data on 208 species of hummingbirds from a variety of sources, Collins and Patton (1989) found the mean (± SD) mass to be 5.1 ± 2.9 g. The frequency of mass classes was 54.3 for <5.0 g and 42.8 for 5.0–9.9 g. Of the 88 species of Apodidae listed by Dunning (2008), 46 (52%) fell within the size range of hummingbirds (297 species), and of the 297 species of hummingbird, 149 (50%) fell within the range of swifts (4.9–108 g). Thus, "small size," without qualification, is not a diagnostic feature of the family Trochilidae (contra Mayr 2004), and *Eurotrochilus* was comparable in size to both modern hummingbirds and swifts.

Evolution of nectarivory and hovering.—The above considerations and the list of features in which *Eurotrochilus* differs from "crown-group Trochilidae" presented by Mayr (2004) allow alternative interpretations of phylogeny and behavior of the fossil taxa. *Eurotrochilus* (and possibly *Jungornis*) may be part of an adaptive radiation within Apodiformes independent of the hummingbird clade, in which feeding and locomotor methods differed from modern swifts. Alternatively, *Eurotrochilus* may represent a branch of the clade that includes Trochilidae but embodies a stage in which hovering was not yet highly developed, and nectarivory, if present, was supplemental to insectivory.

Assuming aerial, arthropod eating as ancestral in Cypselae, how does one envision the evolution of a nectar-adapted bill, tongue, and hyoid apparatus, and of sustained, controlled hovering in hummingbirds? Cohn (1968:169) proposed that hovering developed in birds that gleaned insects from vegetation, and that maintaining position in the air efficiently would be beneficial for that behavior. Mayr (2003b:148) thought that hovering might have "primarily evolved as an adaptation for gleaning insects from the underside of leaves… or around flowers and as a preadaptation for the highly derived nectarivory of extant Trochilidae (Mayr and Manegold 2002)." Schuchmann (1999:506) suggested that nectarivory, not insectivory, was the major stimulus for evolution of the hummingbird feeding apparatus.

I think it likely that a bill longer than those seen in modern swifts and fossil Cypseli would have improved the efficiency of insect-gleaning from leaves or probing of vegetation. Perhaps in the first stage, a subset of aerial insect hawkers or salliers increased their use of hover gleaning for insects on vegetation, developing a longer bill and improved hovering capability. In a later stage, they may have used the longer bill and more efficient hovering to drink water from vegetation and obtain nectar from flowers. However, an intervening stage may have occurred: a subset of hover-gleaning species with a long bill may have specialized on insects associated with nectar-producing flowers rather than on those in nonfloral vegetation. This behavior might have initiated an introduction to nectar, first through consumption of nectar-eating insects near or in flowers, or nectar-producing insects (aphids or scale insects), and then through direct contact with flowers and nectar. Addition of nectar to the diet could have led to increased selection for improvements in hovering and growing reliance on nectar for energy. Further adaptations of the bill, tongue, and hyobranchial apparatus for nectar eating would make insect capture strangely awkward, as seen in modern hummingbirds, and insect hunting would be focused on situations that provide the greatest success. In my opinion, the available evidence from *Eurotrochilus* would place it in the first stage.

SECTION II. THE DIVERSITY OF HUMMINGBIRDS

In this section, emphasis is on variation between species and among higher-level clades below the family level. Many variations throughout the skeleton within Trochilidae are documented here for the first time. The taxonomic distribution of character states and examples of intraspecific variation are broadly indicated below and further detailed in Appendix 2. Use of generic names as examples for character states indicates that the character state occurs in some, but not necessarily all, of the species. Regrettably, the functions and biological roles of most of the variation catalogued here are currently unknown, but emphasis is on variation that I judged to have the most promise for further study. For convenience and continuity with the previous section, data are again organized topographically, and I continue to use the informal terms "Hermit" and "Trochiline" (see Fig. 1). In addition, I refer to subclades supported by anatomical characters but not shown in Figure 1 as (1) the *Anthracothorax* group (*Polytmus* through *Eulampis*) within Mangoes and (2) the *Amazilia* group (*Chlorestes* through *Hylocharis*) within Emeralds (see Appendix 1 for a list of included species).

SIZE

General body size, represented by body weight, is temporally and sometimes geographically variable within each species. Nevertheless, the sample of published weights presented by Dunning (2008) provided a useful approximation of size variation within the named clades of hummingbirds. Both the largest and smallest weight classes are apparently derived within Trochilidae, but polarity of size categories within clades is not firmly established. Size ranges in grams are as follows: Hermits (2.3–10.9), Topazes and Mangoes (3–12.6), Brilliants (3–11.4), Coquettes (2.3–9.1), Patagona (20), Mountain Gems and Bees (1.9–9.2), and Emeralds (2.2–9.8). Note that each clade includes species within the size range of Bees (1.9–4.3).

SYRINX

The following notes on syringeal variation are based on cursory examination of a small sample of hummingbird taxa (*Eutoxeres aquila, Glaucis hirsutus, Threnetes ruckeri, T. leucurus, Phaethornis malaris, P. superciliosus, Anthracothorax dominicus, Chrysolampis mosquitus, Florisuga mellivora, Colibri coruscans, Doryfera lucovicae, D. johannae, Coeligena coeligena*, and *Mellisuga minima*). Among these genera, (1) internal division of the bronchial drum occurs only in *M. minima*, (2) the lateral lamella is fully ossified only in Hermits, (3) the drum is short or long (variable within genera), (4) the drum may exhibit a dorsolateral ridge (*C. coruscans* and *D. johannae*). The tympanic ossicle varies in shape and occurrence: anvil-like in Hermits, slender and curved to knobby in Trochilines, and absent in *F. mellivora*. The mid-dorsal and midventral lengths of the drum are nearly equal and the pessulus rises almost vertically in Trochilines, whereas the midventral portion of the drum is longer and the pessulus slopes rostrodorsally from its ventral attachment in *Apus* and Hermits.

BILL

In general, hummingbirds have long bills in relation to cranial length, but they also exhibit a wide range of bill lengths (*Ramphomicron* to *Ensifera*) and a lesser range of bill widths. Both variables may have ecological significance (Temeles et al. 2002). Hummingbirds are also noted for other differences in bill shape, from strong decurvature (*Eutoxeres*), moderate decurvature (most *Phaethornis*), or terminal recurvature (*Avocettula recurvirostris, Opisthoprora euryptera*) to no curvature (many genera). In this they differ from passerine nectarivores, almost all of which have variously decurved bills.

Differences in the form of the upper mandible, such as presence of a hook, terminal recurvature, tomial serrations (Ornelas 1994, R. L. Zusi unpubl. data), and lateral compression into a blade (*Heliothryx* and *Augastes*), are primarily or completely restricted to the rhamphotheca. Similarly, extended basal feathering (e.g., *Heliodoxa* and *Ensifera*) and fleshy dermal expansions (*Trochilus* and *Cynanthus*) over the craniofacial bending zones are not reflected in the skeleton. Ventral expansion of the caudal rhamphotheca of the upper mandible of *Anopetia* may or may not have an osteological counterpart (no skeletons were available). Of special interest are the pronounced, opposing hooks on the mandibles of adult male *Ramphodon* and *Androdon* (Fig. 21) that are little developed or absent in immature males and in females. How do adult males perform tongue lapping of nectar in the presence of such opposing hooks? Sazima et al. (1995), Bleiweiss

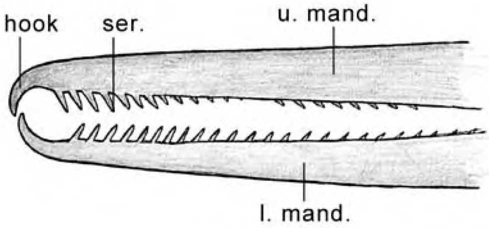

FIG. 21. Rhamphothecal serrations and hooks in a hummingbird. Lateral view of *Androdon aequatorialis*. Serrations and hooks are not reflected in the underlying bone. Although serrations are found in many species, prominent hooks on both mandibles are restricted to adult males of *A. aequatorialis* and *Ramphodon naevius*. The apparent interruption of serrations on the upper mandible is artifactual. Abbreviation: l. mand. = lower mandible, ser. = serration, u. mand. = upper mandible.

et al. (2003), and Ornelas (1994) did not address this problem.

PREPALATAL UPPER JAW

Intermediate part.—Among hummingbirds, the prepalatal upper jaws of *Heliothryx* and *Schistes* have a proportionally long, bony nasal opening in which the flattened plane of the ventral bars is roughly horizontal, and a proportionally short intermediate part in which the plane of the ventral bars is more vertical.

Nasal part.—The transverse section of the dorsal bar in the nasal part may be circular, dorsoventrally compressed, or mediolaterally compressed—configurations that may be modified by the nasal roof. Species in which hyoid horns penetrate the bony nasal opening on either side display an excavation of the ventrolateral portion of the dorsal bar on that side (e.g., *Topaza pella*, *Ensifera ensifera*, *Heliodoxa branickii*, *H. aurescens*, *H. rubinoides*, and *H. leadbeateri*). The dorsal bar at the rostral portion of the nasal region may be uniformly narrow or gradually widened rostrally in dorsal view, and variable in length.

Length of the nasal part, adjusted for body size (indexed by coracoideum length), is modally shorter in Hermits than in Trochilines (R. L. Zusi unpubl. data). The nasal part (Fig. 22A, B) includes the vestibular region (regio vestibularis) and respiratory region (regio respiratoria). Partial separation of the two regions is provided by the nasal crest (crista nasalis), a ventral, transverse ridge of the dorsal bar. The medial wall (paries) of both regions is formed by a continuous, membranous nasal septum. A blind, caudodorsal pouch of the respiratory region represents an olfactory region (regio olfactoria), bounded caudally by the mesethmoidale and ectethmoidale. In hummingbirds, the nasal part includes a broad, lateral, nasal operculum (operculum nasale) that defines the external, membranous nasal opening (naris). The latter is a long, horizontal slit that widens posteriorly, bounded dorsally by the leathery operculum and ventrally by the ventral bar. The respiratory passage traverses the external naris, vestibular region, and respiratory region. Openings in the floor of the respiratory region are the internal nares medially and the antorbital sinus (sinus antorbitalis) laterally. The nasal cavity is partially subdivided transversely into a medial sector (sector medialis) between the nasal septum and the conchae and a lateral sector (sector lateralis) between the

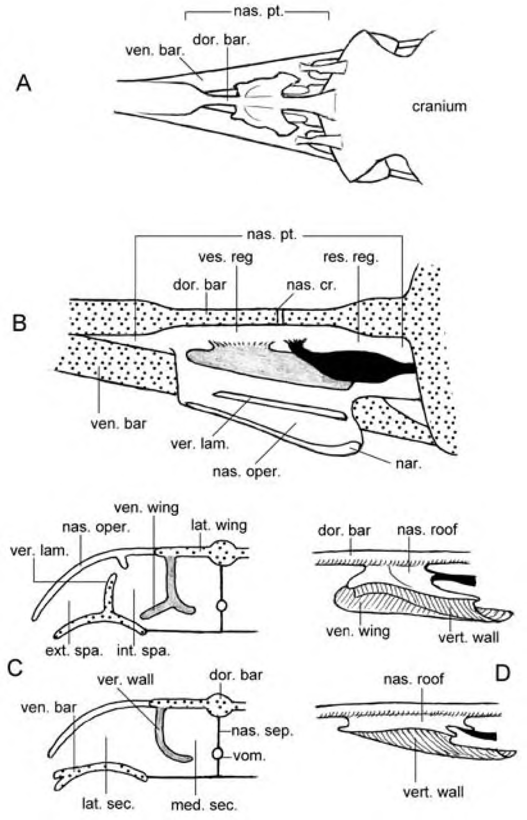

FIG. 22. Structures of the nasal part of the prepalatal upper jaw in hummingbirds. (A) Partial hummingbird skull in dorsal view for orientation of B–D. (B) Diagrammatic composite of left side in dorsal view, with nasal roof and maxillary processes of nasale removed, and nasal operculum added. Bone is stippled, rostral concha is gray, and medial concha is solid black. Both conchae are suspended from the dorsal bar and nasal roof. The vertical lamella rises from the ventral bar within the nasal opening of the nasal operculum. (C) Diagrammatic transverse sections through the rostral concha, which may have an inverted T-bar form (above) or a J-bar form (below). (D) Semidiagrammatic representations of the left rostral concha in dorsolateral view; inverted T-bar form above, and J-bar form below. The base of the medial concha in solid black. Variations shown have no known functional significance. Abbreviations: dor. bar = dorsal bar of upper jaw, ext. spa. = external space, int. spa. = internal space, lat. sec. = lateral sector, lat. wing = lateral wing, med. sec. = medial sector, nar. = external nasal opening, nas. pt. = nasal part of upper jaw, nas. roof = roof of nasal region, nas. oper. = nasal operculum, nas. cr. = nasal crest, nas. sep. = nasal septum, res. reg. = respiratory region, ven. bar = ventral bar, ven. wing = ventral wing, ver. lam. = vertical lamella, vert. wall = vertical wall, ves. reg. = vestibular region, vom. = vomer.

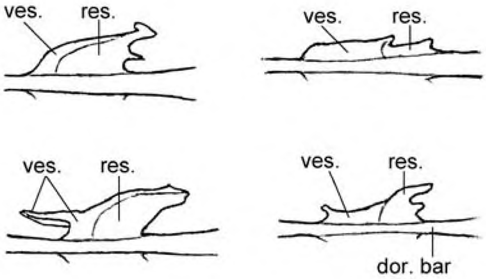

FIG. 23. A sample of variation in the ossified nasal roof in Trochiline hummingbirds. Right side, dorsal view; rostral direction to left. The vestibular and respiratory portions are highly variable in size and shape within Trochilidae, but some patterns reflect phylogeny at various levels. Patterns often found in *Anthracothorax*, *Eriocnemis* (above, left and right), *Heliodoxa*, and *Chlorostilbon* (below, left and right). See also Figures 4, 6, and 8. Abbreviations: dor. bar = dorsal bar of the upper jaw, res. = respiratory roof, ves. = vestibular roof.

conchae and naris. The main air passage between lateral and medial sectors lies just anterior to the rostral concha, and a more restricted passage continues caudally as a narrow space between the ventral border of the rostral concha and the ventral bar. In outgroups and Hermits the nasal roof and conchae are largely cartilaginous. However, all hummingbirds have part of the roof of both the vestibular and respiratory regions ossified in the vicinity of the nasal crest, and ossification of the nasal roof and conchae in Trochilines is usually extensive (Fig. 23).

The rostral concha is suspended from the roof of the vestibular region by a vertical wall (paries verticalis) and continues, unsupported, into the respiratory region. The rostral concha is cartilaginous in outgroups, Hermits (except *Eutoxeres*), and some Mangoes (*Androdon*, *Colibri*, *Schistes*, and *Augastes*), and is ossified in *Eutoxeres*, *Florisuga*, some Mangoes, and all Neotrochilines. The medial concha (concha nasalis medialis) is suspended anteriorly from the roof and sides of the respiratory chamber by an ossified, rod-like base, and passes caudally, unsuspended and cartilaginous, to its attachment on the posterior wall of the combined respiratory and olfactory chambers. I found that, in general, the vestibular region is lined with stratified squamous epithelium, the respiratory region with ciliated cuboidal or ciliated columnar epithelium, and the olfactory area with olfactory epithelium. An olfactory concha (concha nasalis caudalis) is lacking in hummingbirds and in *Collocalia* (Bang 1971), but its status in other apodiforms is unknown. There is no fusion of nasal structures with the ventral bars (as noted also in *Archilochus alexandri* by Shufeldt (1885).

The conchae are a rich source of variation in hummingbirds. In most Trochilines the medial concha becomes broader and ribbon-like caudally and scrolls along its long axis from less than one turn to one-and-a-quarter turns. Scrolling is absent in most Hermits, *Heliothryx*, *Androdon*, *Heliactin*, *Topaza*, and some *Colibri*; instead, the free margin of the shelf-like concha is thickened and rod-shaped and contains venous sinuses. In all hummingbirds the medial concha narrows caudally and terminates on the ectethmoidale.

In transverse section, the rostral concha (Fig. 22C) exhibits either an inverted T-shape (most hummingbirds) or a J-shape with the ventral curve directed medially (*Florisuga*, *Anthracothorax*, *Eulampis*, *Chrysolampis*, some *Heliodoxa* and *Coeligena*, and the *Amazilia* group). For brevity I shall refer to the inverted T-shape of the rostral concha simply as a "T-bar," and to the J-shape as a "J-bar." Intermediate states occur. For example, the ventral wing (ala ventralis) of the T-bar may be reduced or missing in some portion of the concha; or the ventral wing may taper anteriorly and disappear at, or near, the anteroventral limit of the concha. Some form of intermediacy is found in *Glaucis*, *Threnetes*, *Androdon*, *Heliothryx*, many Brilliants, *Patagona*, and some species in the *Amazilia* group. All states may be found within the *Heliodoxa* group, and the genus *Campylopterus* is also highly variable.

Among the species with a T-bar, the ventral wing of the rostral concha (Fig. 22D) may protrude anteriorly beyond the vertical wall of the concha (*Doryfera*, various Brilliants and Coquettes, *Eugenes*, *Lamprolaima*, and Bees). Uniquely to *Lampornis* and *Lamprolaima*, the anterior portion of the ventral wing is marked ventrally by a groove that curves anteromedially and produces a notch in the rostral tip of the concha. The vertical wall may curve laterally at its anterior extremity (*Ensifera*, *Phlogophilus*, *Sephanoides*, *Lophornis*, *Urosticte*, most Coquettes, *Eugenes*, Bees, *Cynanthus*, and *Basilinna*). Species with a T-bar usually have a well-developed vertical lamella (lamella verticalis)—a vertically oriented, longitudinal baffle arising from the ventral bar in the caudal part of the vestibular region just inside the external naris and oriented parallel to the concha. This lamella partially subdivides the lateral sector into external and internal spaces (spatium externum and spatium internum). Species with a baffle also may have one or more tubercles or ridges that descend from the nasal operculum to cross or embrace the caudodorsal margin of the lamella. In species with a J-bar the vertical lamella is reduced typically to a low, roughly horizontal ridge that does not divide the lateral sector. The J-bar apparently is a derived state within Trochilidae, primarily through loss of the ventral wing of a T-bar and of the vertical lamella.

The roof of the nasal part of the upper jaw may be largely unossified (*Androdon*), but ossification associated with both the vestibular and respiratory regions occurs in most hummingbirds, in various patterns (Figs. 7B, 8, 22, and 23).

Flower mites.—Flower mites (Ascidae) are known to travel from one flower to another (phoresis) in the nasal cavity of hummingbirds and passerine nectarivores, gaining access to or departing from flowers by running along the bill of the feeding bird. Mites may be found in any part of the nasal chambers in spirit specimens of hummingbirds, possibly having wandered after death and before fixation of the bird; their locations in the living bird are not well known. The biology of flower mites has been investigated by various authors (e.g., Colwell 1985, Colwell and Naeem 1993), but little is known about the relation of mites to nasal anatomy of the carrier. The lateral section of the nasal cavity of hummingbirds (Fig. 22C), lined with stratified squamous epithelium, may serve to house mites in a location that permits their rapid departure and that isolates them from the respiratory region and its ciliated epithelium.

Craniofacial hinge.—The amount and location of decalcification in the nasale during posthatching development, discussed in Section I, probably differs within Trochilines and probably explains different forms of the caudal portion of the bony naris—long and slit-like in *Eutoxeres*, narrow and pointed in *Androdon*, or broad and delimited by the ectethmoidale. In some (e.g., *Heliodoxa*), the bony narial opening stops just short of the craniofacial hinge and is broadly rounded within the nasal bone. The slit-like bony nasal opening of *Eutoxeres* occasionally extends to, or transects, the craniofacial hinge. Characterization of Hermits and Trochilines as strictly holorhinal and schizorhinal, respectively, is therefore somewhat ambiguous and simplistic.

The middle portion of the craniofacial hinge, comprising the frontal processes of the premaxillares and premaxillary processes of the nasales, is underlain by the mesethmoidale. Flexibility of that portion of the hinge is lost in some genera (*Eutoxeres, Doryfera, Eugenes, Coeligena,* and *Ensifera*) by fusion of mesethmoidale and premaxillare, a specialization associated with "distal rhynchokinesis" in some Charadrii (Zusi 1984).

PALATUM

Vomer.—The rostral profile of the vomer from dorsal or ventral view (Fig. 24A) varies from rounded (most Hermits, Topazes, Mangoes, some Brilliants and Coquettes, some Mountain Gems and Bees) to angular (some Mangoes, Brilliants, Coquettes, Mountain Gems, Bees, and Emeralds), and the angles may be enhanced by spicules (some *Heliodoxa*; see Graves and Zusi 1990). The body may comprise little more than a juncture of the pterygoid processes (most Hermits, *Topaza*, Mangoes, Brilliants, Coquettes, Mountain Gems, and Bees) or it may be a variably extensive plate (Emeralds). *Eutoxeres* is distinguished among hummingbirds by a long, narrow vomeral body that becomes spatulate rostrally. Huxley (1867:454) stated that "Trochilus has the true Passerine vomer, with its broad and truncated anterior, and deeply cleft posterior end." Since then, other workers have overemphasized the systematic importance of an angular profile of the vomeral body and the presumed aegithognathous palate in hummingbirds. For example, Lowe (1939) accepted Huxley's conclusion after dissecting species from eight genera, three of which actually have a rounded or nearly rounded vomer (*Eulampis, Ensifera,* and *Patagona*).

The vomeral spine of hummingbirds is short in *Colibri*, Brilliants, some Coquettes and Bees, *Panterpe, Campylopterus,* and some other Emeralds, and long in Hermits (except *Eutoxeres*), Topazes, the *Anthracothorax* group, *Heliodoxa, Coeligena, Patagona,* and some Emeralds. A bony spine is absent from *Eutoxeres*, but I found a cartilaginous spine in a poorly cleaned skeleton of *E. condamini.*

Maxillare.—The palatal process of the maxillare may extend dorsally or dorsomedially beyond its co-ossification with the rostral process of the palatinum, as either a slight ridge or a short hook (most Hermits, Topazes, Mangoes, and Brilliants). In some species, the hook expands caudally and lies parallel and medial to the palatinum (some Brilliants and

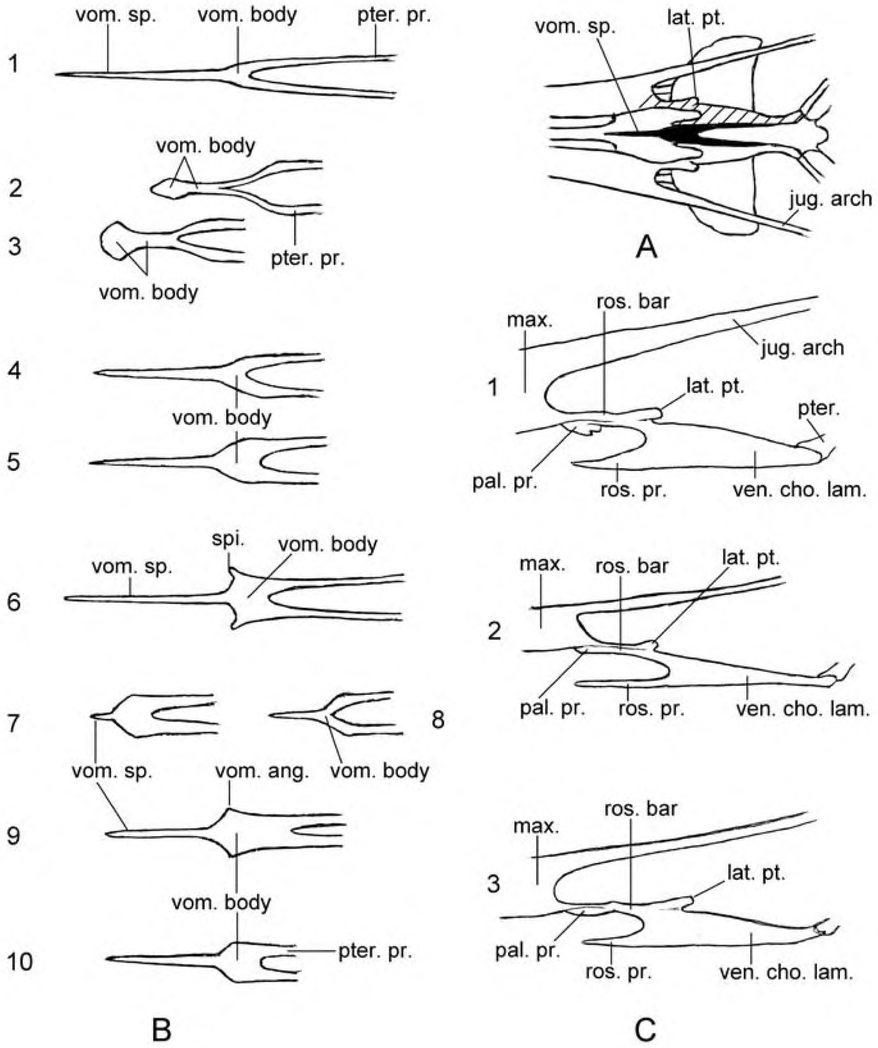

FIG. 24. Examples of variation in shape of the vomer, palatal process, and palatinum in hummingbirds. (A) Ventral view of hummingbird palate for orientation in B and C. Most of upper jaw (to left) not shown. Left palatinum obliquely hatched, vomer in solid black, rostral is to left. (B) Vomers in dorsal or ventral view: (1) *Phaethornis guy*, (2) *Eutoxeres aquila*, (3) *Eutoxeres condamini*, (4) *Topaza pella*, (5) *Florisuga mellivora*, (6) *Heliodoxa leadbeateri*, (7) *Colibri delphinae*, (8) *Panterpe insignis*, (9) *Eupetomena macroura*, (10) *Trochilus polytmus*. Note lack of vomeral spine in *Eutoxeres*. Except for the latter, a vomeral spine is found in all species of hummingbird. Otherwise, no particular vomeral shape characterizes Trochilidae. (C) Variation in shape of palatal process of maxillare and location of lateral process of palatinum (left, ventral view), scaled to similar length of palatinum; vomer absent and pterygoideum incomplete. The patterns are exemplified by (1) *Lampornis amethystinus*, (2) *Phaethornis hispidus*, and (3) *Anthracothorax mango*. Note that the caudal extremity of the palatal process fuses with the rostral bar of the palatinum and assumes various shapes. The lateral part of the palatinum may lie (1) between the rostral bar and ventral choanal lamella of the palatinum (mostly in Neotrochilines), (2) on the rostral bar (mostly in Hermits), or (3) on the ventral choanal lamella (mostly in Mangoes). Abbreviations: jug. arch = jugal arch, lat. pt. = lateral part of palatinum, max. = maxillare, pal. pr. = palatal process of maxillare, pter. = pterygoideum, pt. pr. = pterygoid process of vomer, ros. bar = rostral bar of the palatinum, ros. pr. = rostromedial process of the palatinum, spi. = spicule, ven. cho. lam. = ventral choanal lamella of the palatinum, vom. ang. = vomeral angle, vom. body = vomeral body, vom. sp. = vomeral spine.

Coquettes). The extended portion may be irregular in outline, possibly indicating ossification of its surrounding membrane (*Patagona*, all Mountain Gems, Bees, and Emeralds; Fig. 24C: 1).

Palatinum.—The lateral part of the palatinum usually lies near the junction of the ventral choanal lamella and rostral bar, but it may lie farther caudally on the lamella or more rostrally on the rostral bar (Fig. 24C). It serves for insertion of m. pterygoideus (pars ventralis medialis), which originates on the medial process of the mandibula in both swifts and hummingbirds (Morioka 1974, Zusi and Bentz 1984: fig. 3a). The more rostral position of the latter part probably reflects a longer pterygoideus muscle in Hermits and *Androdon*, which also have conspicuously large adductor mandibulae muscles. By contrast, a markedly caudal position of the lateral part is found in Topazes and Mangoes (except *Androdon*).

Pterygoideum.—A syndesmotic, intrapterygoid articulation occurs in all outgroups. In a minority of hummingbird species the articulation is present in adults, but in the majority the articulation is obliterated by fusion. The articulation, although variable in its occurrence in adults of many species, is commonly found in *Eutoxeres*, *Colibri*, *Schistes*, some Brilliants and Coquettes, *Patagona*, *Lampornis*, some Bees, *Orthorhynchus*, and *Klais*. Individuals that lack the intrapterygoid articulation have a pterygopalatine arch without articulations or well-defined hinges.

Jugal arch.—In adults of *Aegotheles*, Hemiprocnidae, and Apodidae and a juvenile hummingbird (*Chlorostilbon swainsonii*) the jugal arch consists of a long quadratojugale extensively sutured with a long jugal process (processus jugalis) of the maxillare. The jugale is absent. Adult hummingbirds differ from other Apodiformes in that the two bones forming the arch are fused. A minor and variable lateral or medial widening of the rostral portion of jugal arch in the frontal plane occurs in a few species of hummingbird, most prominently in *Ramphodon* and many species of *Phaethornis*, possibly in relation to the insertions of enlarged pterygoideus muscles.

MANDIBULA

In its least differentiated form, the intermediate part of the mandibular ramus is laterally compressed and the tomial and ventral margins somewhat swollen and rod-shaped (thus roughly hourglass-shaped in transverse section). In most species the ramus gradually widens caudally, becoming oval in transverse section, but the caudal part may exhibit a more abrupt pneumatic inflation, the most extreme examples manifesting also a large rostral mandibular fenestra (some Mangoes, most Brilliants and Coquettes, Patagona, Mountain Gems, Bees, and some Emeralds). In Hermits, the free rami are narrowly oval in transverse section throughout, vertically oriented caudally, and becoming more horizontal toward the symphysis. The rostral mandibular fenestra is absent or small in relation to the depth of the ramus in Hermits, and largest in *Heliothryx*, *Aglaeactis*, *Ensifera*, *Coeligena*, *Pterophanes*, *Boissonneaua*, *Discosura*, *Loddigesia*, *Lesbia*, *Ramphomicron*, *Oxypogon*, *Patagona*, Mountain Gems, and some Bees. Lateromedial bending of the rami occurs between the rostral mandibular fenestra and the inflated portion of the caudal ramus in many Trochilines, but the zone of bending is less restricted in Hermits. In them, the fenestra is lacking or minimal.

Although I did not measure the length of the mandibular symphysis in most species, *Threnetes ruckeri* is probably unique in having a symphysis that occupies almost half the length of the bill (that of *T. leucurus* is about one fifth) (Fig. 25). In *T. ruckeri* the ventral surface of the symphysis is planar and forms an abrupt 90° angle with the lateral portion. The planar symphysis fills the space between the ventral bars of the prepalatal upper jaw, and presumably the bright yellow rhamphotheca of the enlarged symphysis is conspicuous in display. The symphysial part of the prepalatal upper jaw is not correspondingly elongate.

CRANIUM

Cranial shape.—In dorsal view (Figs. 4, 26A, and 27A) the rostral contour of the ectethmoidale usually slopes caudolaterally from the transvere axis of the craniofacial hinge, but in many Coquettes it nearly parallels the hinge axis and forms a right angle with the supraorbital margin (margo supraorbitale). The profile of the frontal, extending from the lateral limit of the ectethmoidale to the caudal margin of the orbit, in dorsal view, may resemble a medially concave V (most Hermits, Topazes, Mangoes, most Brilliants, some Coquettes, and Bees), a medially concave _/ (some *Heliodoxa*, many Coquettes, Mountain Gems, Bees, and Emeralds), or a medially concave

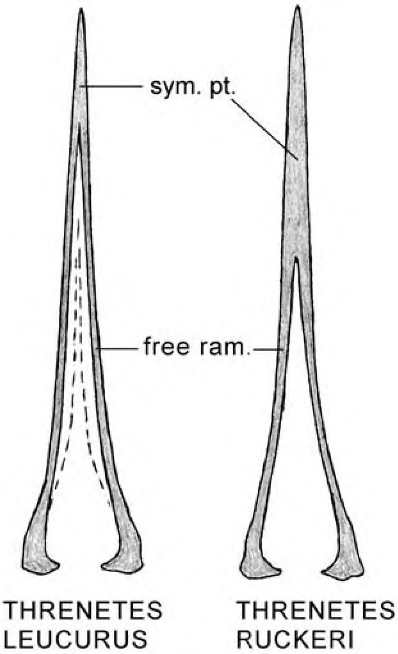

FIG. 25. Mandibular variation in *Threnetes*. The symphysial part of the mandibula of *T. ruckeri* is proportionally much longer than that of *T. leucurus*, in which the rami may be spread (while drinking nectar?) as shown in the gray-shaded mandibula, or relaxed as shown by the dashed line. In *T. ruckeri* the long and broad symphysis maintains a mandibular profile similar to that of the spread state in *T. leucurus*, and the flattened, bright yellow, ventral surface of the symphysis may represent a display feature. Abbreviation: free ram. = free ramus of mandibula, sym. pt. = symphysial part of mandibula.

U (*Eutoxeres*, *Ramphodon*, some *Phaethornis*, some *Campylopterus*, and *Pterophanes*).

The cranium in adults of almost all hummingbird species is fully ossified dorsally but unpneumatized medially. However, within the otherwise pneumatized, rostral portion of the frontal bones, a frontal fenestra (fenestra frontalis) occurs in a few genera (*Polytmus*, *Anthracothorax*, *Eulampis*, *Chrysolampis*, and possibly *Avocettula*; Fig. 26A). Apparently, ossification (and pneumatization) of this fenestra progresses slowly because most adult specimens of each species exhibit the fenestra, but occasionally it is reduced or absent. I have found no similar fenestra in other avian families.

The cranium in hummingbirds varies in the length in relation to the width of both the ethmoidal region and the brain case. In *Phaethornis* the cranium of all but the smaller species is proportionally long, narrow, and caudally tapered, with deep grooves that house the hyoid horns (cornu branchiale). The orbitocranial fonticulus (fonticulus orbitocranialis) may be narrower lateromedially (Hermits and some Mangoes), wider (most hummingbirds), or almost circular (many Coquettes; Fig. 26B). A partial separation of the optic foramen (foramen n. opticum) from the orbitocranial fonticulus is least prominent in Hermits, some Mangoes, and some Coquettes, and more prominent in other hummingbirds. Skulls of the smaller Coquettes are proportionally short and spherical. Although the profile of the cerebellar prominence of most hummingbirds is evenly curved in lateral view, a few species show a contour that is caudally blunt (*Heliodoxa*, *Sternoclyta*, *Patagona*, and *Schistes*; Fig. 26B). In rostral view (Fig. 27A) the lateral margins of the ectethmoidales may be vertically parallel (Hermits, Topazas, some Mangoes, Brilliants, *Patagona*, Bees, and Emeralds) or may slope to varying degrees, always converging dorsally (especially Coquettes).

Occiput and Basicranium.—Midventrally the curve of the cerebellar prominence terminates at the foramen magnum, either without modification (most hummingbirds) or with a swelling (Fig. 26B) associated with pneumatization along the dorsal rim of the foramen (e.g., *Ramphodon*, *Phaethornis*, *Doryfera*, *Chrysolampis*, *Coeligena*, *Urochroa*, *Ensifera*, *Heliodoxa*, and *Ocreatus*). In the internal brain cavity (endocranium), a feature sometimes visible through the foramen magnum (Fig. 27B) is the caudal wall (dorsum sellae) of the hypophysial recess (sella turcica). The caudal wall is ligamentous, but its dorsal rim may be ossified fully to form a bony bridge (*Florisuga*, *Colibri*, *Chrysolampis*, *Eulampis*, and many Coquettes). The ossified bridge is partial or absent in most other hummingbirds, including *Topaza*. It is absent or present in swifts.

Processes, crests, and fossae.—The size of m. adductor mandibulae externus (Fig. 10C) is related to the size of the temporal fossa (fossa temporalis musculorum), reflected in part by its defining crests, and by the distance between the postorbital (processus postorbitalis) and zygomatic processes (processus zygomaticus; Figs. 4A and 26B). All of these features are most developed in *Glaucis*, *Ramphodon*, and *Androdon*, but only *Ramphodon* has a midsagittal crest (crista nuchalis sagittalis). *Androdon* exhibits a uniquely short and broad-based zygomatic process (Fig. 26B, middle row left).

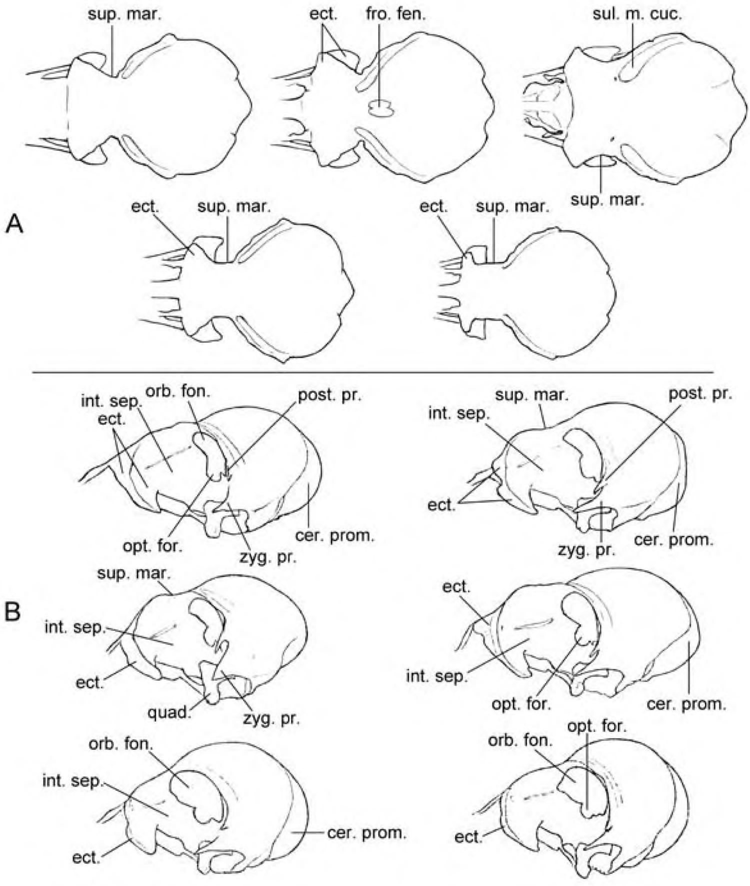

FIG. 26. Examples of variation in the cranium of hummingbirds. Jugal arch and most of the upper jaw not shown. (A) Dorsal view. Above, left to right: *Glaucis*, *Anthracothorax*, *Eutoxeres*; below, left to right: *Amazilia* and *Metallura*. Examples of the genera illustrated are intended to show variations in shape of the supraorbital margin and adjacent margin of the ectethmoidale that sometimes typify genera or groups of genera. The frontal fenestra is found only in *Polytmus*, *Anthracothorax*, *Eulampis*, *Chrysolampis*, and possibly *Avocettula*. (B) Left lateral view. Left to right, top: *Phaethornis* and *Heliodoxa*; middle: *Androdon* and *Ensifera*; bottom: *Chalcostigma* and *Mellisuga*. Examples from the genera illustrated were selected to show variations discussed in the text; for example, *Androdon* has a uniquely short and broad-based zygomatic process. Variations in the labeled features are largely unexplained. Abbreviations: cer. prom. = cerebellar prominence, ect. = ectmethmoidale, fro. fen. = frontal fenestra, int. sep. = interorbital septum, opt. for. = optic foramen, orb. fon. = orbitocranial fonticulus, post. pr. = postorbital process, quad = quadratum, sul. m. cuc. = sulcus of cucullaris capitis muscle, sup. mar. = supraorbital margin, zyg. pr. = zygomatic process.

Mid-dorsally on the cranium, a shallow depression indicates the origin of m. stylohyoideus (Fig. 4B), a muscle that lies between and below the two hyoid horns. In species with shorter horns, the depression is about midway on the brain case; in those with long horns it is near or anterior to the craniofacial hinge. Even when the horns extend far forward into the nasal or intermediate regions of the upper mandible, the anterior limit of origin of m. stylohyoideus remains at or slightly anterior to the craniofacial hinge.

Interorbital septum and parasphenoidal rostrum.—Lateral expansion and pneumaticity of the interorbital septum, rostral tympanic recess (recessus tympanicus rostralis), and parasphenoidal rostrum vary within the family (Fig. 27C). In general, character states of the three variables are highly correlated. Expansion and pneumaticity

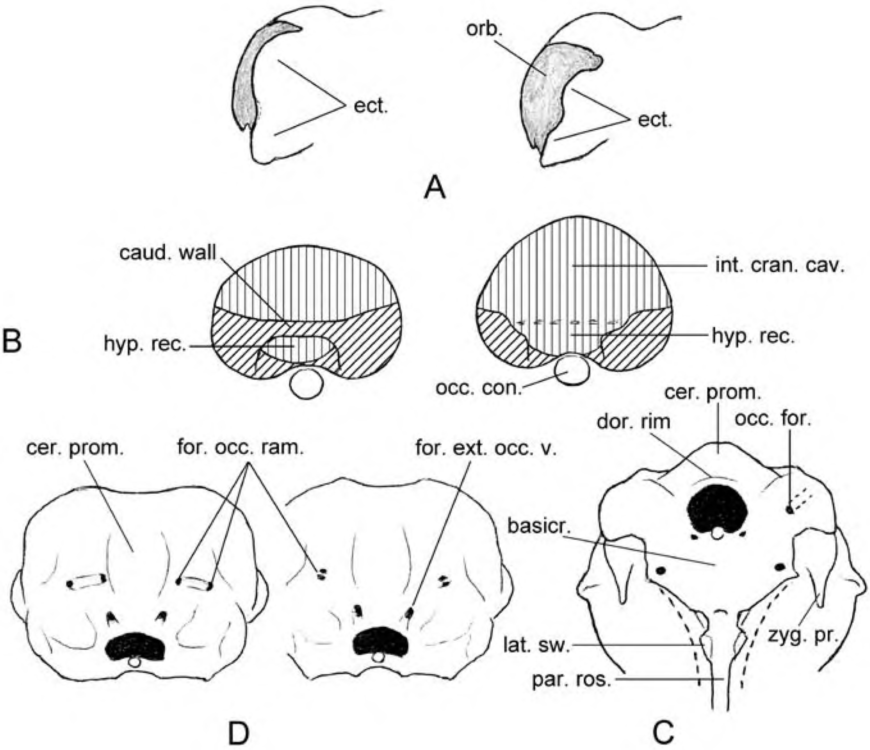

FIG. 27. Variation in cranial characters of hummingbirds. The drawings illustrate extreme states of continuous variation found in several characters, and they do not represent particular species. The significance of the variations is largely unknown. (A) Rostral view of the cranium (right side only) to show a nearly vertical lateral margin of the ectethmoidale (left) versus one that slopes toward the midline dorsally (right). (B) Semidiagrammatic. Internal bony structures (oblique hatching) of the cranial cavity (vertical hatching), showing presence or absence of a bony, caudal wall of the hypophysial recess, as seen through the foramen magnum; dashed line is a ligament. (C) Ventral view of cranium. Dashed line shows the extent of pneumatic inflation of the parasphenoidal rostrum found in some species. The occipital foramen is an opening of a previously undescribed vascular tube peculiar to Trochilidae; the foramen may be absent. This drawing shows the abrupt swelling on the parasphenoidal rostrum that supports the palatum in hummingbirds, and has been mistaken for basipterygoid processes. (D) Caudal view of crania showing vascular foramena. In C and D the foramen magnum is solid black. Abbreviations: basicr. = basicranium, caud. wall = caudal wall of hypophysial recess, cer. prom. = cerebellar prominence, dor. rim = dorsal rim of foramen magnum, ect. = ectethmoidale, for. ext. occ. v. = foramen of external occipital vein, for. occ. ram. = foramen of occipital ramus of ophthalmic artery, int. cran. cav. = internal cranial cavity, lat. sw. = lateral swelling on parasphenoidal rostrum, occ. con. = occipital condyle, occ. for. = occipital foramen of vascular tube, orb. = orbit, par. ros. = parasphenoidal rostrum, sul. nas. = sulcus of nasolacrimal ducts, zyg. pr. = zygomatic process.

are especially pronounced in *Pterophanes*, *Heliangelus*, *Aglaiocercus*, *Sappho*, *Lesbia*, *Ramphomicron*, *Chalcostigma*, and *Boissonneaua*, and least developed in Hermits, *Florisuga*, *Androdon*, *Urochroa*, *Heliodoxa*, *Sternoclyta*, *Patagona*, *Eugenes*, and *Heliomaster*. Regardless of lateromedial breadth, the interorbital septum of hummingbirds is always complete. Relationships of these variables to size and orientation of the eyes and bill length might reveal a functional complex related to feeding behavior.

Other conformations of the rostrum may be independent of pneumatization. The parasphenoidal rostrum typically is flat or slightly concave ventrally, occupying the entire space between the pterygoid processes of the vomer. However, the midsection of the rostrum may be narrowed (especially *Eutoxeres*, *Ramphodon*, and some *Phaethornis*), creating a lateral space between it and the pterygoid processes (*Ramphodon* and *Phaethornis*). *Doryfera, Schistes,* and *Goldmania* have a basally broad rostrum that narrows rostrally to form a keel. In lateral view, the midventral contour of the mesethmoidale may be smoothly continuous with that of the parasphenoidal rostrum, or it may angle upward more or less abruptly from the tip of the rostrum toward the dorsal bar of the upper jaw. Abrupt angling is extreme in *Lafresnaya, Oreotrochilus, Lesbia, Ramphomicron, Metallura,* and *Chalcostigma*.

Foramena and Fenestrae.—The medial orbitonasal foramen (foramen orbitonasale mediale), located at the rostral end of the olfactory sulcus (sulcus n. olfactorius), is double in *Hemiprocne, Cypseloides,* Hermits, Topazes, *Androdon, Colibri,* and *Schistes*; typically, it is single in other hummingbirds, but some intermediacy occurs. Bilaterally on the occiput, the occipital ramus (ramus occipitalis) of the ophthalmic artery (a. ophthalmica) is associated with one or two foramena (Fig. 27D) that may be closely, moderately, or widely spaced and connected by a roughly horizontal sulcus. Single or closely spaced foramena typify *Hemiprocne, Cypseloides,* Hermits, *Polytmus,* and *Chrysolampis,* whereas widely spaced foramena typify *Florisuga, Doryfera,* many Brilliants and Coquettes, and many Mountain Gems and Bees. Moderate separation occurs in Topazes and *Patagona*.

Vascular tube.—Apart from its apomorphic status in hummingbirds among Apodiformes, the vascular tube exhibits topographic variations of its foramina on the cranium. An occipital foramen (foramen occipitalis), located bilaterally on the occiput dorsolateral to the foramen magnum (Fig. 27C), is found in Hermits, *Heliothryx, Androdon, Heliactin, Eulampis, Anthracothorax, Chrysolampis,* and *Polytmus*. When absent, an alternative foramen may occur in the external acoustic meatus (meatus acusticus externus). Documentation, analysis of variation, and function of the vascular tube are beyond the scope of the present study.

HYOBRANCHIAL APPARATUS

The retracted tongue reaches almost to the tip of the bill. Photographs and published statements (e.g., Davis 1958:33) indicate that many species are capable of protruding almost the entire tongue beyond the bill tip. Pronounced extension of the tongue and hyoids is accomplished by contraction of m. branchiomandibularis, which inserts on most or all of the epibranchiale. Measurement of the curved epibranchiale can be made on cleared and stained specimens by straightening the fragile bone without danger of damage. Measurements (in relation to cube root of body weight) of the bill and hyobranchial elements of single specimens of nine species in the USNM cleared-and-stained collection are summarized in Table 2. In this sample the epibranchiales are roughly three or more times longer than the combined basihyale and ceratobranchiale. Length of the basihyale is roughly two-thirds that of the ceratobranchiale, and both elements show little variation in this proportion (Table 2). In addition, regardless of relative bill length, relative lengths of the basihyale and ceratobranchiale are approximately constant, and the relative length of the epibranchiale is highly variable among the species of *Heliodoxa*. *Heliodoxa jacula* and, especially, *H. leadbeateri* have relatively long epibranchiales, although relative bill length in the genus is moderate and approximately constant. Measurements from a large sample of species would probably reveal interesting patterns and adaptations.

The epibranchiales in most hummingbirds extend dorsally along the occiput on either side of the cerebellar prominence and rostrally over the frontale, ending short of the craniofacial hinge (Fig. 28). In some, however, the two epibranchiales continue forward along the dorsal surface of the nasal region (Figs. 28 and 29A) on different sides of the dorsal bar (symmetry; most *Phaethornis*), or on the same side (asymmetry; some *Phaethornis, Topaza, Eugenes, Ensifera, Sternoclyta,* some *Heliodoxa,* and *Coeligena*). The epibranchials were symmetrical in nine species of *Phaethornis* and one of *Threnetes*. When they extend rostrally beyond the nasal region asymmetrically, the horns enter the same bony naris and regain bilateral symmetry anteriorly, within a dorsomedial sheath of the upper mandible (*Topaza, Ensifera, Sternoclyta,* and some *Heliodoxa*; Fig. 29B). Asymmetry of both epibranchials to the right side was modal in nine species of the *Heliodoxa* group, but extension of the epibranchials into the nasal region varies within the *Heliodoxa* group.

Bilateral asymmetry of the nasal skeleton is an indication of long epibranchiales. Epibranchiales that enter the bill through the nasal opening of one side are associated with depression of the nasal roof on one side and erosion of the

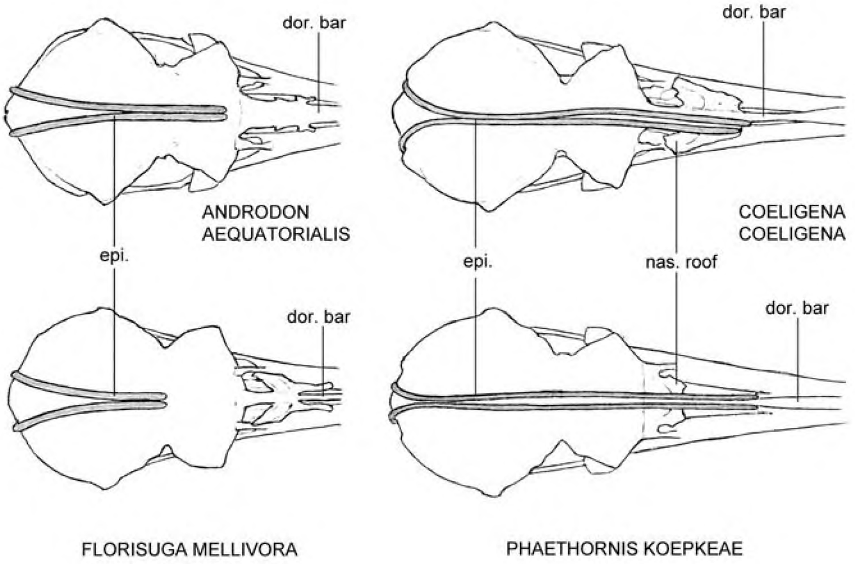

FIG. 28. Variation in the epibranchiales of hummingbirds. Dorsal view of the cranium and base of upper jaw, scaled to similar cranial width. The epibranchiales curve ventrally and then rostrally around the cranium to articulate with the ceratobranchiales below the cranium. In hummingbirds the epibranchiales are the most variable in length of all hyoid bones, and they are shown here as positioned with the tongue retracted. Upon contraction of m. branchiomandibularis, the dorsal portions of the epibranchiales seen here move caudally, the hyoid apparatus is pushed forward, and the tongue is protruded from the bill. Abbreviations: dor. bar = dorsal bar of upper jaw, epi. = epibranchiale, nas. roof = roof of the nasal region.

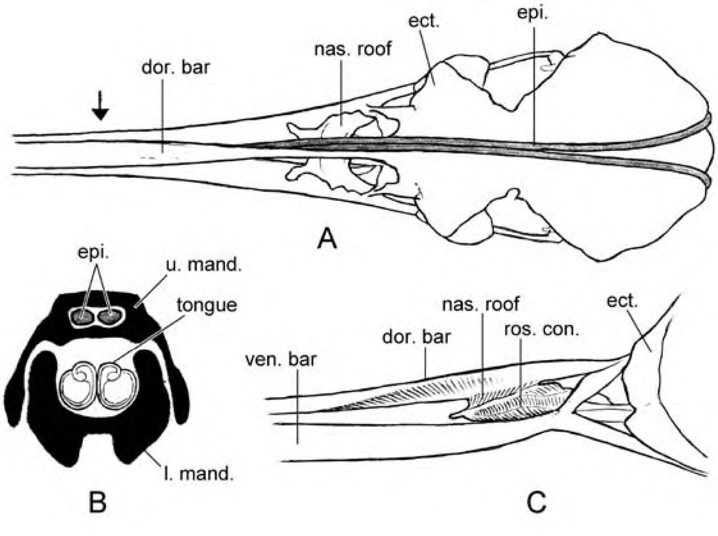

FIG. 29. Asymmetry of the epibranchiales in *Heliodoxa leadbeateri*. (A) Dorsal view of cranium; rostral portion of upper jaw missing. Arrow shows rostral limit of epibranchiales when the tongue is retracted. The long, paired epibranchiales pass on one side of the dorsal bar and enter a medial chamber in the connective tissue of the intermediate part of the upper mandible. (B) Semi-diagrammatic transverse section of the mandibles and tongue, showing the intermediate part of the upper mandible containing the epibranchiales. Mandibles are solid black. (C) Right lateral view of nasal part showing excavated dorsal bar and depressed rostral concha associated with asymmetry of the epibranchiales (drawing reversed for comparison with A). Abbreviations: dor. bar = dorsal bar of upper jaw, ect. = ectethmoidale, epi. = epibranchiale, l. mand. = lower mandible, nas. roof = roof of nasal region, ros. con. = rostral concha, u. mand. = upper mandible, ven. bar = ventral bar of upper jaw.

ventrolateral portion of the dorsal bar on the same side (Fig. 29C). This asymmetry is found not only in *H. leadbeateri*, *H. jacula*, and *H. xanthogonys*, but also in *H. schreibersii*, *H. rubinoides*, and *H. aurescens*. Lesser depression of the nasal roof and an unaltered dorsal bar indicate shorter epibranchials that barely penetrate the nasal opening or do not reach it, as in *H. gularis* and *H. branickii*, respectively. *Clytolaema* has still shorter epibranchials and shows no asymmetry (*Heliodoxa imperatrix* and *Hylonympha macrocerca* were not available). On the basis of comparison with *Urochroa*, elongation of the epibranchial of *Heliodoxa jacula* and its extreme elongation in *H. leadbeateri* are both derived conditions within the phylogeny of *Heliodoxa* by McGuire et al. (2007). A detailed presentation of evolution within the *Heliodoxa* group is not possible without inclusion of *Clytolaema* and *Hylonympha* in the analysis.

VERTEBRAE

Cervical.—The cervical vertebrae (vertebrae cervicalis) are defined as all vertebrae of the neck region rostral to the first vertebra attached to the sternum by a complete rib (costae completae)—that is, one having both vertebral and sternal segments. The cervical vertebrae number 14 in outgroups and 14 in hummingbirds. Relative lengths of the necks in hummingbirds have not been measured. In general, Hermits have shorter cervical costal processes than Trochilinae (Fig. 30) in relation to the depth of the vertebral body.

Thoracic.—Free thoracic vertebrae (vertebrae thoracicae liberae) begin with the first connected to the sternum by a complete rib and end with the last that is not fused in any way to the pelvis and synsacrum (Fig. 31). These vertebrae are characterized by a large, rectangular spinous process (processus spinosus) and a prominent transverse process (processus transversus). They number 4 in outgroups; 4 in *Eutoxeres*; 3 in other Hermits and in most Mountain Gems, Bees, and Emeralds; and 4 in most Coquettes, Brilliants, and *Patagona*. Mangoes are variable, with 3 in *Polytmus*, *Anthracothorax*, *Eulampis*, *Chrysolampis*, *Colibri*, *Schistes*, *Heliothryx*, and *Androdon*, 4 in *Doryfera*, and 4 or 3 in Topazes. Thoracic vertebrae of the synsacrum number 3 or 4 in Aegothelidae, Hemiprocnidae and some Apodidae, and 2–5 in other Apodidae. There are 3 (rarely 4) in Hermits and 3 or 4 in Trochilines. The number of thoracics (free and fused) is modally 6 in Hermits and 7 in Trochilines. Different degrees of fusion can be found between vertebrae of the rostral portion of the synsacrum, and most variation within species and between closely related species, in numbers of free and synsacral vertebrae probably results from presence or absence of fusion of a vertebra into the synsacrum.

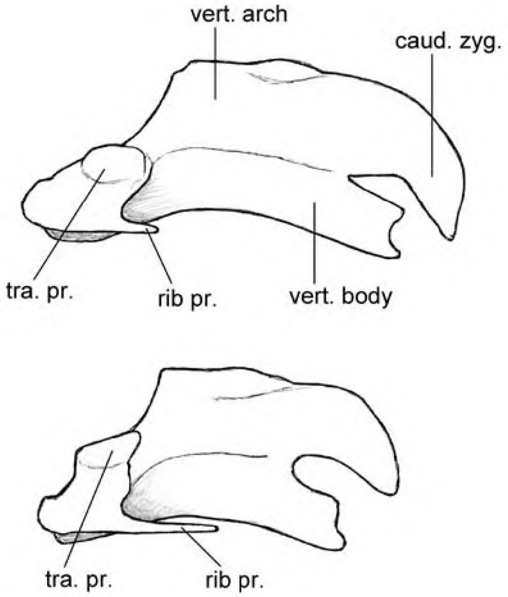

FIG. 30. Variation in length of rib processes of cervical vertebrae in hummingbirds. In Hermits the rib processes are typically shorter than those of Trochilines, as exemplified here by *Threnetes leucurus* (above) and *Coeligena wilsoni* (below). Abbreviations: caud. zyg. = caudal zygapophysis, rib pr. = rib process, tra. pr. = transverse process, vert. arch = vertebral arch, vert. body = vertebral body.

COSTAE

Numbers and polymorphism.—When present, ribs on the first 12 cervical vertebrae consist of rib processes, whereas the last two cervical vertebrae (13 and 14) bear articulated vertebral ribs. On vertebra 13 the rib is very short, and it may be disarticulated (and lost) as an artifact of skeletal preparation. The incomplete vertebral rib from vertebra 14 is longer and spine-like.

True complete ribs (costae completae verae) of the thorax are composed of two sections: a vertebral rib (costa vertebralis) articulating with the vertebra, and a sternal rib (costa sternalis) articulating syndesmotically with the tip of the

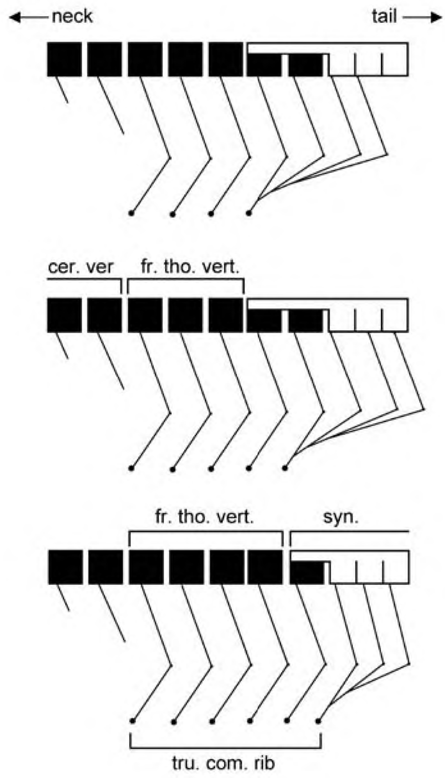

FIG. 31. Patterns in hummingbirds of free and synsacral thoracic vertebrae, and their association with thoracic ribs. Diagrammatic. The synsacrum (white) may incorporate one or two relatively unmodified thoracic vertebrae (solid black rectangles). Dots on the ribs represent articulations with the sternum (not shown) and indicate true compound ribs. Ribs that terminate on other ribs lack dots and represent false compound ribs. The top pattern is common in Hermits, the middle pattern typifies most Trochilines, and the bottom pattern characterizes many Brilliants and Coquettes (Andean Trochilines). Abbreviations: cer. ver. = cervical vertebrae, fr. tho. vert. = free thoracic vertebrae, syn. = synsacrum, tru. com. rib = true complete ribs.

vertebral rib and synovially with the sternum. Caudally, those sternal ribs that do not reach the sternum are false complete ribs (costae completae spuriae) in which the tip of the sternal rib abuts the preceding sternal rib (Fig. 31). In hummingbirds false complete ribs number 3 or 2.

Numbers of true complete ribs in outgroups are as follows: Aegothelidae (2 spp.), 3 or 4; Hemiprocnidae (4 spp.), 5; Cypseloidinae (4 spp.), 5; Apodini (14 spp.), 5, 4, or bilateral asymmetric 5/4 in *Collocalia esculenta*); and *Cypseloides senex*, 6. Outgroup species typically are sexually monomorphic with respect to numbers of true, complete ribs. In Trochilidae the number of true complete ribs varies from 4 to 7 pairs. In the present study, coverage of taxa that include at least one specimen of each sex is as follows (number of genera precedes number of species): Hermits, 4/17; Mangoes, 10/14; Brilliants, 12/24; Coquettes, 11/16; Mountain Gems, 4/8; Bees, 7/11; and Emeralds, 21/46. Sample sizes were 1 to 13, but most commonly of 1 to 4 per sex. Modal numbers of true, complete ribs and some variants within clades are summarized below.

Hermits.—Both sexes 4; males of some species either 4 or 5; *Eutoxeres*: both sexes 5.

Topazes.—*Topaza pella*: both sexes 5; *Florisuga mellivora*: males 6, females 5.

Mangoes.—Both sexes 5 (some species 4 or 5 and others 5 or 6); *Florisuga*, males 6, females 5; *Heliothryx*: males 4, females 4.

Brilliants.—Males 6, females typically 5 or 6.

Coquettes.—Males 6, females 6 or 5.

Patagona.—Both sexes 6.

Mountain Gems.—Males 6, females 5 or 6; *Panterpe*, both sexes 5 or 6.

Bees.—Males 6, females 5 or 6.

Emeralds.—*Amazilia* group: males 5 or 6, females 5, a few 6; Other Emeralds: both sexes 5.

Hermits, Mangoes, many Coquettes, and the *Chlorostilbon* group of Emeralds probably are modally sexually monomorphic. Presence of 5 both in outgroups and *Eutoxeres*—the latter, sister to the remaining Hermits (McGuire et al. 2007, R. L. Zusi unpubl. data)—suggests that the apomorphic state in Hermits is 4, whereas the presence of 5 in outgroups and Mangoes suggests that 6 or more represents the apomorphic state in most Trochilines.

Given sexual dimorphism within a species or clade, the larger number of true, complete ribs usually occurs in males. An example of this pattern is *Eutoxeres condamini*, in which 10 males and 8 females had five pairs, one male had six, and four females had four. Similarly, in male *Thalurania furcata*, 12 males had six and 1 had five; among females, 10 had five and 1 had six. When polymorphism occurs in both sexes, individuals with a higher number are usually males, and those with a lower number females.

Functional considerations.—Any attempt to produce a functional explanation for the curious pattern of sexual dimorphism in the number of true, complete ribs should include the main function of the ribs, which interconnect the vertebral column and sternum. Muscles of the rib cage (thorax) cause the ribs to push the sternum away from the vertebral column or, with help from abdominal muscles, to draw it toward the vertebrae, thus expanding and compressing posterior air sacs like a bellows during breathing (Brackenbury 1982, Fedde 1987, Brown 1999). Although powerful flight muscles originate on the sternum and pectoral girdle, the muscles associated with thoracic and abdominal compression and expansion comprise an essentially independent functional system (Duncker 1971, Brown 1999). Addition of one true, complete rib and its associated muscles to the rib cage probably would significantly increase the overall power of the ribs during respiration.

Male behaviors that might benefit from such enhancement are singing, which occurs during exhalation, and high-energy displays (e.g., Pizo 2012) that increase the breathing rate. "There is…a synchrony between abdominal muscle activity and the changes in air sac driving pressure, air flow and sound volume…. The magnitude of these physical parameters varies greatly between different types of vocalization" (Brackenbury 1989:204–205). Thus, if singing produces an extra burden on the normal process of exhalation in males, it is likely that inhalation would also be stressed. At present, there is no experimental support for these speculations on sexual dimorphism.

Sternum

Carina.—The lateral profile of the carinal apex and the angle of the carinal pillar to the plane of the sternal plate are variable (Fig. 32A). The carinal apex is usually more extensive in larger species of

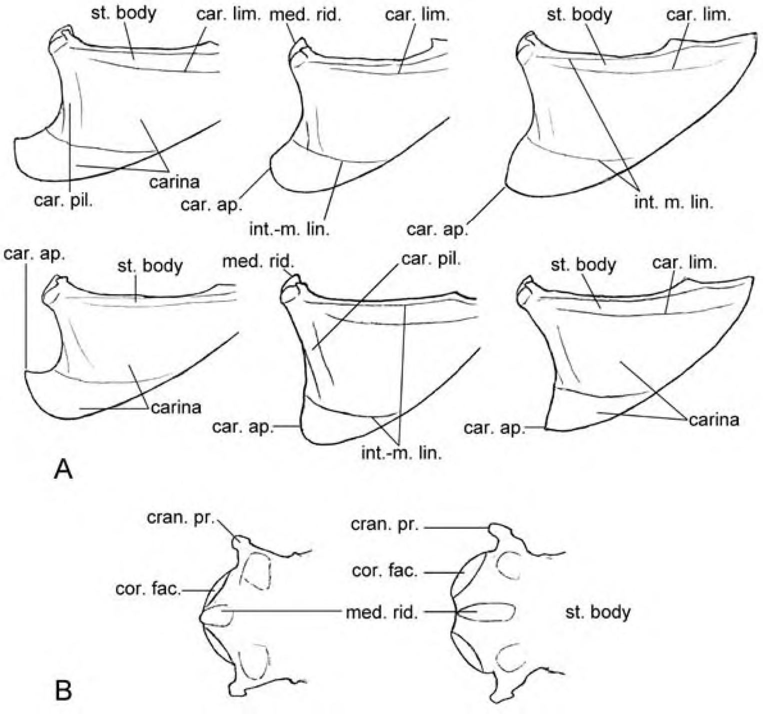

Fig. 32. Patterns of variation in sternal characters of hummingbirds. (A) Shape of the carinal apex and inclination of the carinal pillar; left lateral view. Sternae are scaled to similar length, but caudal portions of some sternae are not shown. Above, left to right: *Heliodoxa leadbeateri*, *Florisuga mellivora*, *Topaza pella*; below, left to right: *Patagona gigas*, *Myrtis fanny*, *Metallura williami*. The species are chosen to exemplify major differences in carinal shape, but more than one shape may be found within a genus or even within a species. (B) Rostral portion of sternum in dorsal view showing lateral separation of coracoidal articular facets; scaled to similar sternal width. Left: *Colibri serrirostris*; right: *Campylopterus hyperythrus*. Separated facets are common in the genus *Campylopterus*, a fact of unknown significance. Abbreviations: car. ap. = carinal apex, car. lim. = dorsal limit of carina, car. pil. = carinal pillar, cor. fac. = coracoidal articular facet, cran. pr. = craniolateral process, int.-m. lin. = intermuscular line, med. rid. = medial ridge, st. body = sternal body.

hummingbird, possibly incorporating partial ossification of the sternoclavicular ligament. Although intraspecific variation is common, a particular profile of the carinal apex may characterize taxa at generic or higher levels (Fig. 32A). A short and bluntly pointed apex occurs in some Hermits and Bees; a longer, broadly rounded protrusion typifies *Heliothryx*, *Florisuga*, *Coeligena*, and some *Heliodoxa*; and a sharply pointed profile is found in many Brilliants, Coquettes, and Mountain Gems and in some bees and Emeralds. A profile intermediate between sharply pointed and broadly rounded occurs in some species of most major clades. In them the apex has a rostral convexity that meets the upturned ventral margin of the keel at an angle (*Topaza*, some Mangoes, and some Emeralds). The long apex of *Patagona* and some species of *Heliodoxa* is rounded rostrally, concave dorsally, and pointed rostrodorsally (canoe-shaped). Species may be sexually dimorphic in keel shape, as exemplified by *Trochilus polytmus*— males: 10 convex and angled, two pointed; females: 14 pointed, 2 slightly convex and angled.

Coracoidal facets.—The coracoidal facets of most swifts and hummingbirds are separated from the midsagittal plane of the sternum only by the medial ridge, which slopes dorsocaudally to form a caudal peak. However, the facets of some hummingbirds are laterally displaced (Fig. 32B) from the ligamental ridge and connected by a transverse, rostral shelf. Prominent separation typifies at least *Phaeochroa cuvierii*, *Campylopterus rufus*, *C. hyperythrus*, *C. largipennis*, *C. hemileucurus*, *Eupetomena macroura*, *Aglaeactis*, and *Phlogophilus*. Moderate separation is unusual and occurs only in a few Emeralds, Brilliants, and Coquettes. Although the coracoidal facets on the sternum were markedly separated from the midline in *Jungornis* (swift-like birds from the Lower Oligocene; see Karhu 1988), separation is evidently apomorphic within modern Trochilidae. Greater separation would enlarge the angle between the sternoprocoracoidal ligament and the coracoideum and increase its mechanical advantage for resisting lateroventral displacement of the coracoid. *Campylopterus* is known for its highly modified, widened rachis of the leading-edge primary feathers, of possible significance "for strengthening of the wing during their fast, swift-like gliding among semi-open vegetation, a common feature of these hummingbirds" (Schuchmann 1999:477), but no functional explanation for separation of facets in *Campylopterus* has been proposed.

Costal facets.—Bilateral asymmetry in number of sternal articular processes (processus articularis sternocostalis) involves the rostralmost of the false complete ribs, in which the sternal rib abuts the sternal rib of the adjacent true complete rib on one side, and abuts the sternal plate on the other. Additional sternal ribs are added caudally. New sternal facets are small and nearly adjacent to the larger, penultimate facet.

HUMERUS

Proportions.—Apart from the humeral characters unique to hummingbirds, the humerus exhibits considerable variation in shape within the family (Fig. 33A–H). Differences in relative stoutness of the entire humeral shaft (Fig. 33C and E vs. D and H) or in different parts of the shaft (Fig. 33G) are pronounced. Other variation is detailed below.

Pneumaticity.—Pneumaticity of the bicipital crest caudoventrally on the humerus is present in *Aegotheles* and Apodiformes. Homologous pneumaticity in hummingbirds (Fig. 34A) is manifested by at least one pneumatic foramen within a caudal recess along the ventral process. In addition, hummingbirds may possess at least one prominent pneumatic foramen on the caudodorsal surface of the humerus between the humeral head and the deltopectoral crest. This deltopectoral foramen (Fig. 34A) is usually absent from Hermits (except *Eutoxeres*) and present in Trochilines. A third area of pneumaticity lies just distal to the ventral portion of the capital tuberculum, where the small to moderately large foramen may be partially hidden by the tuberculum (Fig. 34A). This foramen is commonly found in Hermits, *Florisuga*, and the *Anthracothorax* group and may be polymorphically present or absent. Another pneumatic foramen may be present on the base of the ventral process. It occurs sporadically and is often polymorphic. Finally, a foramen just distal to the dorsal portion of the capital tuberculum may be present—usually small but occasionally prominent, and sometimes closely proximate to the foramena near the deltopectoral crest. All of the above foramena may be found in some specimens of *Phaethornis*, *Eutoxeres*, and the *Anthracothorax* group. Additional pneumatic foramina occur uniquely near the distal condyles of the humerus in all species of *Boissonneaua*, where the patterns are polymorphic and often bilaterally asymmetrical.

Processes.—The distal end of the ventral process (Fig. 34B) may be truncate (or slightly notched), or markedly notched symmetrically

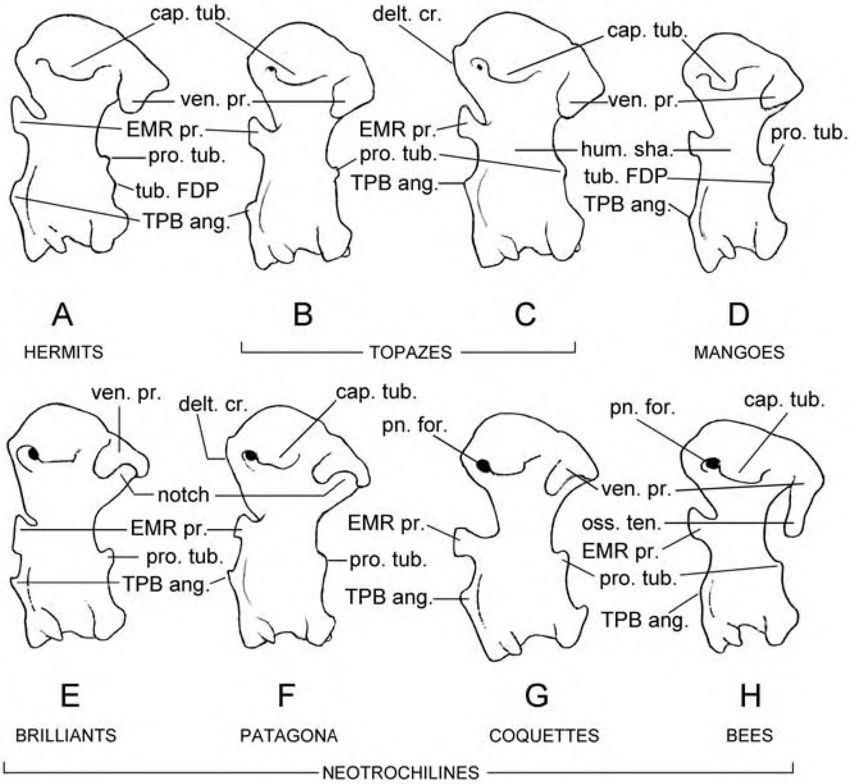

FIG. 33. Variation in shape of the humerus within hummingbirds. Caudal views; scaled to similar humeral length. (A) *Phaethornis*. (B) *Topaza*. (C) *Florisuga*. (D) *Heliothryx*. (E) *Pterophanes*. (F) *Patagona*. (G) *Metallura*. (H) *Microstilbon*. These examples are chosen to emphasize differences within Trochilidae, but variation also occurs within each major clade. Pneumatic foramena on the deltopectoral crest and a notch on the ventral process are most prevalent in Neotrochilines. Nothing is known at present about the functional significance of intrafamiliar variation. Abbreviations: cap. tub. = capital tubercule, delt. cr. = deltopectoral crest, EMR pr. = process of extensor metacarpi radialis muscle, hum. sha. = humeral shaft, oss. ten. = ossified tendon (probably of the subcoracoideus muscle), pn. for. = pneumatic foramen, pro. tub. = pronator tubercle, TPB ang. = angle of tensor propatagialis brevis muscle, tub. FDP = tubercle of m. flexor digitorum profundus, ven. pr. = ventral process.

or asymmetrically. When asymmetric, the dorsal arm (crus dorsale fossae) of the ventral process is slightly longer than the ventral arm (crus ventrale). Many species are polymorphic for unnotched versus symmetrically notched; others are polymorphic for symmetrically versus asymmetrically notched. The ventral process is unnotched in outgroups, variable (from unnotched to moderately notched) in Hermits, Topazes, Mangoes, *Lophornis* and *Discosura*, some *Chlorostilbon* and *Cynanthus*, and Bees. It is symmetrically notched in *Campylopterus*, most of the *Chlorostilbon* group, and in many other Emeralds, whereas asymmetrical notching is most prevalent in Brilliants, Coquettes, and *Patagona*. The dorsal arm of some Bees is variably elongate distally, probably by ossification of the tendon (tendo ossificans) of m. subcoracoideus (Fig. 33H).

Although the differences described above are small and variable, they may be significant because the ventral process is strongly developed in swifts and hummingbirds. In swifts, m. scapulohumeralis caudalis inserts along the bicipital crest near the base of the ventral process, but in hummingbirds it inserts on the ventral arm of the ventral process, and m. coracobrachialis caudalis inserts on the tip of the dorsal arm (Fig. 34C). The latter muscle effects supination of the humerus, and the former effects pronation. Both muscles influence the rotation angle of the

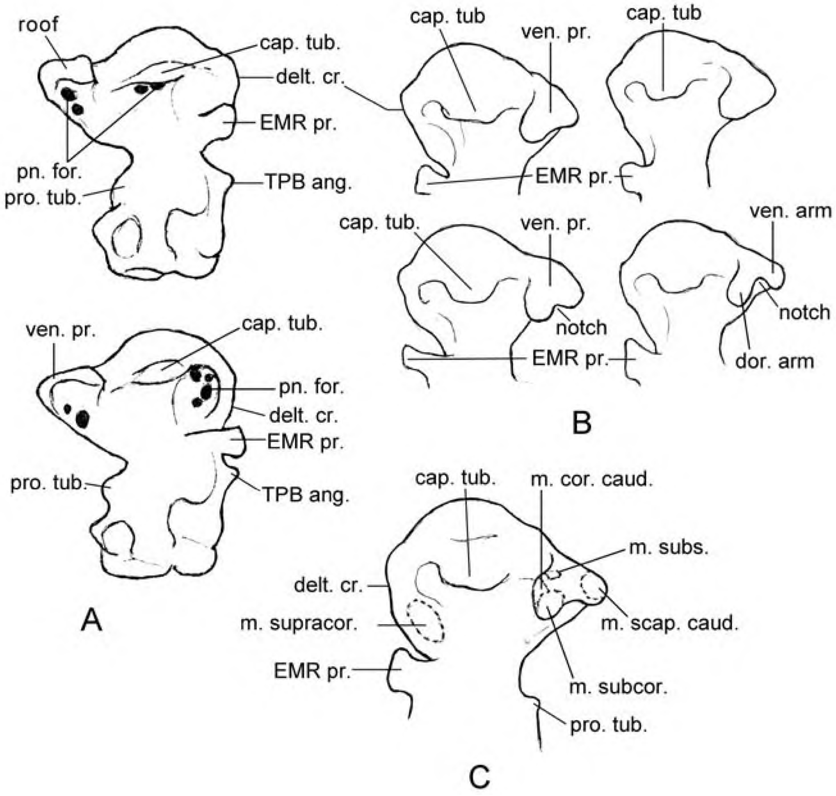

FIG. 34. Processes, pneumatic foramena, and muscle insertions on the humerus of hummingbirds. (A) Proximocaudal view of right humerus. Pattern of pneumatic foramena common in Hermits (above) and common in Trochilines (below). Additional foramena may accompany these basic patterns. (B) Variation in shape of the distal end of the ventral process; left humerus, caudal view. Upper left: *Anthracothorax mango*; upper right: *Heliothryx aurita*; these species show little or no notching on the ventral process and are typical of Hermits, Mangoes, and Bees. Presence of a distal notch may reflect roughly symmetrical dorsal and ventral arms on the ventral process, shown in lower left (*Chlorostilbon mellisuga*) and typical of most Neotrochilines, or asymmetrical arms, shown in lower right (*Coeligena violifer*), typical of many Brilliants and Coquettes. (C) Muscle insertions on the ventral process and deltopectoral process; caudal view. These muscles influence positions and axial rotation of the humerus, but the functions of those on the ventral process are not fully understood. Abbreviations: cap. tub. = capital tuberculum, delt. cr. = deltopectoral crest, dor. arm. = dorsal arm of ventral process, EMR pr. = process of extensor metacarpal radialis muscle, m. cor. caud. = coracohumeralis caudalis muscle, m. supracor. = supracoracoideus muscle, m. scap. caud. = scapulohumeralis caudalis muscle, m. subcor. = subcoracoideus muscle, m. subs. = subscapularis muscle, pn. for. = pneumatic foramen, pro. tub. = pronator tubercle, TPB ang. = m. tensor propatagialis brevis angle, ven. arm = ventral arm of ventral process, ven. pr. = ventral process.

wing throughout the wing stroke (Cohn 1968). As antagonists, isolation of the two muscles on different arms may improve efficiency of their respective actions. The roles of m. subcoracoideus and m. subscapularis, also inserting distally on the ventral process, are not well documented.

The deep, pneumatic recess of the ventral process is bounded by dorsal and ventral walls. At the tip of the process the recess is partly enclosed by a roof (tectum fossae; Fig. 34A) connecting the two walls in Hermits, Topazes, and Mangoes (except *Colibri*, *Schistes*, and *Doryfera*). The roof is smaller in *Lophornis*, *Discosura*, and Bees, and absent in *Colibri* and most other Trochilines.

In most avian families, the origin of m. extensor metacarpi radialis (EMR) is from an indistinct part of processus supracondylaris dorsalis, located dorsally near the distal end of the humeral shaft. By contrast, in Apodidae and Trochilidae it is from an enlarged, isolated process

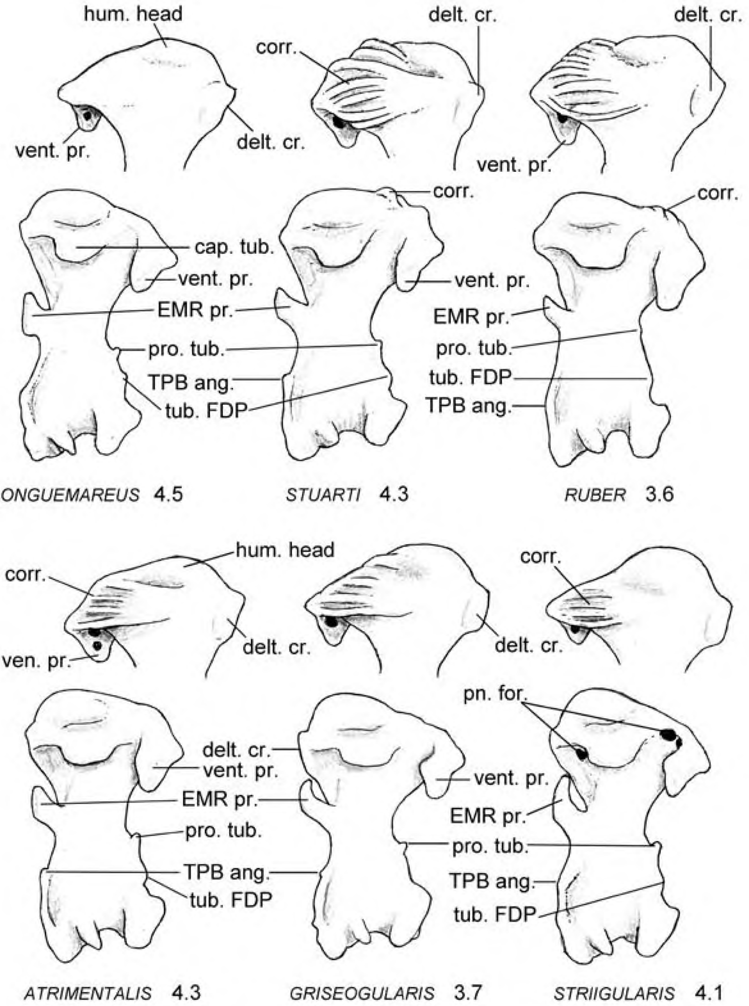

FIG. 35. Variations of the humerus in the Hermit genus *Phaethornis*. Incomplete depictions are in cranial view; complete humeri are shown in caudal view, scaled to similar humeral length. Numbers represent mean lengths (mm) of the humeri. Corrugations on the humerus of the species shown are unique within Trochilidae and define a subgroup (*Pygmornis* group) within *Phaethornis*. Variation in the processes shown probably serve to identify each species of the *Pygmornis* group. Abbreviations: cap. tub. = capital tuberculum, corr. = corrugation, delt. cr. = deltopectoral crest, EMR pr. = process of extensor metacarpi radialis muscle, hum. head = humeral head, pn. for. = pneumatic foramen, pro.tub. = pronator tubercle, TPB ang. = angle of tensor pronator superficialis muscle, tub. FDP = tubercle of the flexor digitorum profundus muscle, ven. pr. = ventral process.

(EMR process) positioned more proximally on the shaft. Well developed in hummingbirds (Figs. 15, 33, and 34B), it projects dorsally from the humeral shaft, perpendicular to, or more often angled proximad to, the long axis of the shaft (Fig. 15). The process is located variously along the shaft (Fig. 33)—opposite the midpoint (most Brilliants, Coquettes, *Panterpe*, *Campylopterus*, *Chalybura*, and *Trochilus*), proximad (most Hermits, Topazes, Mangoes, *Patagona*, Bees, and Emeralds), or further distad (*Urochroa*, *Pterophanes*, *Metallura*, *Aglaeactis*, *Lafresnaya*, *Boissonneaua*, and *Phlogophilus*). It is notably long and narrow in *Oreotrochilus*, *Aglaiocercus*, *Lesbia*, *Sappho*, and *Polyonymus*. Sometimes it ends bluntly, often with terminal expansions proximally and distally. Rarely, the proximal expansion of the EMR process is extreme (and the distal one absent) such that the tip of the process approaches the deltopectoral crest rostrally (many *Phaethornis*) or abuts it (*P. striigularis*; Fig. 35).

The tensor propatagialis, pars brevis muscle of hummingbirds arises from an angular projection (henceforth TPB angle) on the dorsal surface of the humeral shaft (Fig. 33) and is variously positioned between the distal end of the humerus and the EMR process. A crest along the dorsal margin of the humeral shaft joins the process and angle. The TPB angle is located more distally on the shaft in Hermits, *Heliothryx*, *Topaza*, and *Phlogophilus* than in other hummingbirds. Usually it projects less dorsally from the shaft than the EMR process, but in *Coeligena* and *Heliodoxa* the reverse is true. Located on the ventral surface of the humerus are the pronator tubercle (tubercle of m. pronator superficialis) and FDP tubercle (tubercle of m. flexor digitorum profundus). These tubercles may be strongly separated (Hermits), moderately separated (Topazes and most Mangoes), or closely spaced (sometimes inseparable) in other hummingbirds.

Pygmornis *group.*—Among Hermits the largest genus (*Phaethornis*) includes a group of species that differ in their smaller size, several plumage features, and body proportions (Hinkelmann 1990). They have been treated variously as a separate genus or subgenus (*Pygmornis*). Hinkelmann and Schuchmann (1997) proposed a subgenus *Pygmornis* comprising 10 species, but according to McGuire et al. (2007) these species are not monophyletic or sister to all other *Phaethornis*. Within subgenus *Pygmornis*, Hinkelmann and Schuchmann (1997) included a clade of five species, *Phaethornis striigularis*, *P. atrimentalis*, *P. griseogularis*, *P. stuarti*, and *P. ruber*, and placed *P. longuemareus* in another clade. Of the five, *P. striigularis*, *P. atrimentalis*, and *P. longuemareus* were lumped under *P. longuemareus* in the classifications of Peters (1945) and Morony et al. (1975). For comparison, I include *P. longuemareus* in a "*Pygmornis* group" because of its taxonomic history, along with the other five species.

While examining skeletons of *Phaethornis*, I noted that features of the humerus of specimens labeled *P. longuemareus* permitted recognition of three groups, each characterized by specimens collected from the allopatric distributions of Hinkelmann's *P. longuemareus*, *P. atrimentalis*, or *P. striigularis* (Hinkelmann 1990). In addition, the humeral characters of *P. ruber*, *P. griseogularis*, and *P. stuarti* in specimens from allopatric portions of their respective distributions proved to be diagnostic for each species (Fig. 35).

The proximocranial side of the humerus in five members of the *Pygmornis* group, *Phaethornis striigularis*, *P. atrimentalis*, *P. griseogularis*, *P. stuarti*, and *P. ruber*, exhibits a series of roughly parallel ridges separated by grooves (corrugations). The corrugations extend from the ventral extremity of the ventral process toward the deltopectoral crest and follow the course of the tendon of insertion of m. pectoralis major. The corrugations are absent from about the mid-longitudinal axis of the humerus to the deltopectoral crest (Fig. 35). Numbering three to six, the corrugations are deeper when more numerous. In the latter case, I found that the adjacent surface of the isolated tendon of m. pectoralis major was also ridged to mesh with the grooves; in species with weak corrugations the isolated tendon was weakly ridged or unridged. *Phaethornis longuemareus* exhibits the plesiomorphic condition of a humerus and tendon without corrugations; typically, *P. griseogularis* has three ridges, *P. striigularis* has four or three, and *P. atrimentalis*, *P. stuarti*, and *P. ruber* have six.

The EMR process in *P. longuemareus* lies in the proximal half of the humerus, where it is short, stout, and expanded terminally. It is less stout and expanded in *P. atrimentalis*, longer and more slender in *P. stuarti*, slender and tapered in *P. ruber*, and extremely long and curved proximocraniad in *P. griseogularis* and *P. striigularis*. In some specimens of the latter two species its distal tip reaches the crista deltopectoralis and forms an arch between the process and caput humeri.

Farther distad on the dorsal surface of the humerus is the TBP angle, which varies from sharply angular in *P. longuemareus*, *P. stuarti*, and *P. atrimentalis* to more rounded in *P. ruber*, *P. griseogularis*, and *P. striigularis*. Also variable are the ventrally situated tuberculum of m. pronator superficiallis and a more distal tuberculum FDP. These tubercles are in closest proximity to each other in *P. longuemareus*; they are in lesser proximity in *P. stuarti*, *P. atrimentalis*, *P. griseogularis*, and *P. striigularis*; and in least proximity in *P. ruber*. The tuberculum of pronator superficialis is peg-like in all but *P. ruber*, in which it is very short and inconspicuous.

Another variable within the *Pygmornis* group is the pattern of proximal, pneumatic foramina; most *Phaethornis* have one or more pneumatic foramina within the ventral process, but in *P. striigularis* additional foramina are usually present medial to the ventral process and near the deltopectoral crest (Fig. 34). A foramen just distal to the tuberculum capitis may be present or absent in *P. longuemareus*, *P. griseogularis*, and *P. striigularis*.

Mean lengths of the humerus, based on samples of 1 to 7, differ within the *Pygmornis* group, with

Phaethornis ruber shortest (3.5 mm), *P. griseogularis* slightly longer (3.7 mm), and the others ranging between 4.2 and 4.5 mm.

Although states of these five characters are not perfectly correlated among the species of the *Pygmornis* group, each species studied here (two to five specimens per species) has a unique combination of states that apparently permit identification by the humerus alone. The question of a sister relationship of *Phaethornis longuemareus* or *P. atrimentalis* to the recently named *P. aethopyga* (Piacentini et al. 2009) might be answered by presence or absence of corrugations on the humerus of *P. aethopyga*, and the other characters might clarify its relationships within the *Pygmornis* group. However, humeri are unavailable for *Phaethornis aethopyga, P. r. rupurumii, P. idaliae, P. griseogularis zonura, P. s. striigularis,* and *P. ruber nigricinctus*. Apart from their relevance to systematics and taxonomy, these variables are of interest as a rare case of species-specific diversity of the humerus within closely related species of a genus. As mentioned above, determination of species limits in the *Pygmornis* group is important because, for several decades, three species were lumped under *Phaethornis longuemareus* in museum collections of skeletons, spirit specimens, and tissue samples, as well as in publications on phylogeny, behavior, ecology, and other subjects.

Functional considerations.—In *Glaucis* and the smaller *Phaethornis,* hovering sometimes occurs with the body axis horizontal and the tail raised—the so-called "boat" posture (Skutch 1951, Stiles and Wolf 1979:65–66). This form of hovering, used in displays, was described for *G. hirsutus* (Snow 1973a), *P. longuemareus* (Snow 1968), *P. striigularis saturatus* (Skutch 1951), and *P. ruber* (Mobbs 1971, Snow 1973b). It represents *extreme* hovering because, as suggested above, the wing is most strongly supinated with the body horizontal. The flattened tendon of insertion of m. pectoralis passes over the cranial surface of the humerus before inserting on the deltopectoral crest, and the angle of this passage would become more acute during the upstroke and with increasing supination of the humerus. Pressure of the tendon on the humerus is probably greatest at the beginning of the downstroke, and especially when the humerus is supinated in the boat posture. Precise guidance of the tendon near its insertion by corrugations as seen in members of the *Pygmornis* group may improve efficiency at high wingbeat rates during extreme hovering. However, comparative data on boat posture behavior and hovering mechanics between species with and without ridges are not available.

TARSOMETATARSUS

The size of the foot (pes) in relation to body size varies considerably within Trochilidae. Using tarsal length divided by coracoidal length to represent foot size in relation to body size, I found that foot size in Hermits (except *Eutoxeres*) and Emeralds was small; in Bees small to medium; in *Eutoxeres, Panterpe,* and most Brilliants and Coquettes medium; and in *Lophornis, Discosura, Chalcostigma, Oreotrochilus, Lesbia, Adelomyia,* and *Aglaeactis* large (R. L. Zusi unpubl. data). Species with large feet often cling to a flower or other substrate while feeding, and *Oreotrochilus estella* is known to roost while clinging to vertical rock surfaces (Carpenter 1976). Among Hermits, *Eutoxeres* is a habitual perch-feeder (Gill 1985). However, many hummingbirds occasionally cling to flowers while feeding (e.g., Pyke 1981, Mobbs 1989, Zusi and Hamas 2001), regardless of foot size.

PHALANGES

In most hummingbirds the number of phalanges (phalanx) in digits of the foot follows the formula 2,3,4,5 for digits I, II, III, and IV, respectively. However, some taxa display only four phalanges in digit IV. The smaller number results from fusion of phalanges 3 and 4 (counting from the base), as shown by adult specimens that exhibit early stages of fusion between phalanges (Fig. 36). Phalanges of a cleaned skeleton may be tightly conjoined but separable after hydration; partially fused but retaining the flexor tubercle (tuberculum flexorium) of phalanx 4; fully fused but retaining reduced, tubercular swelling of phalanx 4; or fused with no trace of former trochleae of phalanx 4. The length of the fused phalanx roughly equals that of its two progenitors. Reduction to four phalanges in digit IV appears consistently in Hermits (*Eutoxeres*), Mangoes (*Schistes* and *Augastes*), Brilliants (*Boissonneaua*), Coquettes (*Discosura* and *Lophornis*), *Patagona,* and Mountain Gems (*Panterpe*), and sporadically in various species. By contrast, reduction is widespread in Emeralds of the Amazilia group (*Chlorestes* through *Hylocharis* in Appendix 1).

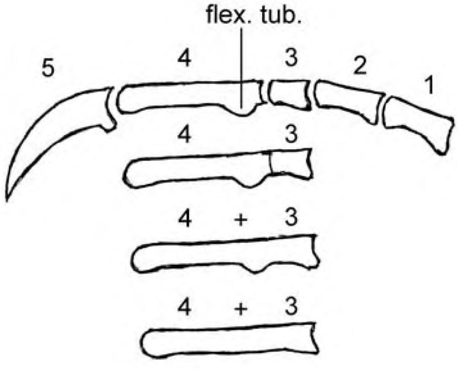

FIG. 36. Fusion in phalanges of the fourth toe of some hummingbirds. Phalanges are numbered, starting at the base. The top figure shows the five phalanges found in most species. Lower figures show successive stages in fusion of phalanges 3 and 4 found polymorphically in some species and suggest the evolutionary path to a fourth toe of only four phalanges. The latter state is derived within hummingbirds and has evolved in parallel repeatedly within the family. Abbreviation: flex. tub. = flexor tuberculum.

Several species in Apodidae also depart from the usual phalangeal formula (2,3,4,5). I found five phalanges in digit IV of two specimens of *Streptoprocne zonaris* (YPM 7572, 8197), and four in another (YPM 7573), that may have resulted from loss of a phalanx. Zehntner (1890) found developmental reduction of phalanges in *Apus melba* (phalangeal formula 2,3,4,5 in 10-day chick to 2,3,3,3 in adult) to result from fusion of phalanges differing from those of hummingbirds. Adults of *Aeronautes saxitilis* also have 2,3,3,3.

INTRASPECIFIC VARIATION

Within a species, variation may be related to geographic isolation, sexual dimorphism, or age differences. Specimens used in the present study were of adult size, although some had more pronounced sutures in the craniofacial region and more slender construction of the skeleton, suggesting younger age. Using these criteria, I compared variation in samples of specimens of apparently younger versus older individuals of a variety of species. The samples included both sexes and were collected within a restricted geographic range. In a variety of characters, I found the same kinds of character variation in samples of both younger and older individuals, and I conclude that most variation (polymorphism) that is detailed in Appendix 2 and discussed below is largely individual variation independent of sex, age, or geographic origin. The following are selected examples that exclude sexual dimorphism.

(1) In Hermits the rostral concha has a weakly developed ventral wing (T-bar); the ventral wing is either enlarged or lost within Trochilines, in which both conditions are probably derived. One stage in its loss retains only a reduced ventral wing near the midpoint of the concha. Reduction or complete loss of the wing occurs polymorphically within some species of Trochilines (e.g., *Sternoclyta cyanopectus, Heliodoxa aurescens, Damophila julie*, and *Amazilia tzacatl*).

(2) The body of the vomer in dorsal view may be anteriorly rounded, angled, or with spicules. Rounded and angled are polymorphic in some species (e.g., *Archilochus colubris*); presence or absence of spicules are polymorphic in others (*Heliodoxa branickii, H. rubinoides, Urosticte benjamini, Ocreatus underwoodii, Amazilia candida, A. amazilia, A. tzacatl, Damophila julie*, and *Basilinna leucotis*).

(3) Examples of intraspecific variation in position of the epibranchiales in relation to the dorsal bar are as follows: symmetrical vs. both left (*Phaethornis hispidus, P. philippii*, and *P. syrmatophorus*); symmetrical vs. both right (*P. superciliosus*); symmetrical vs. both on right or left (*P. guy*); both right vs. both left (*Coeligena violifer, C. torquata, Ensifera ensifera, Heliodoxa rubinoides, H. branickii*, and *H. gularis*).

(4) Examples of intraspecific polymorphism in presence or absence of the intrapterygoid articulation are *Adelomyia melanogenys* (17 of 19 with articulation) and *Metallura theresiae* (39 of 42 with articulation).

(5) In dorsal view, the supraorbital margin on each side may be V-shaped (sometimes U-shaped) or \/-shaped. These two states are polymorphic in some species. In *A. melanogenys*, 20 specimens were \/, 5 specimens V, and 8 specimens intermediate; *Archilochus colubris* had 16 V, 15 \/, and two intermediate.

(6) Free thoracic vertebrae usually number 3 or 4. Polymorphic 3 or 4, and 4 or 5, occur in some species. I noted instances of 3/4 polymorphism of the free thoracic vertebrae in two to six species each of Hermit, Mangoes, Coquettes, and Emeralds; 3/2 polymorphism occurred in *P. guy*, and 4/5 in *Doryfera ludovicae*.

(7) Polymorphism in the number of true, complete sternal ribs within each sex is widespread within hummingbirds. Examples in the major clades are as follows: Hermits—males 4/5, 5/6;

females 4/5. Mangoes—males 4/5, 5/6; females 5/6. Brilliants—males 5/6, 6/7; females 5/6. Coquettes—males 5/6, 6/7; females 5/6. Mountain Gems—males 6/7, females 5/6. Bees—males 5/6, 6/7; females 5/6. Emeralds (*Chlorostilbon* group)—males 5/6; females 4/5, 5/6. Emeralds (*Amazilia* group)—males 5/6; females 5/6.

(8) A foramen may be present or absent just distal to the tuberculum capitis. Presence (most Hermits) and absence (most Trochilines) are polymorphic in some species (e.g., *Glaucis hirsutus, P. philippii, P. ruber, P. striigularis, P. yaruqui, Florisuga mellivora, Colibri coruscans, Anthracocorax dominicus, Eulampis jugularis, E. holosericeus, Chrysolampis mosquitus, Haplophaedia aureliae, Eriocnemis luciani, Aglaeactis cupripennis, Pterophanes cyanoptera, Heliangelus exortis, Ramphomicron microrhynchum, Oreotrochilus estella, M. theresiae,* and *Eupetomena macroura*). Separately, a foramen may be present or absent on the deltopectoral crest. Presence and absence are sometimes polymorphic (e.g., *Eutoxeres aquila, G. hirsutus, Phaethornis ruber,* and *Ramphodon naevius*).

(9) Ventrally on the humeral shaft are tubercles of origin for m. pronator superficialis and flexor digitorum profundus. The tubercles may be adjacent, moderately separate, or distinctly separate. The states "moderately separate" and "adjacent" are sometimes polymorphic (e.g., *Doryfera ludovicae, F. mellivora, Colibri coruscans, Anthrothorax dominicus, Eulampis jugularis, Heliothryx auritus, Chlorostilbon maugaeus, Cynanthus latirostris, Thalurania furcata, Damophila julie,* and *Trochilus polytmus*).

(10) The process of m. extensor metacarpus radialis may be sited distally on the humeral shaft (outgroups), about midway on the shaft, or proximally on the shaft (most Trochilines). Polymorphism of midway and proximally cited is most common in species of Brilliants and Coquettes.

(11) Phalanges of digit IV may number 4 or 5, and polymorphism occurs in *G. hirsutus, Heliodoxa aurescens, Heliangelus amethysticollis, Ocreatus underwoodi, Basilinna leucotis, Campylopterus largipennis,* and *T. polytmus*. One specimen each of *Colibri delphinae* and *T. polytmus* was bilaterally asymmetrical (4/5).

States of characters that are synapomorphic for higher-level categories within Trochilidae may occur as intraspecific variation, variation among congeners, or differences between genera of a clade. As shown in Table 3, character states that distinguish Trochilines (+) from Hemiprocnidae, Apodidae, and most Hermits (–) are also found as intraspecific variation (polymorphism) within one or more genera of Hermits (Table 3, characters 2 and 3). In character 3, different species of *Phaethornis* show different states (–, +, or polymorphic +/–). A character state that distinguishes Neotrochilines (+) from Hermits, Topazes, and Mangoes (–) is polymorphic in *Eutoxeres* (character 4) and differs between genera within both Topazes and Mangoes (characters 4 and 5). Thus, there is strong support for the concept that many phenotypic differences at multiple phylogenetic levels had their origins in species-level variation.

TABLE 3. Distribution of skeletal characters in higher-order clades of Apodiformes and of Trochilidae, as shown in Figure 1. Note high levels of variation in Hermits, Topazes, and Mangoes.

		Trochilidae			
			Trochilines		
Character	Hemiprocnidae and Apodidae	Hermits	Topazes	Mangoes	Neotrochilines
1. Fusion of nasal roof with nasale ±	NA or +	+	–	–	–
2. Nasal opening transects craniofacial hinge ±	–	–[a]	+	+	+
3. Pneumatic foramen(a) on deltopectoral crest ±	–	–, +, or ±	+	+	+
4. Rostral concha ossified ±	–	–[b]	+ or –[c]	+ or –	+
5. Medial concha scrolled ±	+	–	+ or –	+ or –	+

[a] *Eutoxeres* polymorphic +/–.

[b] *Eutoxeres* +.

[c] *Topaza* –, *Florisuga* +.

Discussion

Apomorphies of major clades.—In contrast to the many skeletal characters that support monophyly of Trochilidae within Apodiformes (Appendix 1), few or none support each major clade within Trochilidae. The clade of Neotrochilines (Fig. 1) is only weakly supported by skeletal characters (Table 3), and even the traditional view of Hermits and Trochilines as sister taxa (Phaethornithinae and Trochilinae, respectively) is supported by only three characters for Trochilinae (Table 3). The latter dichotomy is contradicted by molecular evidence for Topazes as sister taxon to all other hummingbirds (McGuire et al. 2007). However, developmental change within a Trochiline (*Chlorostilbon swainsonii*) from holorhinal nares of the nestling to schizorhinal nares of the adult, largely achieved by bone resorption, is consistent with bony nasal openings that transect the craniofacial hinge as a derived condition of Trochilines (Table 3). According to Bleiweiss (1998), divergence of Hermits and Trochilines occurred in the Miocene. Inferences about polarity of morphological characters rely mainly on structure of extant outgroups (Hemiprocnidae and Apodidae) that probably diverged from a hummingbird line in the Oligocene. Even if *Eurotrochilus* should prove to be the oldest known member of the hummingbird clade, its visible character states are not necessarily pertinent to polarity of modern character states that distinguish Hermits from Trochilines. Eventually, additional fossils from the late Miocene might prove to be informative about polarity.

Within each of five major clades of Trochilidae, individual genera or groups of genera are supported as clades by independently evolved synapomorphies (Table 4).

Diversity within major clades.—The following summary reiterates the high level of interspecific and intergeneric variation within major hummingbird clades. As noted earlier, each of these clades contains species of a wide range of body sizes. Qualitative diversity of the skeleton within Hermits is largely between *Eutoxeres* and all other genera. *Eutoxeres* differs in having the most strongly decurved bill, bony nasal opening slit-like caudally, a proportionally short and broad cranium, a spatulate form of the vomeral body and lack of a vomeral spine, modally five pairs of true thoracic ribs, and four phalanges in pedal digit IV. Other Hermits display minor variations of the skeleton, most notably the presence of corrugations on the humeral head in the *Pygmornis* group of *Phaethornis*. Especially in *Glaucis*, *Threnetes*, and *Ramphodon*, the temporal fossa is extensive, its defining crests well developed, and the postorbital and zygomatic processes widely separated. These features reflect the larger size and strength of the superficial mandibular adductor muscles, and a presumed stronger bite—functions that may support insect gleaning from bark and epiphytes. The two genera of Topazes differ in form of the rostral and medial concha, ossification of the hypophysial

Table 4. Derived character states of genera or generic groups within major clades of Trochilidae.

Character	Genera	Major clade
Vomeral body spatulate	*Eutoxeres*	Hermits
Nuchal crest present	*Ramphodon*	Hermits
Corrugations on humerus	Subset of *Phaethornis* [a]	Hermits
Four phalanges in digit IV	*Eutoxeres*	Hermits
	Amazilia group [b]	Emeralds
Zygomatic process short and broad-based	*Androdon*	Mangoes
Frontal fenestra present	*Anthracothorax* group [c]	Mangoes
Rostral concha lacks ventral wing	*Florisuga*	Topazes
	Anthracothorax group [c]	Mangoes
	Amazilia group [b]	Emeralds
Pneumatic foramena distally on humerus	*Boissonneaua*	Brilliants
Ventral groove on ventral wing of rostral concha	*Lampornis*, *Lamprolaima*	Mountain Gems

[a] *Phaethornis atrimentalis*, *P. striigularis*, *P. griseogularis*, *P. ruber*, and *P. stuarti*.
[b] *Chlorestes* through *Hylocharis* in Appendix 1.
[c] *Polytmus* through *Eulampis* in Appendix 1.

wall, symmetry of nasal region, carinal shape, and humeral pneumaticity. Mangoes are a highly diversified clade showing extremes of variation in shape of the caudal rim of the bony nasal opening, structure of the nasal conchae, size of the rostral mandibular fenestra, craniocaudal position of the lateral part of the palatinum, many features of the braincase, bill length and shape, relative length of the epibranchiales, shape of the sternal carina, pattern of humeral pneumatic foramena, and number of phalanges in pedal digit IV. Brilliants show considerable difference in bill length and shape, size of the rostral mandibular fenestra, features of the cranium and palate, relative length of the epibranchiales within *Heliodoxa*, and number of phalanges in pedal digit IV. Within Coquettes there is variation in bill length and shape, development of the ventral wing of the rostral concha, size of the rostral mandibular fenestra, and degree of pneumatic inflation of the cranium. Mountain Gems show some variation in the cranium and in number of phalanges of pedal digit IV. Bees exhibit variation in rostral concavity of the ectethmoidale and in tendinal ossification associated with the humeral ventral process. Variation among Emeralds includes shape of the rostral concha (T-bar versus J-bar), presence or absence of a vertical lamella, shapes of interorbital margins, and number of phalanges of pedal digit IV.

Parallelism.—As one would expect when considerable diversity exists within major clades of a family, parallelisms occur. Examples among hummingbirds, in the context of the McGuire et al. (2007) phylogeny, are shown in Table 5.

Structural adaptation and community ecology.—Although synapomorphies of the upper jaw, palatum, mandibula, hyobranchial apparatus, and wing that distinguish Trochilidae within Apodiformes probably represent basic adaptations for feeding and hovering flight, variations within these complexes may represent finer-grade adaptations within Trochilidae. For example, observations on bill structure, flower structure, and feeding ecology of captive and free-living birds have engendered and confirmed hypotheses on ecological causation of sexual dimorphism and on coadaptation (e.g., Snow and Snow 1980; Temeles et al. 2000, 2002; Temeles and Kress 2003), and Stiles (2008) has explored adaptations of the flight mechanism for life at higher elevations within major hummingbird clades. Variations in poorly known skeletal complexes—those of the nasal region, trunk, foot, and syrinx—may constitute other adaptations, although morphologies divorced from specific adaptation are not ruled out.

Hummingbirds' specializations for hovering and nectarivory provide them a unique eco-space. Within that eco-space, relatively simple changes in bill length and shape almost certainly contribute to establishment of hierarchies of coexistence (Colwell 2000, Temeles and Kress 2003, Temeles et al. 2010). On a broader scale, Bleiweiss (1990) has argued that the generalized feeding ecology and high vagility of Trochilines (as opposed to Hermits) predisposed them to exploit diverse habitats and nectar sources, leading to speciation, specialization in feeding, and increased diversity. The use of clades to represent phylogenetic diversity of hummingbird communities in different ecological and biogeographic contexts (Graham et al. 2009) may provide a template for future analysis of morphological variation and adaptation in hummingbird communities. One difficulty for future analyses is that the named clades of hummingbirds are not equivalent in age or diversity.

CONCLUSIONS

This monograph has identified special problems in the morphology of hummingbirds, notably those listed below. Detailed descriptions of kinematics and functional analyses of articulations are key to many of these problems. Fortunately, hummingbirds are relatively amenable to captivity, and many new anatomical methods remain to be applied.

(1) Functional significance of syringeal structures unique to hummingbirds, requiring observation and cinematography of syrinx during vocalization.

(2) Functional analysis of holorhinal and schizorhinal prepalatal upper jaws, including measurement of bending of tip of upper jaw while drinking, and movement of entire upper jaw when opened widely, with special attention to differences between Hermits and Trochilines.

(3) Comparative study of posthatching development of upper jaw in Hermits as well as Trochilines, with special attention to nasale and craniofacial hinge.

(4) Functional anatomy of the jaw articulation in relation to cranial kinesis and streptognathism. Precise motions of the quadrate and mandible with respect to each other would be necessary. Measurement of torsion in the free rami of the mandibula and electromyography of jaw muscles

TABLE 5. Parallel occurrence of selected characters among major clades of Trochilidae.

Character state	Hermit	Topazes	Mangoes	Brilliants	Coquettes	Patagona	Mountain Gems and Bees	Emeralds
Rostral conch lacks ventral wing		*Florisuga*	*Anthracothorax* group[a]	Some *Heliodoxa* and *Coeligena*				*Amazilia* group[b]
Truncate cerebellar prominence			*Schistes*	*Sternoclyta*, some *Heliodoxa*		*Patagona*		
Four free thoracic vertebrae	*Eutoxeres*	*Florisuga*	*Doryfera*	Most species	Most species	*Patagona*		
Four phalanges in digit IV	*Eutoxeres*		*Schistes*	*Boissonneaua*	*Discosura*, *Lophornis*	*Patagona*	*Panterpe*	*Amazilia* group[b]
Four attached complete ribs	Hermits[c]		*Androdon*, *Heliothryx*					

[a] *Polytmus* through *Eulampis* in Appendix 1.

[b] *Chlorestes* through *Hylocharis* in Appendix 1.

[c] Except *Eutoxeres*.

during cranial kinesis and mandibular streptognathism would be instructive.

(5) Apparent conflict between developmental restructuring of prepalatal upper jaw for nectar transport and the effectiveness of rhynchokinesis for bill-tip motion. Measurement of movement of ventral and dorsal bars during kinesis would be crucial, and elasticity of connective tissue connecting the two bars should be measured. Any difference between motion of dorsal and ventral portions of ventral bar should be determined.

(6) Analysis of motion and transmission of forces throughout pterygopalatine arch and prepalatal upper jaw during cranial kinesis. Powered by jaw muscles, the kinetic mechanism consists of several kinematic chains that include also jugal arch and mandibula, quadromandibular articulation, and associated ligaments.

(7) Measurement of calcium content of bone in flexible portions (hinges) of jaws compared to adjacent portions.

(8) Functional significance of inflation of the caudal part of mandibular ramus. Precise description of jaw muscle insertions and ligaments on species with different morpholgies of the caudal part of mandibular ramus are needed. Torsion in the caudal portion of mandibular rami may be a factor.

(9) Further analysis and ecological significance of jaw mechanisms of Hermits and Trochilines. If differences between Hermits and Trochilines are found in the above studies 2–7, field work might reveal correlated differences in uses of mandibles.

(10) Mechanism and possible role of mandibular downbending during insect capture. Measure downbending precisely, and determine precise motion of mandibular ramus at jaw articulation during downbending. Measure torsion in mandibular rami.

(11) Evaluate hypothesis of two hyobranchial mechanisms, one for tongue lapping and another for full protrusion of tongue. Observe and measure details of tongue protrusion during feeding under different levels of nectar volume and availability at feeders and flowers. Electromyography of intrinsic and extrinsic muscles of the hyobranchial apparatus would be important.

(12) Functional and ecological significance of variation in epibranchial lengths within *Heliodoxa*. Measure maximum protrusion of tongue in species with proportionally different lengths of the epibranchiales. Field studies are needed throughout the range of each species, concentrating on flower structure and nectar reservoirs.

(13) Functional analysis of nasal region and its various morphologies. Measure airflow in various parts of the nasal region during breathing and singing. Determine location of flower mites in nasal region of live birds in the field.

(14) Analysis of influences on cranial shape, including, at least, variation in bill length, ethmoidal region, and overall cranial pneumaticity. Size and orientation of eye, and bill length and shape, may be important correlates of cranial pneumaticity and ectethmoidale shape.

(15) Role of neck in special positioning of head during nectarivory and insect capture. Laboratory and field observations and slow-motion cinematography during feeding would be needed.

(16) Function of lateral displacement of coracoidal facets of sternum in some species. Look for other parameters of shoulder girdle that relate to coracoidal separation. Field study of *Campylopterus* might suggest its significance.

(17) Significance of different numbers of free thoracic vertebrae. Look for functional correlates.

(18) Functional significance of general trends and sexual dimorphism in numbers of true complete ribs. Increase sample sizes of specimens and species measured. Analyze rib function and explore behavioral differences in the sexes that are related to respiration.

(19) Detailed kinematics of shoulder and humerus during flight. Precise motions of wing elements, incuding axial rotation, should be determined at each wing joint for different forms of hovering. Determine the relation of capital tuberculum to glenoid socket during the wingbeat.

(20) Functional significance of notched humeral ventral process and its associated muscles. In combination with study 16 above, electromyography of muscles to ventral process of humerus would be valuable.

(21) Function of corrugations on humeral head in the *Pygmornis* group of *Phaethornis*. Determine the relation of the insertion tendon of m. pectoralis to corrugations during normal and extreme hovering, and between species with and without corrugations.

(22) Functional significance of synostosis of phalanges in digit IV of the foot. Detailed observation of positions of phalanges of all digits during perching and clinging. Are there functional differences between the four- and five-phalanx versions of digit IV?

(23) Relate functional findings on wing skeleton to different parameters of feathered wing, and to different behavioral parameters.

(24) Posthatching and postfledging developmental changes and rates for all structural complexes and associated behavioral changes related to parental feeding, nectarivory, tongue protrusion, and hovering. For example, is the prokinetic upper jaw of nestling Trochiline hummingbirds especially efficient for wide-mouthed food begging?

In a broader perspective, new techniques for three-dimensional imaging and measurement of anatomical complexes applied to skeletons and spirit specimens of hummingbirds may allow more rigorous study of angular relationships of cranium and jaws, eye-size and orientation, lengths of hyobranchial elements and tongue, length and functional properties of neck segments, and other parameters in taxon-rich comparisons. Such data would relate directly to efficiency of access to corollas and nectar, and indirectly to community ecology. Using traditional techniques, these anatomical topics have been explored in other families of birds by Marinelli (1928), Boas (1929), Duijm (1951), and Zusi (1962), among others.

This monograph documents developmental change in the prepalatal upper jaw essential for efficient nectar eating in hummingbirds. Similarly, the tongue develops its terminal, nectar-gathering lamellae and adult length only after fledging (Scharnke 1931a). Although growth of a long bill and tongue is constrained within the egg, there is no obvious reason why rotation of the ventral bars could not have occurred before hatching. Growth of the epibranchiales may also be delayed and occur within a short period, but measurements of the hyobranchial elements of known-age fledglings are lacking and the role of the epibranchiales in nectarivory has not been firmly established. Feeding of fledglings by the adult female probably provides the necessary supplemental energy before the nectar-eating mechanism is maximally efficient:

> When they are flying well, often shortly after the fifth day after fledging, the female prolongs the feeding intervals, teaching the young by loud calls to come for food.... Between feeding bouts, young hummingbirds are often seen to probe at twigs or red parts of leaves.... This exploratory behaviour is maintained throughout adolescence and ultimately leads them to new nectar sources. (Schuchmann 1999:513–514)

Further comparisons of the developmental rates of feeding and hovering adaptations are needed, as well as comparisons of changes in behavior and physiology during maturation. Also lacking is a detailed account of the development of techniques for insect capture by fledglings.

The growing fields of developmental physiology and genetics have provided valuable insights into mechanisms that produce adult morphologies from single cells. In addition, they elucidate the bases for both morphological stasis and variability and promise to reshape our views on adaptation and natural selection (see Badyaev 2011, and references therein). Although hummingbirds have not yet been the subjects of such investigations, even the minimal data on developmental anatomy offered in the present study elucidate gross aspects of the origin of unique features of the bill that pertain to nectarivory in adult hummingbirds. Ultimately, regardless of the analytical approach applied or the source of data employed, explication of evolutionary history will benefit from a broadly comparative approach.

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APPENDIX 1

TAXA STUDIED, COLLECTION SOURCES, AND SPECIMEN NUMBERS

The species of hummingbirds and outgroups studied for this monograph are listed below, grouped by the major trochilid clades recognized by McGuire et al. (2007). Order of the species follows Remsen et al. (2007) and American Ornithologists' Union (1998), except where genera are clustered to reflect similarity in anatomical characters (*Anthracothorax* group: *Polytmus* through *Eulampis*; *Amazilia* group: *Chlorestes* through *Hylocharis*). All species of a major clade are grouped together. Reference numbers and acronyms of source collections for anatomical specimens are as follows:

1.—USNM (National Museum of Natural History; Washington, D.C.)
2.—LSU (Lousiana State University Museum of Natural History; Baton Rouge)
3.—AMNH (American Museum of Natural History; New York)
4.—FMNH (Field Museum of Natural History; Chicago)
5.—UMMZ (University of Michigan Museum of Natural History; Ann Arbor)
6.—UKMNH (University of Kansas Museum of Natural History; Lawrence)
7.—MVZ (Museum of Vertebrate Zoology, University of California; Berkeley)
8.—SDSNH (San Diego Society of Natural History)
9.—YPM (Yale Peabody Museum; New Haven)
10.—LACM (Los Angeles County Museum)
11.—ROM (Royal Ontario Museum; Toronto)
12.—CAS (California Academy of Sciences; San Francisco)
13.—CMNH (Carnegie Museum of Natural History; Pittsburgh)
14.—IRSNB (Institut Royal des Sciences Naturelles de Belgique)
15.—UWBM (University of Washington Burke Museum; Seattle)
16.—DMNH (Delaware Museum of Natural History; Wilmington)
17.—BC (Pierce Brodkorb collection, University of Florida; Gainesville)
18.—MG (Museu Paraense Emelio Goeldi; Belem, Brazil)
19.—ANSP (Academy of Natural Science of Philadelphia)
20.—UWZM (University of Wisconsin Zoological Museum; Madison)
21.—BMNH (Natural History Museum; Tring, UK)

In the species list below, numbers following "S" (skeleton) identify the numbered collections, listed above, from which skeletal data were obtained. Numbers following "A" (alcohol or spirit specimen) similarly identify collections rather than specimens. In both cases, museum numbers of specimens examined for multiple characters are enclosed in parentheses, following the collection number. A subset of these species, identified by inclusion of a capitalized species acronym, was used in the frequency matrix (Appendix 2). Museum numbers of specimens examined for only a few selected characters are not given here. Asterisks indicate species included in the molecular phylogeny of McGuire et al. (2007).

AEGOTHELIDAE

Aegotheles insignis (Feline Owlet-nightjar) AEGOCRIS. S: 9 (6906).

A. crinifrons (Moluccan Owlet-nightjar). S: 1.

A. albertisi (Mountain Owlet-nightjar). S: 9 (6904–5).

A. cristatus (Australian Owlet-nightjar). S: 1 (560816, 612637, 612708, 620228); 4 (337190); 7 (143441, 149017). A: 1 (542627).

HEMIPROCNIDAE

Hemiprocne coronata (Crested Treeswift). S: 1 (320840).

H. longipennis (Gray-rumped Treeswift). S: 1.

H. comata (Whiskered Treeswift) HEMICOMA. S: 1 (488343, 488940); 9. A: 1 (510349).

H. mystacea (Moustached Treeswift). S: 1 (558294, 560829); 9 (7039, 7040); 22.

APODIDAE

Cypseloides niger (Black Swift) CYPSNIGE. S: 1 (290999, 555770). A: 1 (511010).
C. phelpsi (Tepui Swift). S: 1.
C. senex (Great Dusky Swift). S: 9.
Streptoprocne rutila (Chestnut-collared Swift). S: 1 (614122); 12.
S. zonaris (White-collared Swift). S: 1 (614120, 490031); 4; 9; 12 (71845–7).
S. semicollaris (White-naped Swift). S: 1; 12 (62883, 63221). A: 1 (512823).
Collocalia esculenta (Glossy Swiftlet). S: 1. A: 1 (506737).
C. troglodytes (Pygmy Swiftlet). S: 1.
Aerodramus francicus (Mascarene Swiftlet). S: 1.
A. spodiopygius (White-rumped Swiftlet). S: 1.
Hirundapus caudacutus (White-throated Needletail). S: 1.
Chaetura spinicaudus (Band-rumped Swift). S: 1.
C. vauxi (Vaux's Swift). S: 12 (42764, 70803, 71851).
C. pelagica (Chimney Swift). S: 1 (431936, 492655); 12 (71663). A: 1 (512808).
Aeronautes saxatalis (White-throated Swift). S: 1; 8.
Tachornis phoenicobia (Antillean Palm Swift). S: 1.
T. squamata (Fork-tailed Palm Swift). S: 1.
Cypsiurus parvus (African Palm Swift). S: 1.
Apus apus (Common Swift). S: 1.
A. pallidus (Pallid Swift) APUSPALL. S: 1 (582349, 582352–4, 582357). A: 1 (540245).
A. caffer (White-rumped Swift). S: 1.
A. affinis (Little Swift). A: 1.

TROCHILIDAE

HERMITS

*Eutoxeres aquila**+ (White-tipped Sicklebill) EUTOAQUI. S: 1 (428580, 430611, 432173, 500607, 560020, 613297); 2 (86388, 89732); 3 (6078). A: 1 (510579); 2 (117911).

*E. condamini** (Buff-tailed Sicklebill). S: 2 (74844, 79757, 118197); 6 (80543); 8 (37585). A: 1 (511929, 512283).

Ramphodon naevius+ (Saw-billed Hermit) RAMPNAEV. S: 1 (562754, 562759, 612046–9). A: 1.

*Glaucis aeneus** (Bronzy Hermit). S: 1 (612305); 2 (48563, 50745, 77731, 77733).

*G. hirsutus**+ (Rufous-breasted Hermit) GLAUHIRS. S: 1 (344138–9, 492298, 492346, 500586, 555682–3, 562547, 562735); 2 (70194); 9. A: 1 (641471).

*Threnetes ruckeri** (Band-tailed Barbthroat). S: 1 (500583, 500585, 611575, 611582–3, 611586, 611588, 612317, 613372, 613377); 2. A:1 (510573).

*T. leucurus** (Pale-tailed Barbthroat) THRELEUC. S: 1 (492278–9, 492327, 429378–9, 500500, 560023, 560042); 2; 9 (8064).

Phaethornis squalidus (Dusky-throated Hermit). S: 1 (612040).

P. longuemareus (Little Hermit). S: 1 (560160–1, 562500–1); 5 (156545, 158230).

*P. atrimentalis** (Black-throated Hermit). S: 2 (75536, 86386, 106988, 111171).

P. striigularis (Stripe-throated Hermit). S: 1 (430590, 430942, 490208, 612310, 613382–4); 2 (31864, 108740); 4 (337121); 5 (153097); 6 (29235); 7 (156637).

*P. griseogularis** (Gray-chinned Hermit). S: 3 (18143); 11 (114822). A: 2 (91476).

*P. ruber** (Reddish Hermit) PHAERUBE. S: 1 (345257–8, 562453, 562757); 2 (101262–3, 131463–4); 3: (19420, 19421); 4 (320687). A: (616329, 641470).

P. stuarti (White-browed Hermit). S: 2 (70199, 101264).

P. subochraceus (Buff-bellied Hermit). S: 2 (125716–7); 4 (334395).

*P. augusti** (Sooty-capped Hermit). S: 1 (344553); 11 (128034).

P. pretrei (Planalto Hermit). S: 1 (202037, 562755, 612041); 2 (125715).

P. eurynome (Scale-throated Hermit). S: 1 (555946–7, 556425–6, 558793).

*P. anthophilus** (Pale-bellied Hermit). S: 16 (61817, 62990).

*P. hispidus** (White-bearded Hermit). S: 2 (111159, 111161, 121004); 5 (200598).

*P. yaruqui** (White-whiskered Hermit) PHAEYARU. S: 1 (492395–6, 500467, 610457); 2 (68728, 68731). A: 1 (505460).

*P. guy** (Green Hermit). S: 1 (560018, 562498–9, 613288 613295); 2 (63180, 86691, 106984, 118182).

*P. syrmatophorus** (Tawny-bellied Hermit). S: 2 (89424, 89727, 97462); 3 (8232).

*P. koepckeae** (Koepcke's Hermit). S: 2 (118190, 118192); 4 (320664–5).

*P. philippii** (Needle-billed Hermit). S: 2 (93875, 118335); 3 (10241–2). A: 2 (131777).

*P. bourcieri** (Straight-billed Hermit). S: 2 (111162–3); 3 (18001); 4 (318733).

*P. longirostris** (Long-billed Hermit). S: 1 (500581, 500584, 612308–9).

P. superciliosus (Long-tailed Hermit) PHAESUPE. S: 1 (492254, 492314, 492336, 562441, 562444–6, 621397). A: 1.

*P. malaris** (Great-billed Hermit). S: 2 (111139, 111149, 125710–1).

TOPAZES

*Topaza pella** (Crimson Topaz) TOPAPELL. S: 11 (107531, 112538). A: 1 (505574).

T. pyra (Fiery Topaz). S: 4 (318845). A: 1 (505573).

*Florisuga mellivora** (White-necked Jacobin) FLORMELL. S: 1 (344142–3, 430918, 501331, 554690, 611569); 2 (50750); 9 (7921–3). A: 1 (505502).

F. fusca (Black Jacobin) FLORFUSC. S: 1 (552560, 562760); 4 (105686); 14 (37763).

MANGOES

*Doryfera ludovicae** (Green-fronted Lancebill) DORYLUDO. S: 1 (491584); 2 (63176, 64840, 64925, 106949). A: 1 (511956, 512143).

*D. johannae** (Blue-fronted Lancebill). S: 2 (89714–5, 118178–9).

*Schistes geoffroyi** (Wedge-billed Hummingbird) SCHIGEOF. S: 1 (560034); 2 (68832, 83979, 86390, 89850); 4 (291776). A: 2 (98030).

Augastes lumachella (Hooded Visorbearer). S: 8 (155178); 10.

*Colibri delphinae** (Brown Violetear). S: 1 (344144, 428699, 428728); 2 (50763, 118204). A: 1 (505506).

*C. thalassinus** (Green Violetear). S: 2 (64844, 70203, 81209); 8 (37780).

*C. coruscans** (Sparkling Violetear) COLICORU. S: 1 (428732, 428764, 428847, 559970); 2; 8 (36296); 10 (89178). A: 1 (505505).

C. serrirostris (White-vented Violetear). S: 7 (155174).

*Androdon aequatorialis** (Tooth-billed Hummingbird) ANDRAEQU. S: 2 (104613); 16 (57988, 57990). A: 16 (63070).

*Heliactin bilophus** (Horned Sungem) HELIBILO. A: 18 (4214).

Heliothryx auritus (Black-eared Fairy) HELIAURI. S: 1 (344145); 4 (315397); 6 (71534); 9 (7612, 8288); 11 (125774–5). A: 1 (541604).

*H. barroti** (Purple-crowned Fairy). S: 2; 5.

*Polytmus guainumbi** (White-tailed Goldenthroat) POLYGUAI. S: 2 (125744); 4 (289178, 334406); 11 (109532). A: 1 (505527).

P. milleri (Tepui Goldenthroat). S: 3.

*P. theresiae** (Green-tailed Goldenthroat). S: 5 (156141); 6 (34841). A: 18 (3342).

*Chrysolampis mosquitus** (Ruby-topaz Hummingbird) CHRYMOSQ. S: 1 (555695); 13: (8484); 4 (105393, 105395). A: 1 (318125).

Anthracothorax viridigula (Green-throated Mango). S: 1 (345259, 345260); 4 (104251–2). A: 13 (1448).

A. prevostii (Green-breasted Mango). S: 2 (31866); 11 (112891).

*A. nigricollis** (Black-throated Mango). S: 1 (555686–7, 555695, 562502); 2 (64994); 6 (34825).

A. dominicus (Antillean Mango) ANTHDOMI. S: 1 (501714, 501755, 501760, 501851, 501857, 501901, 554619, 555779, 555783, 555785–6). A: 1 (506174).

A. viridis (Green Mango). S: 1 (501785, 501798, 501827, 501830).

*A. mango** (Jamaican Mango). S: 1 (558870–1); 7 (149980).

*Eulampis jugularis** (Purple-throated Carib) EULAJUGU. S: 1 (487942, 487945, 487948, 487969, 488010, 488035, 556601, 556603, 556633). A: 1 (542587).

*E. holosericeus** (Green-throated Carib) EULAHOLO. S: 1 (487962–3, 488000, 488006, 555023, 555033, 557665). A: 1 (318101).

BRILLIANTS

*Haplophaedia aureliae** (Greenish Puffleg) HAPLAURE. S: 1 (428851, 428868, 560029, 560030); 2; 7 (141747); 10 (89183). A: 2 (104769).

*H. lugens** (Hoary Puffleg). S: 3; 10 (105695). A: 3 (7239).

Eriocnemis nigrivestis (Black-breasted Puffleg). S: 3.

*E. vestita** (Glowing Puffleg). S: 1 (501558–9); 2; 3 (8230, 8280); 10 (99894).

E. cupreoventris (Coppery-bellied Puffleg). A: 11 (105392).

*E. luciani** (Sapphire-vented Puffleg) ERIOLUCI. S: 1 (559963–5); 2 (81222, 99328, 112877); 3 (7060). A: 1 (505424).

*E. mosquera** (Golden-breasted Puffleg). S: 1 (559962).

*E. alinae** (Emerald-bellied Puffleg). S: 2 (107089, 129817–9). A: 2 (129522).

*Aglaeactis cupripennis** (Shining Sunbeam) AGLACUPR. S: 1 (559972–4, 614842–3); 2; 3 (7053–4); 9 (7851). A: 1 (505439).

*A. castelnaudii** (White-tufted Sunbeam). S: 2 (113660, 129791–2).

*Coeligena coeligena** (Bronzy Inca). S: 1 (491510, 491752–3, 560035); 2 (97466, 129797); 7 (141746). A: 1 (512168).

*C. wilsoni** (Brown Inca). S: 1 (501555, 610458); 8 (38331); 11 (118770).

*C. torquata** (Collared Inca). S: 1 (428869, 428882, 560051); 2 (89772).

C. violifer (Violet-throated Starfrontlet). S: 2 (74857, 89792); 3 (7038, 7332).

C. iris (Rainbow Starfrontlet) COELIRIS. S: 2 (79771, 81223, 81225, 86476–7); 3; A: 3 (7262).

C. phalerata (White-tailed Starfrontlet). S: 8 (38332).

*C. lutetiae** (Buff-winged Starfrontlet). S: 1 (501556); 2; 3 (6063, 6067, 6071). A: 3 (7267).

*Lafresnaya lafresnayi** (Mountain Velvetbreast) LAFRLAFR. S: 1 (428898, 614844–5); 2 (75608, 97465, 129793); 3 (8228, 8270). A: 1 (505576, 615934).

*Ensifera ensifera** (Sword-billed Hummingbird) ENSIENSI. S: 1 (428880, 501557); 2 (157292); 3 (8259, 8541). A: 1 (505429).

*Pterophanes cyanopterus** (Great Sapphirewing) PTERCYAN. S: 1 (501561); 2 (79763–5, 101267, 113659, 129794); 3 (7056–7). A: 1 (505488).

*Boissonneaua flavescens** (Buff-tailed Coronet). S: 1 (428897, 559988); 3 (6069, 8286); 9 (4136); 11 (118767). A: 3 (7283).

*B. matthewsii** (Chestnut-breasted Coronet) BOISMATT. S: 2 (74861, 93901, 107081–2); 5 (210493). A: 2 (91484).

B. jardini (Velvet-purple Coronet). S: 3 (17653).

*Ocreatus underwoodii** (Booted Racket-tail) OCREUNDE. S: 1 (428754, 491583, 501647, 559990); 2; 3 (17651); 7; 8 (37446); 9 (2071). A: 1 (505457, 512389).

*Urosticte benjamini** (Purple-bibbed Whitetip) UROSBENJ. S: 2 (118208, 157298); 3 (1764). A: 3 (4700).

*Urochroa bougueri** (White-tailed Hillstar) UROCBOUG. S: 2; 3 (6075); 8 (36639, 36948, 37700–1); 11 (118774). A: 3 (9701).

*Heliodoxa xanthogonys** (Velvet-browed Brilliant). S: 3 (18152, 18155, 18157–8); 4 (318840, 339638). A: 1.

H. gularis (Pink-throated Brilliant). S: 2 (89755–6).

*H. branickii** (Rufous-webbed Brilliant). S: 1 (491590–1); 2 (107023); 4 (315387, 320908). A: 1 (512076).

*H. schreibersii** (Black-throated Brilliant). S: 2 (118346); 3; 4 (315367, 320877). A: 3 (7234).

*H. aurescens** (Gould's Jewelfront) HELIAURE. S: 2 (93889, 107015, 118345); 4 (315362, 320851). A: 1.

*H. rubinoides** (Fawn-breasted Brilliant). S: 1 (501565; 2; 3 (6079, 8235, 8306); 8 (36726); 10. A: 1 (512157).

*H. jacula** (Green-crowned Brilliant). S: 1 (500466, 501562–3); 2; 8.

*H. leadbeateri** (Violet-fronted Brilliant) HELILEAD. S: 1 (491567, 501564, 560016–7, 560031); 2 (68736, 83969); 6 (80847); 13 (2422). A: 1 (505623).

Clytolaema rubricauda (Brazilian Ruby). S: 1.

Sternoclyta cyanopectus (Violet-chested Hummingbird) STERCYAN. S: 1 (501646); 5 (210814). A: 1 (505039).

COQUETTES

*Heliangelus amethysticollis** (Amethyst-throated Sunangel) HELIAMET. S: 1 (559996); 2 (97480, 107084); 3 (6074, 6909); 10 (99893). A: 1 (511966).

H. strophianus (Gorgeted Sunangel). S: 1 (559984–5); 4 (106388).

*H. exortis** (Tourmaline Sunangel). S: 1 (428884); 2 (97481–2); 3 (8238); 9. A: 13 (1974).

H. viola (Purple-throated Sunangel). S: 1 (491386); 8 (37664–5). A: 3 (7237).

*Sephanoides sephaniodes** (Green-backed Firecrown) SEPHSEPH. S: 1 (322956); A: 1 (508250).

*S. fernandensis** (Juan Fernandez Firecrown). S: 15 (35366); A: 1 (322907).

*Discosura conversii** (Green Thorntail) DISCCONV. S: 3 (5744); 17 (927800). A: 3 (4771).

*D. popelairii** (Wire-crested Thorntail). S: 1 (501567); 2 (157296).

D. langsdorffi (Black-bellied Thorntail). S: 2 (109390, 111176, 132099). A: 1 (616367, 616534).

Lophornis helenae (Black-crested Coquette) LOPHHELE. S: 2 (31867).

L. ornatus (Tufted Coquette). A: 1 (81493).

L. adorabilis (White-crested Coquette). S: 5 (133762, 153098–9).

L. gouldii (Dot-eared Coquette) LOPHGOUL. S: 1 (562447). A: 18 (5529).

L. magnificus (Frilled Coquette). S: 1; 4 (105685).

*Phlogophilus hemileucurus** (Ecuadorian Piedtail) PHLOHEMI. S: 1 (560021); 2 (86389, 86692, 157299). A: 2 (85958).

P. harterti (Peruvian Piedtail). S: 4 (320834–5, 320843).

*Adelomyia melanogenys** (Speckled Hummingbird) ADELMELA. S: 1 (428896, 559582–3, 560036, 560050); 2 (93885, 129787–8). A: 1 (615317).

*Aglaiocercus kingi** (Long-tailed Sylph) AGLAKING. S: 1 (428825, 428858); 2; 3 (429, 6065); 5 (213992); 8; 9 (4158). A: 1 (512427).

*A. coelestis** (Violet-tailed Sylph). S: 1: 2 (95373, 101275); 3 (17648, 17650); 5 (209220); 8 (43861). A: 1 (227969).

Sappho sparganura (Red-tailed Comet) SAPPSPAR. S: 2 (95373, 101275); 3 (17648, 17650); 5 (209220), 8 (43861). A: 1 (227969).

Polyonymus caroli (Bronze-tailed Comet) POLYCARO. S: 2 (86481, 97479). A: 2 (86213).

*Oreotrochilus estella** (Andean Hillstar) OREOESTE. S: 2 (93893, 114251, 120852); 3 (6070, 7049, 7050); 5 (212728). A: 1 (505434, 505451).

O. melanogaster (Black-breasted Hillstar). S: 2 (106938); 5 (156828).

Loddigesia mirabilis (Marvelous Spatuletail) LODDMIRA. A: 19 (192473, 192474).

*Opisthoprora euryptera** (Mountain Avocetbill) OPISEURY. S: 2 (87579, 93938).

*Lesbia victoriae** (Black-tailed Trainbearer) LESBVICT. S: 1; 2 (93903); 3 (6057, 8460); 5 (210492); 10 (89184). A: 1 (505447).

*L. nuna** (Green-tailed Trainbearer). S: 2 (83977); 3 (7061–2); 6 (80901); 9 (7852).

*Ramphomicron microrhynchum** (Purple-backed Thornbill) RAMPMICR. S: 1 (559975); 2 (71577, 129820, 157350); 3 (6061, 6066, 6068). A: 2 (113730).

*Chalcostigma ruficeps** (Rufous-capped Thornbill). S: 2 (70215, 89849, 93936, 101278). A: 2 (79537).

C. olivaceum (Olivaceous Thornbill). S: 2 (114252–3). A: 2 (70610).

C. stanleyi (Blue-mantled Thornbill) CHALSTAN. S: 2 (79789, 93937). A: 1 (505476).

*Oxypogon guerinii** (Bearded Helmetcrest) OXYPGUER. S: 3 (9500). A: 3 (4637).

*Oreonympha nobilis** (Bearded Mountaineer) OREONOBI. S: 3 (7075); 4 (324113). A: 2 (79540).

*Metallura tyrianthina** (Tyrian Metaltail). S: 1 (559966–8); 2 (81214–5, 129841, 129844); 3 (7074); 10 (99896). A: 1 (505444).

*M. williami** (Viridian Metaltail). S: 1 (428821); 2; 3 (6058). A: 11 (112064).

M. odomae (Neblina Metaltail). S: 2 (89835).

M. theresiae (Coppery Metaltail) METATHER. S: 2 (81219, 89837, 93914, 113663, 120899, 120912–3, 120916). A: 2 (120716).

M. eupogon (Fire-throated Metaltail). S: 2 (129829, 129833–4, 129839); 3 (7064–5).

*M. aeneocauda** (Scaled Metaltail). S: 2 (79776, 95374–6).

*M. phoebe** (Black Metaltail). S: 2 (114260, 120835); 3 (7067, 7069).

PATAGONA

*Patagona gigas** (Giant Hummingbird) PATAGIGA. S: 1 (322105, 343093); 2 (120849); 3 (7063); 4 (324112); 5 (156737); 7 (158796). A: 1 (505465).

MOUNTAIN GEMS

*Eugenes fulgens** (Magnificent Hummingbird) EUGEFULG. S: 2 (62777, 63140, 64846, 131282); 3 (12735); 6 (30887); 7. A: 1 (5061130).

*Panterpe insignis** (Fiery-throated Hummingbird) PANTINSI. S: 1 (613296); 2 (48570, 50757, 51328, 62776, 63138, 64845); 3 (12711–2); 7. A: 1 (542828); 2 (63690).

*Heliomaster longirostris** (Long-billed Starthroat) HELILONG. S: 1 (500582, 559695, 612951); 2 (31891); 5 (133791, 153110, 218953). A: 3.

H. constantii (Plain-capped Starthroat). S: 2 (31890, 50764); 3 (10316); 7 (85772, 154290). A: 1 (506366).

H. furcifer (Blue-tufted Starthroat). S: 1 (556414); 2 (151657); 5 (202055). A: 3 (7231).

Lampornis clemenciae (Blue-throated Hummingbird). S: 2; 5(159127); 6; 8(37443); 10. A: 11 (118323).

L. amethystinus (Amethyst-throated Hummingbird). S: 4 (105158); 6 (30886); 7. A: 11 (113216).

L. viridipallens (Green-throated Mountain-gem). S: 1 (560217–9, 560220); 6 (69624, 69645); 9 (8141–2).

*L. hemileucus** (White-bellied Mountain-gem). S: 5 (133784, 133787).

*L. castaneoventris** (Variable Mountain-gem) LAMPCAST. S: 1 (613292–3); 2 (157295); 3 (12791); 5 (133783, 219567). A: 1 (542827).

Lamprolaima rhami (Garnet-throated Hummingbird) LAMPRHAM. S: 1 (611758); 6 (40549); 7 (85747). A: 6 (040545).

BEES

*Myrtis fanny** (Purple-collared Woodstar) MYRTFANN. S: 2 (81213, 93939, 113666); 3 (7083–5); 5 (156833). A: 1 (505463).

Eulidia yarrellii (Chilean Woodstar). S: 1 (500846).

Myrmia micrura (Short-tailed Woodstar) MYRMMICR. S: 2 (93940). A: 2 (89429).

*Rhodopis vesper** (Oasis Hummingbird) RHODVESP. S: 2 (100535); 3 (7076–8); 4 (105915). A: 3 (9775–7).

Thaumastura cora (Peruvian Sheartail) THAUCORA. S: 2 (65301, 114250, 157351); 3 (7079, 7080). A: 2 (114290).

Calothorax lucifer (Lucifer Hummingbird) CALOLUCI. S: 1 (559710, 560942); 5; 6 (29236). A: 11 (110097).

C. pulcher (Beautiful Hummingbird). S: 7 (154291).

Doricha enicura (Slender Sheartail) DORIENIC. S: 1 (11643); 6 (69654).

D. eliza (Mexican Sheartail). S: 15 (37715). A: 6 (89338).

Calliphlox evelynae (Bahama Woodstar) CALLEVEL. S: 1 (555533–4); 2 (71050, 71247, 80151, 86684); 17: (37570). A: 1 (505046).

*C. mitchellii** (Purple-throated Woodstar). S: 20. A: 20.

C. amethystina (Amethyst Woodstar). A: 1 (505591); 21.

Chaetocercus mulsant (White-bellied Woodstar) CHAEMULS. S: 1 (559971); 2 (105820, 129848). A: 1 (505414).

C. bombus (Little Woodstar). A: 1.

C. jourdanii (Rufous-shafted Woodstar) CHAEJOUR. S: 1 (344155–6); 13 (2634).

Microstilbon burmeisteri (Slender-tailed Woodstar) MICRBURM. S: 1 (645254); 5 (157954). A: 1 (645151).

Tilmatura dupontii (Sparkling-tailed Woodstar). S: 1. A: 1 (541082).

Mellisuga minima (Vervain Hummingbird) MELLMINI. S: 1 (226929, 292586, 555789, 555790–1). A: 1 (225892, 225926, 291395, 318952).

M. helenae (Bee Hummingbird). S: 1; A: 1 (229945–8, 225950).

*Archilochus colubris** (Ruby-throated Hummingbird) ARCHCOLU. S: 1 (347968, 498793, 502142, 553900, 560941, 610988, 612009); 2; 3 (11057). A: 1 (319894).

*A. alexandri** (Black-chinned Hummingbird). S: 1 (17073, 226374–5, 346514–5, 555737).

*Calypte anna** (Anna's Hummingbird). S: 2 (130850); 7 (41356, 69531, 77234, 120370).

*C. costae** (Costa's Hummingbird) CALYCOST. S: 1 (20344, 499022, 553913, 555620, 621308); 2; 3 (5735, 8499, 13775); 10 (102419). A: 1 (23475).

Atthis heloisa (Bumblebee Hummingbird) ATTHHELO. S: 4 (343216); 5 (214389); 11 (109634). A: 1 (506367).

*Stellula calliope** (Calliope Hummingbird) STELCALL. S: 1 (489879, 498990, 571158); 2 (95267); 3 (15979); 7 (69324–5). A: 1 (18651).

*Selasphorus rufus** (Rufous Hummingbird) SELARUFU. S: 1 (558426, 558428, 558431–2, 610991, 621310); 2 (122561); 5 (204596); 7 (125538); 9 (2231); 12 (68669). A: 1 (81518).

S. sasin (Allen's Hummingbird). S: 2 (118768); 7 (125538); 9 (5753, 6279); 10 (103144); 12 (68989).

*S. platycercus** (Broad-tailed Hummingbird). S: 1 (17076–7, 450076, 498881); 2 (122199); 3 (5457, 16639); 7 (41412, 153908).

*S. flammula** (Volcano Hummingbird). S: 2 (48518, 48573, 64847); 3 (12697, 12724); 5 133794); 7.

S. scintilla (Scintillant Hummingbird). S: 5 (219569).

EMERALDS

Chlorostilbon canivetii (Canivet's Emerald). S: 1 (432179), 2 (118529, 1131465); 5 (153100); 7 (85738, 153912). A: 1 (541030).

*C. mellisugus** (Blue-tailed Emerald) CHLOMELL. S: 1 (428762); 2 (118529, 131465); 3 (6064, 7035); 4 (317158); 9 (4143). A: 1 (505461); 13 (1350).

C. aureoventris (Glittering-bellied Hummingbird). S: 2; 4 (105325); 5 (200684, 202039, 202040); 10 (104434).

C. ricordii (Cuban Emerald). S: 1 (553356, 555178–9, 562473, 6122530); 4 (105612, 105747). A: 1 (542501).

C. bracei (Brace's Emerald). S: 1 (553485, 553488).

C. swainsonii (Hispaniolan Emerald). S: 1 (555787); 9 (6495, 12107). A: 1 (291045).

C. maugaeus (Puerto Rican Emerald). S: 1 (501773–4, 501786–7, 501813). A: 1 (504029).

Cynanthus sordidus (Dusky Hummingbird). S: 5 (210412, 210528); 7 (153913).

C. latirostris (Broad-billed Hummingbird) CYNALATI. S: 1 (489886); 4 (317859); 6 (19042, 29809, 30883, 35634); 7. A: 1 (226755).

Cyanophaia bicolor (Blue-headed Hummingbird) CYANBICO. S: 1 (487926, 487978, 488044). A: 1 (508024).

*Orthorhyncus cristatus** (Antillean Crested Hummingbird) ORTHCRIS. S: 1 (487958, 487992, 555008, 555016, 555019, 555021, 558096, 558100, 612556). A: 1 (81180).

*Klais guimeti** (Violet-headed Hummingbird) KLAIGUIM. S: 1 (559997); 2 (50765, 86440, 157297); 3 (17236); 4 (320773); 14 (37762). A: 2 (81180).

Stephanoxis lalandi (Plovercrest) STEPLALA. S: 1 (555948, 555950, 558794–5); 5 (200683); 9 (6432). A: 1 (505203).

Abeillia abeillei (Emerald-chinned Hummingbird) ABELABEI. S: 1 (560211–2); 6 (69643). A: 1 (540578).

Basilinna leucotis (White-eared Hummingbird) BASILEUC. S: 1 (500617); 2; 3 (8084, 8086–7, 13766); 5; 10 (89179). A: 1 (506361).

B. xantusii (Xantus's Hummingbird). S: 2 (127198); 7 (55204–5, 55207). A: 1 (87685).

Phaeochroa cuvierii (Scaly-breasted Hummingbird) PHAECUVI. S: 1 (430229); 2 (32041, 50751); 7 (155746).

Campylopterus curvipennis (Wedge-tailed Sabrewing). S: 2; 6 (28954); 9 (9887–8, 9890, 9892). A: 3 (7279).

*C. largipennis** (Gray-breasted Sabrewing) CAMPLARG. S: 1 (492310, 492317, 492324, 492338, 620144–5); 2; 6 (71829, 72047); 9 (7872, 8286). A: 1 (511221).

C. rufus (Rufous Sabrewing). S: 12 (71555). A: 1 (506222).

*C. hyperythrus** (Rufous-breasted Sabrewing). S: 3 (9495); 4 (339630–1). A: 1 (505622).

*C. hemileucurus** (Violet Sabrewing). S: 1 (7050, 560209, 560210); 3 (10305, 15664); 5 (210638); 6 (29297); 7; 8 (25626); 12. A: 1 (506219).

C. ensipennis (White-tailed Sabrewing). S: 1 (344140–1).

C. falcatus (Lazuline Sabrewing). S: 1 (491751). A: 1 (615309, 615311).

*C. villaviscensio** (Napo Sabrewing). S: 1 (501553, 560014); 2 (118200–1). A: 3 (7280).

C. duidae (Buff-breasted Sabrewing). S: 3 (18144, 18148, 18150–1); 4 (318777, 318781). A: 1 (505499, 505596).

Eupetomena macroura (Swallow-tailed Hummingbird) EUPEMACR. S: 1 (345894, 490018, 561285, 562761); 2 (125728); 4 (334990–1); 7; 14 (37775–6). A: 2 (85953).

*Chlorestes notata** (Blue-chinned Sapphire) CHLONOTA. S: 1 (344149, 344150, 562503–4, 612946); 2; 4 (313624–5); 6 (71827, 71902). A: 1 (542677).

*Chalybura buffonii** (White-vented Plumeleteer) CHALBUFF. S: 1 (428756, 490206, 610226–7); 2; 5 (218384–6). A: 1 (615313).

*C. urochrysia** (Bronze-tailed Plumeleteer). S: 1 (428231); 5 (133779, 133782).

*Thalurania colombica** (Violet-crowned Woodnymph). S: 1.

*T. furcata** (Fork-tailed Woodnymph) THALFURC. S: 1 (344153, 345895, 345897, 501333, 560022, 562450–1, 613385, 613387–8); 2; 9 (8047–8). A: 1 (505523).

T. glaucopis (Violet-capped Woodnymph). S: 1; 7.

Trochilus polytmus (Red-billed Streamertail) TROCPOLY. S: 1 (502867, 502872, 502874, 502876, 558876, 558880, 559187). A: 1 (505181).

*Eupherusa eximia** (Stripe-tailed Hummingbird) EUPHEXIM. S: 1 (490214, 560215–6); 4 (69629, 69671); 6; 12 (71908). A: 1 (542825).

*E. nigriventris** (Black-bellied Hummingbird). S: 1 (613299, 613300); 3 (5661); 5 (133778).

*Microchera albocoronata** (Snowcap). S: 5 (153107, 156028).

*Elvira chionura** (White-tailed Emerald) ELVICHIO. S: 1 (613301); 2 (50762). A: 1 (542829).

*E. cupreiceps** (Coppery-headed Emerald). A: 1 (510679).

*Aphantochroa cirrochloris** (Sombre Hummingbird) APHACIRR. S: 8; 10 (89181).

*Taphrospilus hypostictus** (Many-spotted Hummingbird) TAPHHYPO. S: 2 (116620); 4 (315355). A: 4 (291588).

Leucochloris albicollis (White-throated Hummingbird) LEUCALBI. S: 4 (105681, 105683–4); 5 (200694). A: 1 (505195).

Leucippus fallax (Buffy Hummingbird). A: 1 (505528).

L. baeri (Tumbes Hummingbird). S: 1; 2 (75603, 77723, 93880); 3 (7039). A: 2 (75459).

L. taczanowskii (Spot-throated Hummingbird). S: 2 (981208, 93881); 3 (7040). A: 2 (75461).

L. chlorocercus (Olive-spotted Hummingbird) LEUCCHLO. S: 2 (48763, 111172, 121020, 121023–4, 121030, 121032). A: 2 (120575).

*Amazilia chionogaster** (White-bellied Hummingbird). S: 2 (70208, 73052, 125745, 125747, 125749, 125751); 3 (9145). A: 1 (19412).

A. viridicauda (Green-and-white Hummingbird). S: 2 (48762, 129785).

*A. rutila** (Cinnamon Hummingbird). S: 1 (210524); 2 (31883, 50755, 51330); 3 (10313); 5 210524); 6 (36532); 7 (85757).

A. yucatanensis (Buff-bellied Hummingbird). S: 6 (24927, 30884); 11 (112895). A: 13 (1608).

*A. tzacatl** (Rufous-tailed Hummingbird) AMAZTZAC. S: 1 (492394, 611570, 613401, 613403, 613405, 613407, 613409, 613411, 613414, 613416); 2. A: 1 (542822).

A. amazilia (Amazilia Hummingbird). S: 1 (492391); 2 (52686); 3 (7045–6). A: 2.

A. leucogaster (Plain-bellied Emerald). S: 3 (17661); 6 (34823, 72010, 72012).

*A. versicolor** (Versicolored Emerald). S: 1 (555592, 555951, 558000); 4; 6 (318826).

A. brevirostris (White-chested Emerald). S: 1 (560162); 5 (158228).

*A. franciae** (Andean Emerald). S: 1 (428758, 491387); 8 (36667, 38043); 13 (2427, 2419).

A. candida (White-bellied Emerald) AMAZCAND. S: 1 (288831–3, 288837); 2; 3 (7856, 12567). A: 3 (7294).

A. cyanocephala (Azure-crowned Hummingbird). S: 1 (560214); 2 (31878–9, 31880); 6 (29237).

A. violiceps (Violet-crowned Hummingbird). S: 6 (33143, 35439); 7 (153910–1); 10 (104411).

A. viridifrons (Green-fronted Hummingbird). S: 5 (159125); 6 (69628); 11 (118428, 118436).

*A. fimbriata** (Glittering-throated Emerald). S: 1 (559698–9, 560052); 2; 3; 4 (337126); 11 (105981, 114838).

A. lactea (Sapphire-spangled Emerald). S: 2 (50754, 73208); 3 (7042–3) .

*A. amabilis** (Blue-chested Hummingbird) AMAZAMAB. S: 1 (432603, 500460, 613389, 613983); 5 (133772–4). A: 1 (542239).

*A. saucerrottei** (Steely-vented Hummingbird). S: 1 (347112); 2 (32032, 48572); 5 (153106).

A. cyanifrons (Indigo-capped Hummingbird). S: 1 (428766).

A. edward (Snowy-bellied Hummingbird). S: 1 (432108); 2 (32033, 50752).

A. cyanura (Blue-tailed Hummingbird). S: 2 (31881–2).

A. beryllina (Berylline Hummingbird). S: 3 (8089, 8090); 6 (34802–3, 69652).

*A. viridigaster** (Green-bellied Hummingbird). S: 3 (15115, 18153–4). A: 1 (505543).

A. tobaci (Copper-rumped Hummingbird) AMAZTOBA. S: 1 (555688–9, 555690, 562505–6, 612949, 612950); 4 (104246). A: 1 (346751).

*Chrysuronia oenone** (Golden-tailed Sapphire) CHRYOENO. S: 1 (560053); 2 (70207, 118206); 3 (7037); 4 (291760, 315346, 320808). A: 1 (615312).

Goethalsia bella (Pirre Hummingbird) GOETBELL. S: 1 (559696); 2 (104615, 104665, 108746).

Goldmania violiceps (Violet-capped Hummingbird) GOLDVIOL. S: 1 (432625); 5 (219563–5). A: 1 (432661).

*Lepidopyga coeruleogularis** (Sapphire-throated Hummingbird) LEPICOER. S: 1 (432175, 490211, 610224–5); 3 (6510); 5 (490211). A: 1 (431209).

*Damophila julie** (Violet-bellied Hummingbird) DAMOJULI. S: 1 (491263, 559703, 559708, 610220, 610222); 2; 8 (37379). A: 7 (4104).

*Hylocharis eliciae** (Blue-throated Goldentail). S: 2 (32030–1); 5 (133771). A: 2 (99907).

*H. sapphirina** (Rufous-throated Sapphire). S: 9 (7599).

*H. cyanus** (White-chinned Sapphire) HYLOCYAN. S: 1; 2 (99591); 3 (11946); 5 (209492); 11 (107530). A: 2 (131780).

H. chrysura (Gilded Hummingbird) HYLOCHRY. S: 1 (555949, 556412); 2; 4 (334400–1, 335011); 5; 6 (79270). A: 1 (505979).

*H. grayi** (Blue-headed Sapphire). S: 11 (106267, 114826, 118756). A: 11 (112062).

Appendix 2

Character List for Frequency Matrix

1. Length of dorsal bar of prepalatal upper jaw between nasal crest and intermediate part, in relation to length between nasal crest and craniofacial hinge: (a) longer, (b) similar, (c) shorter.
2. Dorsal bar of prepalatal upper jaw rostral to nasal roof, shape of transverse section: (a) ovate or circular, (b) dorsoventrally compressed, (c) laterally compressed.
3. Maxillare, shape of ventral surface at level of junction with maxillary process of nasale: (a) concave and rounded, (b) concave and angled.
4. Dorsal bar of prepalatal upper jaw rostral to nasal roof, shape in dorsal view: (a) sides parallel, (b) sides diverging rostrally.
5. Mandibula, size of rostral mandibular fenestra: (a) absent or small, (b) medium, (c) large.
6. Mandibular ramus, degree of inflation of caudal part in relation to intermediate part in ventral or dorsal view: (a) slight, (b) moderate, (c) marked.
7. Mandibula, shape of transverse section of intermediate part of ramus rostral to rostral mandibular fenestra: (a) lateromedially compressed with thicker dorsal and ventral margins, (b) oval.
8. Nasal part of upper jaw, conformation of transverse section of medial concha: (a) thin and scrolled, (b) partially scrolled and thickened, (c) thick and unscrolled.
9. Nasal part of upper jaw, rostral concha, status and development of ventral wing: (a) well developed along most or all of vertical wall, (b) weakly developed or reduced to angular ridge in region of nasal crest, (c) absent.
10. Nasal part of prepalatal upper jaw, rostral concha, rostral portion of ventral wing in relation to rostral limit of vertical wall: (a) does not protrude, (b) protrudes moderately, (c) protrudes markedly.
11. Ossified nasal roof: (a) fused caudally with nasale, (b) separated caudally from nasale.
12. Nasal part of prepalatal upper jaw, rostral concha, rostral portion of vertical wall: (a) not flared laterally, (b) moderately flared, (c) strongly flared.
13. Nasal operculum, status and development of tubercles or ridges internally, caudal to external nasal opening: (a) absent, (b) weakly developed, (c) well developed.
14. Nasal part of prepalatal upper jaw, vestibular potion of nasal roof, status and dimensions of ossification: (a) ossification absent, (b) ossification present, length equal to or less than width, (c) ossification present, length greater than but less than twice width, (d) ossification present, at least twice width.
15. Nasal part of upper jaw, rostral concha, status of laterally curved ridge and groove on rostroventral surface of lateral wing: (a) absent, (b) present.
16. Nasal part of upper jaw, status and development of nasal crest, (a) complete, (b) lacking medially, (c) absent or indistinct.
17. Nasal part of upper jaw, rostral limit of ossified nasal roof in relation to rostral limit of rostral concha: (a) equal to, (b) moderately less than, (c) markedly less than.
18. Palatum, lateral part of palatinum, location: (a) on ventral choanal lamella, (b) between ventral choanal lamella and rostral bar, (c) on rostral bar.
19. Palatum, anterior profile of vomeral body in ventral view: (a) rounded, (b) angled, (c) spiked.
20. Palatum, vomeral body length in relation to width: (a) shorter than, (b) equal to, (c) longer than.
21. Palatum, status and length of vomeral spine in relation to length of rostral bar of palatinum: (a) spine absent, (b) longer than, (c) equal to, (d) shorter than.
22. Palatum, palatinum, shape of dorsomedial margin and its relation to pterygoid process of vomer: (a) curved, smoothly merging with caudal half of pterygoid process, (b) curved, meeting caudal third of pterygoid process at obtuse angle, (c) straight, meeting caudal end of pterygoid process at acute angle.
23. Palatum, pterygoideum, status of intrapterygoid articulation: (a) present, (b) absent.
24. Palatum, pterygoideum, breadth of shaft in ventral view: (a) narrow throughout, (b) broader caudally, (c) broad throughout.

25. Jugal arch, shape of rostral portion in ventral view: (a) gradually widened, (b) abruptly and moderately widened, (c) abruptly and markedly widened.
26. Palatum, palatal process of maxillare, relation to rostral bar of palatinum: (a) fused and undifferentiated, (b) fused as dorsal and/or medial ridge, without caudomedial extension, (c) fused as dorsal and/or medial ridge, with caudomedial extension.
27. Cranium, status of ossification of caudal wall of hypophysial recess: (a) absent or incomplete, (b) complete bridge.
28. Cranium, supraoccipitale, dorsal margin of occipital condyle: (a) not thickened, (b) slightly thickened, (c) prominently thickened.
29. Cranium, frontale, conformation of supraorbital rim in dorsal view: (a) angled, rounded, or notched, (b) straight and approximately parallel to sagittal plane of cranium.
30. Cranium, ectethmoidale, conformation of caudal margin in dorsal view: (a) moderately angled to sagittal plane of cranium, (b) nearly perpendicular to sagittal plane of cranium.
31. Cranium, surface of parasphenoidal rostrum between pterygoid processes of vomer in ventral view: (a) flat to rounded, (b) with median ridge.
32. Cranium, mesethmoidale, orientation of rostroventral margin in relation to ventral contour of parasphenoidal rostrum in lateral view: (a) markedly angled (~ 45°) to, (b) moderately angled (10–40°) to, (c) approximately collinear with.
33. Cranium, degree of lateral inflation of skull base, parasphenoidal rostrum, and interorbital septum: (a) none or slight, (b) moderate, (c) great.
34. Cranium, status of fonticulus in frontale: (a) absent, (b) present.
35. Cranium, caudal profile of cerebellar prominence in lateral view: (a) evenly curved, (b) truncate.
36. Cranium, parasphenoidal rostrum, conformation between pterygoid processes of vomer in ventral view: (a) broad, (b) slightly narrowed on midportion, (c) markedly narrowed in midportion.
37. Cranium, ectethmoidale, rostral profile in lateral view, status and extent of protrusion ventral to nasolacrimal sulcus: (a) absent or slight, (b) moderate, (c) marked.
38. Cranium, ectethmoidale, portion of rostral surface lateral to olfactory chamber: (a) abruptly convex, (b) approximately flat, (c) concave.
39. Cranium, extent of temporal fossa in relation to cerebellar prominence in caudal view: (a) distinctly lateral to, (b) near or with slight encroachment, (c) considerable encroachment (approaching midsagittal plane of cranium), (d) reaching midsagittal plane, forming nuchal crest.
40. Cranium, foramen of occipital ramus of ophthalmic artery: (a) single, (b) double and closely spaced, (c) double and moderately spaced, (d) double and widely spaced.
41. Cranium, caudolateral wall of foramen for maxillomandibular nerve: (a) unossified, (b) slightly ossified, (c) fully ossified.
42. Cranium, medial orbitonasal foramen: (a) double, (b) single.
43. Cranium, status and number of pneumatic foramena on otic pillar: (a) none, (b) few, (c) many.
44. Thoracic vertebrae, number rostral to synsacrum: (a) four (rarely five), (b) three (rarely two).
45. Cervical rib processes, length in relation to depth of vertebral body: (a) greater than, (b) equal or less than.
46. Sternum, extent of lateral separation between coracoidal facets: (a) none, (b) slight, (c) moderate, (d) great.
47. Sternum, costal margin, modal number of sternocostal articular processes on each side (reflecting number of attached thoracic ribs): (a) four (or three), (b) five, (c) six (or seven).
48. Sternum, shape of carinal apex in lateral view: (a) short and rounded, (b) sharply pointed, (c) dorsally convex and angled, (d) long and broadly rounded.
49. Humerus, status and extent of roof over recess of ventral process: (a) present and broad, (b) present and narrow, (c) absent.
50. Humerus, status of pneumatic foramena near distal end of shaft: (a) absent, (b) present.
51. Humerus, status of pneumatic foramen (a) immediately distal to capital tubercle: (a) present, (b) absent.

52. Humerus, status of pneumatic foramen caudally on base of deltopectoral crest: (a) absent, (b) present.
53. Humerus, status and proximity of the tubercle of m. flexor digitorum profundus to the pronator tubercle: (a) present and strongly distal to, (b) present and moderately distal to, (c) closely spaced or not distinguishable.
54. Humerus, position of process of extensor metacarpi radialis muscle in relation to midpoint of long axis of humeral shaft: (a) proximal to, (b) even with or distal to.
55. Humerus, position of angle of tensor propatagialis brevis muscle in relation to midpoint of humeral shaft between process of extensor metacarpi radialis muscle and the dorsal condyle: (a) distal to, (b) even with, (c) proximal to.
56. Humerus, cranioproximal surface of head: (a) not corrugated, (b) corrugated.
57. Humerus, status and shape of notch on tip of ventral process: (a) absent, (b) present and symmetrical, (c) present and asymmetrical.
58. Hindlimb, status of fusion of phalanges 2 and 3 of digit IV: (a) absent, (b) present.
59. Nasal region, position of caudal limit of bony nasal opening in relation to craniofacial hinge: (a) rostral to, (b) reaches or transects craniofacial hinge.
60. Nasal part of upper jaw, rostral concha, degree of ossification: (a) unossified, (b) ossified.

Frequency Matrix of Character States

The frequency matrix is available online at dx.doi.org/10.1525/om.2013.77.1.1. For identification of species acronyms see Appendix 1.

Appendix 3

Tensor Propatagialis Brevis Muscle

Muscles.—M. tensor propatagialis, pars brevis (TPB), displays considerable variation within hummingbirds (Zusi and Bentz 1982). It originates from the head of the coracoid as a broad, strap-like belly that terminates on the belly of m. extensor metacarpi radialis. From this attachment it sends a tendon distally in association with m. extensor metacarpi radialis that fuses with the tendon of insertion of that muscle. This tendon varies from a poorly defined, aponeurotic sheet (Type I), to a well-defined broad sheet (Type II), to a well-defined, narrow tendon (Type III). The distal tendon has not been reported in other avian families. Taxonomic distribution of the three types corresponds exactly to the Hermits (I), Topazes and Mangoes (II), and Neotrochilines (III) (Beiweiss 2002, McGuire et al. 2007). However, I found a weak development of the Type II tendon in one specimen of *Eutoxeres aquila* (USNM 510579).

In addition, TPB sends a tendon in the opposite direction that inserts on the humeral tubercle of m. tensor propatagialis, pars brevis. The humeral tendon crosses the aponeurosis of origin of m. extensor metacarpi radialis on its way to insertion on the TPB angle. Where this tendon emerges from the belly it may be free of the aponeurosis of origin of EMR, bound to it, or fused with it. The humeral tendons of a few genera were said by Zusi and Bentz (1984) to be fused completely with that of EMR and to attach on the EMR process (Type IV). However, additional dissections have revealed that in those genera the humeral tendon is absent or vestigial. Vestigial tendons attach on the humerus distal to the EMR process or lose definition without making attachment. The TPB angle is correspondingly poorly defined or absent.

Species examined during the present study, but not included in Zusi and Bentz (1982), are listed below, with genera not previously listed shown in bold.

Type I. (Hermits)—*Eutoxeres aquila, Phaethornis griseogularis, P. guy, P. superciliosus.*

Type II. (Mangoes)—***Heliactin*** *bilophus, Heliothryx auritus, Polytmus theresiae, Anthracthorax viridigula,* ***Schistes*** *geoffroyi.*

Type III. (Brilliants)—*Eriocnemis cupreoventris, E. alinae, Coeligena iris, C. lutetiae,* ***Boissonneaua*** *flavescens, B. matthewsii,* ***Urosticte*** *benjamini,* ***Urochroa*** *bougueri, Heliodoxa schreibersii, H. aurescens, H. rubinoides, H. leadbeateri.*

(Coquettes)—*Heliangelus exortis, Sephanoides sephanoides, S. fernandensis,* ***Discosura*** *conversii, D. longicaudus, Lophornis gouldii,* ***Phlogophilus*** *hemileucurus,* ***Adelomyia*** *melanogenys,* ***Polyonymus*** *caroli,* ***Oreotrochilus*** *estella,* ***Loddigesia*** *mirabilis,* ***Ramphomicron*** *microrhynchum,* ***Chalcostigma*** *ruficeps, C. olivaceum, C. stanleyi,* ***Oxypogon*** *guerinii,* ***Oreonympha*** *nobilis, Metallura williami, M. theresiae.*

(Mountain Gems)—*Heliomaster constantii, Lampornis clemenciae, L. amethystinus,* ***Lamprolaima*** *rhami.*

(Bees)—***Rhodopis*** *vesper,* ***Thaumastura*** *cora,* ***Doricha*** *eliza,* ***Myrmia*** *micrura, Mellisuga helenae, Archilochus colubris,* ***Atthis*** *heloisa.*

(Emeralds)—*Chlorostilbon canivetti, C. mellisugus, C. ricordii,* ***Klais*** *guimeti,* ***Abeillia*** *abeillei,* ***Basilinna*** *leucotis, B. xantusii,* ***Chlorestes*** *notata, Campylopterus curvipennis, C. largipennis, C. rufus, C. hyperythrus, C. hemileucurus, C. falcatus, C. villaviscensio,* ***Eupetomena*** *macroura,* ***Eupherusa*** *eximia, Elvira chionura,* ***Taphrospilus*** *hypostictus, Leucippus baeri, L. taczanowskii, L. chlorocercus, Amazilia chionogaster, A. yucatanensis, A. candida, A. tobaci, Hylocharis eliciae, H. cyanus, H. grayi.*

Type IV. (Bees)— *Calliphlox mitchellii,* ***Microstilbon*** *burmeisteri,* ***Tilmatura*** *dupontii.*

Type IV is actually an apomorphic modification of Type III. All of its species also possess plumage features (white flank patches) not found in other Bees. Consequently, they are listed consecutively (*Calliphlox mitchellii* through *Tilmatura dupontii*) in Appendix 1. If this hypothetical clade were substantiated, *Calothorax* would be polyphyletic.