

The osteology and phylogeny of the Hawaiian finch radiation (Fringillidae: Drepanidini), including extinct taxa

HELEN F. JAMES*

Division of Birds, National Museum of Natural History, Washington, DC 20013–7012, USA, and Edward Grey Institute of Field Ornithology, South Parks Road, Oxford OX1 3PS, UK

Received February 2003; accepted for publication December 2003

The monophyly and phylogeny of the adaptive radiation of Hawaiian finches (Fringillidae: Drepanidini; honeycreepers, auct.) were studied using parsimony analysis of comparative osteology, combined with Templeton (Wilcoxon signed-ranks) tests of alternative phylogenetic hypotheses. Eighty-four osteological characters were scored in 59 terminal taxa of drepanidines, including 24 fossil forms, and in 30 outgroup species. The optimal phylogenetic trees show considerable agreement, and some conflict, with independently derived ideas about drepanidine evolution. The monophyly of a large Hawaiian radiation was upheld, although one fossil taxon from Maui fell outside the drepanidine clade. The finch-billed species were placed as basal drepanidine taxa, and continental cardueline finches (Carduelini) were identified as the radiation's closest outgroups. The study found anatomical as well as phylogenetic evidence that the radiation had a finch-billed ancestor. The optimal trees identify the red-and-black plumage group as a clade, and suggest that the tubular tongue evolved only once in the radiation. Because comparative osteology provides too few characters to strongly support all the nodes of the tree, it was helpful to evaluate statistical support for alternative hypotheses about drepanidine relationships using the Templeton test. Among the alternatives that received significant statistical support are a relationship of the drepanidines with cardueline finches rather than with the Neotropical honeycreepers (Thraupini), classification of the controversial genera *Paroreomyza* and *Melamprosops* as drepanidines, and a secondary loss of the tubular tongue in *Loxops mana*. The hypothesis of monophyly for all the Hawaiian taxa in the study was not rejected statistically. The study provides a framework for incorporating morphological and palaeontological information in evolutionary studies of the Drepanidini. © 2004 The Linnean Society of London, *Zoological Journal of the Linnean Society*, 2004, 141, 207–255.

ADDITIONAL KEYWORDS: adaptive radiation – comparative anatomy – evolution – fossils – Hawaiian honeycreepers – island biogeography – morphology – palaeontology – Passeriformes.

INTRODUCTION

The Hawaiian finches or honeycreepers (Passeriformes: Fringillidae: Drepanidini) are a classic example of adaptive radiation in insular vertebrates. The most striking aspect of diversification in this tribe of nine-primaried oscine songbirds is in the bill shape and method of feeding. The tribe includes species with bills that resemble such disparate continental taxa as grosbeaks, bullfinches, hawfinches, cowbirds, mead-

owlarks, woodcreepers, parrots, warblers and honeycreepers. Drepanidines such as the akipolaau, *Hemignathus wilsoni*, and Lanai hookbill, *Dysmorodrepanis munroi*, have bill morphologies that are unique among birds. The group is also diverse in plumage, song, tongue structure, and other attributes (see, for example, Perkins, 1903; Amadon, 1950; Richards & Bock, 1973).

Compared with most tribes of passerine birds, the drepanidines have an excellent fossil record. Four genera and 15 species have been described from fossils (James & Olson, 1991, 2003), raising the documented diversity of the radiation to 20 genera and 51 species (these figures varying slightly according to the classi-

*Correspondence address: Bird Division, NHB MRC-116, Smithsonian Institution, PO Box 37012, Washington, DC 20013-7012, USA. E-mail: james.helen@nsmnh.si.edu

fiction used; James & Olson, 1991: 80, followed here). Fossil collections also include specimens of five or more species that remain undescribed (James & Olson, 1991; H. F. James, pers. observ.). The drepanidine fossil record is Quaternary in age, the great majority of fossils coming from Holocene (<10 000 years old) deposits in lava caves, eolian dunes and karstic cavities. These fossils represent birds that became extinct in recent millennia, and would probably still be part of the living avifauna were it not for prehistoric human settlement of the islands and the attendant extinctions. Following upon these prehistoric extinctions, 11 or more species of drepanidines have become extinct in historic times.

The drepanidines have long attracted the attention of evolutionary biologists. Patterns in their comparative morphology and geographical distributions were used to illustrate the allopatric model of speciation (Amadon, 1950), the superspecies concept (Amadon, 1950), character displacement (Bock, 1970; Schluter, 1988), dynamic equilibrium theory in biogeography (Juvik & Austring, 1979), and the processes underlying macroevolutionary change (Amadon, 1950; Bock, 1970, 1979). Molecular genetic data were used to correlate drepanidine genetic diversity and phylogenetic history with the historical geology of the archipelago (e.g. Tarr & Fleischer, 1993; Fleischer, McIntosh & Tarr, 1998; Lovette, Bermingham & Ricklefs, 2002). The inferences made in these types of studies depend on accurate information about diversity and biogeography, yet evolutionary analyses of the drepanidines remain largely innocent of the wealth of new information provided by fossils.

Before the fossils can be effectively integrated in evolutionary studies, a phylogenetic hypothesis is needed that encompasses all the taxa, living and extinct. Beyond a mere hypothesis of relationships, a taxonomically inclusive osteological database would be useful for comparative studies of morphological and genetic data. Accordingly, I undertook a phylogenetic analysis of drepanidine osteology with the objectives of: (1) examining whether osteological characters will identify the Drepanidini as a monophyletic group, including the fossil taxa; (2) developing a phylogenetic hypothesis for the entire radiation; and (3) providing a database on the osteology of drepanidines for use in further phylogenetic, biogeographical, and comparative studies.

The fossils examined are from Holocene sites on Kauai, Oahu, Molokai, Maui and Hawaii (Fig. 1). The Pleistocene locality at Ulupau Head on Oahu has also produced drepanidine fossils (James, 1987), but these have not yet been thoroughly studied and are not included here. By nondestructively removing skulls and partial skeletons from old museum skin specimens (Olson *et al.*, 1987), it was possible to include the

taxa that became extinct in historic times, even though no skeletal specimens were originally preserved for some of them (e.g. *Chloridops*, *Rhodacanthis*, *Ciridops*). Thus, the taxa included here represent the radiation as it would exist today, were it not for the elevated extinction rates of the human era (excepting undiscovered fossil taxa, of course).

HISTORY OF DREPANIDINE SYSTEMATICS

Unlike the case of the relatively uniform Galapagos finches, the Hawaiian finches were not widely recognized as a related group of species until about a century after their discovery. The first specimens that came to Europe with returning voyages in the late 18th century were described as members of the familiar continental genera that they superficially resemble (*Certhia*, *Loxia*, *Fringilla*). In the 19th century, as awareness of island endemism grew, most Hawaiian passerines were assigned to endemic Hawaiian genera (see Olson & James, 1991: 8–10). Yet the idea that all the disparate drepanidine morphologies belong to a single adaptive radiation was not generally accepted until the astute field naturalist R. C. L. Perkins published his arguments in 1901 and 1903, richly supported with field observations from his several years of collecting natural history specimens in the islands.

Comparative anatomical study of the drepanidines was begun by Gadow (1899), who described the pterylosis, bill serrations, nostril shape, nasal operculum, corneous tongue, bony palate and gross morphology of the alimentary tract in ten species, although at the time he failed to recognize all of them as members of a single group. He placed two finch-like species, *Loxioides bailleui* and *Psittirostra psittacea*, in the Fringillidae, while giving the eight thin-billed species in his study group the rank of a family, Drepanididae. All but one of these eight possess a tubular tongue, so Gadow sought the closest relatives of his Drepanididae among other tubular-tongued birds. Only two other groups of birds possess both the tubular tongue and a vestigial tenth primary, like the drepanidines. Additional characters of the tongue and bill lead Gadow to ally the drepanidines with the Neotropical honeycreepers (the former Coerebidae, now recognized as a polyphyletic assemblage of nectarivorous tanagers, Emberizidae: Thraupini; Beecher, 1951a; Burns, 1997), rather than with the Australasian flowerpeckers (Dicaeidae). In so doing, he not only gave the drepanidines their widely used common name, the Hawaiian honeycreepers, but he also defined the debate over the relationships of the tribe. Once it became generally accepted that the finch-like species are part of the same radiation, the question became: Are the drepanidines derived from finches, or from tubular-tongued nectarivores ('Coerebidae')?

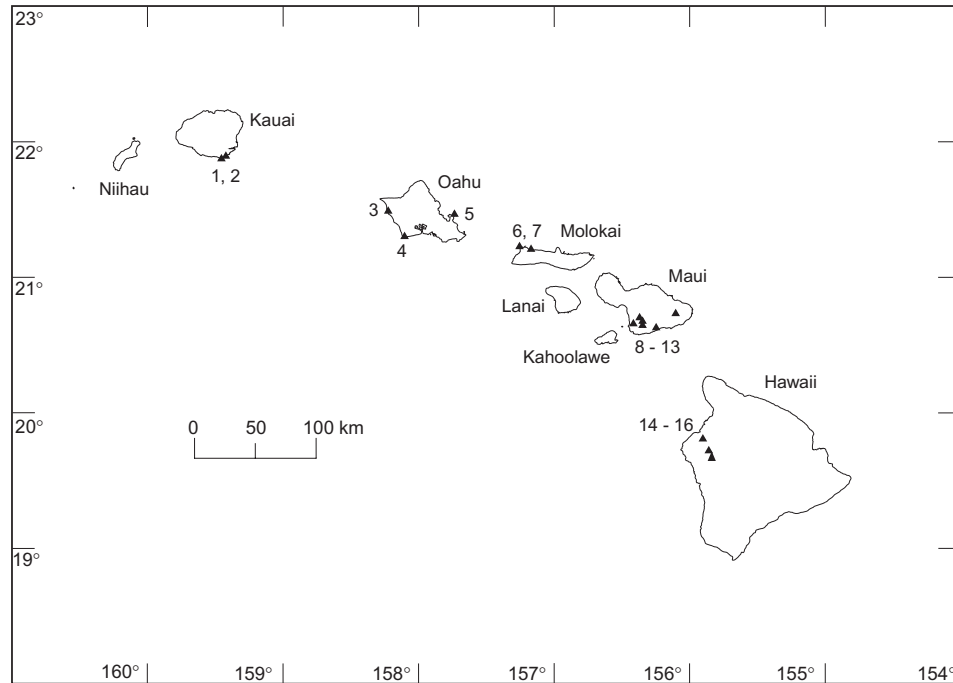


Figure 1. Map of the Hawaiian Islands showing the principal collecting localities for fossil drepanidines. From west to east, the localities are (1) the Makawehi Dunes (Olson & James, 1982; Hearty *et al.*, 2000), (2) Mahaulepu Cave (Burney *et al.*, 2001), (3) sediments of mixed origin exposed near Ohikilolo Point (Storrs Olson, pers. comm.), (4) karstic solution pits and caves on the Ewa Plain near Barber's Point (Olson & James, 1982; Athens *et al.*, 2002), (5) Pleistocene wetland sediments at Ulupau Head (James, 1987), (6) perched dunes at Ilio Point (Olson & James, 1982; Hearty *et al.*, 2000), (7) the Moomomi Dunes (Olson & James, 1982; Hearty *et al.*, 2000), (8) Puu Naio Cave (James *et al.*, 1987), (9) Puu Makua Cave (Olson & James, 1991), (10) Lua Lepo Cave (Olson & James, 1991), (11) Auwahi Cave (Olson & James, 1991), (12) Crystal Cave (Olson & James, 1991), (13) Pukamoa (Medeiros, Loope & James, 1989), (14) Owl Cave (Jon Giffin, pers. comm.), (15) Umii Manu (Giffin, 1993), and (16) Petrel Cave (James & Olson, 2003). Localities (8) to (16) are lava tubes.

Given the tremendous morphological diversity of the drepanidines, identifying their sister group was certain to be controversial. Gadow himself had noted similarities in the bony palate between the thin-billed drepanidines and continental finches such as *Coccothraustes*, *Cardinalis* and *Estrilda*. Sushkin (1924, 1929), who studied the skull and horny palate, was the first to advocate a relationship between the Drepanidini and the Carduelini, a cosmopolitan though mainly Palaearctic group of finches that includes such familiar types as crossbills (*Loxia*), goldfinches (*Carduelis*) and bullfinches (*Pyrrhula*). In 1950, Amadon published an important monograph of the Drepanidini. Drawing strongly upon the work of Perkins and Gadow, he emphasized the taxonomic value of the tubular tongue, and favoured an origin of the Drepanidini from the Neotropical honeycreepers or from similar thraupine stock.

Amadon's influential monograph secured the placement of the Drepanidae following the Coerebidae in systematic lists of the 1950s and 1960s, yet contrary evidence and contrary opinions continued to emerge.

Beecher (1953) noted similarities between the jaw muscles of *Psittirostra cantans* and the cardueline finches, but he attributed them to convergence. Tordoff (1954) and Bock (1960) studied the bony palate and, like Sushkin, favoured a cardueline relationship. Sibley (1970) found the electrophoretic patterns of drepanidine egg white proteins to match those of carduelines more closely than tanagers.

Important anatomical studies of the drepanidines were published in the 1970s. Richards & Bock (1973) described the cranial myology and osteology of the species in Amadon's genus *Loxops* in relation to functional morphology and feeding behaviour. Bock (1972, 1978) described the anatomy of the tongue in *Ciridops anna* and *Melamprosops phaeosoma*. Raikow (1976, 1977a) described the appendicular myology of a selection of drepanidine species, and used this information in combination with characters of the tongue, plumage, nostril, bill form, and odour, in the first cladistic analysis of the group (Raikow, 1977b). The authors of these anatomical papers favoured a cardueline relationship for the drepanidines. Raikow's evidence is

particularly compelling because he made broad comparisons within the nine-primaried oscines (Raikow, 1978). Also, in a paper characterizing the interorbital septum of cardueline finches, Zusi (1978) found that the drepanidines group with the carduelines.

In the 1980s, molecular systematics came to the forefront. Sibley & Ahlquist (1982) used DNA–DNA hybridization to study the outgroup relationships of the Drepanidini, comparing the drepanidine *Himatione sanguinea* (the radiolabelled taxon) with 31 species chosen to survey the oscine passerines. *Himatione* came out closest to the cardueline finches once again. Three subsequent studies of genetic relationships among the nine-primaried oscines also included *Himatione sanguinea* to represent the Drepanidini (Bledsoe, 1988, DNA–DNA hybridization; Groth, 1998, cytochrome *b* sequences; Yuri & Mindell, 2002, cytochrome *b* sequences), and all three confirmed that *Himatione* has an affinity for the cardueline finches. Johnson, Marten & Ralph (1989) examined the allozymic variability and evolutionary relationships of ten species of drepanidines. In a departure from most modern studies, this study found support for an emberizine rather than cardueline relationship for the drepanidines. Fleischer *et al.* (2001) analysed cytochrome *b* sequences from 18 species of drepanidines, and found the drepanidine clade to be genetically closer to the two carduelines in their study than to the emberizines. Pratt's (1979) review of traditional systematic characters, and James & Olson's (1991) monograph describing new fossil species of drepanidines, also favour the cardueline relationship. Thus, a strong consensus has emerged from anatomical, genetic and behavioural data that the Drepanidini are related to cardueline finches.

The monophyly of the radiation was challenged by Pratt (1979, 1992a, 1992b) and Chu (2002). Chu selected one finch-billed drepanidine (*Telespiza cantans*) and three nectarivorous/insectivorous drepanidines (*Loxops virens*, *Himatione sanguinea*, and *Vestiaria coccinea*) to include in his phylogenetic analysis of morphological characters in the cardueline finches. These two very distinct drepanidine morphotypes joined his trees as independent clades. Pratt argued that two extant genera, *Paroreomyza* and *Melamprosops*, might not be members of the radiation, pointing out that these genera lack the musty 'drepanidine odour' that is characteristic of other drepanidines, that their calls and plumage may be atypical (although see Engilis *et al.*, 1996), and that their corneous tongues have a pair of caudal projections that most drepanidines lack. Despite these doubts, more recent genetic and morphological analyses have favoured placing *Melamprosops* and *Paroreomyza* in the Drepanidini (Fleischer *et al.*, 2001; Pratt, 2001).

Similar doubts could be raised about the relationships of the recently named fossil genera *Orthiospiza*, *Xestospiza*, *Vangulifer* and *Aidemedea* (James & Olson, 1991). These taxa were placed in the Drepanidini based on their phenetic resemblance to one or another member of the radiation, but they obviously differ enough to inspire the introduction of new genera. The present study was conceived partly to investigate whether *Paroreomyza*, *Melamprosops* and the four new fossil genera are correctly classified as Drepanidini.

With regard to the relationships of the drepanidines *inter se*, Perkins (1903) introduced several themes that have been influential ever since. He divided the drepanidines into two groups: division one, the 'chlorodrepanine group', and division two, the 'melanodrepanine group'. The melanodrepanine group includes *Ciridops*, *Palmeria*, *Himatione*, *Vestiaria* and *Drepanis*. These are highly nectarivorous birds, distinguished by meliphagid-like songs, red and/or black in the adult plumage, and the lack of sexual plumage dimorphism, among other traits. (The extinct genus *Ciridops* is included in the melanodrepanine group although almost nothing is known about its feeding behaviour, and the possibility of sexual plumage dimorphism cannot be ruled out based on the five preserved skin specimens.) The chlorodrepanine group was characterized by Perkins as having green immature and (usually) adult female plumages, lacking truncate apices of the primaries, and often showing sexual plumage dimorphism, among other traits. Perkins emphasized that his two groups are so distinct from one another that they might represent separate colonizations of the archipelago, although he favoured a single colonization. Amadon (1950) argued for a single colonization, but he assigned subfamilial rank to Perkins' two groups, and both authors represented the melanodrepanine and chlorodrepanine groups as a basal dichotomy in their depictions of drepanidine phylogeny.

The greatest resistance that Perkins faced to his argument for monophyly of the drepanidines was to the notion of a close relationship between the thin-billed species and the finch-billed species. To overcome this, he proposed that *Hemignathus* (= *Heterorhynchus* of Perkins), with its thin, overhanging maxillary rostrum, and *Pseudonestor*, with its thick, overhanging maxillary rostrum, are transitional taxa that bridge the morphological gap. This idea of a complex transition involving evolution and then loss of the overhanging maxillary rostrum was favoured by Amadon (1950) and Bock (1970, 1979). Raikow (1977b) proposed a different phylogeny, in which *Pseudonestor* is a specialized offshoot of the finches, *Hemignathus* is a specialized offshoot of the thin-billed birds, and neither is considered 'transitional'. More recently, Pratt's

(2001) weighted parsimony analysis of traditional morphological characters placed *Pseudonestor* near *Hemignathus* and distant from the finches. Thus, the phylogenetic history of *Pseudonestor* is at once highly contested and pivotal to some of the published hypotheses for the history of morphological change in the radiation.

A comprehensive species-level phylogeny of the drepanidines based on molecular genetic data is not yet available. The molecular genetic studies that have been published employed allozymes (Johnson *et al.*, 1989), restriction fragments of mitochondrial DNA (Tarr & Fleischer, 1993, 1995) and nucleotide sequences of the cytochrome *b* gene (Feldman, 1994; Freed, 1999). Each of these studies encompasses fewer than a dozen drepanidine species. By extracting ancient DNA from museum study skins, Fleischer *et al.* (2001) expanded the taxon sample for cytochrome *b* gene sequences to 18 species, but they found disappointingly low bootstrap support for most nodes of the phylogeny, a common problem in phylogenetic studies of the drepanidines.

Many of the extant drepanidines share a specialized tubular tongue, useful for taking up nectar. The tube is formed out of the sides of the corneous tongue, which rise up and overlap at the midline. The drepanidines that lack tubular tongues include the finch-like species and a diverse group that feeds on such items as arthropods, snails and fruit (*Telespiza*, *Loxioides*, *Chloridops*, *Rhodacanthis*, *Pseudonestor*, *Psittirostra*, *Melamprosops*). Five thin-billed insectivorous species (*Oreomystis bairdi*, *Paroreomyza montana*, *P. maculata*, *P. flammea* and *Loxops mana*) also lack tubular tongues. In these five species, the corneous tongue is long, relatively flat, and dissected at the tip, thus resembling the tongues of many other insectivorous passerines (Gardner, 1925). The systematic relationships of these species have long been controversial (compare Amadon, 1950; Pratt, 1979, 1992b, 2001; Olson & James, 1982; Conant, Pratt & Shallenberger, 1998; Fleischer *et al.*, 1998). Intriguingly, most molecular genetic studies place one or two of these five as basal taxa in the radiation (*Oreomystis bairdi* and *Paroreomyza montana*; Johnson *et al.*, 1989; Feldman, 1994; Tarr & Fleischer, 1995; Fleischer *et al.*, 1998), suggesting either that the ancestor of the radiation was a thin-billed insectivore, or if it was a finch-billed species, that adaptation to insectivory occurred very early in the radiation and probably more than once.

METHODS

CHARACTER SCORING

Osteological characters with clearly discrete states or with strongly bimodal or multimodal distributions

were sought and scored, in most cases by visual comparison of the bones under a binocular dissecting microscope. The characters were chosen to emphasize finer points of osteology, rather than general attributes like 'finch-like bill' or 'sickle-shaped bill.' Character states that appear to divide the taxa into functional groups were favoured. For example, straight vs. arched dorsal maxilla was accepted as a character whereas moderately arched vs. strongly arched dorsal maxilla was not.

If a few species were found to have intermediate conditions between two otherwise distinct states, an additional 'intermediate' state was created rather than rejecting the character. The weight assigned to characters with intermediate states in the phylogenetic analyses was adjusted to avoid giving intermediate conditions undue influence during tree-building (see Methods/Phylogenetic analyses). For some characters it was difficult to score all the diverse outgroup species in the study, usually because some of the outgroup species were distinctive enough in their morphology to create doubt about character homology. In such cases, the score was recorded as missing for the outgroup taxa in question.

When highly repeatable scores could not be produced through visual comparisons, an attempt was made to develop an osteometric standard for scoring. An appropriate measure or index (either a logarithmic ratio of two dimensions, an angle, or a measurement of curvature) was taken, and its distribution examined graphically to identify an appropriate gap or valley for separating the states. Distributions of morphometric traits typically reveal outliers (for example, see character 5), but these were not assigned separate character states. Instead, the original, functional definition of character states was maintained (such as straight vs. arched; rather than straight, moderately arched, strongly arched, and so on).

In composing the character list, autapomorphies were not emphasized because they are uninformative in cladistic analysis, although some striking autapomorphies were included in order to canvass the breadth of osteological variation in the drepanidines. Characters were not rejected based on the investigator's perception that the character exhibited too much homoplasy, a practice that can prejudice the results in favour of a priori ideas about relationships. The most common reason for rejecting characters was my failure to achieve high repeatability in scoring. Every effort was made to describe and, where helpful, illustrate the method of scoring. However, for some characters it would not be possible to repeat the scoring without re-examining a series of comparative specimens.

Characters that express intraspecific polymorphism were rejected unless the polymorphism was found in a

small number of taxa, or mainly in the outgroups. Despite this discrimination, approximately 1/3 of the characters do express intraspecific polymorphism. Two options for coding and analysing the polymorphic characters were tried (for a discussion of the options available, see Wiens, 1999, 2000). First, I assigned the polymorphic taxa a separate, intermediate state between the two fixed states, making the assumption that the evolutionary transition from one fixed state to another involves a polymorphic stage (Mabee & Humphries, 1993). This is similar to the assumption I applied to characters with intermediate conditions, and again, characters with polymorphic states were appropriately down-weighted in phylogenetic analyses (see Methods/Phylogenetic analyses). Secondly, I allowed PAUP* to assign either of the two fixed states to the polymorphic taxon, depending on the most parsimonious resolution of the other data in the matrix. Exploratory heuristic searches using matrix B (see Results) found no conflict in the relationships supported by the two options, but the number of equally parsimonious trees was higher using the first option. The second option was chosen for subsequent analyses because, for these data, it provides better resolution of relationships.

TAXON SAMPLING

Characters were scored in all species of drepanidines recognized as valid by James & Olson (1991: 80), excepting *Akialoa ellisiana* and *Akialoa lanaiensis*, for which skeletons are not available, and *Paroreomyza maculata*, which closely resembles *Paroreomyza montana* in osteology. In order to evaluate their systematic relationships, characters were also scored in nine fossil taxa that have not been formally described and named (e.g. those mentioned by James & Olson, 1991; Burney *et al.*, 2001). Some of these are clearly diagnosable as new species (e.g. *Loxioides* sp., Hawaii; Maha'ulepu finch; and *Chloridops* sp., Maui), while others represent new island populations that may be referable to existing species upon further evaluation (e.g. *Rhodacanthis* aff. *flaviceps*, *Rhodacanthis* aff. *palmeri*, *Akialoa* cf. *lanaiensis* and *Akialoa* aff. *upu-pirostris*). Such taxonomic decisions are deferred to future publications.

In order to thoroughly examine whether the Drepanidini can be recognized as a monophyletic group with respect to the Carduelini, 20 species of cardueline finches were included as outgroups, representing 14 of the 19 genera in the tribe. Nine additional outgroup species were chosen to canvass the Emberizinae and Fringillini. Some of these were chosen to be the same as those used by Bledsoe (1988), to facilitate comparisons of different types of data. *Passer domesticus* was included as an outgroup to the nine-primaried oscines.

A list of specimens examined is given in Appendix 1. Binomials for the Drepanidini follow James & Olson (1991), except that the genus *Akialoa* is used for the akialoas, as suggested by Olson & James (1995), and the Oahu amakihi is recognized as a full species (*Loxops flavus*), as suggested by Tarr & Fleischer (1995). Binomials for outgroup taxa and the names for suprageneric taxa follow Sibley & Monroe (1990). Informal names and brief descriptions are given for fossils that have not been formally described and assigned Latin binomials.

ANATOMICAL TERMINOLOGY

Many of the features of cranial osteology mentioned in the text are identified in Figures 2 and 3. The hyoid osteology is illustrated by Bock (1972, 1978) and Richards & Bock (1973). Anatomical terminology is taken primarily from the chapter on osteology in the *Handbook of Avian Anatomy* (Baumel & Witmer, 1993), with most terms translated into English vernacular as suggested by King (1993). The term *fonticuli interorbitales* was translated as *interorbital fenestrae*, following Zusi (1978). I also follow previous authorities on drepanidine osteology (Gadow, 1899; Richards & Bock, 1973) in using the term *transpalatine process* rather than referring to the caudal process of the palatine as the *angulus caudolateralis*. The term *palatine process of the premaxilla* is taken from Bock (1960); it is unclear whether the *os premaxillare*, *proc. palatinus* in the handbook is a synonym.

Baumel & Witmer (1993) do not name the ridges, troughs and sulci on the ventral surface of the maxilla. James & Olson (1991, fig. 9) referred to these features with informal English names, but here I offer the following new terms for them, composed to be consistent with the terminology of the handbook:

Cristae ventralis maxillaris – a pair of ridges or crests, orientated anteroposteriorly, on the ventral face of the maxilla. See ventral crest, Figure 3.

Sulcus lateralis maxillaris – sulcus or depression between the Crista tomialis and the Crista ventralis of the maxilla. See lateral sulcus, Figure 3.

Fossa medianus maxillaris – fossa or depression occupying the medial space between the two Cristae ventralis maxillaris. See median fossa, Figure 3.

Sulcus neurovascularis medianus – a narrow sulcus or furrow extending sagittally from the posterior to the anterior end of the ventral surface of the maxilla. See median neurovascular sulcus, Figure 2.

PHYLOGENETIC ANALYSES

Phylogenetic analyses were performed with PAUP* software (Version 4.0B10; Swofford, 2002) using the parsimony criterion. Heuristic searches were repli-

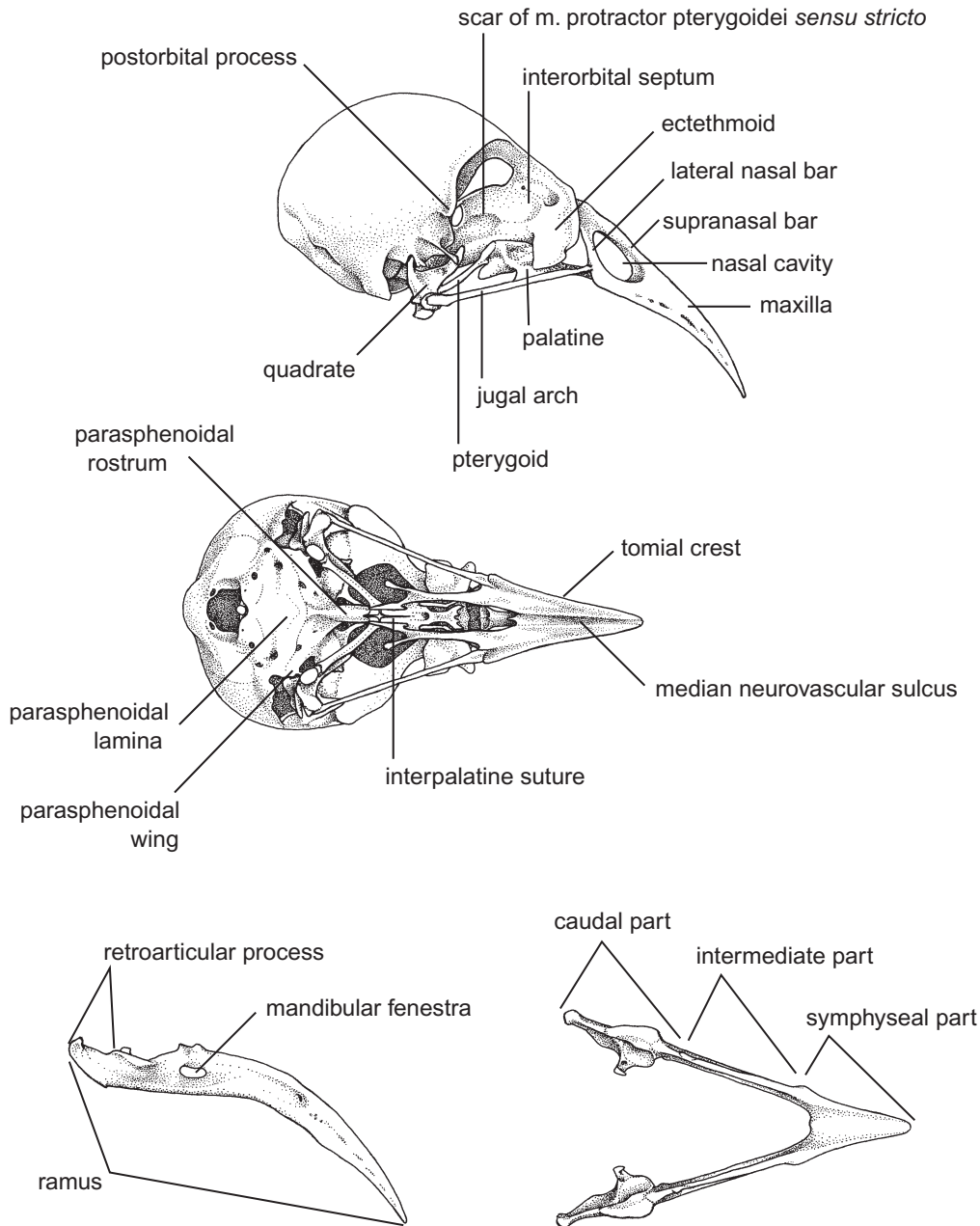


Figure 2. Osteological terminology illustrated on the skull and mandible of *Loxops stejnegeri* (USNM 502195).

cated 100 times, with initial trees constructed by random addition of taxa (with ten trees held at each step), and improved upon with tree-bisection-reconnection branch swapping (with the retention index set to eight). Multistate characters with sequential states (e.g. small, medium, large) were run as ordered in the PAUP* analyses. All other characters were unordered. Most characters were treated as unweighted, so that a transformation from one state to another (or for ordered characters, from one state to the next in the sequence) cost one step in tree

length. An exception was made for characters that were originally defined with binary states, but that proved to be hard to score as binary characters because a few intermediate conditions were encountered. These were scored with three states (see Methods/Character scoring), and were run as ordered characters with a weight of 0.5 in the heuristic searches. In this way, characters with intermediate states were accorded no greater potential influence on tree length than a binary character without intermediates would have.

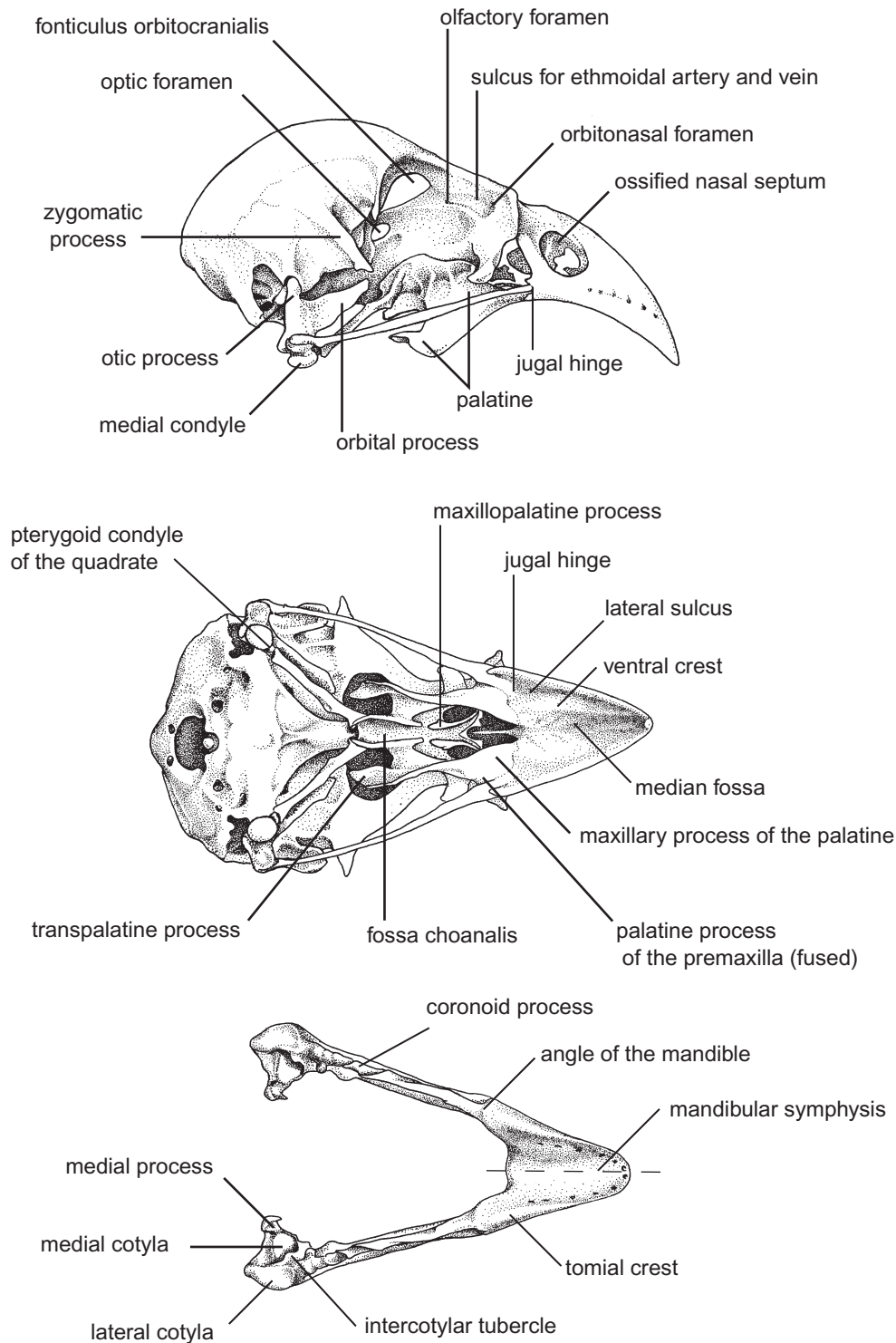


Figure 3. Osteological terminology illustrated on the skull and mandible of *Telespiza cantans* (USNM 502223).

Character matrices that have a large number of taxa, a proportionately small number of informative characters, and a great deal of missing data, generally produce poorly resolved trees with weak character

support for the nodes (Novacek, 1992; Chu, 1995; Wilkinson, 1995). Heuristic searches of such matrices can be inefficient because of the large number of equally parsimonious trees. Anticipating these prob-

lems, the more fragmentary fossils were excluded from the analyses addressing outgroup relationships of the drepanidines, and conversely most of the outgroups were excluded from analyses addressing the phylogenetic position of fragmentary fossils.

In the analyses that address monophyly of the Drepanidini, *Passer domesticus* was included as an outgroup for rooting the trees. In the analyses that address relationships within the drepanidine clade, *Carpodacus purpureus* and *Pinicola enucleator* were included as outgroups for rooting the trees. However, throughout the text, the term outgroup is used to refer to all the nondrepanidine taxa in the study, and the term ingroup is used to refer to the drepanidine taxa.

Character support for nodes of the trees was evaluated with Bremer support indices (Bremer, 1994) and with 500 bootstrap replications. Bootstrap and Bremer support were determined using ten replications of random addition sequences, with ten trees held at each step, and tree-bisection-reconnection branch swapping. AUTODECAY 4.0 (Eriksson, 1998) was helpful in calculating Bremer support, and McClade 3.0 (Maddison & Maddison, 1992) was helpful for viewing character state optimizations.

EVALUATING ALTERNATIVE HYPOTHESES

The literature on the drepanidines is rich with hypotheses about their systematic relationships, some of which conflict with the optimal trees supported by the osteological data. The Wilcoxon signed-ranks test (Wilcoxon & Wilcox, 1964), first applied to phylogenetic contrasts by Templeton (1983) and therefore commonly called the Templeton test in this context, was used to evaluate the strength of character conflict with important a priori alternative hypotheses. A one-tailed test was applied because one of the two trees in each comparison was the optimal tree for the data (Templeton, 1983). The more powerful Kishino-Hasegawa test, based on parametric statistics, is inappropriate in this situation (Goldman, Anderson & Rodrigo, 2000).

For the statistical tests, heuristic searches with topological constraints were used to find trees consistent with each alternative hypothesis (Swofford, 2002). A single binary tree was needed for the statistical comparison, however, both the constrained and unconstrained searches often found more than one optimal tree. In these cases, a binary tree was selected that had the minimum symmetric difference (available in PAUP*) from the unconstrained majority rule tree, to ensure that the trees used in statistical comparisons were close to each other and to the optimal trees for the data in their topology.

DESCRIPTIVE OSTEOLOGY

FACIAL SKELETON

1. *Maxillary rostrum much longer than mandibular rostrum; absent (0), intermediate (1), present (2)*. Ordered, weight = 0.5. In many types of birds, the tip of the maxillary rostrum extends slightly beyond the mandibular rostrum when the jaws are closed. The maxillary rostrum greatly overextends the mandibular rostrum in many raptors, parrots and seabirds, but in passerine birds this condition is extremely rare, occurring only in certain species of drepanidines. Character state (1) was assigned to two heavy-billed species, *Pseudonestor xanthophrys* and *Dysmorodrepanis munroi*, and three thin-billed species, *Hemignathus wilsoni*, *H. lucidus* and *H. vorpalis*, a recently described fossil species from the island of Hawaii (James & Olson, 2003). An intermediate character state was assigned to *Psittirostra psittacea*.

The genus *Akialoa* was assigned character state (0), although arguably state one could have been assigned because the mandibular rostrum in these long-billed species is usually noticeably shorter than the maxillary rostrum (Amadon, 1950). This was not done because elongation of the maxillary rostrum in *akialoas* mainly affects the rhamphotheca and not the bone, so it could not be scored in fossils.

2. *Diastema between the maxillary and mandibular rostra, with the jaws in closed position; absent (0), present (1)*. The drepanidine species *Dysmorodrepanis munroi* has a most unusual bill shape, in which the maxillary rostrum is strongly hooked and the mandibular rostrum is re-curved, leaving a diastema between the jaws when the bill is closed. *Dysmorodrepanis* is known from a single skin specimen from the island of Lanai (Perkins, 1919). James, Zusi & Olson (1989) showed that the bill could have been used in the manner of pincers or ice-tongs, because the bill tips would touch each other if both the maxillary and mandibular rostra were depressed. The bill shape of *Dysmorodrepanis* is not dissimilar to that of a snail kite (*Rostrhamus sociabilis*), discounting the diastema, and James *et al.* (1989) suggest that a diet of Hawaiian land snails may be the source of selection that led to this unusual bill form. The only other birds with a diastema between the closed jaws, to my knowledge, are the open-billed stork, *Anastomus lamelligeris*, and Lafresnaye's vanga, *Xenopirostris xenopirostris*, both of which have long, straight bills, very different from that of *Dysmorodrepanis*.

3. *Bilateral asymmetry of the bill, in which the tips of the maxilla and mandible bend towards opposing sides; absent (0), present (1)*. Included in the present

study are both of the avian species groups that have crossed bill tips: the cardueline crossbills, *Loxia*, and the drepanidine akepas, *Loxops coccineus* and *Loxops caeruleirostris*. Because these groups are classified in the same subfamily, we might expect to find a number of parallelisms in their bill osteology, yet close comparison reveals more differences than similarities. For example, the crossbills have deep bills in which lateral deflection of the bill tips involves the bony rostra as well as the rhamphotheca (state 1), while in the akepas the bill shape is more conical, and lateral deflection of the bill tips involves only the rhamphotheca. Other differences include the presence of long retroarticular processes and of greater asymmetry in the lateral cotylae of the mandible in the akepas.

4. *Foreshortening of the conical bill; absent (0), intermediate (1), present (2)*. Ordered, weight = 0.5. The bullfinches, genus *Pyrrhula* (Carduelini), have distinctive, very short and strongly arched finch-like bills (state 2). Among the drepanidines, similarly foreshortened bills occur in *Loxioides bailleui* and in an undescribed fossil taxon from the island of Kauai ('Maha'ulepu finch'). An undescribed fossil taxon from the island of Hawaii (*Loxioides* sp., Hawaii) has a somewhat foreshortened conical bill, and was assigned the intermediate state.

MAXILLA

5. *Dorsosagittal profile of the premaxilla; moderately to strongly arched (0), straight (1)*. To standardize scoring of this character, the degrees of arc of the premaxilla were measured using a modification of Feduccia's (1993) method for measuring degrees of arc in avian claws. In Figure 4, point a is the midpoint of the supranasal bar; point b is the tip of the premaxilla; line c–d is a perpendicular drawn to bisect chord a–b; and point X is the intersection of line c–d with the dorsal premaxilla. The angle θ between lines a–b and b–X, times two, is a measure of the degrees of arc of the premaxilla. Data on degrees of arc are graphed in Figure 5. Species with values of 13° or less were scored as having straight premaxillae, while those with values of 17° or greater were scored as having curved premaxillae.

By this strict criterion, the drepanidines with straight premaxillae are *Xestospiza fastigialis*, *Aidemia chascax*, *Aidemia lutetiae*, *Loxops coccineus* and *Loxops mana*. Of the outgroup taxa in the study, *Agelaius phoeniceus*, *Mniotilta varia* and *Chlorophanes spiza* have straight premaxillae.

6. *Planar dorsomedial surface; absent (0), slightly developed (1), well developed (2)*. Ordered, weight = 0.5. Some drepanidines with relatively straight bills have

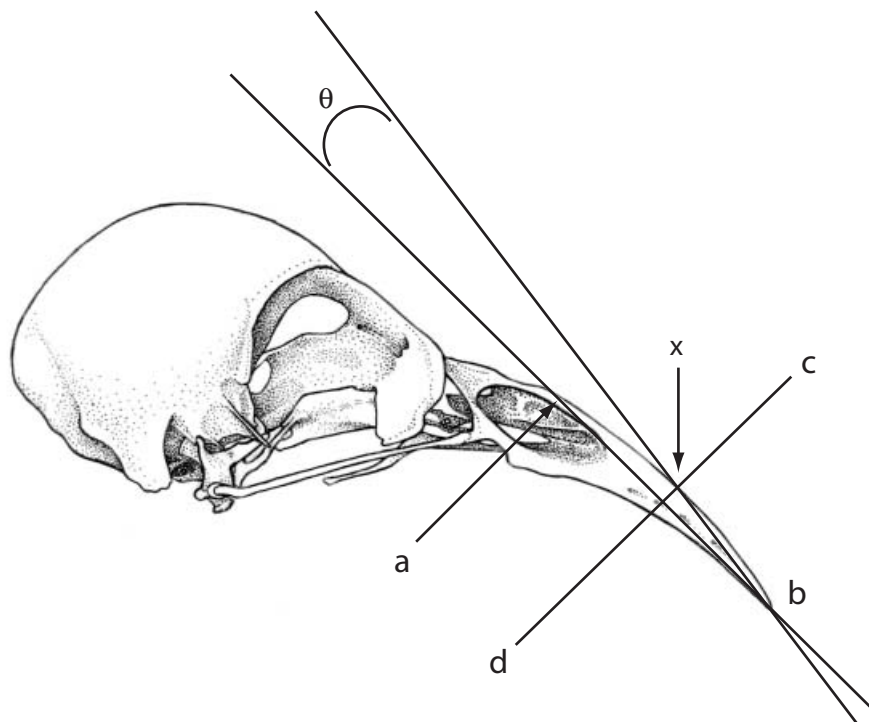


Figure 4. Method of measuring degrees of arc of the premaxilla, illustrated on the skull of *Himatione sanguinea* (MVZ 118858). See character 5.

a flat surface on the dorsal maxilla. The flattened area extends over the anterior part of the supranasal bar and the posterodorsal part of the premaxilla. This trait is quite noticeable in the long-billed gaping species, *Aidemia lutetiae*, and present also in two conical-billed finches, *Xestospiza conica* and *Xestospiza fastigialis*. It is present but less well developed in *Aidemia chascax*, which was scored intermediate. James & Olson (1991) point out that the combination of a relatively straight bill with a flattened dorsal surface is reminiscent of certain icterids. Thus, the bill shape of meadowlarks (*Sturnella*) is a good analogue for the straight-billed species of *Aidemia*, while cowbirds (*Molothrus*) are a good analogue for *Xestospiza*.

7. *Nasals only slightly constricted or not constricted anteriorly (0); greatly constricted anteriorly (1)*. Among the most striking bill shapes in the Drepanidini are those with long, sickle-shaped maxillary rostra, a shape that occurs in both the chlorodrepanine group (in *Hemignathus* and *Akialoa*) and the melanodrepanine group (in *Vestiaria* and *Drepanis*). The shape of the maxillary rostrum in sickle-billed species in the two groups is superficially similar, but there are striking differences in underlying osteology. For example, in *Hemignathus* and *Akialoa*, the maxilla becomes narrow very abruptly in the region of the nasal bones, so that the anterior, decurved part of the bill is quite narrow along its entire length. This appears to be an adaptation for probing in crevices for beetle larvae and other invertebrate food. In the nectar-sipping *Drepanis* and *Vestiaria*, the maxilla tapers more gradually towards the tip. Character state one was scored only in *Hemignathus* and *Akialoa*.

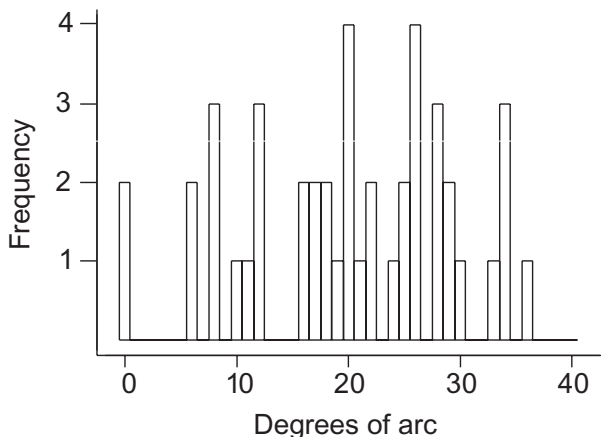


Figure 5. Distribution of measurements of the degrees of arc of the premaxilla. Taxa with greater $>40^\circ$ omitted. See character 5.

8. *Profile of the tomial crest in dorsal or ventral aspect; straight or convex (0), intermediate (1), distinctly concave (2)*. Ordered, weight = 0.5. In most finch-billed birds, the maxilla viewed in dorsal or ventral aspect has a straight or convex lateral contour, while thin-billed birds tend to have concave lateral contours. This division is imperfect, however, because some thin-billed species have a straight lateral contour (e.g. *Aidemia*, *Vangulifer neophasis*.) Holding a straight edge alongside the bone facilitates scoring the character.

9. *Supranasal bar broad anteriorly but becoming narrow before the transverse mid-line of the bar (0), very broad anteriorly and tapering posteriorly to the transverse mid-line of the bar (1), very broad anteriorly and continuing to taper beyond the mid-line of the bar (2)*. Ordered. Slender-billed species and a limited number of the finch-billed species have a strut-like supranasal bar (state 0). Most finch-billed species have a moderately (state 1) or strongly (state 2) tapering supranasal bar. The strongly tapering bar is more frequent in the finch-billed drepanidines (six species) than in the outgroups (two species).

Scoring was facilitated by holding a divider such as a straight pin or needle above the maxilla so as to transversely bisect the supranasal bar. If the portion of the bar just anterior to the mid-line is of about the same width as the portion just posterior to the mid-line, this indicates a strut-like bar and is scored (0). If the bar becomes noticeably wider just anterior to the mid-line but not posterior to it, this indicates a tapering bar and is scored (1). If the bar broadens both anterior and posterior to the midline, a score of two is assigned.

10. *Texture of the lateral edge of the supranasal bar; smooth (0), slightly to distinctly rugose (1)*. The finch-like fossil drepanidine *Xestospiza fastigialis* is distinguished by a pair of rugose ridges that ascend its supranasal bar along the lateral edges (state 1; James & Olson, 1991: 57). Similar rugosities are present in *Agelaius phoeniceus* and *Carduelis carduelis*, which also received state (1). *Passer domesticus* and *Hesperiphona vespertina* have rugosities in at least some individuals, but these are positioned mainly along the anterior margin of the nasal cavity rather than on the supranasal bar, and were considered not to be homologous with character state (1).

11. *Thickness of supranasal bar; comparable with the lateral nasal bar (0), much stouter than the lateral nasal bar (1)*. Some of the finch-billed drepanidines have extremely stout supranasal bars. To score this character in all the diverse species under study, an objective criterion was needed for comparing stoutness of the bar in species with very different bill

shapes. I chose to evaluate the width of the supranasal bar width in relation to the lateral nasal bar. Figure 6 shows the frequency distribution of the logarithmic ratio of these measurements in finch-billed drepanidines and in finch-billed outgroup taxa. The group of drepanidines with stout supranasal bars is clearly identified, and includes *Telespiza*, *Loxioides*, *Chloridops regiskongi* and *Xestospiza conica*, with ratios between 0.3 and 0.6. None of the finch-billed outgroup taxa has a ratio above 0.3.

The distribution of the same index in all drepanidines shows only a small gap centred at 0.3 (Fig. 6). Rather than rejecting the character, I accepted it and scored species with indices equal to or below 0.3 as character state (0), and those with indices above 0.3 as character state (1).

Four additional species of drepanidines, *Pseudonestor xanthophrys*, *Oreomyzta bairdi*, *Aidemia chascax* and *Aidemia lutetiae*, join the finches in having stout supranasal bars (index >0.3). In the outgroup taxa, only *Agelaius phoeniceus* has an index greater than 0.3.

12. *Tomial crest terminates posterior to or even with the lateral part of the jugal hinge (0), terminates anterior to the jugal hinge (1)*. The blade-like tomial crest of the maxilla extends at least as far posteriad as the lateral part of the jugal hinge in most species in the study group. However, some of the thin-billed drepanidines have the posterior end positioned anterior to the lateral part of the jugal hinge. The character was scored by first examining the maxilla in ventral view to determine the posterior extent of the blade-like tomial crest, and then in lateral view to relate this to the lateral part of the jugal hinge.

Character state (1) was assigned to *Paroreomyza*, *Loxops parvus* and *L. virens*, and to all the species in the melanodrepanine group. It was not found in any of the outgroup taxa.

13. *Anterior end of the premaxilla; pointed (0), blunt (1)*. The genus *Vangulifer* accommodates two fossil species from Maui whose with thin, weak maxillae are oddly wide and blunt at the tip (James & Olson, 1991). Pointed maxillary rostra are the norm in birds, so

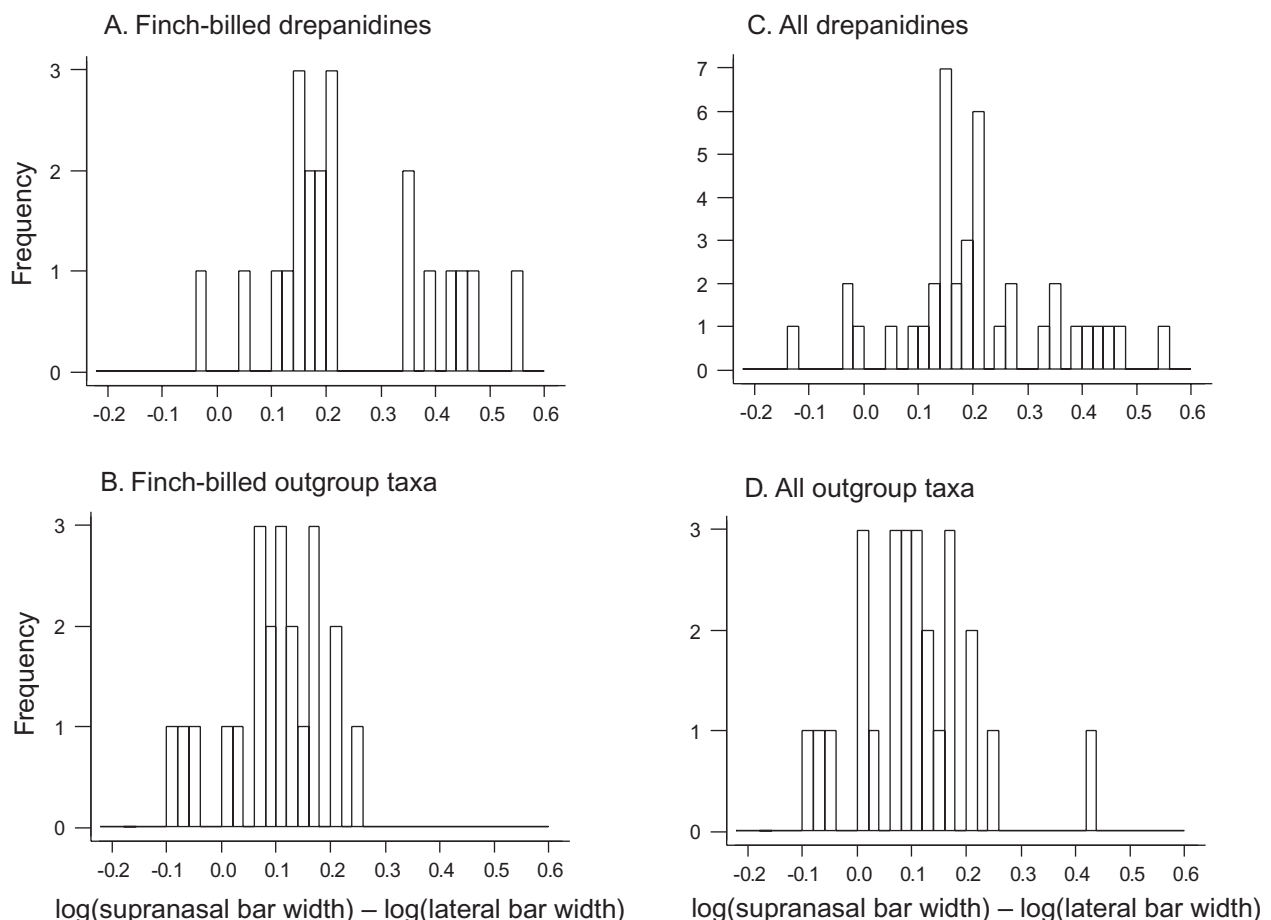


Figure 6. Distribution of measurements of the relative breadth of the supranasal bar. See character 11.

much so that no satisfactory living analogue has been found for the bill shape of *Vangulifer*. James & Olson (1991) speculated that these birds were adapted for catching insects on the wing. Character state (1) was also assigned to *Aidemia lutetiae*, a member of the fossil genus of 'icterid-like gapers' with a fairly blunt tip of the maxilla. The other two species of *Aidemia* may also have blunt bill tips, but this could not be determined because the fossil material is too fragmentary.

14. *Ventral bulge of the tomial crest; present (1), absent (0)*. A slight ventral bulge in the anterior portion of the bony tomial crest is characteristic of the genus *Chloridops*. Where this bulge occurs, about 2/3 of the way to the tip of the rostrum, the tomial crest has a convex contour in lateral aspect, whereas it has a concave contour both anterior and posterior to the bulge. Many finch-like birds have a ventral bulge in the rhamphothecal part of the tomial crest, but in *Chloridops* the bulge is also present in the underlying bone.

Character state (1) was also assigned to the outgroup taxa *Poocetes gramineus* and *Sicalis flaveola*, which have a slight ventral bulge near the bill tip.

15. *Posteroventral edge of the maxilla; recessed medially (0), straight (1)*. The posteroventral edge of the maxilla between the jugal hinges is usually recessed, but in *Orthospiza howarthi* it is almost perfectly straight, providing a linear zone of contact with the jugals and palatines. Other species that approach this condition are *Chloridops wahi*, in the ingroup, and *Hesperiphona vespertina*, *Mycerobas melanoxanthos* and *Agelaius phoeniceus* in the outgroup, all of which received character state one.

16. *Median fossa on the ventral surface; deeply excavated (0), shallow to moderately excavated (1), not excavated (2)*. Ordered. The median fossa (fossa medianus maxillaris) lies between the ventral crests (cristae ventralis maxillaris), or between the tomial crests anteriorly if the ventral crests do not extend to the bill tip. The depth of this fossa varies greatly in the species under study, although the most common score is character state (1), shallow to moderately excavated. The distribution of the deeply excavated fossa suggests that this condition has arisen more than once. For example, deep fossae occur in a group of heavy-billed finches (*Chloridops regiskongi*, *Rhodacanthis*) as well as in the nectar-sipping species of the red-and-black group (excepting *Himatione freethii*), and in the wood warbler *Mniotilta varia*. In *Orthospiza howarthi*, *Carpodacus erythrinus* and *Serinus mozambicus*, there is no excavation of the medial surface of the ventral maxilla between the ventral crests (state 3).

Two species were scored as missing data because they have unusual configurations of the ventral max-

illa such that the region between the ventral crests, where the fossa normally lies, no longer exists. In *Hemignathus vorpalis* the median sulcus has become an internal canal, and in the process the other features of the ventral maxilla have been lost (James & Olson, 2003; see also character 29). In *Loxia leucopetra*, the ventral crests have moved medially to lie alongside the median sulcus; thus the median fossa is absent.

17. *Width of the median fossa at the transverse midline of the maxilla; less than half the width of the maxilla (0), equal to or greater than half the width of the maxilla (1)*. The narrower median fossa (state 0) occurs in most of the noncardueline outgroup taxa, the only exceptions being *Fringilla coelebs* and *Mniotilta varia*. All Carduelini and Drepanidini have the wider fossa except two genera with heavy, finch-like bills (*Chloridops* and *Orthospiza*), and two species that lack the median fossa altogether and were therefore scored as missing data (see character 15).

Although this difference is subtle and was not scored, the narrow fossa in the outgroup taxa has a somewhat different appearance than in *Chloridops* and *Orthospiza*. In the latter two genera, the fossa is wider and sometimes much deeper, with sloping sides rather than having the fossa bordered by abrupt ridges as in outgroup species such as *Agelaius phoeniceus* and *Sicalis flaveola*.

18. *Ventral ridges with a distinct midline crest (0), intermediate (1), broad and blunt with no distinct midline crest (2)*. Unordered. Among the species with well-developed ventral ridges (principally the finch-billed species), some have the ridges very broad and blunt, while in others each ridge achieves a fairly sharp crest along its midline. The broad, blunt condition is fully expressed only in the grosbeak-like drepanidines *Chloridops kona* and *C. wahi*, the only taxa that were scored state (2). Sharply crested ridges occur in a variety of finch-like bill shapes, e.g. in *Rhodacanthis palmeri*, *Xestospiza conica* and *Telespiza*. This diversity of ventral ridge morphology in the finches probably relates to the variety of seeds eaten and the methods used to manipulate and crack them.

In the unusual finch-like species *Orthospiza howarthi* and in many of the thin-billed drepanidines, ventral ridges are a relatively unimportant topographic feature on the maxilla, making it difficult to determine the character state. Most of the thin-billed species have weak but discernible ridges, with a distinct medial line; in those cases I assigned state (0). Because the ridges are all but indiscernible in *Akialoa* and *Melamprosops*, I scored the latter taxa as missing data.

19. *Lateral sulci; shallow (0), intermediate (1), deep (2)*. Ordered, weight = 0.5. Character state (0) was

reserved for species with very shallow, undeveloped lateral sulci. In the drepanidines, this is the state in most of the thin-billed species and also in a few species with relatively heavy, finch-like bills (*Psittirostra psittacea* and *Melamprosops phaeosoma*). The majority of finch-billed drepanidines and continental carduelines have deep sulci, as do the 'creepers', *Oreomystis* and *Paroreomyza*. The intermediate character state was assigned mainly within the melanodrepanine group.

20. *Ventral crests and lateral sulci extend to, or nearly to, the tip of the maxilla (0), extend about 3/4 of the way to the tip (1), confined posterolaterally (2)*. Ordered. The lateral sulci and ventral crests originate at the posterior end of the ventral maxilla and extend anteriorly, in some species all the way to the tip of the maxilla (state 1). In other species these sulci and crests are insignificant features that reach only half way to the tip or less (state 2).

The former condition is more frequent in finch-billed species, while the latter is more frequent in long, thin-billed species, especially those with decurved maxillae. However, the correlation is imperfect, because the long, thin-billed *Sicalis flaveola* has crests and sulci that extend to the tip, while the finch-billed drepanidines *Xestospiza conica*, *X. fastigialis* and *Melamprosops phaeosoma* have these features confined posterolaterally. A diverse suite of species have an intermediate condition (state 1), including some of the very heavy-billed finches (e.g. *Rhodacanthis* and *Chloridops*) as well as thin-billed leaf-gleaners and bark creepers (*Paroreomyza* and *Oreomystis*).

21. *Anterior rim of nasal cavity; distinct (0), intermediate (1), indistinct (2)*. The anterior rim of the nasal cavity is sharply demarcated in most species under study. In a subset of drepanidines, the border of the cavity loses its definition and develops a slope anteriorly (state 1). Some of these species are extinct and their feeding habits are unknown, but if we consider only the extant species, the indistinct rim is distributed mainly in birds that take nectar. Development of the sloping anterior nasal cavity may be related to design changes in the nostril associated with enlargement of the nasal opercula, a change that tends to accompany the nectar-feeding habit (Amadon, 1950; Richards & Bock, 1973; Raikow, 1977b). Large nasal opercula together with expanded and sometimes ossified nasal conchae are thought to help prevent pollen from entering the nasal cavity.

The intermediate character state was assigned only to *Chloridops kona*, in which the anterior rim of the nasal cavity is curved, but is not gradual and sloping as in the species assigned state (2).

22. *Shape of the opening of the nasal cavity; not anteroposteriorly elongate, either circular/subcircular*

or higher than long (0), anteroposteriorly elongate (1). The shape of the opening of the nasal cavity varies greatly in the drepanidines. For the most part, the differences correlate with overall bill shape: finch-billed species tend to have compact, approximately circular openings, while thin-billed species tend to have the opening elongated in consonance with the general form of the maxilla. The exception is *Hemignathus*, which has a very thin and attenuated maxilla but a circular, finch-like opening.

Scores were assigned based on the logarithmic ratio of height to length of the nasal opening. The drepanidines show a large gap in the distribution of this index, between 0.17 and 0.22 (Fig. 7), so drepanidines with values below 0.17 were scored state (0), and those with values above 0.22 were scored state one. Because the same distributional gap was not observed in the outgroup species (Fig. 7), the score for the species with ratios between (and including) 0.17 and 0.22 was recorded as indeterminate (missing data).

The opening in *Pseudonestor xanthophrys* and *Chloridops regiskongi* (the outlier on the left in Fig. 7) is unusual. These species have very deep maxillae and their nasal cavities are concordantly deep. Clearly, an additional state could be created for these two species ('opening much higher than long'), but instead their condition was regarded as an extreme case of state zero and the binary nature of the character was preserved.

23. *Nasal septum mostly unossified (0), intermediate (1), mostly ossified (2)*. Ordered, weight = 0.5. The continental grosbeaks *Mycerobas* and *Hesperiphona* have extensive ossification of the nasal cartilages, affecting both the septum and the nasal conchae. In the drepanidines, the septum tends to ossify at least partially in some of the heavier-billed finches, in the nectar-sipping species of the melanodrepanine group (see character 21), and in *Oreomystis bairdi* and *Loxops parvus*.

Presence vs. absence of ossification could not be scored because small centres of ossification that are contained within the cartilaginous septum, but not attached to the maxilla, are not preserved in bony specimens. Consequently, the states were defined as 'mostly ossified' vs. 'mostly unossified'. The minimal requirement for a score of mostly ossified was an ossified splint attached to the dorsal nasal bar and extending ventrad nearly to the base of the septum.

24. *Nutrient foramen in the anterior wall of the nasal cavity; absent (0), present at the anterior-most point of the cavity rim (1), present in the anterior wall of the nasal cavity, well medial to the rim (2)*. Unordered. A nutrient foramen in the anterior wall of the nasal cavity (or sometimes multiple tiny foramina) is present in most drepanidines. The foramen is lacking

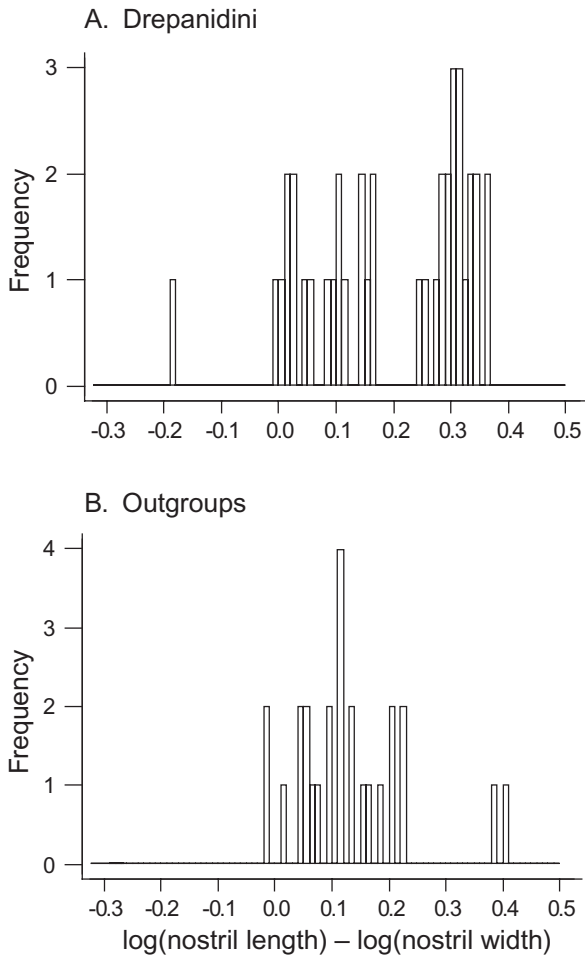


Figure 7. Distribution of logarithmic ratios of the length to height of the narial opening. See character 22.

in some drepanidine species with finch-like bills and in most of the outgroup species. When present, the foramen is usually located at the anterior-most point of the cavity rim (state 1). In some of the finch-billed drepanidines, it is located inside the nasal cavity, well medial to the rim (state 2).

25. *Large opening (fonticulus) in the anterior wall of the nasal cavity; absent (0), present (1).* This recognizes a remarkable autapomorphy of *Pseudonestor xanthophrys*. Unlike other taxa in the study, *P. xanthophrys* has the anterior wall of the nasal cavity essentially unossified. In place of the expected bony wall is a large oval opening that communicates with the internal, trabeculated part of the rostrum. Examination of a skull preserved in alcohol (BBM-240) established that there is no corresponding opening in the cartilaginous capsule that lines the nasal cavity (R. L. Zusi, pers. comm.). Why the bone is unossified here is unclear.

26. *Median neurovascular sulcus; absent (0), shallow (1), moderately developed (2), deep (3).* Ordered. The sulcus (sulcus neurovascularis medianus; see Methods) is a narrow groove that conducts neurovascular tissue to the bill tip. It varies in development from being the dominant feature of the ventral maxilla in some species to being absent in others.

In drepanidines, the degree of development of the sulcus correlates well with what we know about feeding habits. Crevice-probing and nectar-sipping species that make constant use of the bill tip and rely on its sensitivity have the greatest development of the sulcus (i.e. *Drepanis*, *Vestiaria*, *Akialoa*, *Hemignathus*). Finch-billed species that use the more posterior parts of the rostra to a greater extent (maxillary and mandibular tomia, ventral ridges) tend to have shallow sulci. This is also true of most Carduelini, except that in crossbills (*Loxia*) the sulcus is well incised. Crossbills perform fine manipulations with their bill tips, so that where exceptions occur, they tend to find ready explanation in feeding behaviour.

27. *Accessory neurovascular impressions radiating anterolaterad from the median neurovascular sulcus; faint or absent (0), very distinct, reaching toward the tomial crests (1), very distinct, reaching to the ventral crests (2).* Unordered. The fossil drepanidine *Vangulifer mirandus* has an unusual development of the median neurovascular sulcus on the ventral maxilla. In most species the sulcus has a simple form, extending straight from the posterior to the anterior end of the maxilla, but in *V. mirandus* this central stream develops numerous side branches that reach anterolaterally toward the tomial crests (state one). These side branches apparently function to supply neurovascular tissue to the lateral edges of the maxilla (James & Olson, 1991).

Although the branching of the sulcus is much more developed in *V. mirandus* than in any other drepanidine species, faint traces of a branching pattern can be seen in a number of other species under a dissecting microscope. These traces are clearest *Vangulifer neophasis*, but I did not create an intermediate state for this species because the faint traces of *V. neophasis* differ little from the rather fainter traces of some other species. Dissection of the nerves and vessels in drepanidines and carduelines would probably reveal that branching of the neurovascular tissue occurs in quite a few species, but that only in *V. mirandus* have these side branches become important enough to leave distinctive impressions in the bone.

A similar phenomenon occurs in the bullfinch *Pyrrhula erythaca*, which also has a well-incised pattern of side branches radiating anterolaterally from the median sulcus. In this case the branches extend not to the tomial crests but to the ventral crests of the max-

illa (state 2). My examination of skeletons of other carduelines in the USNM collections suggests that this radiating pattern is characteristic of the genus *Pyrrhula*.

28. *Ossification of the floor of the nasal cavities: only the anterior part is ossified medially (1), the floor is entirely ossified or nearly so (0), the floor is almost entirely unossified medially (2)*. Ordered. The unossified medial space is typical of birds with thin, weak bills. In contrast, some heavy-billed finches have the maxilla completely ossified in this region.

29. *Median neurovascular sulcus enclosed ventrally along most of its length to form an internal canal; absent (0), present (1)*. Conversion of the median sulcus to an internal canal is a unique condition found in *Hemignathus vorpalis*, a fossil drepanidine from the island of Hawaii (James & Olson, 2003). This remarkable species has a very long and narrow, slightly decurved maxillary rostrum, coupled with a much shorter mandibular rostrum. On its maxilla, bone has grown across the narrow ventral surface to enclose the median neurovascular sulcus, so that the sulcus has become an internal canal.

30. *Median crest on the ventral surface; absent (0), present (1)*. In a limited subset of the outgroup taxa (*Passer domesticus*, *Poocetes gramineus*, *Cardinalis cardinalis* and *Sicalis flaveola*), a slight crest replaces the median sulcus along at least part of its length.

MANDIBLE

31. *Angle of the symphysis to the internal ramus; subparallel (0), deflected (1)*. Most finch-billed drepanidines have the mandibular symphysis orientated on a line that roughly parallels the ventral border of the internal portion of the mandibular ramus (the intermediate and caudal parts). In contrast, the thin-billed drepanidines have the symphysis angled downward to varying degrees. *Hemignathus wilsoni*, with its thin maxilla but stout, straight mandible, groups with the finches in this respect. In addition, a number of species with generally finch-like bills group with the thin-billed species (*Xestospiza fastigialis*, *Melamprosops phaeosoma*, *Loxops coccinea* and *L. caeruleirostris*). These species are of interest because the deflection implies that bill function differs in some respects from that in the more typical finch-billed drepanidines. Also, deflection of the symphysis in these finch-like species may be a precursor condition to the evolution of thinner bill shapes, considering that deflection is present in almost all thin-billed drepanidines.

In order to develop a standard for scoring deflection of the symphysis, the angle of the symphysis to the ventral border of the internal portion of the ramus was

measured (lateral view). For curved symphyses, the line of the symphysis was taken to be the chord of the arc (Fig. 8). Three things are striking about the histograms showing the distribution of these measurements (Fig. 9). First, the range of measurements is much greater in the drepanidines than in the outgroup species, attesting once again to the breadth of adaptive radiation in the Hawaiian birds. Second, both histograms show a peak at zero degrees. This is unimportant because it is an artefact of the method of data recording. Because angles that are nearly parallel are hard to measure, these were not measured but were simply recorded as zero.

Third, there are extreme outliers at both ends of the range in the drepanidines. Outliers at the low end are *Chloridops kona* and *Chloridops regiskongi*, two species with hyper-development of the finch-like bill. Outliers at the high end are *Akialoa stejnegeri*, *Vestiaria coccinea*, *Drepanis pacifica* and *Drepanis funerea*, four species with strongly sickle-shaped bills. These are not traits that need to be distinguished in scoring this character, which pertains only to presence or absence

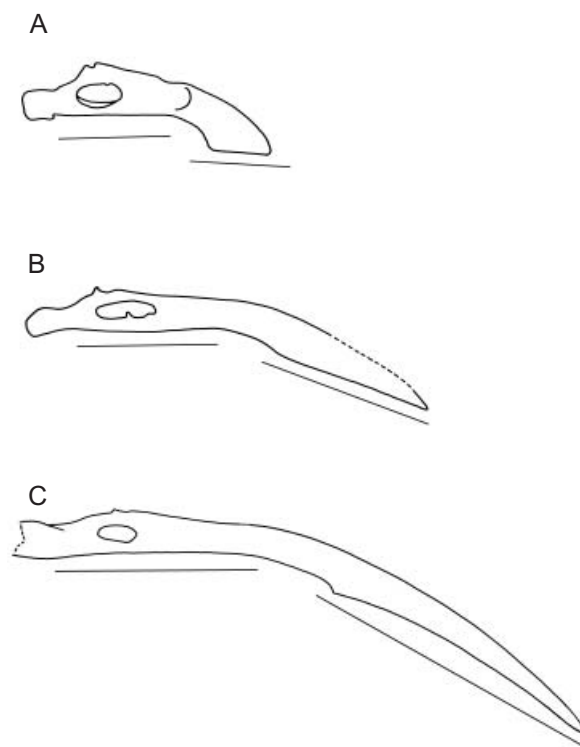


Figure 8. Method of measuring the angle of the mandibular symphysis to the internal ramus. Mandibles, in lateral view, are of *Telespiza ypsilon* USNM 254736 – subparallel (A), *Vangulifer mirandus* USNM 445808 – deflected (B), and *Aidemia zanclops* BBM-X 155160 holotype – deflected (C). See character 31.

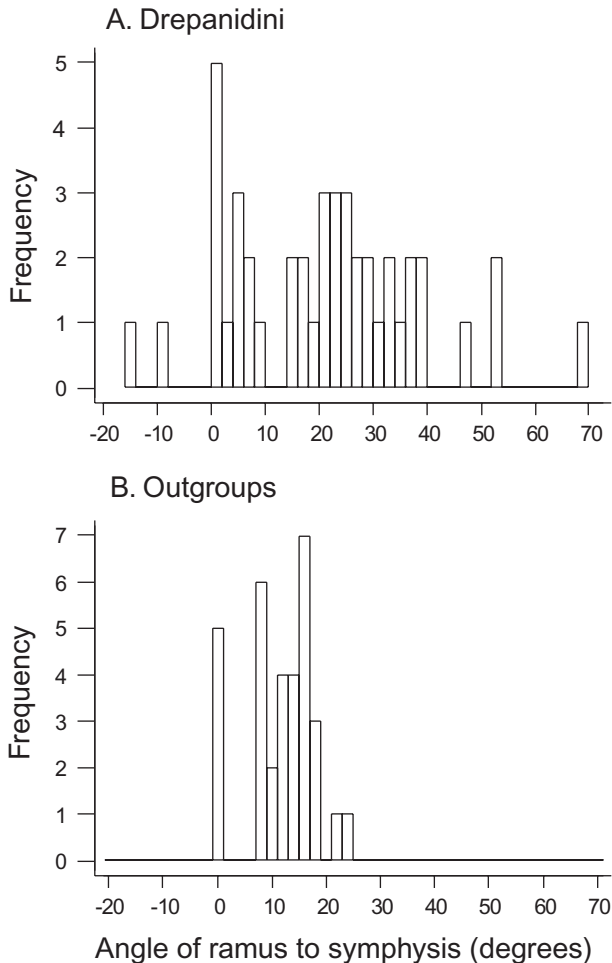


Figure 9. Distribution of measurements of the angle of the mandibular symphysis to the internal ramus. See character 31.

of significant deflection of the symphysis. Therefore, rather than assigning separate character states to the outliers, they were lumped with their neighbours.

The gap between 9° and 14° in the drepanidine histogram effectively divides species with little or no deflection from those with substantial deflection. Accordingly, drepanidines with an angle of 9° or less were assigned character state (0), while those with an angle of 14° or more were assigned state (1). Outgroup species with angles between 9° and 14° were recorded as missing data.

32. Posterior margin of the mandibular rostrum; curved or angular (0), straight (1). This is best observed in ventral view. The posterior margin of the mandibular rostrum is an unbroken arc in most species, but in some finches and in *Drepanis funerea*, it extends in a relatively straight line directly from the intermediate part of one ramus to the other. The

straight posterior margin occurs mainly in species with large, robust bills.

33. Ramus height at the coronoid process; much greater than height at lateral cotyla (0), intermediate (1), only slightly greater than height at lateral cotyla (2). Ordered, weight = 0.5. In finches and other birds with robust bills, the dorsal ramus rises steeply anterior to the articular fossa to form a distinct angle at the coronoid process. In birds with long or weak bills the ramus is much less produced here.

To standardize scoring, the height of the mandible at the coronoid process was compared with its height at the lateral cotyla. The logarithmic ratios of these two dimensions for drepanidines have a bimodal distribution (Fig. 10A). The gap between values of 0.22 and 0.24 most appropriately divides the distribution into two parts. This gap disappears when all of the outgroup species are added to the histogram (Fig. 10B), although the bimodal distribution remains much the same. Accordingly, species with log-ratios equal to or below 0.22 were assigned character state zero, the two outgroup species with log-ratios between 0.22 and 0.24 were assigned the intermediate character state (1), and species with log-ratios equal to or exceeding 0.24 were assigned character state (2).

34. Sides of the mandibular rostrum; not very thick (0), intermediate (1), very thick (2). Ordered, weight = 0.5. Sturdy-billed finches, almost by definition, have very thick mandibular rostra. I find that repeatable scoring of this characteristic can be achieved by examining the rostrum in posterior view. Mandibles with very thick rostra present a broad, flat posterior surface at the juncture between the rostrum and the intermediate part of the ramus, on the lingual side (state 2). This flat surface is lacking in thinner rostra (state 0). A few finch-billed species exhibit an intermediate condition (state 1).

35. Retroarticular process; absent (0), present but insignificant (1), long and blade-like (2). Ordered. A retroarticular process is present in nearly all of the thin-billed insect-eating and nectar-sipping drepanidines, but is absent in species with typical finch-like bills. *Vangulifer mirandus* is an exception, having a very thin, weak bill but lacking a retroarticular process. *Pseudonestor xanthophrys* breaks the rule in the opposite manner, by having a well-developed retroarticular process despite its thick and rather finch-like bill.

The process occurs much less frequently in the outgroup taxa, in which it is 'present but insignificant' in *Agelaius phoeniceus*, *Spinus pinus*, *Carduelis carduelis* and *Loxia curvirostra*. In most species that have a well-developed process, its main function is probably

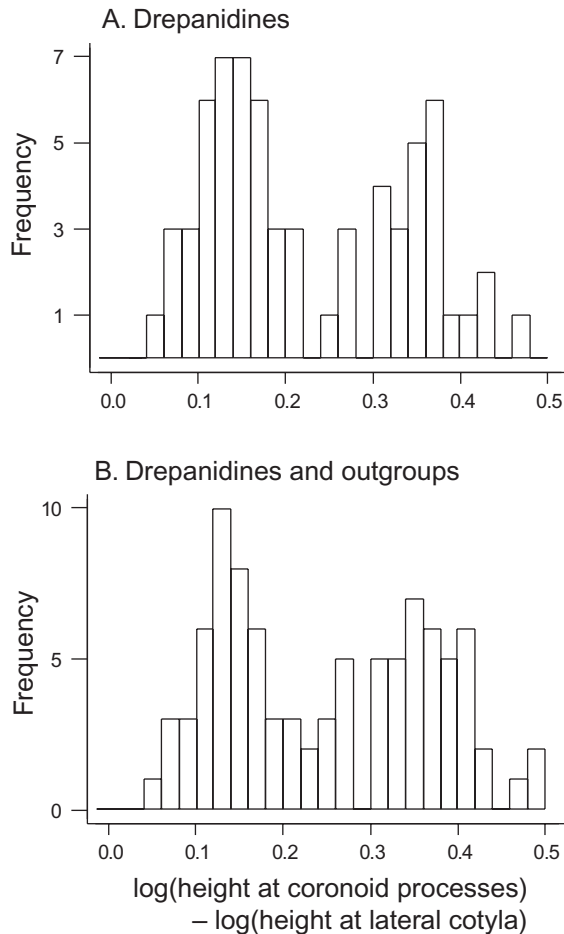


Figure 10. Distribution of logarithmic ratios of the height at the coronoid processes to the height at the lateral cotyla. See character 33.

to enhance the force available for opening the bill against pressure (Beecher, 1951b; Zusi, 1967).

36. *Ossified fascia for attachment of musculus pseudotemporalis profundus; absent (1), present below and encroaching on the mandibular fenestra (0), present below and extending far anterodorsal to the mandibular fenestra (2).* Unordered. *Musculus pseudotemporalis profundus* originates on the orbital process of the quadrate and inserts on the medial surface of the mandible, both above and below the mandibular fenestra (Richards & Bock, 1973: 63; James *et al.*, 1989). Its contraction simultaneously raises the mandible and depresses the maxilla. In finch-billed species that use the bill forcefully in this manner, the muscle tends to develop an ossified fascia below the mandibular fenestra. Ossification of the fascia occurs in all the sturdy-billed drepanidine finches, in the Carduelini with a few exceptions, and in a limited number of additional species.

In the drepanidines and the noncardueline outgroup species, when ossification of the fascia occurs, it is confined to the region of the fenestra (state 0). In the Carduelini, it extends far beyond the mandibular fenestra along an anterodorsal line (state 2). This is a minor difference, and sometimes the anterodorsal extension is faint.

37. *Mandibular fenestra; present (0), absent (1).* The mandibular fenestra is absent in *Mycerobas melanoxanthos* and *Hesperiphona vespertina*, which instead have this region of the mandibular ramus penetrated only by a very small foramen. All other species in the study group have an unmistakable mandibular fenestra.

38. *Dorsal profile of the ramus between the mandibular fenestra and the tomial crest; concave (0), straight or convex (1).* A straight edge held above the mandible is helpful in scoring this character. The concave profile (Fig. 11A) was observed only in the outgroup species *Passer domesticus*, *Agelaius phoeniceus*, *Poocetes gramineus*, *Tachyphonus rufus* and *Chlorophanes spiza*.

39. *Medial face of the mandibular rostrum; deeply excavated (0), very shallow or unexcavated along the anterior half of the rostrum (1).* The medial face (facies medialis) of the rostrum accommodates the tongue and is deeply excavated in most birds. An unusual condition occurs in a fossil akialoa from Kauai and Oahu, *Akialoa upupirostris*, which has the medial face of the mandibular rostrum unexcavated anteriorly and only very shallowly excavated posteriorly (James & Olson, 1991: 60–62). Filling in of the sulcus with bone in this species may increase the strength of its long, thin probing bill.

Two additional fossil akialoas have been found since 1991. The first of these is represented by a single, damaged mandible from Maui (*Akialoa* aff. *upupirostris*) with a virtually unexcavated medial surface, very similar to *A. upupirostris* but not quite as extreme. It might represent an undescribed species, and in any case its discovery extends the distribution of *upupirostris*-like akialoas from Kauai and Oahu to Maui.

The second new akialoa (*Akialoa* sp., Hawaii), represented by six or more beautifully preserved fossil skeletons found in a lava cave on the island of Hawaii (Giffin, 1993), is markedly larger than *A. obscurus* of the same island. It has the medial face of the mandibular rostrum well excavated along most of its length, but near the tip the sulcus becomes shallow and at the tip it is absent. I assigned character state (0) to this fossil taxon rather than creating an intermediate category.

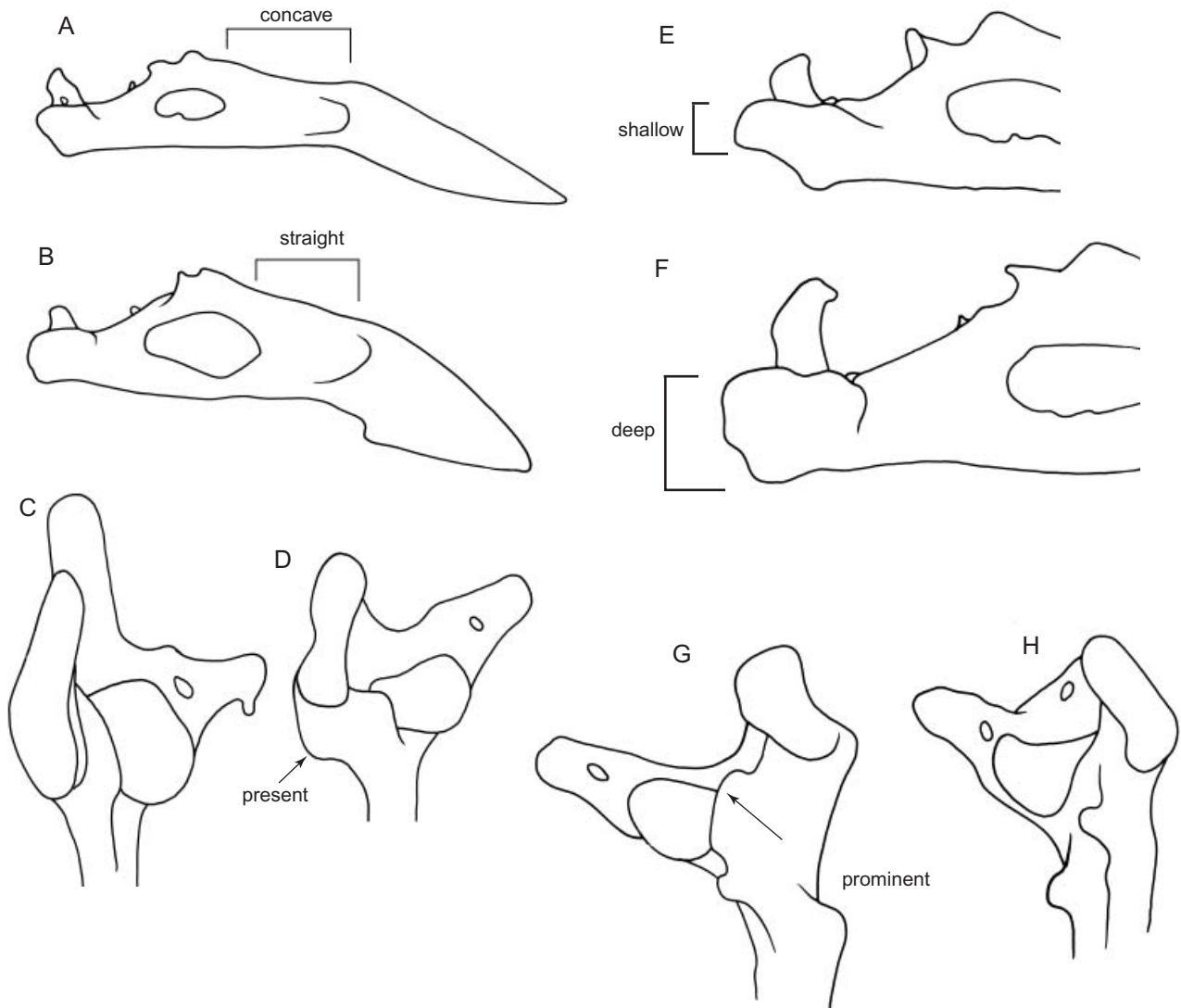


Figure 11. Illustration of states for mandible characters 38, 40, 43, and 44. Mandibles of *Passer domesticus* USNM 561838 (A) and *Telespiza cantans* USNM 289278 (B) in lateral view, illustrating the concave vs. straight dorsal profile (character 38). The articular end of the mandible in *Oreomystis bairdi* USNM 553183 (C) and *Sicalis flaveola* USNM 556091 (D) in dorsal view, illustrating presence (D) vs. absence (C) of lateral inflation anterior to the lateral cotyla (character 40). The articular end of the mandible in *Poecetes gramineus* USNM 555444 (E) and *Leucosticte tephrocotis* USNM 501466 (F) in dorsal view, illustrating the deep vs. shallow development of bone below the lateral cotyla (character 43). The articular end of the mandible in *Cardinalis cardinalis* USNM 554219 (G) and *Telespiza cantans* USNM 561510 (H) in anterodorsal view, illustrating a prominent intercotylar tubercle vs. a weakly developed one (character 44).

40. Lateral inflation of the mandibular ramus in the area just anterior to the lateral cotyla; present (0), absent (1). The two states are illustrated in Figure 11C, D. Lateral inflation does not occur in continental carduelines or in drepanidines, but it is the common condition in the other nine-primaried oscines in the study group, excluding only *Cardinalis cardinalis* and *Fringilla coelebs*.

41. Pronounced bilateral asymmetry in the shape of the lateral cotylae, in which one cotyla is longer

than the other; absent (0), present (1). In the akepas (*Loxops coccineus* and *L. caeruleirostris*) the lateral cotyla on one side of the mandible is much longer than on the other. Asymmetry of the cotylae is less pronounced in *Loxia*. Richards & Bock (1973) describe some additional asymmetries in the skull of the akepas.

42. Rhamphothecal covering of the medial face of the mandibular rostrum extends from the bill tip to the posterior edge of the symphysis (0); stops short of the posterior edge of the symphysis (1). The symphyseal

part of the mandible is usually covered by rhamphotheca, both above and below. In *Pseudonestor xanthophrys*, however, the rhamphotheca does not cover the posterior area of the medial surface. There is a gap in the rhamphothecal covering here, with skin attaching at each edge of the gap. The presence of such a gap can be detected in the bone, because the bone slopes away posteriorly where it is not covered by rhamphotheca. Character state (1) is pronounced in *P. xanthophrys*, and I also scored it present in *Psittirostra psittacea* and *Dysmorodrepanis munroi*. To varying degrees, these birds all possess parrot-like bills with overhanging maxillary rostra.

To possess such a gap is extremely rare in passerine birds, but it is common in certain other birds with roughly similar bill shapes, for example in parrots and hawks. Because the gap appears to have evolved independently in unrelated birds with parrot-like bills, it may have a similar function in those birds. In parrots at least, the function may be related to tongue movements. Homberger (1986) showed that in *Psittacus erithacus* (African grey parrot), the only muscle that attaches to the mandible within the gap is the musculus (m.) genioglossus, an extrinsic tongue muscle that functions (in parrots) to protract and lower the hyoid. In *Loxops* (*sensu* Amadon), Richards & Bock (1973: 101–102) describe m. genioglossus as a long-fibred muscle originating from the medio-posterior surface of the mandibular symphysis. They comment that the muscle is so long and weak in *Loxops* that its function is hard to discern. Perhaps dissections of *Pseudonestor* and *Psittirostra* will reveal that the muscle has developed an expanded origin on the dorsal surface of the mandibular symphysis in these species, and a function similar to that in parrots.

43. *Mandibular ramus below the posterior part of the lateral cotyla; shallow posteriorly (0), intermediate (1), deep posteriorly (2)*. Ordered, weight = 0.5. All drepanidines and nearly all carduelines have the ramus beneath the posterior part of the lateral cotyla about as deep as beneath the anterior part (state 2, Fig. 11E). In most other nine-primaried oscines, the ramus tapers upward to become shallower posteriorly (state 0, Fig. 11F). The exceptions to the rule are *Mycerobas*, *Hesperiphona*, and related taxa sometimes lumped under the genus *Coccothraustes*, which have the shallow posterior ramus, and also *Pinicola enucleator*, scored as intermediate.

44. *Intercotylar tubercle; prominent (0), insignificant or absent (1)*. The small but distinct, sharp dorsal projection of the mandible between the lateral and medial cotylae is here identified as the tuberculum intercotylaris (Fig. 11G; Baumel & Witmer, 1993: 74). The tubercle is prominent in all the noncardueline

outgroup taxa. Its development in the carduelines is variable: seven of the species examined have a prominent tubercle and 11 do not. In drepanidines, the tubercle is either not very prominent or not even discernible as an osteological feature (Fig. 11H).

45. *Medial cotyla extends from the anterior to the posterior edge of the fossa that contains it (1), does not reach the posterior edge (0)*. In the species under study, the medial cotyla of the mandible lies in a distinct fossa. In most of the species, the cotyla does not occupy the full length of the fossa, stopping short of its posterior edge. In *Aidemia*, however, it reaches all the way from the anterior to the posterior edge of the fossa.

In order to score this character, it was necessary to observe the mandible under at least 3× magnification. Intermediate states were not recognized, even though some species (e.g. *Loxops stejnegeri*, *L. sagittirostris*) have the cotyla relatively longer than others do.

46. *Shape of the medial cotyla; approximately oval (cup-shaped) (1), distinctly wider than long (2), distinctly longer than wide (0)*. Ordered. The shape of the medial cotyla was assessed by contrasting anterior-posterior length with medial-lateral width, with the mandible in dorsal view. A fairly compact or cup-shaped cotyla characterizes the outgroup taxa and the finch-billed drepanidines, with a few exceptions. For the most part, the insect-eating and nectar-eating drepanidines have elongate cotylae. The third character state was created to accommodate a few species of nondrepanidine finches (*Cardinalis cardinalis*, *Mycerobas melanoxanthos*, *Carduelis sinica*) with very wide cotylae.

47. *Median fossa along the dorsal symphysis; absent (0), present (1)*. A very distinctive, slot-like fossa in the dorsal symphysis occurs in most of the drepanidine 'grosbeak' finches of the genus *Chloridops* (e.g. *C. kona*; James & Olson, 1991: 39). In osteology, these species give every impression of being adapted for cracking hard seeds with the bill. *Chloridops kona* is the only species in the genus that survived long enough for its feeding habits to be observed and recorded. This species fed mainly on the very hard seeds of the false sandalwood or naio tree (*Myoporum sandwicense*) (Henshaw, 1902; Perkins, 1903; Olson, 1999). Perhaps the slot-like fossa in the mandible of *Chloridops* had a function related to seed-eating, such as accommodating a specialized tongue that helped place the seeds in an advantageous position for cracking.

48. *Medial cotyla orientated dorsally (0), orientated posteroventrally (1)*. The medial cotyla of the mandible is orientated with its planar surface facing dorsad in all the taxa studied except *Hemignathus wilsoni*

and *Dysmorodrepanis munroi*, in which the medial cotyla faces posteroventrad. *Hemignathus wilsoni* uses its chisel-like mandible for hammering and prising up pieces of bark in quest of invertebrate prey (Perkins, 1903.) According to Zusi (1987), the posteroventral orientation of the medial cotyla in this species helps to stabilize the joint when forces are transferred from the tip of the mandible posteriad to the cranium during hammering. *Dysmorodrepanis munroi* has a strongly re-curved mandible that is ill suited to hammering. In *Dysmorodrepanis*, reorientation of the medial cotyla is associated with additional design changes in the articular fossa, which James *et al.* (1989) interpret as functioning to limit mobility of the quadrate-mandibular joint, and thus helping to maintain occlusion of the rostra.

49. *Dorsal flange on the intermediate part of the mandibular ramus; absent (0), present (1).* In the sickle-billed nectarivorous drepanidines *Vestiaria coccinea*, *Drepanis pacifica* and *D. funerea*, the intermediate part of the mandibular ramus has a distinct arc or flange along its dorsal border, positioned slightly posterior to the angle of the mandible. Species that have the dorsal margin of the ramus generally bowed, rather than having a discrete arc that is limited in extent to the area slightly posterior to the angle of the mandible, were assigned state (0) (i.e. *Chloridops*, *Pseudonestor*, *Psittirostra*, *Dysmorodrepanis*, *Loxia curvirostra*). *Palmeria dolei* was assigned state (0) based upon an illustration of the mandible in lateral view, at 3× magnification. This is a tentative assignment pending direct examination of the skeleton.

CRANIUM

50. *Muscle scar for the origin of m. protractor pterygoidei sensu stricto on the interorbital septum; a depression with a distinctly raised border anteriorly and dorsally (0), an indistinct muscle scar (1), not visible (2).* Ordered. The origin of m. protractor pterygoidei *sensu stricto* extends forward and upward from the posterior part of the parasphenoidal rostrum onto the interorbital septum (Richards & Bock, 1973: 54–55; Zusi, 1989). Most drepanidines have a very well delimited scar for the origin of this muscle (Fig. 2; the protractor pterygoid scar of Richards & Bock, 1973). In drepanidines, the scar typically occupies a distinct depression that has a raised edge anteriorly and dorsally (and sometimes even posteriorly; state 1). In carduelines, either the scar is indistinct because the raised border is lacking, or the scar is not discernible at all. These conditions were lumped as state (0).

It is worth noting that, while the m. protractor pterygoidei *sensu stricto* is the only muscle with an

attachment on the interorbital septum in most birds, Zusi (1989) found an expanded origin of the m. pterygoideus retractor on the interorbital septum in *Pseudonestor xanthophrys*. This muscle attachment leaves no visible scar on the bone, and consequently was not coded for the present study. Zusi (1989) offers further comparisons of the scar for m. protractor pterygoidei *sensu stricto* in the drepanidines and carduelines.

51. *Scar for the origin of m. protractor pterygoidei sensu stricto on the interorbital septum; does not expand far anteriorly or narrows anteriorly (0), expands anteriorly to form a more extensive scar on the interorbital septum (1).* Most of the finch-like drepanidines and all of the outgroup taxa have the scar for this muscle limited to the posteroventral part of the septum (state 0). In certain drepanidines the scar extends, and becomes wider, anteriorly (state 1, e.g. *Loxops coccinea*). This condition is found in many species in the chlorodrepanine group of drepanidines but is absent in the melanodrepanine species. One outgroup species, *Carduelis dominicensis*, has a somewhat expanded scar, though not extensive enough to earn a score of state (1). Taxa with no visible scar were assigned state (0).

52. *Interorbital septum entirely double-walled (2), partly single-walled (1), entirely single-walled (0).* Ordered. A thick interorbital septum is characteristic of cardueline finches. Zusi (1978) described a suite of cranial traits associated with thickening of the interorbital septum, by which cardueline finches can be distinguished from other finches, with the caveat that comparisons must be made among species of similar bill shape and cranium size, since the septum tends to be thicker in birds with large skulls and broad, strongly constructed bills, regardless of the taxonomic group.

Finch-billed drepanidines have thick septa that are very similar to those of carduelines. In most cases, these septa have two separate walls that are supported internally by bony trabeculae (state 2). In drepanidines with thinner, weaker bills, the septum is either partly, or essentially entirely, single-walled. The single-walled condition (state 0) is also prevalent in the outgroups other than carduelines, the only exception being *Cardinalis cardinalis*.

53. *Ventral interorbital fenestra, with connection to the optic foramen, absent (0), present (1).* In many birds with relatively weak skulls, the interorbital septum does not ossify completely, so that one or more fenestrae (fonticuli interorbitales) can be seen in the cleaned skulls. These openings, when present, are always independent of the optic foramen and the fonticuli orbitocraniales in the carduelines and drepanidines. Most other nine-primaried oscines have a ventral interorbital fenestra that is continuous with

the optic foramen (state 1). In *Tachyphonus rufus* and *Sicalis flaveola*, a slender strut of bone divides the optic foramen from the ventral interorbital fenestra in some individuals. These species were scored as polymorphic.

Because the systematic position of *Fringilla* has long been debated, it is worth mentioning that this genus resembles emberizines in having the ventral interorbital fenestra open to the optic foramen. *Passer domesticus* lacks an interorbital fenestra (state 0), even though it is a bird of roughly similar skull size and bill shape to *Fringilla coelebs*.

As with character 52, this character is useful for separating the emberizine branch of nine-primaried oscines from the cardueline branch, with the caveat that emberizine finches with heavily fortified skulls (e.g. *Cardinalis cardinalis*) resemble carduelines in having the interorbital septum completely ossified (Zusi, 1978).

54. *Interorbital fenestrae, with no connection to the optic foramen or fonticuli orbitocraniales: small to medium in size or absent (0), very large fenestra present, extending over most of the interorbital area (1).* Although interorbital fenestrae are uncommon in carduelines and finch-billed drepanidines, one or more small openings are sometimes present in some of the species in these groups, especially in females and juveniles. The openings are more common and tend to be larger in drepanidines that have thin bills and weak skulls, such as the species of *Loxops* and the melanodrepanine species. Unlike the openings that occur in many emberizines, those in the carduelines and drepanidines are never continuous with the optic foramen or with the fonticuli orbitocraniales (see above). Because of frequent polymorphism in this feature, the presence vs. absence of independent fenestrae was rejected as a character.

The controversial genus *Paroreomyza* stands out because it has the interorbital septum almost completely unossified (state 1). In this genus, one large fenestra covers most of the interorbital area, creating a superficial resemblance between the septa of *Paroreomyza* and thin-billed emberizines such as *Mniotilta*. There is an important difference, however. The fenestra in *Paroreomyza* is formed in the manner observed in carduelines and drepanidines, not in the manner observed in emberizines. Although one large fenestra occupies most of the interorbital area, it does not join the optic foramen or the fonticuli orbitocraniales (see above).

55. *Angular dorsal process of the interorbital septum, projecting into the fonticuli orbitocraniales along their anteroventral margin; present (0), absent (1).* This refers to a distinct, angular projection lying at

about the mid-point of the rostroventral edge of the fonticuli orbitocraniales. The character was first identified by Zusi (1978). It is present in the majority of nine-primaried oscines and also in *Passer domesticus*, but absent in the carduelines and drepanidines. Note that some skulls have the rostroventral edge of the fonticuli orbitocraniales bowed, or elevated sagittally. If the edge was bowed or arched but lacked an angular projection, I assigned character state one.

56. *Large dorsal interorbital fenestra, open to the fonticuli orbitocraniales posteriorly and extending forward across the anterior part of the interorbital septum; absent (0), present (1).* Several outgroup species have a dorsal interorbital fenestra that does not occur in drepanidines or carduelines. This opening is broadly continuous with the fonticuli orbitocraniales, making it difficult to distinguish the presence of a small dorsal fenestra from its absence in dried skeletons. Consequently, only the presence of an extensive dorsal fenestra was distinguished as a character state. Character state one was assigned to *Mniotilta varia*, *Poocetes gramineus* and *Sicalis flaveola*. In these species, the dorsal fenestra extends from the fonticuli orbitocraniales more than half way across the interorbital septum.

57. *Parasphenoidal rostrum near the parasphenoidal lamina (ventral view); curved or flat posteriorly with no median crest (0), raised medially and sometimes slightly pinched (1), with a very distinct, sharp sagittal crest (2), with the rostrum and interorbital septum blade-like (3).* Ordered. Seen in ventral view, the posterior part of the parasphenoidal rostrum is raised medially in nearly all drepanidines and carduelines. In many species the rostrum appears to be slightly pinched in this area. Character state (1) was assigned to all species with a medially raised or pinched rostrum, a fairly broad category encompassing species with the rostrum raised but not really pinched (e.g. *Carduelis carduelis*), those with the rostrum only slightly pinched (e.g. *Carpodacus purpureus*), as well as those with the rostrum very clearly pinched (e.g. *Loxops parvus*, *L. mana*).

In some species, the posterior part of the parasphenoidal rostrum is more than merely pinched. Rather, it forms a very distinct, sharp sagittal crest (state 2). This condition is present in *Hemignathus lucidus*, *H. wilsoni*, *Akialoa stejnegeri* and *A. obscurus* within the drepanidines, and in *Mycerobas melanoxanthos* and *Hesperiphona vespertina* within the carduelines. As mentioned above, some of the drepanidines that were assigned character state one actually approach this condition, but among the carduelines no such 'transitional' taxa were found.

The development of the sagittal crest is carried a step farther in *Pseudonestor xanthophrys*, in which the parasphenoidal rostrum becomes blade-like posteriorly, in conformity with the narrow interorbital septum (state 3, also observed by Zusi, 1989).

State zero, the absence of a sagittal crest on the posterior parasphenoidal rostrum, was observed in all the nine-primaried oscines other than carduelines and drepanidines, and in a few species in the latter two groups. In difficult cases, distinguishing character state (0) from state (1) can be accomplished by rubbing a needle across the parasphenoidal rostrum to feel whether it is raised medially.

58. *Postorbital process sharp and well developed, projecting lateroventrally from the posterior rim of the orbit (0), either weaker and more blunt or not developed as a distinct, pointed process (1).* The postorbital process provides an attachment point for the postorbital ligament and for part of the adductor musculature of the mandible (musculus adductor mandibulae externus rostralis temporalis and m. adductor mandibulae externus rostralis lateralis; Richards & Bock, 1973: 56–57). Richards & Bock suggest that its degree of development in *Loxops* (*sensu* Amadon) may correlate with the size of m. adductor mandibulae externus rostralis temporalis, a muscle that adducts the mandible and probably also retracts the maxilla.

A well-developed process (state 0) was scored if the process projects out from the skull and has an acute angle between its two edges (lateral and medioventral), or in the most extreme development, has these edges approximately parallel. State (1) was assigned to birds with a moderate development of the process, defined as one in which the angle between the two

edges is approximately 90° or greater. Birds that lack a distinct, pointed process and instead have a curved posteroventral rim of the orbit in this region were also assigned state (1).

59. *Ventral lobe of the ectethmoid; narrow (0), intermediate (1), broad (2).* Ordered, weight = 0.5. In the species under study, the ectethmoid has a mediolateral notch that effectively divides the bone into dorsal and ventral lobes. The ventral lobe is usually either narrow or broad (Fig. 12). Richards & Bock (1973) have suggested that deep mediolateral notches (and presumably narrow ventral ectethmoids) have an adaptive value in improving the capacity for unobstructed stereoscopic vision.

60. *Rostral face of the ectethmoid; not inflated (0), intermediate (1), inflated (2).* Ordered, weight = 0.5. The ectethmoid is a relatively thin, double-walled plate of bone in most drepanidines. Its rostral face has an irregular surface in all the species examined, but in some species this face is quite inflated, so that the ectethmoid on each side of the skull projects forward, and together they form the posterolateral walls of a relatively narrow antorbital space surrounding the vomer and maxillopalatines.

Among drepanidines, inflation of the ectethmoid is most pronounced in the highly nectarivorous species of the melanodrepanine group (state 1 in *Palmeria*, state 2 in *Vestiaria*, *Himatione* and *Drepanis*), and also present in certain other species that rely on nectar to a lesser degree (state 1 in *Paroreomyza flammea*, *Loxops parvus* and *L. virens wilsoni*). This suggests an association with nectar feeding, but the correlation is imperfect because not all drepanidines that take nec-

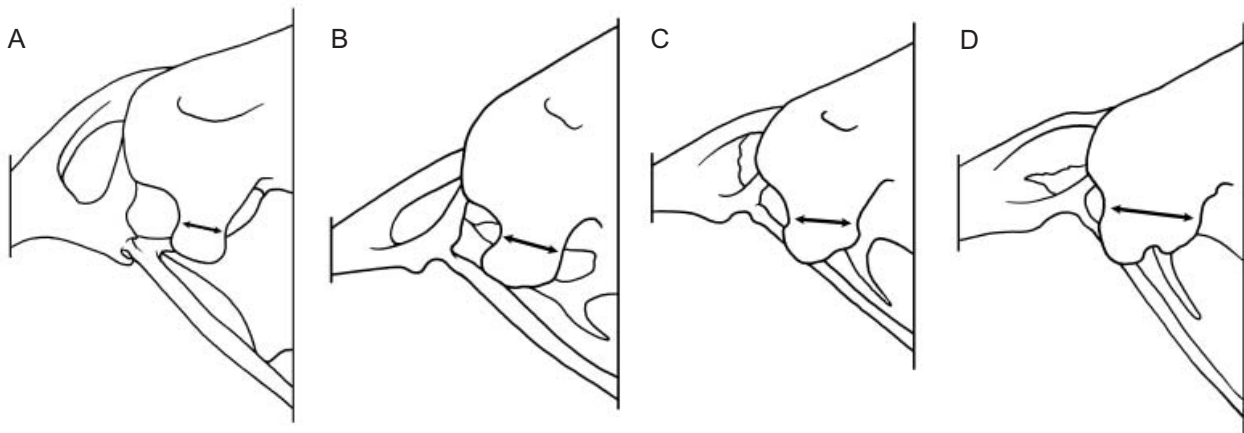


Figure 12. Posterolateral view of the ectethmoid and surrounding bones in selected drepanidines, illustrating the narrow vs. broad ventral lobe of the ectethmoid. The specimens illustrated are *Telespiza cantans* USNM 289283 – narrow (A), *Paroreomyza montana* USNM 502188 – narrow (B), *Loxops* vs. *virens* USNM 553212 – broad (C), and *Himatione sanguinea* USNM 553218 – broad (D). See character 59.

tar have inflated ectethmoids (state 0 in *Loxops virens virens*, *L. flavus* and *L. stejnegeri*).

61. *Orbitonasal foramen undivided posteriorly (0), divided into two distinct foramina both anteriorly and posteriorly (1)*. The olfactory and ophthalmic nerves and the ducts of the nasal gland pass from the orbital cavity to the antorbital space through this foramen or canal (Baumel & Witmer, 1993: 72), sometimes also called the ectethmoid foramen (Richards & Bock, 1973: 37). In most carduelines and drepanidines, the anterior opening is divided into a lateral and a medial foramen. The presence or absence of an anterior division of the foramen exhibits considerable intraspecific variation (also observed by Richards & Bock, 1973), and was not coded for the present analysis.

In *Loxioides bailleui*, the foramen is divided into separate lateral and medial foramina both anteriorly and posteriorly (state 1). This condition also occurs in some of the emberizine outgroup species. The completely divided foramen apparently arises by extension of the anterior bony wall through to the orbital cavity. Baumel & Witmer (1993) state that, in birds with separate foramina, the medial one conducts the olfactory nerve and the medial ramus of the ophthalmic nerve, whereas the lateral one conducts the lateral ramus of the ophthalmic nerve and the duct(s) of the nasal gland.

Of the two fossil specimens ascribed to the genus *Loxioides* from the island of Hawaii, the foramen is completely divided in the adult, and divided anteriorly only in the juvenile. Assuming that the divided foramen is present only in fully adult individuals, I assigned this taxon character state (1) rather than recording it as polymorphic. In some skulls, the bony wall extends nearly but not quite through to the orbital cavity. I scored these as character state (0).

62. *Opening of the orbitonasal foramen to the orbital cavity: slit-like, sometimes divided by a bony wall (0); a wide, oval opening (1)*. The wide, oval opening was observed in the outgroup taxa *Coccothraustes*, *Mycerobas*, *Fringilla*, *Cardinalis*, and *Tachyphonus*.

63. *Olfactory nerve passes through the fonticulus orbitocranialis (0), penetrates the interorbital septum (1)*. Transmission of the olfactory nerve from the brain case to the orbital cavity takes place by two very distinct routes in the species under study. In one set of taxa, the nerve travels through the fonticulus orbitocranialis (state 0). In these birds, the small, often faint olfactory sulcus can usually be seen on the septum, extending between the anterior-most part of the fonticulus orbitocranialis and the orbitonasal foramen.

This sulcus is often superimposed on the larger, more distinctive sulcus that transmits other tissues (apparently including the ethmoidal artery and vein and the ophthalmic nerve) across the interorbital septum from the fonticulus orbitocranialis to the orbitonasal foramen.

In the second group, the nerve leaves the brain case by penetrating the interorbital septum through its posterior face, and then emerges from the interorbital septum on its lateral face within the orbital cavity (state 1). Character state one is easily recognized by the presence of a small olfactory foramen on the lateral face of the interorbital septum, located in or near the larger sulcus mentioned above. In addition, a very small olfactory sulcus can often be observed extending forward from the olfactory foramen toward the orbitonasal foramen.

The olfactory nerve penetrates the interorbital septum in all the drepanidines in which the interorbital septum can be observed. Other than in the drepanidines, penetration of the septum occurs, within the study group, only in four species of cardueline finches (present in *Pyrrhula erythaca*, *Mycerobas melanozanthos* and *Pinicola enucleator*, polymorphic in *Carduelis carduelis*).

Because state one appears to be universally present in drepanidines and shared with only a few species of Carduelini, the character state in genera whose drepanidine affinities have been questioned is of great interest. *Melamprosops phaeosoma* and *Paroreomyza flammea* express state (1), exactly as in the other drepanidines. Penetration of the septum also occurs in *Paroreomyza montana*, although in the three individuals I examined it is bilaterally asymmetrical. The interorbital septum is extremely thin and almost entirely unossified in this species, and an ossified canal leading to a small foramen occurs on one side of the septum only. It is remarkable that the olfactory nerve still penetrates the septum in this species with barely any ossification of the septum at all.

PALATE

64. *Pneumatization of the posterior face of the otic process of the quadrate; absent (0), present (1)*. Many passeriform quadrates have pneumatic openings on the posterior face of the otic process. These openings range from only a single tiny foramen to multiple, large foramina across the entire posterior face. Pneumatization is much more prevalent in the outgroups (present or polymorphic in 22 of 27 taxa) compared with the drepanidines (present or polymorphic in five of 31 taxa). Extensive openings were observed in 12 outgroup species, whereas the few drepanidine specimens with pneumaticity had only a single tiny foramen or a few small openings. Polymorphism in this

character occurs both among individuals of some species, and occasionally between the right and left quadrates of the same individual. The polymorphism involves both the extent of the openings and their presence vs. absence, but only the presence vs. absence was scored for this study. A more thorough accounting of variation in the pneumatic openings might provide additional useful information for systematics.

65. *Medial condyle of the quadrate compact (round/oval) (0), intermediate (1), anteroposteriorly elongate (2)*. Ordered, weight = 0.5. In most outgroups and in the finch-billed drepanidines, the medial condyle of the quadrate has a compact shape, with a circular, oval or sometimes almost square outline (ventral view, state 0).

Within the Drepanidini, many of the thin-billed taxa have an anteroposteriorly elongated medial condyle, although there are some interesting exceptions. Anteroposterior elongation is also present in a few specialized, heavy-billed drepanidines (*Psittirostris psittacea* and *Dysmorodrepanis munroi*), and it reaches its extreme in *Pseudonestor xanthophrys*, which resembles parrots in this respect.

66. *Pterygoid condyle of the quadrate positioned nearly level with medial condyle (1), dorsal to medial condyle (0)*. The pterygoid condyle is a small, distinct knob, usually located dorsal to the medial condyle of the quadrate. In *Pseudonestor xanthophrys*, *Hemignathus lucidus* and *H. wilsoni*, it is positioned more ventrally, nearly level with the anterior edge of the medial condyle.

67. *Pterygoids straight (0), slightly to distinctly bowed (1)*. Slightly bowed pterygoids are present in *Mniotilta varia* and *Akialoa stejnegeri*. Data are missing for the other species of *Akialoa*. In *Hemignathus lucidus*, the pterygoids are distinctly bowed.

68. *Palatine bones joined medially by fusion of the partes choanalis (0), not fused medially, either separated by an open suture or not in contact with each other (1)*. Ankylosis of the interpalatine suture is the rule in the finch-billed drepanidines and the carduelines. Fused palatines were also observed in a variety of other drepanidines with differing bill shapes (e.g. *Pseudonestor xanthophrys*, *Akialoa stejnegeri*, *Oreomyztes bairdi* and *Vestiaria coccinea*). No outgroup species other than carduelines have the suture closed. Amadon (1950: 217) commented that fusion of the palatines in many of the thin-billed drepanidines is a finch-like characteristic.

69. *Transpalatine process, present (0), absent (1)*. The primitive condition in the species under study is almost certainly to possess a very distinct transpalatine process. The process provides part of the surface

for attachment of the pterygoideus muscle (Richards & Bock, 1973). It varies from long and attenuated in nectar-sipping species to short and stout, with a cup-like posterior end, in heavy-billed finches. It is present in all the outgroup species, and in all but two species of drepanidines for which the palatines are known. The process is absent in *Hemignathus lucidus* and *H. wilsoni*. Loss of the transpalatine process in these species may relate to their extreme capacity for cranial kinesis (raising and lowering the maxilla by moving palatal bones).

70. *Palatine process of the premaxilla; absent (= fused) (0), present, attached to the maxillary process of the palatine by an open suture (1), present, free of the maxillary process of the palatine (2)*. Unordered. Perhaps no feature of the passerine skull has received more intense study than the palatine process of the premaxilla, which is the principal subject of two doctoral dissertations (Tordoff, 1954; Bock, 1960). Tordoff made comparisons of the palate in the Fringillidae and allied groups, and concluded that the configuration of the palatine process of the premaxilla ('palatomaxillary') is a good indicator of systematic relationships. Bock showed that the process can have a complex ontogeny. In some species it develops as a free process in embryos but is later joined with the maxillary process of the palatine in mature individuals. When this happens, in some species a suture remains open between the palatine process of the premaxilla and the maxillary process of the palatine in most adults, while in others the suture almost always closes, giving the impression that the palatine process is absent whereas in reality it has become fused. To further complicate matters, the process migrates posteriad during ontogeny in some emberizines such as *Pooecetes*, so that its connection with the premaxilla is lost. After this migration, the process may fuse with the palatine in mature birds, obscuring its complex history and once again giving the impression that it is absent. Unfortunately, distinguishing species in which the palatine process simply fuses in adults from those in which it migrates posteriad during ontogeny and then fuses in adults would require a far better ontogenetic series of specimens than I had available. Consequently, these two conditions were assigned the same score (state 0).

71. *Maxillary process of the palatine broadens anterolaterally to nearly touch the jugal arch (0), flares anterolaterally to articulate with the jugal arch (1), flares anterolaterally but fails to touch the jugal arch (2), relatively narrow anteriorly, does not come near the jugal arch (3)*. Unordered. This rather complicated character encodes some of the additional information provided by Bock (1960) about the juncture of the palatines and maxilla. Carduelines and most

drepanidines possess what Bock termed the lateral flange condition, which refers to anterolateral flaring or broadening of the maxillary process of the palatine. Bock showed that this expansion is accomplished through fusion of the palatine process of the premaxilla with the maxillary process of the palatine. The flared condition is one of the traits that led previous researchers to favour a relationship between drepanidines and carduelines.

In most carduelines and in the drepanidine taxa that have typical finch-like bills, the maxillary process of the palatine is strongly flared, so that it articulates laterally with the jugal arch (state 1). The exceptions among carduelines are *Mycerobas* and *Hesperiphona* (and related species not included in the present study), in which the maxillary process is strongly flared but does not extend far enough laterad to contact the jugal arch (state 2). Based on examination of the holotype fossil specimen of *Orthospiza howarthi*, I tentatively assigned this species character state (2) as well. Many of the drepanidines with more derived bill shapes have the process either flared or broadened anterolaterally. Bock suggested that the latter condition is derived from the former within the radiation.

72. *Origin of maxillopalatine processes on the maxilla; mostly (usually entirely) obscured in ventral view (0), mostly revealed in ventral view (1).* The maxillopalatines attach to the maxilla by a thin strap of bone near the nasal cavity. In carduelines and most drepanidines, the attachment is positioned dorsally and is not visible in the ventral view of the skull. In a small group of thin-billed drepanidines, the attachment is shifted to the medial side of the jugal arch, where it is visible in ventral view. Because of doubts about homology, this character was not scored in the outgroup taxa other than the carduelines. The noncardueline outgroups have a different configuration of the palate in this region.

HYOID SKELETON

73. *Urohyale short (0), intermediate (1), long (2).* Ordered, weight = 0.5. Among the osteological features of the drepanidines that suggest they are related to cardueline finches is the length of the urohyale. The drepanidines and many of the carduelines in the study have the urohyale considerably shorter than in emberizines. The urohyale was judged to be short if its length, from the free end to the posterior-most part of the articular facets for the ceratobranchials, was less than half the length of the basihyale (state 0). In two cardueline and one drepanidine (*Ciridops anna*) taxa, the urohyale is about half the length of the basihyale (state 1). In emberizines, the urohyale is usually well over half the length of the basihyale (state 2).

74. *Ceratobranchiale: Concavity of the dorsolateral surface insignificant or absent (0), moderate (1), extreme (2).* Ordered, weight = 0.5. Bock (1972, 1978) and Richards & Bock (1973) describe the dorsolateral concavity of the ceratobranchiale in various drepanidines, and highlight this as a condition shared with carduelines. In my comparisons, I found the depression to be deep and extensive in most of the cardueline outgroups and in two finch-like drepanidine genera, *Telespiza* and *Loxioides* (state 2). Most other drepanidines have thinner ceratobranchials, with the depression present but shallower and less extensive (state 1). In *Passer domesticus*, the dorsolateral surface is convex, while it is usually slightly indented in the emberizines. The latter two conditions were scored state (0). Good magnification is required to determine the character state in long, thin ceratobranchials such as those of *Mniotilta* and *Paroreomyza*.

75. *Paraglossals (dorsal view) lie roughly parallel to each other (0), lie parallel anterior of the paraglossal-basihyale articulation but diverge posterior of it (1), converge anterior of the articulation and diverge posterior of it (2), converge anterior of the articulation but lie parallel posterior of it (3); diverge anterior of the articulation and lie parallel posterior of it (4).* All the carduelines examined except the two *Loxia* have the paraglossals parallel to each other (state 0). *Loxia* is unusual in having the bones diverge anterior of the paraglossal-basihyal articulation (state 4). The variations identified as states (1), (2) and (3) are largely confined to the emberizine outgroups, although *Oreomystis* and *Paroreomyza* were scored as state one.

76. *Articulating pair of accessory ossicles between the paraglossals, absent (0), present (1).* In the drepanidine taxa *Loxops virens*, *L. stejnegeri*, and *L. parvus*, a pair of accessory ossicles, formed by condensation of bone within the corneous tongue, lie between and ventral to the anterior branches of the paraglossals (state 1). The posterior member of the pair is a compact rod-like bone, whereas the anterior one is broad and flat. The two articulate with each other.

Two related conditions were observed in other species. In *Passer domesticus*, a broad, flat condensation of bone is present below the paraglossals, but the rod-like bone is absent. Also, in one skeleton of *Vestiaria coccinea*, a broad, flat bone is present well anterior of the paraglossals, still attached by connective tissue. Condensations of bone that are independent of the paraglossals may occur in other species as well. Their presence would be hard to detect because they would become unattached during preparation of the skeleton. Consequently, only the condition described as state (1) (which preserves well in

prepared skeletons) was distinguished with a character score.

The extra bone in the tongue of *Passer* was noted by several previous authors and described in detail by Bock & Morony (1978), who named that bone the preglossale. They observed the preglossale in *Passer*, *Petronia* and *Montifringilla*, and considered it very unlikely that a similar bone would evolve in other types of finches.

77. *Paraglossale forms a dorsal crest (0), presents a flat dorsal surface or slopes ventromedial (1)*. The dorsal crest is present in the cardueline outgroups and in *Telespiza* and *Loxioides*. All other drepanidines for which this bone is available have a flat or ventromedially sloping paraglossal, as do the emberizines.

78. *Paraglossals posterior to the paraglossal-basihyal articulation, long (0), short (1)*. The posterior part of the paraglossale is quite short (state 1) in *Vestiaria*, *Palmeria* and *Himatione sanguinea*, all of which are members of Perkins' melanodrepanine division. It is not so short in *Ciridops anna*, another member of the melanodrepanidine division, nor in any other taxon examined.

79. *Paraglossals curl dorsomedial above and posterior of the paraglossal-basihyal articulation (1), do not curl dorsomedial (0)*. The curling paraglossals are characteristic of cardueline finches. Curiously, they do not occur in any of the drepanidines examined, nor in two of the carduelines *Carpodacus thura* and *Loxia leucoptera*.

POSTCRANIAL SKELETON

80. *Coracoid: Lateral process greatly produced (2), intermediate (1), not greatly produced (0)*. Ordered, weight = 0.5. This was scored by examining the dorsal aspect of the coracoid to gauge how far the lateral process extends (laterad) beyond the sternal articular facet. To maintain consistency in scoring, *Cardinalis cardinalis* (USNM 554219) was used as a standard for character state (1); *Telespiza cantans* (USNM 560948) for character state (0).

81. *Coracoid: Blade-like crest on the medial aspect of the shaft above the angulus medialis, present (2), intermediate (1), absent (0)*. Ordered, weight = 0.5. In certain cardueline and drepanidine taxa, the medial side of the shaft above the angulus medialis displays a ridge (state 1) rather than a curved surface (state 0). In other taxa, the ridge is attenuated to form a blade-like crest (state 2).

82. *Humerus: tricipital fossa with pneumatic openings (1), without such openings (0)*. Nearly all taxa in the study lack pneumatic openings in the tricipital fossa.

The exceptions are the two cardinaline finches, *Cardinalis cardinalis* and *Passerina cyanea*, and one tanager, *Tachyphonus rufus*.

83. *Femur with typical proportions (0), very stout (1)*. The extinct genus *Ciridops* is characterized by a very stout hindlimb. There are other taxa in the study with short, stout tarsometatarsi, but none have the tibiotarsus and femur as stout as in *Ciridops*. The stout femur of *Ciridops* is so distinctive that it can readily be identified in fossil collections (James & Olson, 1991).

84. *Tarsometatarsus: The lateral plantar crest is deep and extends toward or contacts the hypotarsus (1); is shallower and less extensive (0)*. In many of the emberizine taxa, the lateral plantar crest is quite deep, particularly near the proximal end of the bone, and in these tarsometatarsi the crest develops a bony process that extends toward and sometimes contacts the hypotarsus.

RESULTS

THE CHARACTER MATRIX

Eighty-four characters (72 cranial, five postcranial and seven in the hyoid skeleton) were scored in 89 terminal taxa, including 24 fossil taxa in the ingroup. Of 34 multistate characters, 26 were judged to be sequential and were run as ordered in the PAUP* analyses. Sixteen of the ordered characters were down-weighted in the analyses (see Methods/Phylogenetic analyses). The down-weighted characters are identified in the character descriptions.

The complete matrix of character scores along with the number of missing scores for each taxon is given in Appendix 1. Mainly as a result of the inclusion of fragmentary fossil taxa, the proportion of missing scores for the Drepanidini is high (22%, compared with <3% for the outgroups). The complete matrix was reduced to several smaller sets of taxa for the PAUP* analyses (matrices A to C, discussed below). For matrices A to C, the number of taxa included, the number of informative characters, and the proportion of missing scores is given in Table 1. The terminal taxa included in each matrix are identified in Appendix 1.

MONOPHYLY OF THE DREPANIDINI

The first set of analyses addressed the monophyly and outgroup relationships of the Drepanidini using matrix A, which includes all the outgroup taxa plus 43 Hawaiian taxa selected to survey the osteological diversity of the radiation while minimizing the amount of missing data. The most complete specimens

for the fossil and historic genera whose drepanidine affinities are in question were included, as well as one or more representatives of each of the other drepanidine genera except *Drepanis*. *Drepanis* was excluded because no complete specimens are available, it is morphologically very similar to *Vestiaria*, and including it causes instability within the melanodrepanine clade.

Heuristic searches of matrix A found one island of 162 optimal trees, all of which support the monophyly of a large Hawaiian clade, the Drepanidini. This is a qualified monophyly, because one fossil taxon, *Orthospiza howarthi* from Maui, falls outside the Hawaiian clade on all the optimal trees. The other three fossil genera, *Xestospiza*, *Vangulifer* and *Aidemia*, join the trees within the drepanidine clade, as do the two extant genera whose relationships have been questioned, *Paroreomyza* and *Melamprosops*. Nodes within the drepanidine clade are fully resolved in the strict consensus, except for the relationships between three terminal taxa, *Loxops caeruleirostris*, *L. coccineus* and *L. mana* (Fig. 13). However, resolution of nodes among the outgroup species is poor.

The relationships among the outgroup species shown in Figure 13 are consistent with traditional classifications in some respects. The species of Emberizinae, Carduelini and Drepanidini each occupy a different portion of the tree, and *Fringilla* (Fringillini) takes an intermediate position between carduelines and emberizines. However, the Emberizinae and Carduelini are depicted as paraphyletic, and some relationships among the species within each of these groups are inconsistent with traditional classifications. This is unimportant and unsurprising, considering that the taxon sample for these groups may be

too small to reveal all of the useful character variation and to resolve their interrelationships. Also, the apparent paraphyly of the emberizine taxa in this study could be an artefact of the choice of outgroup for rooting the tree.

The strength of character support for including *Paroreomyza*, *Melamprosops*, *Xestospiza*, *Vangulifer* and *Aidemia* in the drepanidine radiation was evaluated statistically. Constrained searches were used to find alternative topologies, each of which excluded one of those taxa from the clade composed of the other drepanidines plus their apparent sister taxon (*Pinicola enucleator*). In each case, the Templeton test rejected the constrained topology at the 0.05 level of significance or higher (Table 2).

Two of the fossil genera, *Xestospiza* and *Vangulifer*, are not depicted as monophyletic on the optimal trees. Consequently, the drepanidine affinities of each species in these genera were tested separately (Table 2). Results rejected the alternatives of excluding individual species of *Vangulifer* from the Drepanidini, but did not reject the alternatives of excluding individual species of *Xestospiza*. The test was also applied to *Chloridops regiskongi*, because this distinctive fossil species did not group with the other *Chloridops* on the optimal trees. In this case as well, the alternative of excluding *C. regiskongi* from the Drepanidini was not rejected (Table 2).

Finally, what about *Orthospiza*, the odd finch-like fossil from Maui that was described as a drepanidine (James & Olson, 1991), but appears on the unconstrained optimal trees as sister to the bullfinch genus *Pyrrhula* (Fig. 13)? The Templeton test was applied to an alternative topology that forced *Orthospiza* to join the clade consisting of the drepanidines plus *Pinicola*. This alternative is only

Table 1. The number of terminal taxa, informative characters and proportion of missing scores for matrices A to C

| Matrix | Terminal taxa | | Missing scores (%) | | Informative characters |
|--------|---------------|----------|--------------------|----------|------------------------|
| | Ingroup | Outgroup | Ingroup | Outgroup | |
| A | 43 | 30 | 14.6 | 2.7* | 78 |
| B | 42 | 2 | 14.4 | 1.2 | 59 |
| C | 59 | 2 | 21.9 | 1.2 | 65 |

*Includes *Orthospiza howarthi*.

Figure 13. Strict consensus of 162 optimal trees for matrix A. The arrow points to *Orthospiza howarthi*, the only taxon from Hawaii that does not join the drepanidine clade. Daggers identify taxa that became extinct in historic times; double daggers identify extinct fossil taxa. The optimal trees have a length of 391 steps and a consistency index of 0.26. *These taxa may now be extinct.

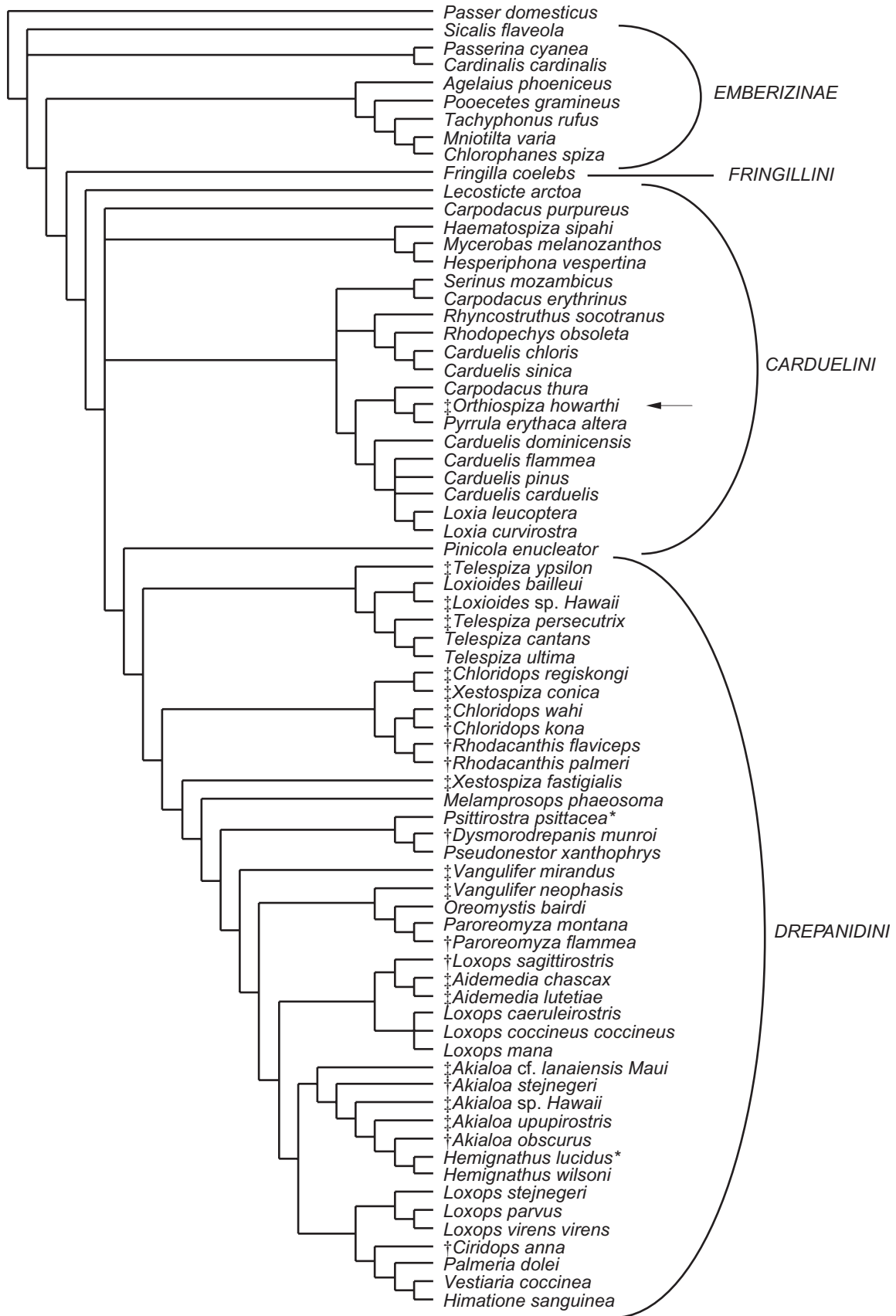


Table 2. Templeton tests of alternative hypotheses for matrix A. Tree topologies consistent with the alternative hypotheses were obtained using monophyly constraints. The probability values are for one-tailed tests. The Methods section (see Evaluating alternative hypotheses) explains how the trees were selected for comparison, when more than one optimal tree was found. The optimal tree length for matrix A is 392 steps

| Alternative hypothesis | Extra steps | <i>N</i> | <i>T</i> | <i>P</i> |
|---|-------------|----------|----------|----------|
| 1. <i>Chloridops regiskongi</i> is not drepanidine | 4.5 | 13 | 30 | 0.12 |
| 2. <i>Xestospiza</i> is not drepanidine | 5.5 | 11 | 14 | 0.03* |
| 3. <i>Xestospiza conica</i> is not drepanidine | 4.5 | 15 | 34.5 | 0.06 |
| 4. <i>Xestospiza fastigialis</i> is not drepanidine | 2.0 | 11 | 27.5 | 0.30 |
| 5. <i>Melamprosops</i> is not drepanidine | 8.5 | 14 | 27 | 0.04* |
| 6. <i>Paroreomyza</i> is not drepanidine | 11.5 | 35 | 207.5 | 0.03* |
| 7. <i>Vangulifer</i> is not drepanidine | 8.5 | 14 | 17 | 0.007** |
| 8. <i>Vangulifer mirandus</i> is not drepanidine | 6.5 | 12 | 15 | 0.02* |
| 9. <i>Vangulifer neophasis</i> is not drepanidine | 8.5 | 10 | 5.5 | 0.006** |
| 10. <i>Aidemia</i> is not drepanidine | 9.5 | 12 | 12 | 0.01* |
| 11. <i>Orthospiza</i> is drepanidine | 0.5 | 12 | 39 | 1.00 |
| 12. Drepanidines and carduelines are sister taxa | 3.0 | 13 | 33.5 | 0.18 |
| 13. Drepanidines are related to emberizines | 12.0 | 26 | 92.5 | 0.01* |

*Significant at the 0.05 level; **significant at the 0.01 level.

half a step longer in tree length compared with the optimal unconstrained trees, and the test showed no statistical support for excluding *Orthospiza* from the Drepanidini (Table 2).

OUTGROUP RELATIONSHIPS OF THE DREPANIDINI

The optimal trees for matrix A show the drepanidine clade embedded within the cardueline finches (Fig. 13), yet most classifications recognize the drepanidines and carduelines as taxa of equivalent rank (e.g. Sibley & Monroe, 1990; American Ornithologists' Union, 1998). Such a classification is consistent with a sister relationship between the two groups but not with the nesting of one within the other, according to phylogenetic principals of classification. A constrained analysis that forced the two groups to be sister taxa produced trees that were only three steps longer than the optimal unconstrained trees, and the Templeton test comparing these alternatives was not significant (Table 2).

The nearly abandoned hypothesis that the drepanidines are related to Neotropical honeycreepers and not to the cardueline finches was also evaluated statistically. The constraint tree required the drepanidines and emberizines to form a clade, without specifying a branching structure within the clade. The test rejected this alternative (Table 2). When forced into confederacy, the Hawaiian and South American nectarivores ('honeycreepers') showed no affinity for each other. Instead, drepanidines remained a monophyletic group, sister to emberizines, with the finch-like species basal.

RELATIONSHIPS AMONG THE DREPANIDINES

Most outgroups were omitted from further analyses. *Orthospiza howarthi*, originally considered a member of the ingroup, was also omitted because this taxon fell outside the drepanidine clade in the analyses of matrix A. *Pinicola enucleator* and *Carpodacus purpureus* were kept in the analyses and were designated as outgroups for rooting the trees. Thus, the taxa in matrix B are exactly the same as in matrix A, but with only two of the outgroup species included.

The analysis of matrix B returned two optimal trees with the same structure for drepanidine relationships as found for matrix A. The two trees differ in the relationships among *Loxops caeruleirostris*, *L. coccineus* and *L. mana*. One of the trees is reproduced as a phylogram in Figure 14, with bootstrap and Bremer support indicated. In interpreting the phylogram, bear in mind that missing data for rare and extinct taxa may contribute to short branch lengths, especially for terminal branches. In addition, low bootstrap support is expected in an analysis with few informative characters in relation to the number of terminal taxa (Table 1). Because character support for most nodes of the trees is weak, the hypothesis of drepanidine relationships derived from parsimony analysis of the osteological data should be viewed as unstable. Nevertheless, the phylogenetic signal from these data can be evaluated through an analysis of congruence and conflict with independent evidence of drepanidine relationships.

To illustrate some of the evolutionary patterns implied by the optimal parsimony trees, 11 clades are identified in Figure 14, and the cranial osteology of

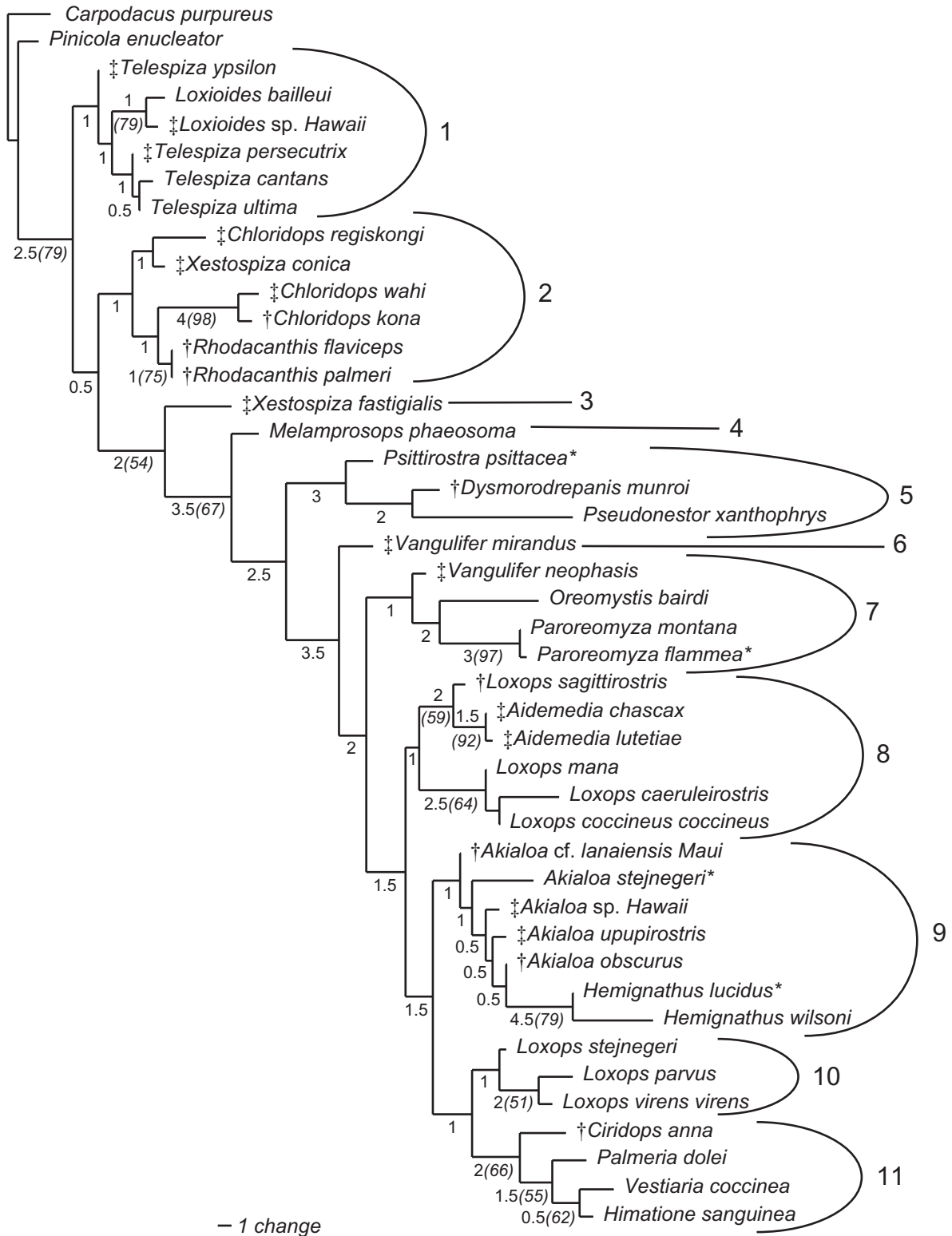


Figure 14. Phylogram showing one of two optimal trees for matrix B (length 193 steps, consistency index 0.42). Eleven clades are identified, and illustrated in Figures 14 and 15. Bremer support (roman numerals) and bootstrap support >50% (italic numbers in parentheses) are indicated. Daggers identify taxa that became extinct in historic times; double daggers identify extinct fossil taxa. The branch lengths were determined with accelerated transformation of states. *These taxa may also be extinct.

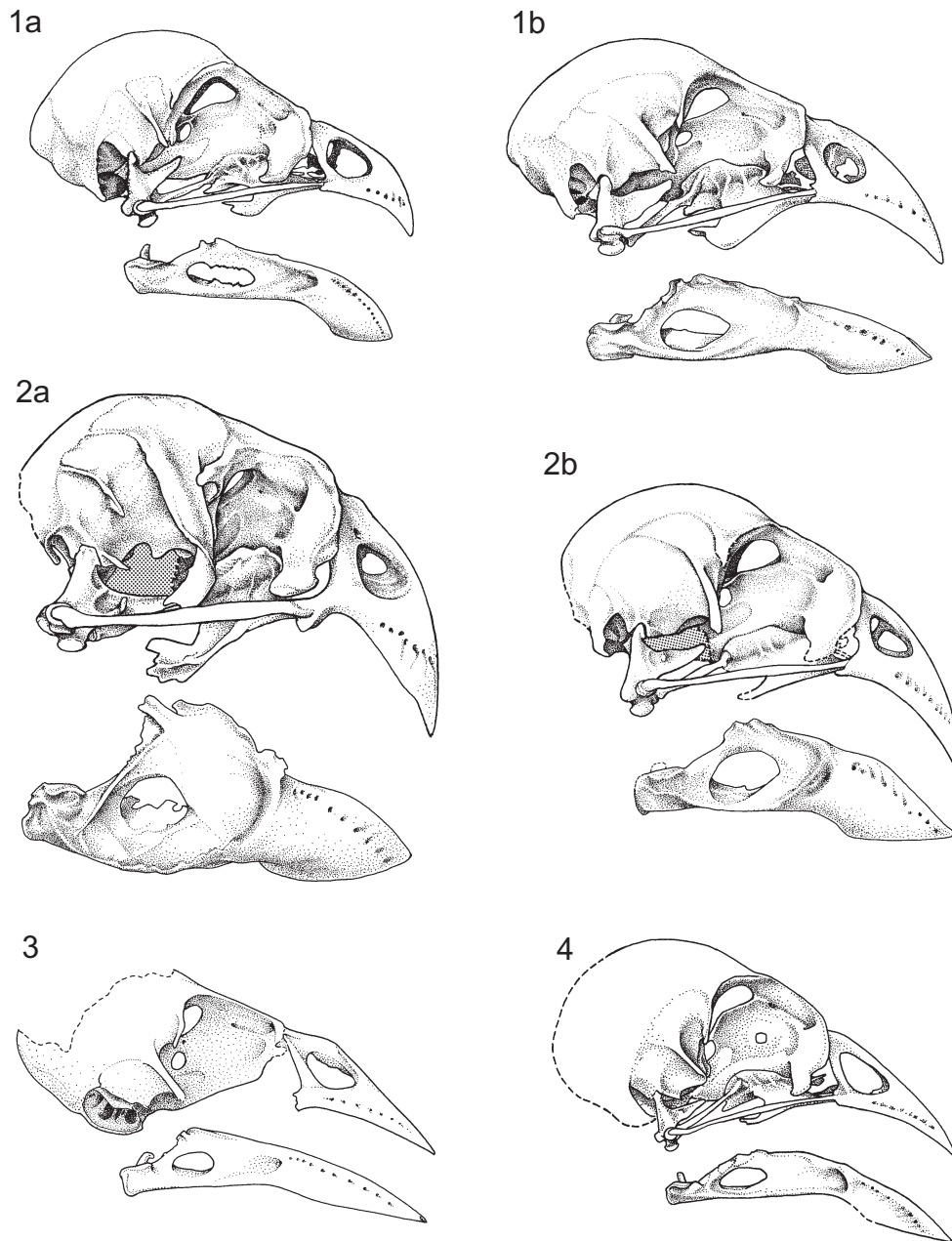


Figure 15. Crania of selected representatives of clades 1 to 4, from Figure 13. Lateral view of the skull and mandible in *Loxioides bailleui* MVZ 122621 (1a), *Telespiza cantans* USNM 502223 (1b), *Chloridops kona* AMNH 453677 (2a), *Rhodacanthis flaviceps* AMNH 453644 (2b), *Xestospiza fastigialis* (3; composite drawing, see material examined), and *Melamprosops phaeosoma* AMNH 810456 (4). Scale bar = 2 cm.

one or two representatives from each clade is illustrated in Figures 15 and 16. The general outline of drepanidine evolutionary history suggested by these results is as follows. The four finch-billed genera *Telespiza*, *Loxioides*, *Rhodacanthis* and *Chloridops* take basal positions on the trees (clades 1 and 2). Two fossil species, *Chloridops regiskongi*, a finch with a

hefty, arched bill from Oahu, and *Xestospiza conica*, a finch with a much straighter, conical bill from Kauai, unexpectedly group together. *Xestospiza fastigialis* and *Melamprosops phaeosoma*, two species that combine finch-like bills with a number of features more common to thin-billed birds, branch off at the next two nodes (clades 3 and 4). Then, the three species of

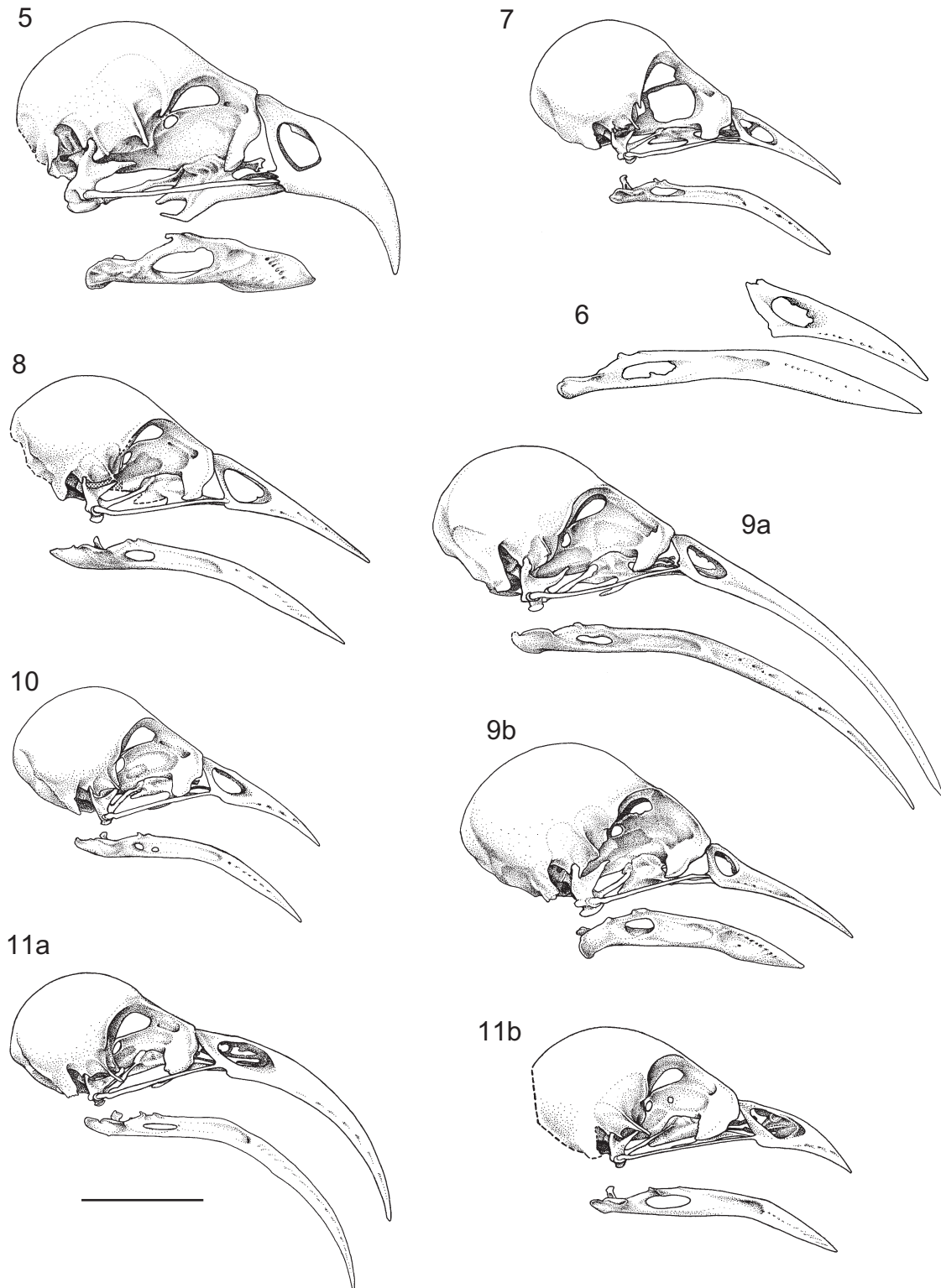


Figure 16. Crania of selected representatives of clades 5 to 11, from Figure 13. Lateral view of the skull and mandible in *Pseudonestor xanthophrys* BMNH S/1961-11-40 (5), *Vangulifer mirandus* USNM 445807 (holotype) and USNM 445808 (6), *Paroreomyza montana* USNM 502188 (7), *Loxops sagittirostris* USNM AMNH 453236 (8), *Akialoa stejnegeri* USNM 19094 (9a), *Hemignathus wilsoni* MVZ 122610 (9b), *Loxops v. virens* USNM 553210 (10), *Vestiaria coccinea* USNM 502204 (11a), and *Ciridops anna* MCZ 10995 (11b). Scale bar = 2 cm.

drepanidines with parrot-like bills (*Psittirostra psittacea*, *Dysmorodrepanis munroi* and *Pseudonestor xanthophrys*) come together in clade 5.

The species in clades 1 to 5 have short, deep bills, whereas those in the large clade that comes next (subsuming clades 6 to 11) predominantly have long, thin bills. Basal in this group are the controversial insectivorous genera *Oreomystis* and *Paroreomyza*, as well as the mysterious fossil genus *Vangulifer* (paraphyletic on these trees; clades 6 and 7). Clade 8 unites birds with straight bills and strong gaping adaptations. (When *Aidemia zanclops* is added to the matrix, with its long decurved bill and strong gaping adaptation, it also joins clade 8; see matrix C, Fig. 17). Clade 9 groups the akialoas and hetero-bills (*Akialoa* and *Hemignathus*), species with long, sickle-shaped maxillae that feed mainly in bark and epiphytes. Clade 10 represents the amakihi complex (Tarr & Fleischer, 1993), excluding only *Loxops sagittirostris*. The placement of *Loxops parvus* in the amakihi complex agrees with traditional classifications (Amadon, 1950; Bock, 1970; Richards & Bock, 1973), but not with more recent genetic and morphological studies (Johnson *et al.*, 1989; Tarr & Fleischer, 1995; Conant *et al.* 1998; Fleischer *et al.*, 2001; Pratt, 2001). Finally, Perkins' melanodrepanine birds come together in clade 11, but this distinct song and plumage group joins the trees at a more proximal node than most previous authors have proposed,

appearing as the sister group of the amakihi complex.

The trees for matrix B show many points of congruence with previous studies, some of which are brought forth in the discussion. The trees also show conflict with previous hypotheses. Important points of conflict were selected for statistical contrasts. For example, a number of genera recognized by James & Olson (1991) are not shown to be monophyletic on the optimal trees. The monophyly of each of these genera was treated as an alternative hypothesis, and the Templeton test was applied (Table 3, alternatives 1–5). In each case, the test failed to reject the hypothesis of monophyly.

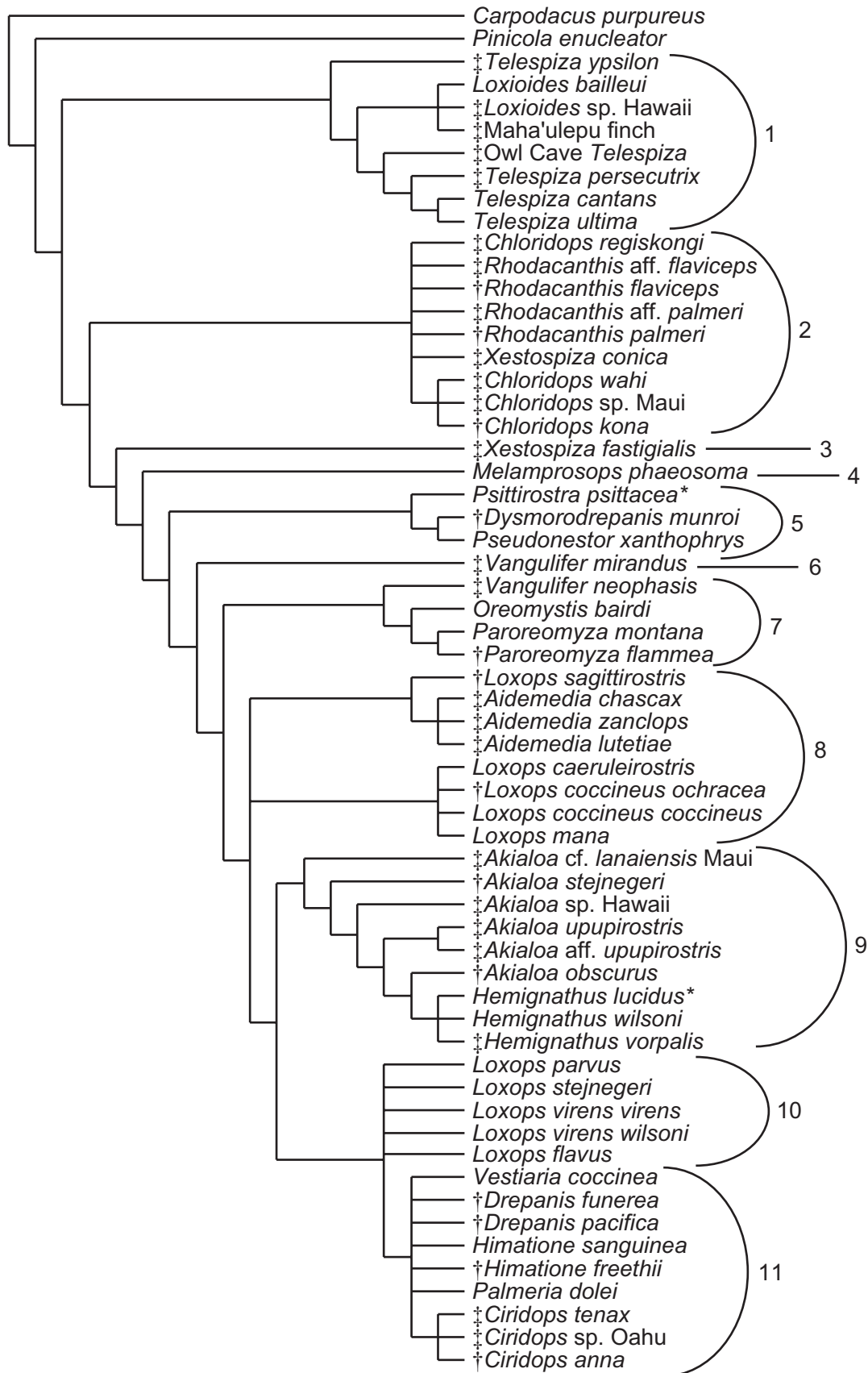
Six genetic studies have produced intriguing findings on the phylogenetic placement of the Kauai and Maui 'creepers' (*Oreomystis bairdi* and *Paroreomyza montana*). Three analyses of genetic data placed these thin-billed insectivores at the base of the drepanidine tree (Johnson *et al.*, 1989; Fleischer *et al.*, 1998; Freed, 1999). A fourth analysis placed *Paroreomyza* basal but not *Oreomystis* (Tarr & Fleischer, 1995). The fifth, which employed essentially the same data as Fleischer *et al.* (1998) but analysed the data with weighted parsimony rather than distance methods, placed both genera higher on the tree in a configuration very similar to the osteological results (Fleischer *et al.*, 2001). The sixth employed the same data as Freed (1999) but used likelihood rather than parsimony analysis, and placed *Oreomystis* but not *Paroreomyza* at the base of

Table 3. Templeton tests of alternative hypotheses for matrix B. Backbone constraints were used to find tree topologies consistent with the alternative hypotheses. The Methods section (see Evaluating alternative hypotheses) explains how trees were selected for statistical comparisons, when more than one optimal tree was found. The optimal tree length for matrix B is 194 steps

| Alternative hypothesis | Extra steps | <i>N</i> | <i>T</i> | <i>P</i> |
|--|-------------|----------|----------|----------|
| 1. Genus <i>Telespiza</i> is monophyletic | 1 | 1 | 0 | 0.16 |
| 2. Genus <i>Chloridops</i> is monophyletic | 1 | 5 | 6 | 0.33 |
| 3. Genus <i>Xestospiza</i> is monophyletic | 3 | 11 | 24 | 0.18 |
| 4. Genus <i>Vangulifer</i> is monophyletic | 2 | 4 | 2.5 | 0.16 |
| 5. Genus <i>Akialoa</i> is monophyletic | 2.5 | 3 | 0 | 0.05 |
| 6. <i>Oreomystis</i> and <i>Paroreomyza</i> are basal taxa | 9 | 15 | 19.5 | 0.006** |
| 7. <i>Paroreomyza</i> is a basal taxon | 13 | 21 | 45.5 | 0.005** |
| 8. Melanodrepanine clade sister to Hemignathini ¹ | 3 | 6 | 4.5 | 0.10 |
| 9. Melanodrepanine clade sister to other drepanidines | 18.5 | 20 | 12.5 | 0.0002** |
| 10. <i>Pseudonestor</i> belongs in Hemignathini ¹ | 4 | 4 | 37.5 | 0.14 |
| 11. Kauai and Hawaii Is. 'creepers' are sisters | 7.5 | 14 | 24 | 0.02* |
| 12. Tubular tongue evolved once and never lost | 5 | 5 | 0 | 0.01* |
| 13. Plantaris muscle lost only once | 1.5 | 4 | 3 | 0.22 |

¹*sensu* Pratt (2001); *significant at the 0.05 level; **significant at the 0.01 level.

Figure 17. Strict consensus of more than 30 000 optimal trees for matrix C. The 11 clades identified in the analysis of matrix B are labelled. The optimal trees have a length of 216.5 steps and consistency index of 0.38. Daggers identify taxa that became extinct in historic times; double daggers identify extinct fossil taxa. *These taxa may also be extinct.



the tree (Lovette *et al.*, 2002). Even though these studies have not converged on a stable tree topology for drepanidine relationships, taken together they suggest that *Paroreomyza* and *Oreomystis* may be basal drepanidine taxa. This alternative hypothesis was evaluated statistically in the context of the osteological data. A constrained topology that forced *Paroreomyza* and *Oreomystis* to compose a basal drepanidine clade was strongly rejected by the Templeton test (Table 3, test 6). A topology that forced *Paroreomyza* alone to be the basal taxon was also strongly rejected (Table 3, test 7).

The parsimony trees recognize a sister relationship between the melanodrepanines and amakihis (clades 11 and 10), a result that agrees with Raikow (1977b) but conflicts with virtually every other previous author. The principal alternatives are Pratt's (2001) weighted topology, in which the melanodrepanine clade is sister to the Hemignathini, and Perkins' idea that the melanodrepanine birds are sister to all other drepanidines (Perkins, 1903; Amadon, 1950). The Templeton test rejected Perkins' placement but not Pratt's (Table 3, tests 8 and 9).

Pratt (2001) separates the thick-billed *Pseudonestor* from *Dysmorodrepanis* and *Psittirostra*, placing it instead with *Hemignathus*. When constrained to seat itself anywhere within the Hemignathini or in the apical melanodrepanine group (clades 8 to 11), *Pseudonestor* did indeed join as sister to *Hemignathus wilsoni*. The Templeton test did not reject this alternative (Table 3, test 10).

The osteological results suggest that the tubular tongue evolved only once in the drepanidine radiation, as it is present only in clades 8 to 11. The trees also show one loss of the tubular tongue, in *Loxops mana*, the only species in clades 8 to 11 without a tubular tongue. (The structure of the corneous tongue is unknown in the fossil taxa, of course.) Several authorities favour the alternative of excluding *L. mana* from clades 8 to 11 and placing it instead in the genus *Oreomystis*, thus requiring only one evolution and no subsequent losses of the tubular tongue (Pratt, 1992b, 2001; Conant *et al.*, 1998). The Templeton test rejected a sister relationship between *L. mana* and *Oreomystis bairdi* (Table 3, test 11), and also rejected a constraint that excluded *L. mana* from clades 8 to 11 (Table 3, test 12).

The plantaris muscle is a very small muscle of the proximal tibiotarsus that has been lost independently several times in the Passeriformes (Raikow, 1978). Presence or absence of the plantaris has been documented in a limited number of drepanidine taxa (Raikow, 1976, 1977b; S. L. Olson, pers. comm.). The limited data available suggest that either it was lost twice, or lost and later regained in the drepanidines, because it is present in clades 5 and 7, absent in clade 8,

present in 9, and absent again in 10 and 11. A constrained analysis required only one loss and no subsequent reappearances of the plantaris by forcing clades 8, 10 and 11 to form a monophyletic group. The Templeton test did not reject this alternative (Table 3, test 13).

DISCUSSION

CONFIDENCE IN THE RESULTS

Some systematists have suggested that convergent and parallel evolution, particularly in the skull and bill, might have obscured the phylogenetic signal from morphological characters in birds (e.g. Mayr, 1958; Sibley & Ahlquist, 1990). Others emphasize that problems with homoplasy in morphological characters could become especially acute within an adaptive radiation such as the drepanidines (e.g. Bock, 1960: 477; Freed, Conant & Fleischer, 1987; Fleischer & McIntosh, 2001). Add to this the perception that morphology provides few useful characters for passerine systematics (Mayr, 1958; Bock, 1962; Groth, 1998), and it is easy to see why so many recent phylogenetic analyses of the oscine passerines have by-passed osteology as data source (exceptions being Cracraft & Feinstein, 2000; Chu, 2002; and James *et al.*, 2003).

In this context, the present study provides encouragement that osteology has continuing relevance to phylogenetic studies of the oscines. Osteological characters provide sufficient information to identify the Hawaiian taxa in the study (excepting one fossil) as monophyletic and to develop a taxonomically inclusive phylogenetic hypothesis for the drepanidine radiation. However, there are too few characters for strong support of all the nodes in the tree. The bootstrap values and Bremer support indices reveal that many branches could be collapsed or moved without tremendous stress to parsimony (Fig. 14). The discussion will consequently focus on identifying aspects of the results in which we can place greater confidence. Confidence is heightened when the results are congruent with independent evidence. In addition, when the nodes supported by the parsimony criterion conflict with specific alternative hypotheses, it can be helpful to evaluate the strength of character conflict statistically.

MONOPHYLY AND ANCESTRY

That the parsimony analysis placed 42 Hawaiian taxa in a clade, and excluded the 30 continental taxa from it, is congruent with the hypothesis of monophyly of a large Hawaiian radiation. Confidence in classifying *Melamprosops*, *Paroreomyza*, *Vangulifer* and *Aidemia* as members of the drepanidine clade is increased by the statistical results. The finding of a single, large Hawaiian clade agrees with many previous studies (Perkins, 1903; Amadon, 1950; Raikow, 1977b, 1978;

Johnson *et al.*, 1989; Tarr & Fleischer, 1995; Fleischer *et al.*, 2001; Pratt, 2001), although the present study includes more taxa and thus defines a larger radiation. The one fossil outlier from Maui, *Orthospiza howarthi*, should be considered *incertae sedis* with respect to tribe (either Carduelini or Drepanidini), but there is no statistical support for excluding it from the Drepanidini. Chu's (2002) recent finding of drepanidine polyphyly may be an analytical artefact, attributable to his sampling only a few drepanidines of widely different morphologies.

The results further corroborate what many previous authors have maintained: that the drepanidine radiation is closely allied with the cardueline finches. The alternative hypothesis that the drepanidines are related to emberizine honeycreepers from South America (Gadow, 1899; Amadon, 1950; Johnson *et al.*, 1989) was strongly rejected by the Templeton test. The optimal trees show the drepanidine clade nested within the cardueline finches, a finding supported by Raikow (1977b) and Groth (1998). However, in terms of statistical confidence, the seating of the drepanidine radiation with respect to carduelines is not resolved by the osteological data.

Characters or character complexes that define major clades are sought and valued by systematists (e.g. Zusi, 1978; Pratt, 1992a, 1992b). Ideally, such characters would change states on the ancestral branch but nowhere else on the tree. Four characters change states unambiguously on the ancestral branch and thus have the potential to diagnose the radiation, but one of the states (undeveloped intercotylar tubercle of the mandible, character 44, state 1) is widely distributed in the carduelines and drepanidines, and therefore not particularly helpful. Two others (extensive muscle scar for *m. pseudotemporalis profundus*, character 36, state 2; dorsomedial curling of the paraglossals, character 79, state 1) help to distinguish the carduelines from other birds in the study, but again do not specify derived conditions unique to the drepanidines. The fourth is more helpful: the scar for *m. protractor pterygoidei sensu stricto* on the interorbital septum is more distinct in nearly all the drepanidines than it is in the other taxa studied (character 50, state 0).

Thus, despite millions of years of isolation in Hawaii (Fleischer *et al.*, 1998), the drepanidines are not distinguished from cardueline finches by an impressive list of osteological differences. This is not really surprising. If the ancestor was a finch that diversified to occupy 'vacant niches' in the Hawaiian Islands, we might expect certain finch-like members of the radiation to persist in the archipelago without undergoing very much morphological change from the ancestral condition. Lineages adapting to insectivory and nectarivory could be expected to undergo much greater morphological change. From this viewpoint, it might

be unrealistic to expect a rapidly diversifying clade such as the drepanidine radiation to be defined by a suite of strict morphological synapomorphies on the ancestral branch.

The path taken by the olfactory nerve as it exits the braincase is arguably the most useful character for diagnosing the Drepanidini. This character also provides insight into the cranial anatomy of the radiation's ancestor. All of the drepanidines plus *Pinicola* have a derived condition in which the olfactory nerve exits the braincase by penetrating through the interorbital septum (character 63, state 1; data are of course missing for the fossil specimens that do not preserve the interorbital septum). All other taxa in the study except a few cardueline finches have the primitive condition in which the nerve exits the braincase through the fonticulus orbitocranialis. The few carduelines with the derived condition are finches with very thick interorbital septa, a condition associated with finch-like bills in the nine-primaried oscines (Zusi, 1978). These facts suggest the following model for evolution of the derived condition. In the primitive state in nine-primaried oscines, the nerve exits the braincase in a sagittal position, through the fonticulus orbitocranialis. With the development of a thick interorbital septum in the carduelines, the fonticulus was displaced laterad, forcing the olfactory nerve out of the sagittal plane as it exits the braincase. Selection to conserve brain anatomy favours maintaining the origin of the nerve in its original sagittal position. In finches with very thick septa, selection thus favours the derived condition in which the nerve regains its more sagittal position by penetrating through the septum. If this interpretation of anatomical evidence is correct, we can infer that the drepanidine radiation had an ancestor with a thick interorbital septum, and a finch-like bill.

Although support for its sister relationship to the Drepanidini is weak, *Pinicola enucleator* (the pine grosbeak) is a reasonable model for the type of bird that could have colonized the Hawaiian Islands and given rise to the radiation. Bock (1960: 477) speculated that the ancestral drepanidines, in order to colonize, 'had to be birds that wander in flocks, preferably erratically, over long distances, and breed at the place to which they have wandered.' The pine grosbeak is a gregarious, Holarctic species that travels in small flocks and sometimes breeds outside its normal range, following irruptive winter movements (Adkisson, 1999). Also important to the success of colonists in a foreign ecosystem may be the ability to tolerate variety in the diet. Pine grosbeaks feed on and near the ground, in trees, and by fly catching, and consume such varied fare as buds, seeds, fruits, insects, spiders and new coniferous leaf tips (Adkisson, 1999). In plumage, pine grosbeaks are likewise good precursors to the radiation: they are sexually dimorphic (true of

most drepanidines), and display both red and yellow carotenoid pigments (common in drepanidines) and streaky plumage (found in *Telespiza*). Crossbills (*Loxia*) are another example of a cardueline genus with many of these characteristics, although with a more specialized bill morphology and feeding niche.

BRANCHING PATTERN WITHIN THE RADIATION

Several experts on drepanidine systematics have expressed concern that phylogenetic analysis of the types of characters used in this study will produce misleading groupings owing to homoplasy (Freed *et al.*, 1987: 196; Fleischer & McIntosh, 2001: 51; Pratt, 2001: 88). Essentially, they worry that morphology will falsely ally birds that have independently evolved, or primitively retained, similar bill shapes and other foraging adaptations. It is therefore worth noting that birds with similar bill shapes do not always group together on the osteological trees. When they do not, they often group instead in ways that are congruent with independent evidence of relationships drawn from plumage, soft anatomy, or genetics. Several examples of this are mentioned below.

The melanodrepanine and chlorodrepanine plumage groups include birds with parallel bill shapes, such as the long, decurved bills of *Drepanis* and *Aki-aloa*, and the short, rather finch-like bills of *Ciridops* and *Loxops caeruleirostris*. Pratt (2001: 88) specifically implied that osteology would fail to correctly segregate birds with similar bill shapes in the two plumage groups. Actually, the osteological trees recognize the melanodrepanine birds as a monophyletic group (clade 11), including the full range of bill shapes from short and conical (*Ciridops*), to dramatically elongated and decurved (*Drepanis*). Clade 8 in the chlorodrepanine plumage group also subsumes birds with diverse bill forms, from relatively short and conical (e.g. *Loxops caeruleirostris*), to long and straight (e.g. *Aidemia chascax*), to long and decurved (e.g. *Aidemia zanclops*). As further evidence that the optimal trees do not simply ally birds of similar bill shape, the trees favour three independent origins of long, thin decurved bills: one in clade 8 – *Aidemia zanclops* (Fig. 17); one in clade 9 – *Aki-aloa*; and one in clade 11 – *Vestiaria* and *Drepanis*. In addition, *Oreomystis bairdi* and *Loxops mana* resemble each other in bill shape, in corneous tongue morphology and in their tree-creeping foraging habit (Pratt, 1992b, 2001; Conant *et al.*, 1998), yet they do not group with each other. Thus, if the osteological trees reflect phylogeny imperfectly, they are imperfect in ways that are subtler than critics have feared.

The optimal trees require only one origination of the tubular tongue, a significant point of congruence with independent evidence because no information on the

form of the corneous tongue was included in the data matrix. Several recent genetic and morphological studies of the drepanidines place one or two of the species that lack tubular tongues within the tubular-tongued clade (*Loxops mana* and/or *Pseudonestor xanthophrys*; Pratt, 2001; Fleischer *et al.*, 1998, 2001; Freed, 1999), implying that if the drepanidine tubular tongue evolved only once, it was secondarily lost at least once. The osteological trees agree in the case of *Loxops mana*, embedding this species in clade 11 with the akepas. The Templeton test rejected the alternative of excluding *Loxops mana* from the tubular-tongued clade and classifying it instead with the other tree-creeping insectivore in the islands, *Oreomystis bairdi* (Pratt, 1992b, 2001; Conant *et al.*, 1998). Independent evolution of the tree-creeping habit in the creepers of Hawaii and Kauai islands is thus favoured by both osteological and genetic data (Fleischer *et al.*, 1998, 2001; Freed, 1999).

In the context of passerine radiations, a trophic adaptation that is even rarer than the tubular tongue is the strongly overhanging maxillary rostrum, which occurs only in the Drepanidini. The optimal trees suggest that it arose twice within the radiation; once in thick-billed birds that lack tubular tongues (*Psittirostra–Dysmordrepanis–Pseudonestor*, clade 5) and once in thin-billed birds that possess tubular tongues (*Hemignathus*, clade 9). This phylogenetic separation of *Psittirostra* and *Pseudonestor* from *Hemignathus* and *Aki-aloa* is inconsistent with the idea that these genera represent stages in the evolutionary transition between the drepanidines with typical finch-like bills and those with typical long, thin bills (Perkins, 1903; Amadon, 1950; Bock, 1970). It agrees with Raikow (1977b), who first pointed out that evolution appears to have accomplished a similar transition several times in other nine-primaried oscines, without taking the complex path of developing and then losing an overhanging rostrum [for example in the Icterini (Beecher, 1951b), 'Geospizinae' (Bowman, 1961), Thraupini (Burns, 1997), and the newly recognized West Indian radiation of Emberizini (Burns, Hackett & Klein, 2002)].

Among the recent phylogenetic analyses of the drepanidines that include at least one species with an overhanging rostrum (Fleischer *et al.*, 1998; Freed, 1999; Fleischer *et al.*, 2001; Pratt, 2001; Lovette *et al.*, 2002), not one interposes these taxa between the finches and the insectivores/nectarivores, so that the idea of a complex morphological transition is not receiving support from any quarter. The studies that include *Pseudonestor* provide inconclusive evidence about its phylogenetic placement, however. In this study, the Templeton test did not reject the alternative hypothesis that *Pseudonestor* is sister to *Hemignathus*, but at the same time, the genetic evidence favouring this alternative is weak due to insufficient taxon sampling. In addition, all of the studies published so far, including

this one, suffer from low character support for the recovered phylogenies. Because of uncertainty about the phylogeny, the evolutionary history of the overhanging rostrum remains poorly understood.

Species with typical finch-like bills were placed at the base of the drepanidine radiation (clades 1 and 2; Fig. 14), in agreement with the topologies published by Raikow (1977b) and Fleischer *et al.* (2001). An intriguing alternative hypothesis is suggested by genetic studies in which certain thin-billed insectivores that lack tubular tongues (*Paroreomyza* and *Oreomystis*) tend to appear at the base of the drepanidine tree (see Results). This could mean either that the original colonist was a thin-billed insectivore, or that it was a finch-billed bird whose early diversification in the archipelago included dramatic morphological adaptation to feeding on arthropods. The latter alternative seems more likely in the case of the drepanidines, in light of the evidence discussed above for a finch-like progenitor of the radiation.

The gene trees that place insectivores at the base of the drepanidine radiation are reminiscent of recent phylogenetic hypotheses for the Galapagos Finches, which place thin-billed warbler finches, *Certhidea*, either as a sister lineage or on basal lineages in relation to the deeper-billed species in that radiation (Sato *et al.*, 1999; Sato *et al.*, 2001; Burns *et al.*, 2002). If the closest outgroups to the Galapagos radiation are finch-billed birds, as indicated by the recent outgroup comparisons of Burns *et al.* (2002), then both of the famous adaptive radiations of passerines in the Pacific may have begun with colonization of a depauperate island ecosystem by a finch, which then rapidly underwent morphological adaptation for the efficient exploitation of arthropods.

While this is an attractive idea, at present it is a poorly supported hypothesis for the drepanidines. The osteological data strongly reject placing *Oreomystis* and *Paroreomyza* as basal lineages, and most genetic studies of the radiation have not included an appropriate taxon sample to resolve the base of the drepanidine tree. In the genetic data set with the largest taxonomic sample, the cytochrome *b* sequences analysed by Fleischer *et al.* (1998, 2001), the inferred tree topology was unstable, with either finches or insectivores appearing on the basal branches depending on the tree-building algorithm and character weighting scheme employed. Thus, a satisfactory resolution of such key questions as the arrangement of taxa at the base of the drepanidine tree, and the evolutionary history of the overhanging rostrum, must await improved sampling of taxa and characters in molecular genetic databases.

CONCLUSION

Adaptive radiation in the Hawaiian finches produced remarkable interspecific diversity in the fine details of

osteology. The present study aimed to encode that diversity in a database and to explore the usefulness of this type of data for systematics. Cranial osteology was emphasized because the morphological divergence among drepanidine species is greater in the cranium than in the postcranial skeleton. The congruence of the parsimony trees with independent evidence such as geographic distribution, presence of a tubular tongue and plumage group, suggests that there is a useful phylogenetic signal in the osteological data. However, the data do not provide strong character support for most nodes in the phylogeny. This is also true of all other recent phylogenetic studies of the radiation, whether genetic or morphological.

The route to a robust and taxon-rich phylogeny for the drepanidines must be through combined analysis of morphological and genetic data, an approach that is not yet feasible because of the limited taxon sample currently available in genetic databases. Fortunately, the extinction of a drepanidine species is not an insurmountable barrier to including it in data sets that draw upon nonosteological characters. Traditional taxonomic characters can be observed in study skins, and ancient DNA can be extracted from them (Fleischer *et al.*, 2001). Considering that fragments of mitochondrial DNA have been recovered from the bones of larger birds from some of the drepanidine fossil sites (for example bones of ducks and geese, see Cooper *et al.*, 1996; Sorenson *et al.*, 1999; Paxinos *et al.*, 2002), sacrificing selected drepanidine fossils for DNA extraction experiments is a promising avenue. The osteological data provided here will enable such combined analyses of the radiation to be taxonomically inclusive, a quality that is frequently needed for inferential studies of evolutionary and ecological processes. In addition, as more genetic data become available, comparative studies of genetic and osteological data should lead to a better understanding of patterns in morphological diversification within this unparalleled adaptive radiation.

ACKNOWLEDGEMENTS

Most of this research was carried out at the National Museum of Natural History, Washington, DC, where I thank Frederick Grady, Mark Florence, James Dean, Robert Fleischer, Sherman Suter, Richard Zusi and especially Storrs Olson for collaboration and support. The project was begun in the Zoology Department, Oxford University, UK, with advice and help from Christopher Perrins, W. J. Kennedy, Thomas Kemp, Jane Pickering, Paul Harvey and E. N. Arnold. I am grateful to many field companions who helped collect the fossils, especially Storrs Olson, Joan Aidem, the Burney family, Michael Severns, Jon Giffin, Pauline Fiene-Severns and the Kikuchi family. Private land-

holders and public land managers in Hawaii who generously granted us access to sites include Pardee Erdman of Ulupalakua Ranch, Lloyd Loope and Arthur Medeiros of Haleakala National Park, Newell Bohnett of Puu Waawaa Ranch, Jon Giffin of the Hawaii Department of Land and Natural Resources, and the managers of Campbell Estates on Oahu.

For the loan of comparative skeletons and fossils in their care, I thank: Ned Johnson, Victoria Dziadosz, Barbara Stein and Carla Cicero of the Museum of Vertebrate Zoology (MVZ; NSF Grant BMS 7200102); Wesley Lanyon, Lester Short and Mary LeCroy of the American Museum of Natural History (AMNH); P. J. K. Burton, Graham Cowles and Ian Galbraith of The Natural History Museum, Tring, UK (BMNH); Allen Allison, Carla Kishinami, Robert Pyle, Terry Lopez and Alan Ziegler of the Bernice P. Bishop Museum (BPBM, BBM, BBM-X); James Dean, Gary Graves, Jann Thompson and Mark Florence of the National Museum of Natural History (USNM); and Raymond Paynter, Jr., of the Museum of Comparative Zoology (MCZ). I owe extra thanks to the staff of the Bishop Museum in Honolulu, who played an enormous role in accessioning and cataloguing fossils and lending them for study. Alan Ziegler established a generous loan program in the early years and Carla Kishinami continues that tradition today.

The stippled illustrations of drepanidine cranial osteology are by Jacquin Schultz (most modern species), Taina Litwak (the fossil species) and Nancy Payzant (*Dysmorodrepanis munroi*). The illustrations are based partly upon photographs by Victor Krantz and John Steiner. My manuscript was improved by comments from Robert Fleischer, Storrs Olson, David Steadman, and Richard Zusi. Financial support came from an Overseas Research Student Fellowship from the British government, the Scholarly Studies Program and Wetmore Funds of the Smithsonian Institution, and NSF DEB-9707260 to David Burney.

REFERENCES

- Adkisson CS. 1999.** Pine Grosbeak (*Pinicola enucleator*). In: Poole A, Gill F, eds. *The birds of North America*, 456. Philadelphia: The Birds of North America, Inc.
- Amadon D. 1950.** The Hawaiian Honeycreepers (Aves: Drepaniidae). *Bulletin of the American Museum of Natural History* **95**(4): 151–262.
- American Ornithologists' Union. 1998.** *Check-list of North American birds*, 7th edn. Washington: American Ornithologists' Union.
- Athens SJ, Tuggle DH, Ward JV, Welch DJ. 2002.** Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai'i. *Archaeology in Oceania* **37**: 57–78.
- Baumel JJ, Witmer LM. 1993.** Osteologia. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, eds. *Handbook of avian anatomy: Nomina Anatomica Avium*, 2nd edn. Cambridge, MA: Nuttall Ornithological Club, Publication 23, 45–132.
- Beecher WT. 1951a.** Convergence in the Coerebidae. *Wilson Bulletin* **63**: 274–287.
- Beecher WT. 1951b.** Adaptations for food-getting in the American blackbirds. *Auk* **68**: 411–440.
- Beecher WT. 1953.** A phylogeny of the oscines. *Auk* **70**: 270–333.
- Bledsoe AH. 1988.** Nuclear DNA evolution and phylogeny of the New World Nine-primaried Oscines. *Auk* **105**: 504–515.
- Bock WJ. 1960.** The palatine process of the premaxilla in the Passeres. *Bulletin of the Museum of Comparative Zoology* **122**: 361–488.
- Bock WJ. 1962.** The pneumatic fossa of the humerus in the Passeres. *Auk* **79**: 425–443.
- Bock WJ. 1970.** Microevolutionary sequences as a fundamental concept in macroevolutionary models. *Evolution* **24**: 704–722.
- Bock WJ. 1972.** Morphology of the tongue apparatus of *Ciriodops anna* (Drepanididae). *Ibis* **114**: 61–78.
- Bock WJ. 1978.** Tongue morphology and affinities of the Hawaiian honeycreeper *Melamprosops phaeosoma*. *Ibis* **120**: 467–479.
- Bock WJ. 1979.** The synthetic explanation of macroevolutionary change – a reductionist approach. *Bulletin of the Carnegie Museum of Natural History* **13**: 20–69.
- Bock WJ, Morony J. 1978.** The preglossale of *Passer* (Aves: Passeriformes) – a skeletal neomorph. *Journal of Morphology* **155**: 99–110.
- Bowman RI. 1961.** Morphological differentiation and adaptation in the Galapagos Finches. *University of California Publications in Zoology* **58**, 1–326.
- Bremer K. 1994.** Branch support and tree stability. *Cladistics* **10**: 295–304.
- Burney DA, James HF, Burney LP, Olson SL, Kikuchi W, Wagner WL, Burney M, McCloskey D, Kikuchi D, Grady FV, Gage R, Nishek R. 2001.** Fossil evidence for a diverse biota from Kauai and its transformation since human arrival. *Ecological Monographs* **71**: 615–641.
- Burns KJ. 1997.** Molecular systematics of tanagers (Thraupidae): evolution and biogeography of a diverse radiation of neotropical birds. *Molecular Phylogenetics and Evolution* **8**: 334–348.
- Burns KJ, Hackett SJ, Klein NK. 2002.** Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evolution* **56**(6): 1240–1252.
- Chu PC. 1995.** Phylogenetic reanalysis of Strauch's osteological data set for the Charadriiformes. *Condor* **97**: 174–196.
- Chu PC. 2002.** A morphological test of the monophyly of the cardueline finches (Aves: Fringillidae, Carduelinae). *Cladistics* **18**: 279–312.
- Conant S, Pratt HD, Shallenberger RJ. 1998.** Reflections on a 1975 expedition to the lost world of the Alaka'i and other notes on the natural history, systematics, and conservation of Kaua'i birds. *Wilson Bulletin* **110**: 1–22.
- Cooper AC, Rhymer J, James HF, Olson SL, Sorenson M,**

- Fleischer RC, McIntosh C. 1996.** Ancient DNA and island endemics. *Nature* **381**: 484.
- Cracraft J, Feinstein J. 2000.** What is not a bird of paradise? Molecular and morphological evidence places *Macgregoria* in the Meliphagidae and the Cnemophilinae near the base of the corvid tree. *Proceedings of the Royal Society of London, Series B* **267**: 233–241.
- Engilis A Jr, Pratt TK, Kepler CB, Ecton AM, Fluetsch KM. 1996.** Description of adults, eggshells, nestling, fledgling, and nest of the poo-uli. *Wilson Bulletin* **108**: 607–619.
- Eriksson T. 1998.** *AutoDecay*, Version 4.0 (program distributed by the author). Stockholm: Department of Botany, Stockholm University.
- Feduccia A. 1993.** Evidence from claw geometry indicating arboreal habits of *Archaeopteryx*. *Science* **259**: 790–793.
- Feldman RA. 1994.** Molecular evolution, genetic diversity, and avian malaria in the Hawaiian honeycreepers. Unpublished PhD Dissertation, University of Hawaii. UMI Dissertation Abstracts number 9519441.
- Fleischer RC, McIntosh CE. 2001.** Molecular systematics and biogeography of the Hawaiian avifauna. *Studies in Avian Biology* **22**: 51–60.
- Fleischer RC, McIntosh CE, Tarr CL. 1998.** Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology* **7**: 533–545.
- Fleischer RC, Tarr CL, James HF, Slikas B, McIntosh CE. 2001.** Phylogenetic placement of the Po'ouli, *Melamprosops phaeosoma*, based on mitochondrial DNA sequence and osteological characters. *Studies in Avian Biology* **22**: 98–103.
- Freed LA. 1999.** Extinction and endangerment of Hawaiian honeycreepers: a comparative approach. In: Landweber LF, Dobson AP, eds. *Genetics and the extinction of species*. Princeton, NJ: Princeton University Press, 137–162.
- Freed LA, Conant S, Fleischer RC. 1987.** Evolutionary ecology and radiation of Hawaiian passerine birds. *Trends in Ecology and Evolution* **2**(7): 196–203.
- Gadow H. 1899.** Remarks on the structure of certain Hawaiian birds, with reference to their systematic position: further remarks on the relationships of the Drepanididae. In (1890–1899): Wilson SB, Evans AH. *Aves Hawaiiensis: the birds of the Hawaiian Islands*. London: R. H. Porter, 219–241.
- Gardner LL. 1925.** The adaptive modifications and the taxonomic value of the tongue in birds. *Proceedings of the United States National Museum* **67**(2591): 1–49.
- Giffin J. 1993.** New species of flightless birds found at Pu'u Wa'awa'a. *Elepaio* **53**: 1–3.
- Goldman N, Anderson JP, Rodrigo AG. 2000.** Likelihood-based tests of topologies in phylogenetics. *Systematic Biology* **49**: 652–670.
- Groth JG. 1998.** Molecular phylogenetics of finches and sparrows: consequences of character state removal in cytochrome *b* sequences. *Molecular Phylogenetics and Evolution* **10**: 377–390.
- Hearty PJ, Kaufman DS, Olson SL, James HF. 2000.** Stratigraphy and whole-rock amino acid geochronology of key Holocene and last interglacial carbonate deposits in the Hawaiian Islands. *Pacific Science* **54**: 423–442.
- Henshaw HW. 1902.** *Birds of the Hawaiian Islands, being a complete list of the birds of the Hawaiian possessions with notes on their habits*. Honolulu: Thos. G. Thrum.
- Homburger D. 1986.** The lingual apparatus of the African Grey Parrot, *Psittacus erithacus* Linné (Aves: Psittacidae): description and theoretical mechanical analysis. *Ornithological Monographs* **39**: 1–233.
- James HF. 1987.** A late Pleistocene avifauna from the island of Oahu, Hawaiian Islands. *Documents de la Laboratoire de Géologie, Lyon* **99**: 221–230.
- James HF, Olson SL. 1991.** Descriptions of thirty-two new species of Hawaiian birds. Part II. Passeriformes. *Ornithological Monographs* **46**: 1–88.
- James HF, Olson SL. 2003.** A giant new species of Nuku-pu'u (Fringillidae: Drepanidini: *Hemignathus*) from the island of Hawaii. *Auk* **120**: 970–981.
- James HF, Ericson GP, Slikas B, Fu-min L, Gill F, Olson SL. 2003.** *Pseudopodoces*, a misclassified terrestrial tit (Paridae) of the Tibetan Plateau: evolutionary consequences of shifting adaptive zones. *Ibis* **145**: 185–202.
- James HF, Stafford TW Jr, Steadman DW, Olson SL, Martin PS, Jull AJT, McCoy PC. 1987.** Radiocarbon dates on bones of extinct birds from Hawaii. *Proceedings of the National Academy of Sciences, USA* **84**: 2350–2354.
- James HF, Zusi RL, Olson SL. 1989.** *Dysmorodrepanis munroi* (Fringillidae: Drepanidini), a valid genus and species of Hawaiian finch. *Wilson Bulletin* **101**: 159–179.
- Johnson NK, Marten JA, Ralph CJ. 1989.** Genetic evidence for the origin and relationships of Hawaiian honeycreepers (Aves: Fringillidae). *Condor* **91**: 379–396.
- Juvik JO, Austring AP. 1979.** The Hawaiian avifauna: biogeographic theory in evolutionary time. *Journal of Biogeography* **6**: 205–224.
- King AS. 1993.** Introduction. In: Baumel JJ, King AS, Breazile JE, Evans HE, Vanden Berge JC, eds. *Handbook of avian anatomy: Nomina Anatomica Avium*, 2nd edn. Cambridge, MA: Nuttall Ornithological Club, Publication 23, xiii–xxiv.
- Lovette IJ, Bermingham E, Ricklefs RE. 2002.** Clade-specific morphological diversification and adaptive radiation in Hawaiian songbirds. *Proceedings of the Royal Society of London, Series B* **269**: 37–42. DOI 10.1098/rspb.2001.1789.
- Mabee PM, Humphries J. 1993.** Coding polymorphic data: examples from allozymes and ontogeny. *Systematic Biology* **42**: 166–181.
- Maddison WP, Maddison DR. 1992.** *MacClade: analysis of phylogeny and character evolution*, Version 3.0. Sunderland, MA: Sinauer Associates.
- Mayr E. 1958.** The sequence of songbird families. *Condor* **60**: 194–195.
- Medeiros AC, Loope LL, James HF. 1989.** Caves, bird bones and beetles: new discoveries in rain forests of Haleakala. *Park Science* **9**: 20–21.
- Novacek MJ. 1992.** Fossils, topologies, missing data, and the higher level phylogeny of eutherian mammals. *Systematic Biology* **41**(1): 58–73.
- Olson SL. 1999.** Kona Grosbeak (*Chloridops kona*), Greater

- Koa-Finch (*Rhodacanthis palmeri*), and Lesser Koa-Finch (*Rhodacanthis flaviceps*). In: Poole A, Gill F, eds. *The birds of North America*, **424**: 1–20. Philadelphia: The Birds of North America, Inc.
- Olson SL, Angle JP, Grady FV, James HF. 1987.** A technique for salvaging anatomical material from study skins of rare or extinct birds. *Auk* **104**: 510–512.
- Olson SL, James HF. 1982.** Prodrromus of the fossil avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology* **365**: 1–59.
- Olson SL, James HF. 1991.** Descriptions of 32 new species of Hawaiian birds. Part I. Non-Passeriformes. *Ornithological Monographs* **45**: 1–88.
- Olson SL, James HF. 1995.** Nomenclature of the Hawaiian Akialoas and Nukupuus (Aves: Drepanidini). *Proceedings of the Biological Society of Washington* **108**: 373–387.
- Paxinos EE, James HF, Sorenson MD, Olson SL, Jackson J, Fleischer RC. 2002.** MtDNA from fossils reveals a radiation of Hawaiian geese recently derived from the Canada Goose. *Proceedings of the National Academy of Sciences, USA* **99**: 1399–1404.
- Perkins RCL. 1901.** An introduction to the study of the Drepanididae, a family of birds peculiar to the Hawaiian Islands. *Ibis, Series 8* **1**(4): 562–585.
- Perkins RCL. 1903.** Vertebrata (Aves). In: Sharp D, ed. *Zoology of the Sandwich (Hawaiian) Isles*, Vol. 1, Part 4. Cambridge: Cambridge University Press, 365–466.
- Perkins RCL. 1919.** On a new genus and species of bird of the family Drepanididae from the Hawaiian islands. *Annals and Magazine of Natural History, Series 9*(3): 250–252.
- Pratt HD. 1979.** A systematic analysis of the endemic avifauna of the Hawaiian Islands. PhD Dissertation, Louisiana State University, Baton Rouge, LA. UMI Microfilms 79-28440.
- Pratt HD. 1992a.** Is the Poo-uli a Hawaiian Honeycreeper (Drepanidinae)? *Condor* **94**: 172–180.
- Pratt HD. 1992b.** Systematics of the Hawaiian 'creepers' *Oreomystis* and *Paroreomyza*. *Condor* **94**: 836–846.
- Pratt HD. 2001.** Why the Hawai'i Creeper is an *Oreomystis*: What phenotypic characters reveal about the phylogeny of Hawaiian Honeycreepers. *Studies in Avian Biology* **22**: 81–97.
- Raikow RJ. 1976.** Pelvic appendage myology of the Hawaiian honeycreepers (Drepanididae). *Auk* **93**: 774–792.
- Raikow RJ. 1977a.** Pectoral appendage myology of the Hawaiian honeycreepers (Drepanididae). *Auk* **94**: 331–342.
- Raikow RJ. 1977b.** The origin and evolution of the Hawaiian honeycreepers (Drepanididae). *Living Bird* **15**: 95–117.
- Raikow RJ. 1978.** Appendicular myology and relationships of the New World nine-primaried oscines (Aves: Passeriformes). *Bulletin of the Carnegie Museum of Natural History* **7**: 1–43.
- Richards LP, Bock WJ. 1973.** Functional anatomy and adaptive evolution of the feeding apparatus in the Hawaiian honeycreeper genus *Loxops* (Drepanididae). *Ornithological Monographs* **15**: 1–173.
- Sato A, O'hUigin C, Figueroa F, Grant PR, Grant BR, Tichy H, Klein J. 1999.** Phylogeny of Darwin's finches as revealed by mtDNA sequences. *Proceedings of the National Academy of Sciences, USA* **96**: 5101–5106.
- Sato A, Tichy H, O'hUigin C, Grant PR, Grant BR, Klein J. 2001.** On the origin of Darwin's finches. *Molecular Biology and Evolution* **18**(3): 299–311.
- Schluter D. 1988.** Character displacement and the adaptive divergence of finches on islands and continents. *American Naturalist* **131**: 799–824.
- Sibley CG. 1970.** A comparative study of the egg-white proteins of passerine birds. *Bulletin of the Peabody Museum of Natural History* **32**: 1–131.
- Sibley CG, Ahlquist JE. 1982.** The relationships of the Hawaiian honeycreepers (Drepanidini) as indicated by DNA-DNA hybridization. *Auk* **99**(1): 130–140.
- Sibley CG, Ahlquist JE. 1990.** *Phylogeny and classification of birds*. New Haven, Connecticut: Yale University Press.
- Sibley CG, Monroe BL Jr. 1990.** *Distribution and taxonomy of birds of the world*. New Haven, CT: Yale University Press.
- Sorenson MD, Cooper A, Paxinos EE, Quinn TW, James HF, Olson SL, Fleischer RC. 1999.** Relationships of the extinct moa-nalos, flightless Hawaiian waterfowl, based on ancient DNA. *Proceedings of the Royal Society, Series B* **266**: 2187–2194.
- Sushkin PP. 1924.** [On the Fringillidae and allied groups.] *Bulletin of the British Ornithologists Club* **45**: 36–39.
- Sushkin PP. 1929.** On the systematic position of the Drepanidae. In: Steinbacher F, ed. *Proceedings of the VI International Ornithological Congress*, Copenhagen, 1926. 379–381. Privately printed, Berlin.
- Swofford DL. 2002.** *PAUP*: phylogenetic analysis using parsimony (*and other methods)*, Version 4.0. Sunderland, MA: Sinauer Associates.
- Tarr CL, Fleischer RC. 1993.** Mitochondrial-DNA variation and evolutionary relationships in the amakihi complex. *Auk* **110**: 825–831.
- Tarr CL, Fleischer RC. 1995.** Evolutionary relationships of the Hawaiian Honeycreepers (Aves, Drepanidinae). In: Wagner WL, Funk VA, eds. *Hawaiian biogeography: evolution on a hot spot archipelago*. Washington: Smithsonian Institution Press, 147–157.
- Templeton AR. 1983.** Phylogenetic inference from restriction endonuclease cleavage site maps with particular reference to the evolution of humans and apes. *Evolution* **37**: 221–244.
- Tordoff HB. 1954.** *A systematic study of the avian family Fringillidae based on the structure of the skull*. Miscellaneous Publication 81. Ann Arbor, MI: Museum of Zoology, University of Michigan.
- Wiens JJ. 1999.** Polymorphism in systematics and comparative biology. *Annual Review of Ecology and Systematics* **30**: 327–362.
- Wiens JJ. 2000.** Coding morphological variation within species and higher taxa for phylogenetic analysis. In: Wiens JJ, ed. *Phylogenetic analysis of morphological data*. Washington: Smithsonian Institution Press, 115–145.
- Wilcoxon F, Wilcox RA. 1964.** *Some rapid approximate statistical procedures*. Pearl River, New York: Lederle Laboratories.

- Wilkinson M. 1995.** Coping with abundant missing entries in phylogenetic inference using parsimony. *Systematic Biology* **44**: 501–514.
- Yuri T, Mindell DP. 2002.** Molecular phylogenetic analysis of Fringillidae, 'New World nine-primaried oscines' (Aves: Passeriformes). *Molecular Phylogenetics and Evolution* **23**: 229–243.
- Zusi RL. 1967.** The role of the depressor mandibulae muscle in kinesis of the avian skull. *Proceedings of the United States National Museum* **123**(3607): 1–28.
- Zusi RL. 1978.** The interorbital septum in cardueline finches. *Bulletin of the British Ornithologists Club* **98**: 5–10.
- Zusi RL. 1987.** A feeding adaptation of the jaw articulation in New World jays (Corvidae). *Auk* **104**: 665–680.
- Zusi RL. 1989.** A modified jaw muscle in the Maui Parrotbill (*Pseudonestor*: Drepanididae). *Condor* **91**: 716–720.

APPENDIX 1

Material examined. The institutions associated with museum acronyms are identified in the acknowledgements.

FOSSIL SPECIMENS EXAMINED

The following fossil specimens formed the primary reference collection for osteological comparisons. Additional specimens at the National Museum of Natural History, Washington, DC, and the Bishop Museum, Honolulu, were also examined. Asterisks identify the fossils that have not been mentioned in the previous literature.

Fringillidae

Fringillinae

Drepanidini

Telespiza persecutrix, skulls, both lacking the palate and maxilla, USNM 523433, 523434. Skull fragments, USNM 523435, 523436. Maxillae: BPBM 158882 (holotype), 177239, 177250, 177254, 177240; BBM-X 155603, 153707, 155885; USNM 255230, 255562, 523437, 523438, 523439. Mandibles: BPBM 177255, 177158, 177194, BBM-X 152693, USNM 253888, 523440, 523442, 523443, 523444, 523445, 523446, 523447, 523448.

Telespiza ypsilon, maxillae: BBM-X 178140, 178141; USNM 253711 (holotype), 253712, 254698, 44579. Mandibles: USNM 254736, 255013, 445718.

*Owl Cave *Telespiza*, partial associated skeleton, BPBM 179438, from Owl Cave, island of Hawaii (c. 250 m a.s.l.; J. Giffin, pers. comm.). The specimen is intermediate in size between *Telespiza persecutrix* and *Telespiza ypsilon*.

**Loxioides* sp., Hawaii, two partial associated skeletons: BPBM 179436 from Umi'i Manu Cave (480 m a.s.l.; Giffin, 1993), and BPBM 179964 from a lava tube near Pu'u Nanaha, Mauna Kea (2683 m a.s.l.; J. Giffin, pers. comm.). This undescribed species has the bill not as foreshortened as in *Loxioides bailleui*.

Chloridops wahi, crania: USNM 523453 (includes skull, maxilla, palatines, pterygoid, quadrate), USNM 523454 (includes skull, maxilla, palatines), USNM 523455 (includes skull, maxilla, pterygoid, damaged palatine. Maxillae: BBM-X 155524 (holotype), 155155, USNM 255568, 445784, 523456, 523457. Mandibles: BBM-X 158681, BPBM 151278, 179521, USNM 253929, 253904, 254980, 445785, 524868. Quadrates: USNM 254981, 254982, 445783, 523451, 524869. Palatines: USNM 254988, 254989, 523452.

Chloridops sp., Maui, mandible: USNM 445786.

Chloridops regiskongi, maxillae: BPBM 158742 (holotype), 158814. Mandibles: BBM-X 151419; USNM 445787, 445788, 445789.

Rhodacanthis aff. *flaviceps*, maxillae: BPBM 158861, USNM 445794. Mandibles: BPBM 179521; USNM 445793, 445796.

Rhodacanthis aff. *palmeri*, cranium: USNM 524870 (includes skull and maxilla). Maxillae: USNM 445792, 524871.

Xestospiza conica, crania: USNM 524872 (includes skull and maxilla), USNM 524873 (includes skull and maxilla). Maxillae: USNM 254881 (holotype), 254951, 524874, 524875. Mandibles: USNM 524876, 524877, 524878, 524879, 524880.

Xestospiza fastigialis, partial skeletons: USNM 445821 (holotype), 394085. Maxillae with frontal attached: USNM 445800, USNM 524881. Maxillae: USNM 322483, 524882. Mandibles: BBM-X 155522, 155728, USNM 445799, 445805.

Melamprosops phaeosoma, partial skeleton, USNM 384745.

Psittirostra psittacea, maxillae: BBM-X 153705, BPBM 158906, USNM 524900. Mandibles: USNM 524896, 524897, 524898, 524899, 524901.

Pseudonestor xanthophrys, partial skeleton: USNM 394089. Quadrate: USNM 524883.

Hemignathus lucidus, maxillae: USNM 524884, 524885, 524894. Mandible: 524895.

Hemignathus vorpalis, partial skeleton: BPBM 179437 (holotype).

Akialoa cf. *lanaiensis*, Maui, maxillae: nearly complete, USNM 508562; posterior half, USNM 508653; anterior fragments, USNM 508564, 508565, 508566. Mandibles: complete specimen, USNM 508661; fragments, USNM 508657, 508658, 508659, 508660.

**Akialoa* sp., Hawaii, partial skeletons: BPBM 179432, 179433, 179434, 179435, all collected from Umi'i Manu, a lava tube cave on Mt. Hualalai (Giffin, 1993). The bill of this species is markedly larger than that of *Akialoa obscurus* of the same island.

Akialoa upupirostris, cranium including skull, maxilla, and damaged palatines, USNM 508665, mandibles: USNM 254171 (holotype), 255211, 255304, 508666, 508557.

**Akialoa* aff. *upupirostris*, mandible (symphyseal part only): BPBM 178865, from Capparris Cave, 2.9 km SSW of Pimoe Cone, East Maui (57 m a.s.l.; F. Howarth, pers. comm.). Like in *Akialoa upupirostris*, the dorsal face of the symphyseal part of the mandible in this specimen is mostly unexcavated.

Vangulifer mirandus, maxillae: USNM 445807 (holotype), 445806. Mandible: USNM 445808.

Vangulifer neophasis, maxillae: USNM 447061 (holotype), 445809, 445810, 445811, 445812. Mandibles: USNM 445813, 524886, 524887, 524888.

Aidemia chascax, maxilla: BBM-X 155844. Mandibles: BBM-X 155523 (holotype), 154918.

Aidemia zanclops, mandible: BBM-X 155160 (holotype).

Aidemia lutetiae, maxillae: BBM-X 152622, BPBM 175622, USNM 445815, 445816, 524889. Mandibles: BBM-X 147441 (holotype), USNM 445817, 445818, 524890, 524891.

Ciridops tenax, maxillae: USNM 254913 (holotype), 254607. Mandibles: USNM 254157, 254158, 254159, 254969, 254971. Femora: USNM 254034, 254035, 254240, 254043, 254044, 254045, 254046, 254047, 254965. Tibiotarsi: USNM 254062, 254079, 254080, 254082. Tarsometatarsi: USNM 254078, 254079, 254080, 254081, 254082, 254083, 254085, 254086, 254167.

Ciridops sp., Oahu, maxillae: BBM-X 155727, USNM 255176, 255179, 255209, 255415. Mandibles: BPBM 155172, USNM 255292, 255429, 255458. Femora: BBM-X 155669, USNM 255124. Tarsometatarsus: BBM-X 155689, USNM 255087, 255257.

**Drepanis funerea*, maxilla: USNM 524892. Mandible: USNM 524893. These two specimens constitute the only records of this species from Maui.

Tribe incertae sedis

Orthospiza howarthi, partial skeleton: BPBM 160712 (holotype). Maxillae: USNM 370557 (imm.), 445797.

Mandibles: USNM 445798, 372838 (imm.)

OSTEOLOGICAL SPECIMENS EXAMINED

The following skeletal specimens formed the primary reference collection for osteological comparisons. A complete list of the skeletons of drepanidines referred to in the course of this study may be found in James & Olson (1991: 25–27). For outgroup taxa, additional specimens in the USNM collections were examined to check for polymorphisms. Characters of the hyoid skeleton in *Ciridops anna* and *Melamprosops phaeosoma* were scored based on the illustrations in Bock's (1972, 1978) anatomical papers.

Passeridae

Passerinae

Passer domesticus (house sparrow, Palearctic), USNM 561838 male, USNM 611663 female.

Fringillidae

Emberizinae

Icterini

Agelaius phoeniceus (red-winged blackbird, North and Middle America), USNM 555417 male, USNM 555411 female.

Parulini

Mniotilta varia (black-and-white warbler, North and South America), USNM 611327 male, USNM 553148 female.

Emberizini

Poocetes gramineus (vesper sparrow, North America and Mexico), USNM 555444 male, USNM 489829 female.

Thraupini

Tachyphonus rufus (white-lined tanager, southern Central America, South America), USNM 612966, USNM 560201 female.

Chlorophanes spiza (green honeycreeper, Middle and South America), USNM 562513 male.

Sicalis flaveola (saffron finch, South America), USNM 556091 male.

Cardinalini

Cardinalis cardinalis (northern cardinal, North and Middle America), USNM 502009 male, 554219 female.

Fringillinae

Fringillini

Fringilla coelebs (chaffinch, Palearctic), USNM 603379 male, USNM 603382 female.

Carduelini

Leucosticte arctoa (Asian rosy-finch, Eurasia), USNM 501467 male, USNM 501466 unknown sex, 498755 unknown sex.

- Pyrrhula erythaca* (grey-headed bullfinch, Himalayas), USNM 319386 male.
Pinicola enucleator (pine grosbeak, Holarctic), USNM 489737 male, USNM 489364 male, USNM 489362 female.
Mycerobas melanozanthos (spot-winged grosbeak, Himalayas), USNM 292174 female.
Hesperiphona vespertina (evening grosbeak, Holarctic), USNM 490808 male, USNM 502235 male, USNM 490244 female, USNM 490800 female.
Carduelis chloris (European greenfinch, western Palaearctic), USNM 226828 male, USNM 492793 female.
Carduelis carduelis (European goldfinch, Palaearctic), USNM 498962 male, USNM 289397 female, USNM 432527 unknown sex.
Carduelis sinica (grey-capped greenfinch, eastern Asia), USNM 291769 male, USNM 318360 female.
Carduelis pinus (pine siskin, North America and Mexico), USNM 490264 male, USNM 490261 female, USNM 499750 female.
Carduelis flammea (common redpoll, Holarctic), USNM 489741 male, USNM 501462 female.
Carduelis dominicensis (Antillean siskin, Hispaniola), USNM 291023 male, USNM 291024 male.
Serinus mozambicus (yellow-fronted canary, Africa), USNM 430417 male, USNM 430362 female.
Carpodacus erythrinus (common rosefinch, Eurasia), USNM 318342 male, USNM 319620 female.
Carpodacus purpureus (purple finch, western North America and Mexico), USNM 491240 male, USNM 501472 female.
Loxia leucoptera (white-winged crossbill, northern Holarctic, Hispaniola), USNM 498863 male, USNM 498846 female.
Loxia curvirostra (red crossbill, Holarctic, Asia, Philippines), USNM 498838 male, USNM 498775 female.
Rhodopechys obsoleta (desert finch, Asia), USNM 289545 female.
Rhyncostruthus socotranus (golden-winged grosbeak, Africa), USNM 488169 unknown sex.

Drepanidini

- Telespiza cantans* (Laysan finch), USNM 289283 male, USNM 561872 female, USNM 560948 sex unknown.
Telespiza ultima (Nihoa finch), USNM 289278 male, USNM 289277 female.
Loxioides bailleui (palila, BBM-X 156555 female, USNM 560602 female, USNM 19098 sex unknown).
Rhodacanthis flaviceps (lesser koa-finch), AMNH 453644 female (bones removed from skin).
Rhodacanthis palmeri (greater koa-finch), AMNH 453623 male (bones removed from skin).
Chloridops kona (Kona grosbeak), AMNH 453677 male (bones removed from skin).
Psittirostra psittacea (ou), USNM 111454 sex unknown (bones removed from skin).
Dysmorodrepanis munroi (Lanai hookbill), BBM 4792 (bones removed from skin).
Pseudonestor xanthophrys (Maui parrotbill), BMNH S/1961.11.46 male, BMNH S. 1961.11.40 female, BBM-240 (skull removed from skin and preserved in alcohol).
Melamprosops phaeosoma (poo-uli), AMNH 810456 immature, sex unknown (bones removed from paratype skin specimen).
Oreomystis bairdi (Kauai creeper), USNM 553183 male, BBM 1231 male.
Paroreomyza montana newtoni (Maui creeper), USNM 502187 male, USNM 502188 male, USNM 502189 male.
Paroreomyza flammea (Molokai creeper), AMNH 453314 sex unknown (bones removed from skin).
Hemignathus lucidus (nukupuu), BMNH S/1961/11.39 sex unknown.
Hemignathus wilsoni (akiapolaau), MVZ 122610 male, MVZ 118830 female.
Akialoa obscurus (lesser akialoa), BBM 4434 male (bones removed from skin).
Akialoa stejnegeri (greater akialoa), USNM 19094 sex unknown.
Loxops caeruleirostris (akekee), BBM 1229 male, USNM 553186, male.
Loxops coccineus coccineus (akepa), BBM 1229 male.
Loxops mana (Hawaii creeper), USNM 19097 sex unknown.
Loxops sagittirostris (greater amakihi), AMNH 453236 sex unknown (bones removed from skin).
Loxops parvus (anianiau), USNM 553188 male, USNM 553190 female.
Loxops stejnegeri (Kauai amakihi), USNM 502195 male, USNM 553193 female.
Loxops virens virens (Hawaii amakihi), USNM 553210 male, USNM 553212 female.
Loxops virens wilsoni (Maui amakihi), USNM 502191 male, USNM 502190 female.
Loxops flavus (Oahu amakihi), BBM-X 145538 female, USNM 553202 female.
Ciridops anna (ula-ai-hawane), MCZ 19095 sex unknown (bones removed from skin).
Himatione sanguinea sanguinea (apapane), USNM 553218 male, USNM 553215 female.
Himatione sanguinea freethii (Laysan honeycreeper), USNM 346246 sex unknown, USNM 301141 sex unknown (bones removed from skin), USNM 301142 sex unknown (bones removed from skin).
Vestiaria coccinea (iiwi), USNM 502203 female, USNM 502204 male.
Drepanis pacifica (Hawaii mamo), BBM 2 sex unknown (bones removed from skin).
Drepanis funerea (black mamo), BBM 4712 sex unknown (bones removed from skin).

APPENDIX 2 *Continued*

| Taxon | Matrix | Missing scores | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|-------------------------------------|--------|----------------|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 0 | 1 | 2 | 3 | 3 |
| 63 <i>Mycerobas melanozanthos</i> | A | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 1 |
| 64 <i>Hesperiphona vespertina</i> | A | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 1 | |
| 65 <i>Carduelis flammea</i> | A | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | ? | 0 | | |
| 66 <i>Carduelis pinus</i> | A | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | |
| 67 <i>Serinus mozambicus</i> | A | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | ? | 0 | ? | | |
| 68 <i>Carduelis chloris</i> | A | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 69 <i>Carduelis carduelis</i> | A | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | |
| 70 <i>Carduelis sinica</i> | A | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | ? | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 71 <i>Loxia leucoptera</i> | A | 4 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | ? | ? | 2 | 1 | 0 | ? | 0 | 2 | 0 | 3 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | |
| 72 <i>Loxia curvirostra</i> | A | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 1 | 0 | 2 | 0 | 3 | 0 | 1 | 0 | 0 | ? | 0 | ? | 0 | |
| 73 <i>Loximistris dominicensis</i> | A | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 74 <i>Haematospiza sipahi</i> | A | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 75 <i>Rhodopechys obsoleta</i> | A | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 76 <i>Carpodacus purpureus</i> | ABC | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | A |
| 77 <i>Rhyncostruthus socotranus</i> | A | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 78 <i>Carpodacus thura</i> | A | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | |
| 79 <i>Carpodacus erythrinus</i> | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 80 <i>Pinicola enucleator</i> | ABC | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | |
| 81 <i>Agelaius phoeniceus</i> | A | 6 | 0 | 0 | 0 | 1 | 2 | 0 | 2 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | ? | 0 | 1 | 0 | ? | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | |
| 82 <i>Passerina cyanea</i> | A | 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | A | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | |
| 83 <i>Cardinalis cardinalis</i> | A | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 84 <i>Mniotilta varia</i> | A | 5 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | ? | 0 | ? | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | |
| 85 <i>Poecetes gramineus</i> | A | 4 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 2 | 0 | 2 | 0 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 0 |
| 86 <i>Tachyphonus rufus</i> | A | 6 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | A | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| 87 <i>Chlorophanes spiza</i> | A | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| 88 <i>Sicalis flaveola</i> | A | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 1 | 0 |
| 89 <i>Passer domesticus</i> | A | 5 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | ? | 0 | 0 | 0 | 0 | 2 | B | 0 | 0 | 0 | 1 | 0 | 1 | ? | 0 | ? | 0 | 0 | |

| 3 3 3 3 3 3 4 4 4 4 4 4 4 4 4 4 5 5 5 5 5 5 5 5 5 5 5 6 6 6 6 6 6 6 6 6 6 7 7 7 7 7 7 7 7 7 7 8 8 8 8 8 | |
|---|--|
| 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 | |
| 0 2 0 2 1 1 0 1 0 0 0 0 2 0 0 0 2 0 2 0 0 1 0 2 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 2 0 0 0 0 ? ? ? ? ? 1 1 0 0 0 | |
| 0 2 0 2 1 1 0 1 0 0 0 0 2 0 0 0 1 0 2 0 0 1 0 2 0 0 0 0 1 0 1 0 0 0 0 0 0 0 2 0 0 0 0 0 0 0 1 0 C 0 0 0 | |
| 0 0 0 C 0 1 0 1 0 0 2 0 0 1 0 0 0 2 0 2 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 2 0 0 0 0 1 0 2 0 0 0 | |
| 0 0 1 C 0 1 0 1 0 0 2 1 0 1 0 0 0 2 0 2 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 2 0 0 0 0 1 1 2 0 0 0 | |
| 0 0 0 2 0 1 0 1 0 0 2 1 0 1 0 0 0 2 0 2 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 2 1 0 0 0 0 0 1 2 0 0 0 | |
| 0 2 0 2 0 1 0 1 0 0 2 0 0 1 0 0 0 1 0 2 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 2 2 0 0 0 0 1 1 C 0 0 0 | |
| 0 1 1 2 0 1 0 1 0 0 2 1 0 1 0 0 0 2 0 1 0 0 1 0 1 0 0 0 0 0 0 A 1 0 0 0 0 0 0 0 1 0 2 2 0 0 0 0 1 0 2 0 0 0 | |
| 0 2 0 2 0 1 0 1 0 0 2 1 0 2 0 0 0 2 0 2 0 0 1 0 1 0 1 0 0 0 0 1 0 0 0 0 0 0 1 0 2 2 0 0 0 1 2 1 0 0 0 | |
| 2 0 0 0 0 1 0 1 0 0 2 1 0 1 0 0 0 2 0 2 0 0 1 0 1 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 1 2 4 0 0 0 0 1 2 0 0 0 | |
| 2 2 1 0 0 1 0 1 0 0 2 1 0 1 0 0 1 2 0 2 0 0 1 0 1 0 1 0 0 0 0 1 2 0 0 0 0 0 1 0 0 1 4 0 0 0 1 1 2 0 0 0 | |
| 0 0 0 ? 0 1 0 1 0 0 2 1 0 1 0 0 0 2 0 2 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 2 0 0 0 0 1 0 2 0 0 0 | |
| 0 1 0 2 0 1 0 1 0 0 0 0 2 0 0 0 1 0 2 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 ? ? ? ? ? 0 1 0 0 0 | |
| 0 2 0 2 0 1 0 1 0 0 2 1 0 1 0 0 0 2 0 2 0 0 1 0 0 0 ? ? 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 ? 0 0 0 0 ? 0 2 0 0 0 | |
| 0 0 0 2 0 1 0 1 0 0 2 0 0 1 0 0 0 0 0 2 0 0 1 0 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 1 0 0 2 0 0 ? 0 1 1 2 0 0 0 | |
| 0 2 0 2 0 1 0 1 0 0 2 1 0 1 0 0 0 2 0 2 0 0 1 0 1 0 0 1 0 0 0 A 0 0 0 0 0 0 0 0 1 0 ? ? ? ? ? 1 0 1 0 0 0 | |
| 0 0 0 2 0 1 0 0 0 1 2 1 0 0 0 0 0 1 0 2 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0 1 0 2 2 0 0 ? 0 0 0 2 0 0 0 | |
| 0 0 0 2 0 1 0 1 0 0 0 1 0 1 0 0 0 2 0 1 0 0 1 0 1 0 1 1 0 0 0 0 1 0 0 0 0 0 1 0 2 2 0 0 0 0 1 0 2 0 0 0 | |
| 0 0 0 2 0 1 0 1 0 0 1 0 0 0 1 0 0 0 1 0 2 0 0 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 2 0 0 ? 0 1 0 2 0 0 0 | |
| 0 0 1 A 0 0 0 0 0 0 2 0 0 0 0 0 0 ? ? 0 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 ? 2 0 2 0 1 0 0 0 2 0 0 1 | |
| 2 0 0 A 0 0 0 1 0 0 0 0 1 0 0 0 C 0 0 A 0 0 1 0 0 0 1 0 A 0 1 0 0 0 1 0 2 3 1 2 0 2 0 ? 0 0 0 2 1 0 1 | |
| 2 0 0 A 0 1 0 1 0 0 0 0 2 0 0 0 2 0 C 0 0 A 0 0 0 0 0 0 1 0 1 0 0 0 1 0 2 0 ? 2 A 3 0 1 0 0 0 2 1 0 1 | |
| 2 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 ? ? 0 1 0 0 1 0 0 2 1 1 0 0 1 1 0 1 1 0 1 3 ? 2 0 2 0 1 0 0 0 2 0 0 1 | |
| 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 ? ? 0 1 0 0 1 0 0 2 1 1 0 0 1 0 0 0 1 0 1 3 ? 2 0 2 0 1 0 0 0 2 0 0 1 | |
| 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 ? ? 0 A 0 0 0 0 0 0 0 1 0 1 0 1 0 0 0 1 0 1 3 ? 2 0 1 0 1 0 0 0 2 1 0 1 | |
| 2 0 0 1 0 1 0 0 0 0 0 0 1 0 0 0 ? ? 0 1 0 0 1 0 0 2 0 1 0 0 1 1 0 0 1 0 1 3 ? 2 0 2 0 1 0 0 0 2 0 0 0 | |
| 0 0 0 A 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 A 0 0 0 0 0 0 1 0 0 0 1 0 0 0 1 0 0 0 ? 2 0 3 0 1 0 0 0 2 0 0 0 | |
| 0 0 0 0 0 0 0 0 1 0 0 B 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 2 0 2 0 ? 0 0 0 2 0 0 0 | |
