FUNCTIONAL ANATOMY AND ADAPTIVE EVOLUTION OF THE FEEDING APPARATUS IN THE HAWAIIAN HONEYCREEPER GENUS *LOXOPS* (DREPANIDIDAE)

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ORNITHOLOGICAL MONOGRAPHS NO. 15

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PREFACE

This study was originally conceived and planned by Lawrence P. Richards as an inquiry into the functional morphology and evolution of the cranial morphology of the Hawaiian Honeycreepers, an aspect of the adaptive radiation of these birds that is still largely unknown. The field studies were conducted in 1951–52, and the initial dissections started in 1952. Soon afterwards, it was apparent that the original plan to cover the entire Drepanididae was not feasible at that time so that the study was restricted to the genus *Loxops*. The resulting thesis "Functional anatomy of the head region of the Hawaiian Honeycreeper genus *Loxops* (Aves, Drepanididae)" was presented in partial fulfillment for the Ph.D. degree, University of Illinois in June 1957. Lack of support and encouragement and, more importantly, lack of suitable publication possibilities precluded its publication at that time. Moreover, the general decline of interest in studies on passerine jaw and tongue musculature in the second half of the 1950's made this period not propitious for such a study. These factors and subsequent development of interest by Richards in other areas of vertebrate biology caused abandonment of the project for several years.

In the fall of 1961, Professor Hobart M. Smith showed Richard's thesis to Walter J. Bock, who had just joined the staff of the Department of Zoology, University of Illinois, expressing his hope that it could be published without further delay. After initial contacts were made, Bock urged Richards to ready his thesis for publication. Further discussions and some work in the summer of 1963 followed, but a series of field trips and changes in position by both Richards and Bock delayed any significant work. Moreover, a number of papers on passerine jaw and tongue muscles and on functional analyses of cranial features necessitated a rather complete review of the thesis and a reworking of several sections.

The task of reviewing the pertinent studies that appeared in the decade since 1957 was formidable in itself, but was rendered impossible by the constant development of new ideas and the modification (some still unpublished) of earlier statements, and by the fact that some of the essential studies (on the redescription of the jaw and tongue muscles) by Bock and his students were still unpublished. Largely because of the latter fact, we decided early in 1968 to work together on the final preparation of this study for publication, so as to bring together the special knowledge of Richards on the natural history and morphology of the Hawaiian Honeycreepers and the special knowledge of Bock on the functional morphology of the passerine jaw and tongue apparatuses. This project occupied most of the summer of 1968. Because the history of each author in this project is quite different and because it became a joint venture late in its development, a few additional comments on responsibilities must be given.

The responsibility and all credit for field observations, obtaining of specimens, dissections of the jaw and the tongue muscles and original descriptions and interpretations belong to Richards. The systems of identification and terminology for the muscles are based upon studies by Bock, but it should be noted that few discrepancies existed between the muscle identifications and terminologies used by Richards in his thesis and those advocated by Bock. Responsibility for the entire paper, functional interpretations and conclusions on the adaptive significances of these cranial features and on the evolution of the group is shared equally as we reviewed, discussed and rewrote the entire manuscript for publication. Hence we look upon this paper as a truly cooperative undertaking in spite of the separate origins of the information and ideas used in reaching the interpretations and conclusions presented herein.

Submitted for publication, April 1970

Final Revision, December 1972

INTRODUCTION

The family of oscine birds endemic to the Hawaiian Islands, the Hawaiian Honeycreepers or Drepanididae, is one of the most spectacular and geographically compact examples of adaptive radiation. Almost the entire range of feeding methods and bill structure known in passerine birds is found within the Drepanididae. This radiation is especially interesting because it has occurred at the low taxonomic level of the family and presumably within a short span of geological time. Although details still remain to be clarified, many evolutionary phenomena are well illustrated by this group of birds—alas, that of extinction is all too well demonstrated by lost members of the Drepanididae (see Greenway, 1967). Consequently, the Hawaiian Honeycreepers have long held the interest of ornithologists and evolutionists, and have been the subject of several monographs (Wilson and Evans, 1890–1899; Rothschild, 1893–1900; Wallace, 1880, 1902; Perkins, 1901, 1903; Henshaw, 1902; Munro, 1944; Amadon, 1950; Baldwin, 1953). Apparently, this family was too poorly known in the middle of the last century to have any role in the initial development of evolutionary ideas; Darwin seems not to have mentioned them at all and Wallace treats them very briefly in the early editions of his "Islands Life." Amadon's (1950) study is of special importance, not only because it is the most recent monograph of the family, but mainly because it is the first (and to date, the only) review of the evolutionary history and classification of the Drepanididae using the ideas generated by recent advances in the New Systematics and the Synthetic Theory of Evolution. He draws together all of the available information on these birds as the foundation for his conclusions on their phylogeny, patterns of speciation, nature and sources of selection forces, and systematics. His monograph is, and quite rightly so, the most authoritative treatment of the Drepanididae and is the source for most discussions of this family in general evolutionary texts. In similar fashion, Baldwin's study is the only analysis of the ecology of these birds using modern approaches to organism-environment interactions. The role of introduced diseases in the widespread and rapid extinction of the Hawaiian Honeycreepers has been discussed elegantly by Warner (1968); his ideas are essential to our conclusions on the adaptiveness of the several species of *Loxops.*

Since fossils of these birds have not yet been discovered, and are not likely ever to be found, the time of original colonization of the Hawaiian archipelago by the form, or forms, ancestral to the present-day drepanidids is not known. Nor can the likely ancestral form be ascertained except by comparative analysis and inference from living birds. Stearns (1946: 2, 85) indicates that the larger Hawaiian Islands were above sea level in

Tertiary times, perhaps as late as the end of the Pliocene epoch of that period. The time of colonization of the Hawaiian Islands by the ancestral stock cannot be dated more exactly than in the Tertiary, but it seems doubtful that colonization took place near either extreme possibility of as early as seventy-five millions of years ago (in the Paleocene Epoch) or as late as the Pleistocene, one million years ago (Knopf, 1949: 8). Zimmerman (1948: 44) considers that land areas capable of supporting forests have been in existence in these islands since late Pliocene times, some five millions of years ago. Carson, Hardy, Spieth and Stone (1970) present an excellent summary of the geological history of the Hawaiian Islands based upon recent findings of global plate tectonics.

Whatever the actual time of colonization, a number of potential empty ecological habitats for passerine birds were present in the Hawaiian Islands. The original habitats may have been the same as those found today or they may have differed somewhat. In any event, some of these habitats were filled by the ancestral drepanidids (along with the few endemic, probably later arriving meliphagids, turdids and muscicapids) to the partial or complete limits of the adaptations and preadaptations of these birds. Subsequent speciation and phyletic evolution into genera and subfamilies (assuming that the Drepanididae are monophyletic) took place with repeated reinvasion of the various islands and with competition for food as a main selection force (Amadon, 1950: 235, 246; 1947: 63, 66).

The combined actions of adaptive radiation and extinction have presumably obliterated traces of the ancestral stock of the Drepanididae and of its early radiation. One cannot simply assume with any justification that any of the extant forms are close representatives of the ancestral stock. No real argument exists today that the Drepanididae arose from the New World nine-primaried complex of oscine birds. Beyond that, most ideas on the possible ancestors of this family may be grouped into two main theories. The earlier one, based largely on the structure and distribution of the tubular tongue, is that the Drepanididae arose from Neotropical Coerebidae or Thraupidae. Because of the vagueness of the Coerebidae and because of the close similarity of at least some of these birds and the Thraupidae, we make no distinction between choice of either of these families as possible drepanidid ancestors in our discussion. Gadow (1891, 1899) was the first worker to advocate this relationship strongly with supporting anatomical data. Amadon (1950: 231–233), Beecher (1951b: 283, 285; 1953: 312–313) and Baldwin (1953: 386–388) accepted Gadow's conclusion and supplied additional support for it, much of it being evidence from jaw muscle patterns provided by Beecher's comparative anatomical studies of the oscine birds. The second and later notion, originally advocated by Sushkin (1929) on the basis of skull and horny palate morphology, is that the Drepanididae evolved from the cardueline finches of the Fringillidae, or from a group directly ancestral to the carduelines (including the genus *Fringilla*). Cardueline relationships of the Hawaiian Honeycreepers has been supported by Bock (1960b: 477–478) on the basis of jaw muscles (in disagreement with Beecher's conclusion), Tordoff (personal communication) on the basis of general nesting habits, and Sibley 1970: 104–105 on the basis of comparative study of several protein systems. For the purposes of this paper, we accept tentatively the cardueline theory for the ancestors of the Drepanididae. The jaw muscles of *Loxops* support this theory better than the thraupid theory, but a sound comparative study must be undertaken before more definite conclusions can be offered. Moreover, we emphasize that the major conclusions of the present study depend to a very minor degree on accepting the cardueline theory of drepanidid ancestry.

Amadon (1950), whose classification we follow, divides the Drepanididae into two subfamilies, the Drepanidinae and the Psittirostrinae. The correct name for this family is the Drepanididae, not the Drepaniidae, following the favorable decision by the International Commission on Zoological Nomenclature (Anon., 1961) on the proposal by Amadon (1960) to place the name Drepanididae Gadow, 1891 on the Official List of Family-Group Names. The Drepanidinae consists of five genera (*Himatione, Palmeria, Ciridops, Vestiaria,* and *Drepanis*) and the Psittirostrinae of four (*Loxops, Hemignathus, Pseudonestor,* and *Psittirostra*).

Amadon (1950: 164–168) merged four genera of earlier workers (*Viridonia, Chlorodrepanis, Paroreomyza,* and *Loxops*) into a single genus *Loxops,* recognizing three subgenera, *Viridonia, Paroreomyza* and *Loxops.* Each of these subgenera are widely distributed throughout the main islands of the Hawaiian archipelago (Fig. 1). While the final draft of this manuscript was being prepared, volume 14 of "Peters' Check-list," containing the Drepanididae was published. Greenway (1968), in treating this family, divided Amadon's *Loxops* into three genera corresponding to the subgenera recognized by Amadon; unfortunately, no reasons were given for this change. Because our study excluded features of the external morphology and many aspects of their behavior and life-history, and because we did not include all members of the family, we are unable to evaluate the merits of Amadon's system versus that of Greenway. Discussions between Bock and Greenway of the reasons underlying Greenway's treatment of the *Loxops* group as opposed to Amadon's could be summarized as differences in opinion on the width of generic limits in the Drepanododae. Our preference is for broader generic limits, but even so, we lack comparative evidence on which to base any argument including the difficult question on the relationship between the members of *Loxops* and the members of *Hemig-*

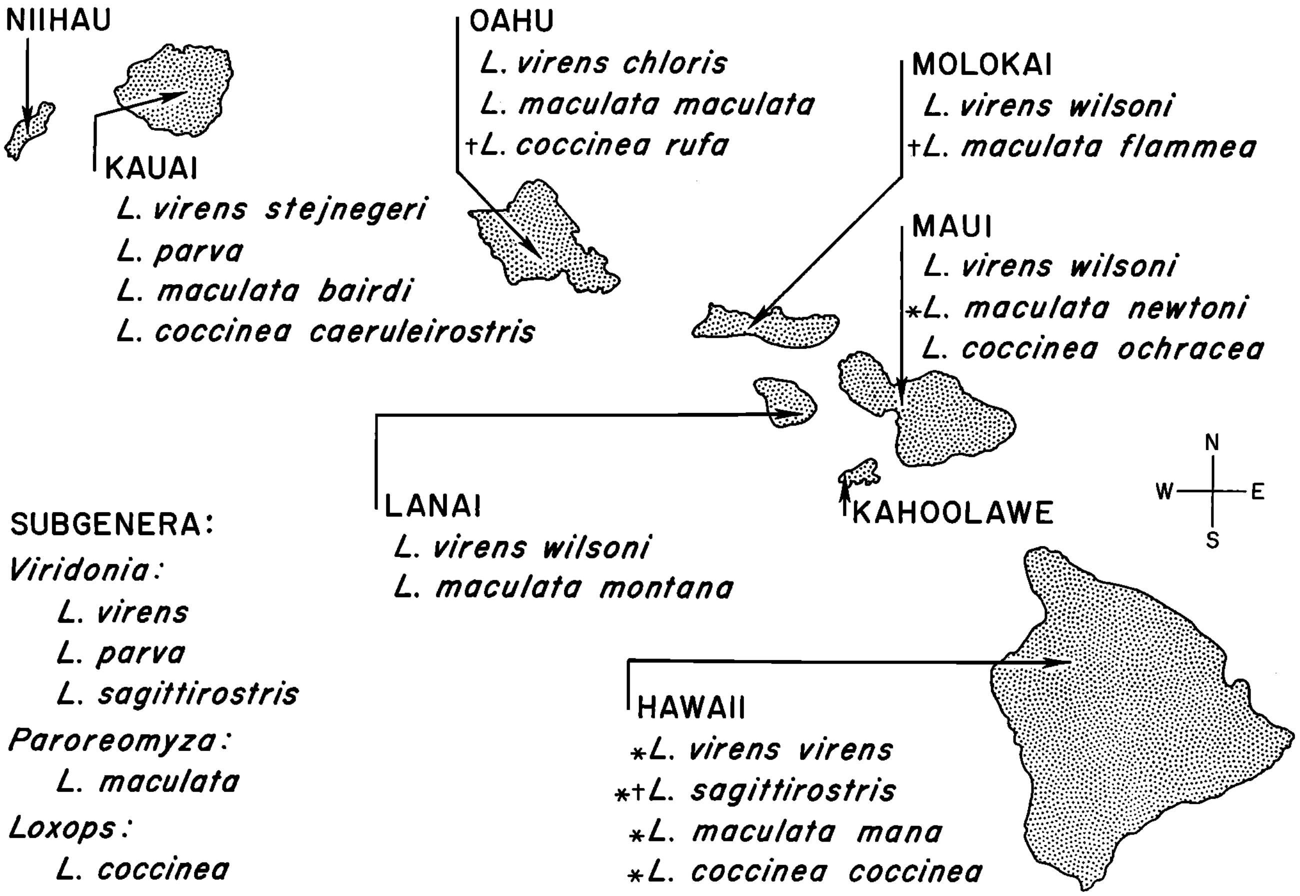

Figure 1. Distribution of the species and subspecies of *Loxops* in the Hawaiian Islands. Extinct taxa are marked with a cross; the forms studied in this analysis are indicated by an asterisk.

nathus. However, because we prefer broader generic limits, and more importantly because of the practical reasons of the ease of style in dealing with one, not three genera, we continue to follow (without prejudice) Amadon's generic treatment of the genus *Loxops.*

The subgenus *Viridonia* contains three species, the Amakihis, *Loxops virens*; the Anianiau, *Loxops parva* (Kauai); and the Greater Amakahi, *Loxops sagittirostris* (Hawaii, extinct). The last two are monotypic species. *L. virens,* however, contains four races which inhabit six islands: *L. v. virens* (Hawaii), *L. v. wilsoni* (Maui, Molokai, Lanai), *L. v. chloris* (Oahu) and *L. v. stejnegeri* (Kauai); *stejnegeri* is quite different in bill structure from other members of *L. virens.* The subgenus *Paroreomyza* contains one species, *Loxops maculata,* the Creepers, which is composed of six subspecies inhabiting six islands: *L. m. mana* (Hawaii), *L. m. newtoni* (Maui), *L. m. flammea* (Molokai, extinct), *L. m. montana* (Lanai), *L. m. maculata* (Oahu), and *L. m. bairdi* (Kauai). The subgenus *Loxops* contains one species, the Akepas, *Loxops coccinea,* which has four races on four islands: *L. c. coccinea* (Hawaii), *L. c. ochracea* (Maui), *L. c. rufa* (Oahu, extinct) and *L. c. caeruleirostris* (Kauai).

The genera of Hawaiian Honeycreepers differ widely with respect to shape and size of the bill and tongue, and presumably in associated anatomical features. In many cases, as might be expected, direct correlations can be made between jaw and tongue morphology in the several genera and the uses (biological roles) to which these structures are put by the birds in obtaining food. However, the details of these correlations and similar intrageneric correlations have not yet been described; such conclusions depend upon a combination of precise field observations, morphological dissections and, if possible, experimental studies.

Considerable field observations on the habitats, food and feeding methods of Hawaiian Honeycreepers are available, most of them done by a few workers who had the opportunity to reside on the Hawaiian Islands for several years. Many of these observations cannot be repeated today because several species of drepanidids are extinct or exist in smaller populations than they did at the time these earlier workers were active. The more important writings on the natural history of the Hawaiian Honeycreepers include Perkins (1893, 1895, 1901, 1903), Munro (1944), Henshaw (1902), Bryan (1908) and Baldwin (1953).

Anatomical investigations of the drepanidids have been scanty, far fewer than the available field observations and far fewer than permitted by long-available materials. In truth most of these anatomical studies should be classed as descriptive external morphology. The earliest and still most extensive work is that of Hans Gadow whose results were published as supplements to Wilson and Evans' great monograph (1891 and 1899:

219–249). Most of the remaining work (Rothschild, 1893–1900: pls. 82 and 83; Hartert, 1893: xx; Lucas, 1897: fig. 3b; Gardner, 1925: 27–28, and pl. 3, fig. 19, pl. 13, fig. 140; Sushkin, 1929: 379–381; and Munro, 1944: 100, 119) deals with the structure of the tongue, rhamphotheca (including the horny palate) and skull structure. Amadon (1950: 213–229) has a section on comparative anatomy in which he discusses and figures those aspects of drepanidid morphology described by earlier workers and comments upon the systematic relevance of these features. Finally, Beecher (1951b: 283, 285, fig. 5; 1953: 310, 312–313, fig. 15) hypothesizes on the relationships of the Drepanididae to the Thraupidae via the medium of jaw musculature pattern, horny palate, tongue architecture and other features.

A detailed investigation of the structural and behavioral adaptations for feeding in this highly interesting example of adaptive radiation has been long overdue. Not only is the amount of published work sadly insufficient for any theorizing on the possible relationships and evolution of this family, but much of it was done many years ago when our understanding of functional morphology, in general, and of the avian jaw and tongue apparatus, in particular, was inadequately known. Moreover, recent developments in many fundamental concepts of comparative morphology have revitalized the entire field and have provided a far sounder basis for comparative anatomical-evolutionary studies. We propose to undertake an extensive investigation of the adaptive radiation of the feeding apparatus in the Drepanididae based upon the recently developed concepts of evolutionary morphology.

As a start into this project, we chose to study the functional morphology and evolution of the feeding apparatus in the genus *Loxops*, concentrating upon the following taxa: *L. sagittirostris* (in part only), *L. virens virens*, *L. maculata mana*, *newtoni*, and *L. coccinea coccinea*. The rhamphothecal, skeletal and muscular features of the jaws and tongue apparatus will be described and compared in detail. Types of food taken and methods of feeding will be correlated as far as possible with the morphological features of the jaws and tongue and with their functional interpretations. Finally, we hope to speculate on the evolution of these feeding adaptations and of the taxa within *Loxops*.

The genus *Loxops* is particularly advantageous for this initial study. It has been long considered as the most primitive group in the Psittirostrinae and close to, if not, the most primitive stock in the whole family. Moreover, members of this genus show considerable variation in their morphology and feeding methods which include: (a) nectarivorous–insectivorous leaf gleaners; (b) insectivorous leaf and bark gleaners; (c) bark and other crevice probers; and (d) cross-billed insectivorous leaf-bud and bean-pod openers. The species of *Loxops* have widespread sympatry with almost every major island possessing races of the three common species (*virens*, *maculata* and *coccinea*). These species are still sufficiently common to permit field observations on their feeding methods. Moreover, several practical reasons determined the choice of this genus and of the particular species studied. Some specimens of *L. virens* and *maculata* were already available to Richards at the outset of the study, and the other forms were sufficiently common to permit taking of additional specimens. Members of *L. virens*, *maculata* and *coccinea* could be observed on Maui and Hawaii, islands on which living accomodations were readily available to Richards as well as possessing sufficient roads allowing travel to the interior of the islands where the birds are found. Moreover, a search for *L. sagittirostris* could be undertaken on Hawaii. Sufficient funds and living accomodations on Kauai were not available to Richards to permit inclusion of *L. parva* in this study.

ACKNOWLEDGMENTS

The unusual development of this study with one author (Bock) joining the project long after completion of the original research and writing of the thesis, necessitates separation of the acknowledgements. Each part of these acknowledgements will be signed and reference of the first person pronouns, be they singular or plural, should be readily apparent.

So many people have aided me in my field work and research in so many ways that it will be difficult to acknowledge all of them for the thanks they are due. I am indebted to many friends and relatives in the Hawaiian Islands who so generously aided and showed me hospitality and gave me access to their homes, mountain cabins, ranch lands and roads, vehicles and saddle horses. Included among these people are my grandmother, Isabelle Jones, my parents, Robert and Catherine Thompson, my uncle and aunt, Howard and Helen Farrar, my friend William Harkins of Maui and a number of the cattlemen of the Kona coast and Mauna Kea, Hawaii: R. L. Hind, Sr. and Jr., Norman Greenwell, Sherwood Greenwell, William Thompson, Herbert Shipman, Hartwell Carter, and Roger Williams. I wish to thank Collin Lennox, Donald Smith and the other members of the Board of Commissioners of Agriculture and Forestry of the Territory of Hawaii for appointing me honorary biologist and issuing permits for the collection of drepanidids in the forest reserves; Robert Hiatt of the University of Hawaii, for giving me equipment and supplies for the preservation of specimens; members of the staff of the Hawaii National Park Service for giving me access to cabins and other facilities at Kilauea and Haleakala;

Edwin H. Bryan, Jr., Curator of Collections at the Bishop Museum Honolulu, for loan of specimens, Alden H. Miller, director of the Museum of Vertebrate Zoology at Berkeley, California, for access to drepanidid skeletal specimens and for generously putting at my disposal photographic equipment and supplies. To my wife, Christina M. Richards, and my good friend, Robert H. S. Glaser of Sacramento Junior College, California, I am grateful for aid in the translation of parts of German publications on avian anatomy. Paul H. Baldwin of Colorado Agricultural and Mechanical College, gave me much valuable advice, information and encouragement before and during the conducting of my field work; furthermore, he put at my disposal sixteen alcoholic specimens of Drepanididae, four of which were used in this study. William Beecher of the Chicago Natural History Museum also passed on to me useful advice and information and answered for me many questions put to him in correspondence. I wish to thank my advisor, Dr. Hobart M. Smith, and former advisors, Drs. Alden H. Miller and Harvey I. Fisher, for their patience, encouragement and helpful advice. This dissertation (Richards, 1957) was written in partial fulfillment of the requirements for the doctor of philosophy degree at the University of Illinois, Urbana.—L. P. Richards.

We wish to thank Mrs. Frances Jewel who devoted much skill and care in assembling, correcting and labeling the original figures drawn by Richards and used in his thesis into the final plates used in this study, and in drawing a number of new plates and text figures that became necessary during the final phases of this study. We would also like to thank Miss Suzanne Budd who completed much of the labeling and undertook the long and arduous task of final corrections and additions to the figures. We would like to thank Drs. H. Morioka, R. S. Hikida, J. L. Cracraft and C. R. Shear for their many helpful comments and suggestions given in the course of many discussions during the summer of 1968 and thereafter. The final manuscript was typed by Mrs. Julia Cracraft who transformed our handwritten scrawl into a clean typescript wonderfully free of mistakes. Dr. Dean Amadon made the facilities of the Department of Ornithology, American Museum of Natural History available to us and provided us with much valuable advice and suggestions from his extensive knowledge of the Drepanididae for which we are most grateful. Support for the completion of this project and for readying the manuscript and figures for publication came from a grant to W. J. Bock from the National Science Foundation (N.S.F.-G.B. 6909X) for studies on the feeding apparatus of the New World nine-primaried oscines. We wish to thank the National Science Foundation for agreeing to changes in the use of these grant funds which was the critical factor permitting the completion and publication of this study.—L. P. Richards and W. J. Bock.

METHODS AND MATERIALS

Field Studies: Because the goal of this study was to correlate some of the anatomical structures of the head region with use of the bill and tongue in feeding, not only were specimens of the Drepanididae needed but also as many recorded observations as possible on the methods of feeding. Even though such men as Perkins, Munro, Henshaw and Bryan recorded much valuable information on feeding behavior, they undoubtedly did not write with the thought in mind that their observations would be used subsequently in studies of functional anatomy. Therefore, it was important that the feeding of these birds be observed personally under natural conditions and the minutiae of use of the bill and tongue recorded as fully as possible from the standpoint of one interested in the muscular and skeletal apparatuses involved.

Between August 11, 1950, and January 17, 1951, a total of 59 days were spent by Lawrence Richards in the forests of Hawaii, Maui and Oahu, collecting and observing drepanidids. Prior and subsequent to this period, five other days were spent for the same purposes. During these periods, 94 pages of species accounts on drepanidids were written, of which 35 were on *Loxops*, and 48 drepanidids were collected, of which 23 were *Loxops*. Paul H. Baldwin gave Richards seven additional alcoholic specimens of this genus, and the Bishop Museum loaned two incomplete alcoholic specimens of *sagittirostris*, on which only the occipital regions of the crania remained. Of these 32 specimens of *Loxops*, 25 were studied: *L. sagittirostris* (2 alcoholics), *L. v. virens* (8 alcoholics), *L. m. mana* (3 alcoholics, 1 skeleton), *L. m. newtoni* (5 alcoholics, 2 skeletons), *L. c. coccinea* (3 alcoholics, 1 skeleton). In addition to these specimens, 27 skeletons of *L. v. virens* and one of *L. m. mana* were available from the Museum of Vertebrate Zoology. Admittedly, the number of specimens of each form available for dissection and study is pitifully small, and these small numbers of specimens had to be used as the basis for statements, suppositions, and conclusions concerning the whole living population of each species or race studied. We realize that this is not necessarily scientifically sound but feel that this study and its conclusions are justified in spite of these small samples because the Board of Commissioners of the Department of Forestry and Agriculture for the Territory of Hawaii allowed under special permit only three specimens of only certain species or subspecies of drepanidids to be collected; because some of the forms of drepanidids collected are practically extinct; because it sometimes was exceedingly difficult to locate the highly localized and sometimes seasonally varying ranges of some of the forms; and because no one had ever attempted such a functional anatomical study on this family nor had (and may never have again in future years) as highly a representative collection of specimens of forms in this genus. All conclusions made concerning any particular race or species studied have been made guardedly and with the reservation due them because of the small size of the sample of available specimens. This fact was kept in mind at all times. It can be surmised that, for a particular subspecies, sexual dimorphism, age, and individual variation would not play important roles in the morphology of those parts of the skeleton and the important divisions of the jaw and tongue musculature studied, with one exception. This one exception is the rare Hawaii Akepa, *Loxops c. coccinea*, in which age and individual feeding behavioral differences might, and probably do, make qute a bit of difference in the ontogenetic development of its asymmetrical rhamphothecae, jaw skeleton and jaw musculature. The study of this form was based mainly on adult males.

The specimens were preserved in the field in one of two ways. They were either skinned, eviscerated and dried to be cleaned subsequently by dermestid larvae as skeletal specimens, or they were preserved as "alcoholics." The latter method involved injection of the abdominal cavity, usually within a few minutes after death with 10 per cent formalin, and later wetting the feathers and skin with soap and water. The specimens were then placed in a fixing and preserved solution composed of 90 parts by volume of 70 per cent ethyl alcohol, five parts full strength formalin and five parts glycerin; the solution was changed once. The specimens were kept in the preserving solution until the end of the field trip and were transferred to 70 per cent ethyl alcohol in the laboratory.

Dissection and Drawing: In the laboratory the heads of the alcoholic specimens were skinned partially and the attachments of the extrinsic tongue musculature separated from the mandible and skull, the floor of the buccal cavity severed from its lateral walls and from the esophagus, and the glossal and laryngeal apparatuses removed. The glossal and attached laryngeal apparatus and head were pinned to the wax bottom of a small plastic dissecting pan, partially filled with 70 per cent ethyl alcohol, and the tongue and jaw musculatures were then dissected under a 20 power binocular dissecting microscope.

Drawings of the tongues were made to scale from the specimens. Drawings of the tongue musculature were made on pencil tracings of ink drawings of glossal skeletons. Drawings of the jaw muscles were made on pencil tracings of ink drawings of the skulls.

The ink drawings of the skulls were made in the following manner: Photographs were made of the best preserved specimen of a skull for every form studied except *sagittirostris*, for which no skull was available. For these photographs the mandibles were glued to the skulls in the closed position. Every skull was photographed in three views—lateral, left front oblique (*i.e.*, looking posteriorly and ventrally into the left orbit from the left front), and ventral. Enlarged prints were made from these negatives so that cranial height in the lateral and oblique views always was kept constant for all species. Cranial width, on the other hand, in the ventral views varied proportionately with the constant cranial height in the four forms studied. (It was assumed that, in a single genus or family of birds of narrowly limited range in body size of the species comprising the group, the cranial height would be proportional, or isometric, to the body size. This assumption appears to be reasonable for the genus *Loxops* whose member species are uniform in height of the brain case; however, it remains to be verified for the whole family.) Thus photographs of the skulls of all species in the genus were then of differing magnifications, allowing differences in shapes and relative sizes of the bills and other, possibly allometric, structures on the skulls to become more evident.

From these photographs ink tracings were made of the three views of the skull, upon which the jaw muscles were drawn.

In the drawings of the glossal skeletons the length of the fused basihyale plus urohyale was kept constant in all species; therefore, magnifications of the drawings of the glossal skeletons of the four forms are not the same. It was reasoned that this length would probably remain most stable in evolutionary lengthening or shortening of the tongue and that it would be isometrically proportional to body size throughout the family. The tongue muscles were drawn on these tracings of the tongue skeleton.

The drawings of the tongues are at different magnifications but are related to the constant length of basihyale plus urohyale in that they were drawn at a magnification twice that of the corresponding drawings of the glossal apparatus, except for the tongue of *L. m. newtoni* which is three times the magnification of the drawing of the glossal apparatus of that form.

All dissections, descriptions and preparations of the figures of the rhamphothecae, jaw skeleton and muscles, and glossal skeleton and musculature were done, with the following exceptions, by Lawrence P. Richards between 1951 and 1956. The skulls of the several taxa studied were jointly described from specimens by Walter J. Bock and Lawrence P. Richards in light of new knowledge of avian cranial kinesis published since 1957. Several additional drawings of the rhamphothecae and of the skull were prepared by Mrs. Frances Jewel.

Plates: To preserve clarity in the figures of the skeletal elements, the pertinent structures were labeled on a separate text figure (Figs. 4, 5, 6 and 12); comparison of this figure with those in the plates should pose no problems. Both the jaw and the tongue musculature are sufficiently complex that the plates of each species had to be labeled fully; however, obvious muscles, such as the m. depressor mandibulae, were not indicated in all plates. The abbreviations used in the text figures and plates and those used in the text are summarized in the glossary.

Unless otherwise specified, the specimens used for illustrating the skull and the glossal mechanism and the outlines of these skeletal elements when drawing the musculature are as follows: *L. v. virens*, juv. ♀, no. MVZ 118, 763; *L. m. mana*, ad. ♂, no. MVZ 118, 823; *L. m. newtoni*, juv.(?) ♂, no. MVZ 122, 615; *L. c. coccinea*, right-billed, ad. ♂, no. MVZ 122, 613; and *L. sagittirostris*, only occipital region of skull, age and sex unknown, no number, BPBM. In the descriptions of the plates of the jaw or the tongue musculature, the museum catalog numbers or the field catalog numbers (of Paul H. Baldwin or Lawrence P. Richards) refer to the specimens used for the dissection and drawings of the soft parts; the age and/or sex of the specimens are stated when known. The magnifications are indicated by an "x" followed by a number giving the degree of magnification. Abbreviations used are MVZ, Museum of Vertebrate Zoology, University of California, Berkeley; BPBM, B.P. Bishop Museum, Honolulu, Hawaii (these specimens do not have catalog numbers); LPR, collected by Lawrence P. Richards and not as yet reposited in a museum; PHB, collected by Paul H. Baldwin, Colorado State University, Ft. Collins, and not as yet reposited in a museum.

Kinetics: In order to measure the kinetics of the skulls (see section under anatomy on osteology of jaws and skull), a machine was designed and built (Fig. 2); details on the construction and operation of this measuring device may be obtained from Richards (1957).

Relative size differences of the jaw muscles: An initial working hypothesis was made that muscle size is, in general, a rough index of muscle strength among homologous muscles. On the basis of this assumption, Richards judged the relative size differences of the jaw muscles in the four taxa of *Loxops* studied; these are summarized in Table 3. The two sides of *coccinea* were considered separately, giving a total of five classes in this comparison. *L. sagittirostris* was excluded from this comparison because only its m. depressor mandibulae was available. This judgement was done by assigning rating numbers, designating relative size, to almost every muscle part for all taxa. The number "1" was given to the species or race (or side of *coccinea*) having the largest muscle or part of a muscle among the series of homologous muscles in the several taxa under study; number "2" was assigned to the taxon with the second largest muscle and so on. If two or more forms has a muscle part of approximately the same size, these two or more were given the same rating.

In this system of rating the relative sizes of homologous muscles, no attempt was made to distinguish quantitative differences among the forms. Furthermore, judgement of the sizes was done visually and not by means

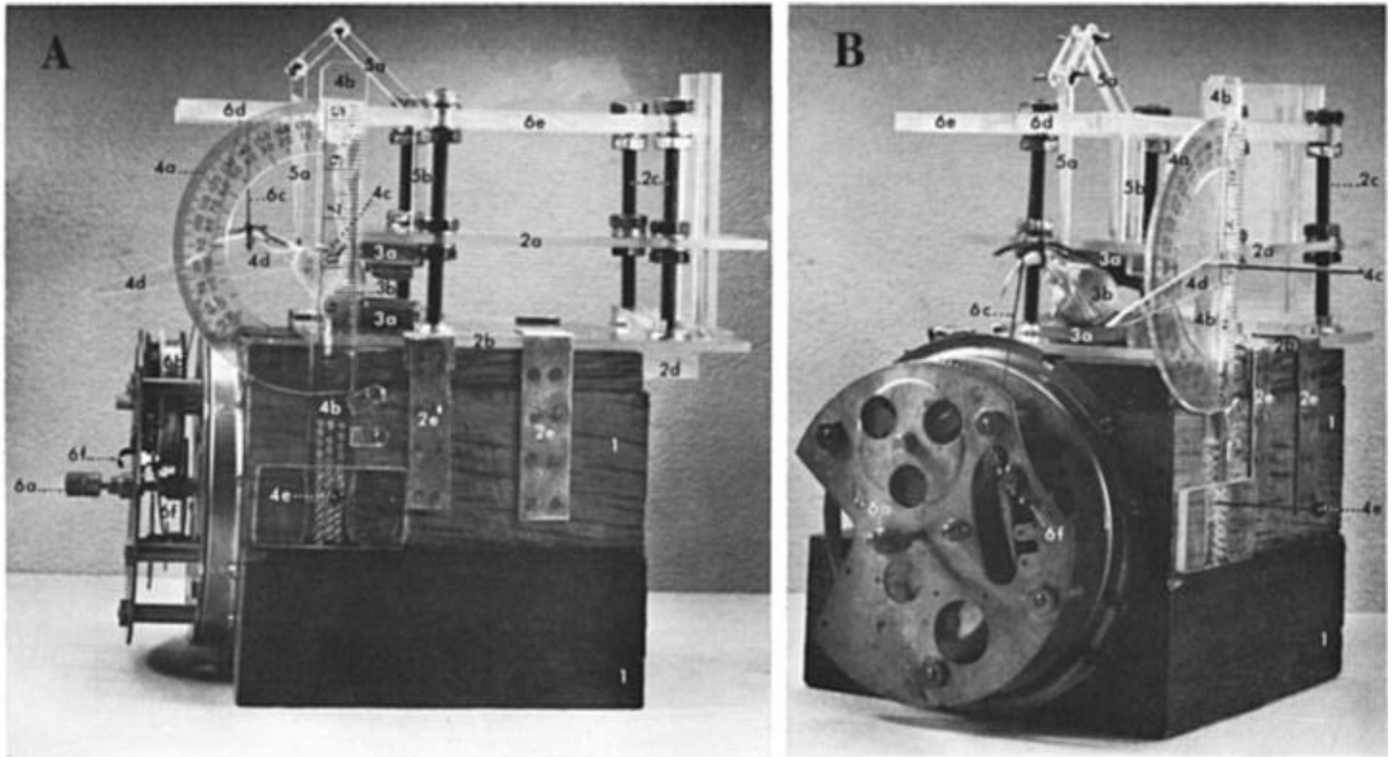

Figure 2. Device used for measurements of skull kinesis. A) View from position of operator while measuring kinesis. B) Oblique view to show gear mechanism and position of the skull in clamp.

Key to abbreviations: 1. base; 2a. upper plate of skull clamp holder; 2b. lower plate of skull clamp holder; 2c. guide bolts of skull clamp holder; 2d. median guide bar of skull clamp holder; 3a. skull clamp; 3b. skull of *Vestiaria coccinea*; 4a. protractor; 4b. vertical supporting bar of protractor; 4c. sighting needle; 4d. angle indicator; 4e. anchor pin for supporting bar of protractor; 5a. nasofrontal hinge pointer; 5b. plastic pillars which support pointer; 6a. winding knob of gear system; 6b. drum on largest cog wheel of gear system; 6c. thread; 6d. pulley; 6e. scaffolding which supports pulley; 6f. brake.

of measuring linear dimensions, volume or mass. The necessary large sample of specimens for determination of size by methods of significant accuracy were not available. Moreover, the attachments of the muscles and the lengths of their moment arms were not considered so that the torques produced by these muscles (Bock, 1968) were not compared; these torques, rather than the forces, produced by the muscles are the more important measurements in comparing the contribution of each muscle to the action of the skeletal system.

The initial assumption used in this comparison is not valid for all comparisons of skeletal muscles as pointed out by Gans and Bock (1965). Rather one should measure the total cross-sectional area of the muscle fibers as an index to force production, the length of the fibers as an index to displacement abilities, and the angle of pinnateness as an index to the force and displacement component along the vector direction of the muscle pull. Unfortunately, these factors are more easily discussed than measured, and we realize fully the shortcomings of our comparisons in not undertaking these measurements. Size as used in these comparsions is a relatively valid measurement of the several functional properties in a series of homologous muscles not too dissimilar in size and fiber arrangement such as those under consideration in this study. And the conclusions reached on the basis of these comparisons are relatively rough ones that do not go beyond the assumptions employed.

TYPES OF FOOD AND FEEDING METHODS

In this section we have not only consulted Richards' field notes but have drawn heavily upon the published observations of ornithologists such as Robert C. L. Perkins, George C. Munro, Henry W. Henshaw, William A. Bryan and Paul H. Baldwin who have studied drepanidids over long periods and at first hand in the field. This information is somewhat scattered in the literature, and we believe a useful purpose is served by summarizing it, in that the ideas of several naturalists based upon extensive observation are brought to bear on the intricacies of feeding behavior in this genus. The original observations reported in this chapter are those of Lawrence P. Richards who assumes primary responsibility for the material presented herein; the pronoun "I" refers to him.

Hawaii Amakihi, *Loxops virens virens*

Types of Food Taken: According to Baldwin (1953: 287) this species feeds on insects and other arthropods, nectar, and juices of fruits in this order of importance. By and large this statement is substantiated by the observations of Perkins (1893, 1903), Henshaw (1902), Munro (1944) and myself.

The most complete data on arthropod foods are given by Baldwin (1953: 314–320). He states that *virens* takes arthropods ranging in length from 1 mm to about 25 mm or more (some caterpillars), the majority of which fall between 1.5 mm and 10 mm in length. Most of these are soft-bodied, nonflying insects; no molluscs were found to be taken. Heteroterans, ants, roaches, beetles, larger wasps and flies, moths, adult lacewings and land snails seemingly were by-passed in large degree despite ready availability. The frequency with which identifiable items of animal food were seen in crop and gizzard contents he indicated by per cent of occurrence which was computed by dividing the number of samples in which a particular item was found by the number of samples examined for the bird. He sampled 63 specimens of *virens* between 1938 and 1944, 1948 and 1949. He also recorded recognizable food fed to young birds. His data are as follows: Homoptera (75%; Auchenorhyncha, Cicadellidae, Delphacidae, Flatidae, Psyllidae, Aphididae, Pseudococcidae, Coccidae, Diaspididae); Lepidoptera (71%; larvae of Pyraustidae (recorded by Perkins), Geometridae, Lycaenidae and other caterpillars plus unidentifed moths); Araneida (33%); Neuroptera (24%; larvae of Hemerobiidae); Coleoptera (11%; Proterhinidae, Curculionidae); Acarina (10%; foliage-inhabiting white mites and Tetranychidae); Corrodentia (10%; Psocidae); Heteroptera (8%; Miridae and others); Diptera (6%); Hymenoptera (3%; Apoidea); and Thysanoptera (2%). It is of interest that the Coccidae are not native to the Hawaiian Islands.

Perkins (1901: 566, footnote) states

> ". . . . Nectar is undoubtedly absolutely necessary to the existence of . . . [*L. virens*] [and other Drepanididae] as they are constituted. . . . Not that nectar is ever the *sole* food, though a most important source of nutriment—so important to the adults of some species that at certain seasons no individual shot contains any trace of insect food."

Perkins (1903: 409) wrote that *virens* takes nectar chiefly from the Ohia Lehua tree, *Metrosideros collina*[1] (Myrtaceae), but that it also obtains nectar from the campanulate blossoms of the native lobelias (Campanulaceae) and other families (Fig. 3), and from blossoms of introduced plants such as the banana, *Musa* sp. (Musaceae); Lantana, *Lantana camara* (Verbenaceae); and canna, *Canna* sp. (Cannaceae). Henshaw (1902: 44) recorded that *virens* visits the Ohia, the banana, and the introduced nasturtium

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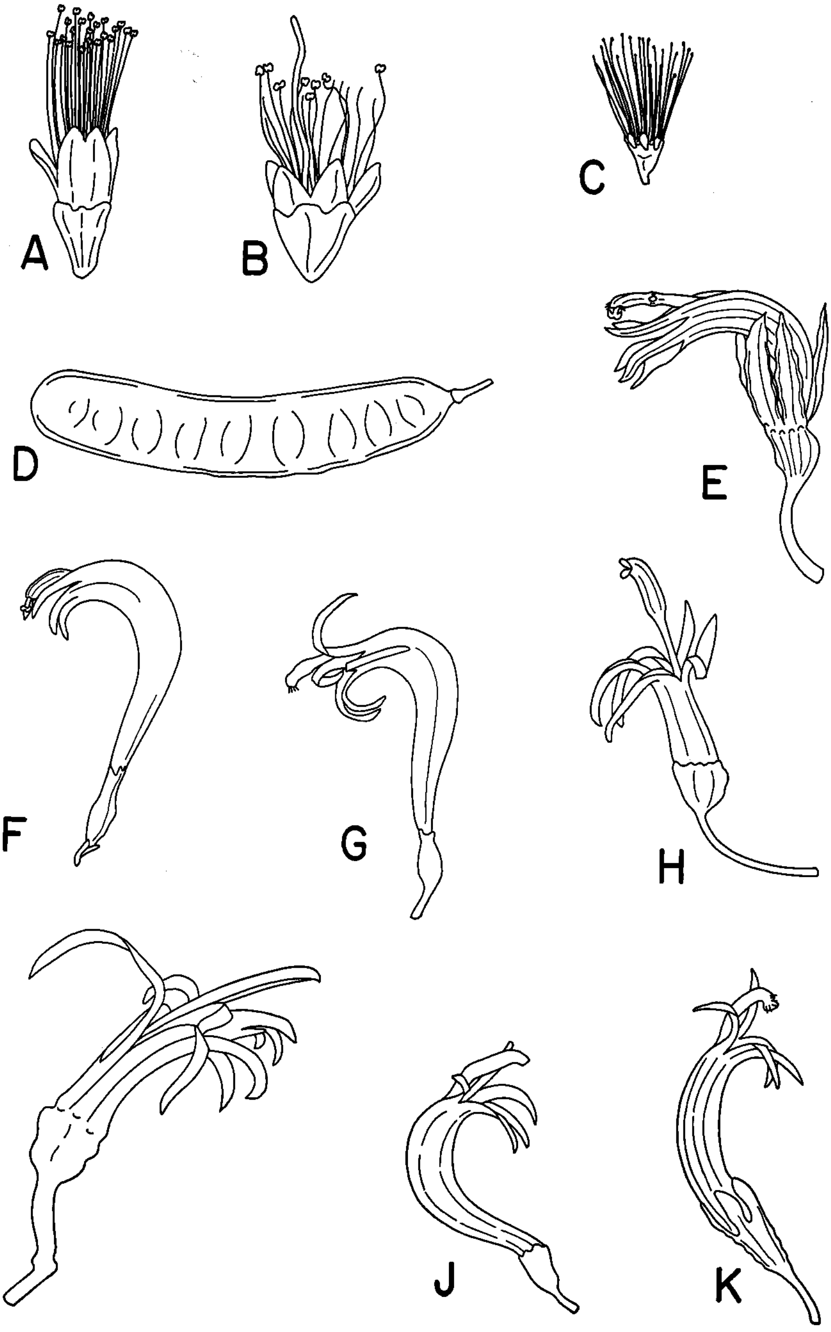
[1] In this study, this species of tree will be referred to either by its abbreviated vernacular name, Ohia, or by its generic name, *Metrosideros*, since it is by far the most common and most important species in the genus found in the Hawaiian Islands (Rock, 1913; Degener, 1932). For similar reasons, the Mamani tree, *Sophora chrysophylla* (Leguminosae), will be referred to by either its vernacular or generic name as will the Naio or Bastard Sandalwood tree, *Myoporum sandwichense* (Myoporaceae), and the Climbing Screw-pine, or Ieie vine, *Freycinetia arborea* (Pandanaceae).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(Tropaeolaceae), a small plant with brilliantly colored blossoms and long corollas. Bryan (1908: 162, 164) wrote that the Amakihi on Molokai, *L. v. wilsoni*, seldom visited lobelia blossoms but frequently visited the blossoms of the Mountain Naupaka bush, *Scaevola* sp. (Goodeniaceae). Munro (1944: 100–102) saw *virens* take nectar from a great variety of flowers, including those of *Metrosideros*; lobelias; the native forest Loulu Palm, *Pritchardia* sp. (Palmaceae); and the Climbing Screw-pine, or Ieie vine, *Freycinetia arborea* (Pandanaceae). Baldwin (1953: 311–312) frequently saw *virens* take nectar from *Metrosideros* and the Mamani tree, *Sophora chrysophylla* (Leguminosae). He also observed it feeding at the flowers of the native Sandalwood tree, *Santalum paniculatum* (Santalaceae); the native vine, Maile, *Alyxia olivaeformis* (Apocynaceae); and the following introduced plants: *Fuchsia magellanica* (Onagraceae); Honeysuckle, *Lonicera japonica* (Caprifoliaceae); Gosmore, *Hypochaeris radicata* (Compositae); Air Plant, *Bryophyllum calicinum* (Crassulaceae). He thinks it probable that this bird also takes nectar from the blossoms of the native shrub *Styphelia Tameiameiae* (Epacridaceae). The blossoms from which I saw *virens* take nectar most often and on many occasions were those of *Metrosideros* and *Sophora.* One specimen shot in an area where many Ohia Lehua trees were in bloom and where many individuals of this race were visiting these blossoms had exuding from its bill a clear liquid, sweet to the taste; undoubtedly this was Ohia nectar. A specimen of the Oahu Amakihi, *L. v. chloris*, shot from a Koa tree (Fig. 3), *Acacia Koa* (Leguminosae), which was in full bloom, as were many other Koas in the same area, also had a clear, sweet-tasting liquid dripping from its bill. It appeared to have been feeding from the Koa blossoms; presumably this liquid was Koa nectar, although *Metrosideros* trees also grow in the same locality. The latter, however, are not mentioned in my field notes as being in bloom on this date. On one occasion I saw *virens* twice dip its bill into a blossom of the Asiatic Thimbleberry bush, *Rubus rosaefolius* (Rosaceae).

Perkins (1903: 409–410) reported *virens* going to the ground for the berries of the introduced Poha plant, *Physalis peruviana* (Solanaceae). He wrote that the more powerfully jaw-muscled Kauai Amakihi, *L. v. stejnegeri*,

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Figure 3. Food sources of *Loxops* and other drepanidids showing some flowers visited for nectar and a koa seed pod used by *L. coccinea.* Identification of plants are: A) *Acacia Koa* (Leguminosae) ♂ flower; B) *Acacia Koa* (Leguminosae), ♀ flower; C) *Metrosideros collina* (Myrtaceae); D) *Acacia Koa* (Leguminosae) seed pod; E) *Cyanea Grimesiana* (Lobeliaceae); F) *Rollandia purpurellifolia* (Lobeliaceae); G) *Rollandia sessilifolia* (Lobeliaceae); H) *Clermontia coerulea* (Lobeliaceae); I) *Clermontia persicifolia* (Lobeliaceae); J) *Rollandia lanceolata* (Lobeliaceae); K) *Cyanea Baldwinii* (Lobeliaceae). Most redrawn from Degener (1932).

feeds on the poisonous berries of the Akia bush, *Wikstroemia* sp. (Thymeleaceae). Baldwin (1953: 312 saw *virens* pierce the fruits and take juice of the exotic Jerusalem Cherry, *Solanum pseudocapsicum* (Solanaceae). Once I saw this bird pecking at the fruits of the Thimbleberry; however, it may have been obtaining small insects from them. At another time I saw *virens* in a *Clermontia* sp. bush (Campanulaceae) which was loaded with the small ripe orange fruits. The bird was not actually seen to eat the fruit, but there were what appeared to be bits of orange fruit pulp adhering to its bill.

Methods of Feeding: The earlier authors referred to above failed to record, at least in their published works, the minutiae of methods of feeding, a knowledge of which is so necessary for a study of this sort.

Concerning the obtaining of animal food, these observers found *virens* hunting for insects mostly among the leaves, both dead and living, and blossoms and along the twigs and smaller branches of the forest trees, especially *Metrosideros* (Perkins, 1893: 108; 1903: 409; Munro, 1944: 102; Henshaw, 1902: 44; Baldwin, 1953: 314, 321). Perkins (1903: 409) and Henshaw (1902: 44) saw *virens* also obtaining insects less frequently from the large limbs and trunks of trees and from shrubbery and ferns, and Henshaw (*loc. cit.*) also observed it hunting over the surfaces of the broad leaves of the banana. Bryan (1908: 162, 164) wrote that the subspecies from Molokai, *L. v. wilsoni*, searched for insects mainly in the foliage of *Metrosideros* but also in low shrubs, especially the leaves and blossoms of the Mountain Naupaka, *Scaevola* sp. (Goodeniaceae).

In my own field notes on *L. virens*, mostly concerning *L. v. virens*, are recorded about twice as many instances of what appeared to be searchings for insects amongst leaves and twigs than upon larger branches and trunks of trees. The former were recorded four times from *Acacia Koa* (including twice for *L. v. chloris*), twice from *Sophora*, once from the Kolea tree, *Myrsine Lessertiana* (Myrsinaceae), and once from the Bastard Sandalwood tree, or Naio, *Myoporum sandwichense* (Myoporaceae). The latter were all observed to take place on the limbs and trunks of *Sophora.*

While feeding either among the smaller plant structures (*i.e.*, blossoms, leaves or twigs) or on the larger structures (*i.e.*, limbs and trunks), for either nectar or insects, the birds are able to maneuver their bodies into almost any imaginable position—right side up or upside down with the axis of the body either vertical or horizontal; the position least observed was that in which the body's axis was vertical and with the head pointing downward. This maneuverability is no doubt an adaptation which allows this form to place its body rapidly in the most satisfactory position for immediate use of its jaws and tongue mechanisms in the taking of animal and plant foods.

While feeding on insects amongst the twigs and leaves, the neck is bent and stretched so that the bill can be thrust between the leaves or probed into masses of hair-like lichens. On one occasion, when a bird was probing among *Sophora* leaves and lichens growing on the twigs, the slender tongue was plainly seen through the opened bill. I think the tongue in this instance was being used as a moistened brush for the capturing of tiny insects, although I could not actually see the prey. On three occasions I observed *virens* capture larger insects or larvae by prying with the bill amongst lichens growing on limbs or plucking them from the bark of *Sophora* branches or trunks. These larger insects were grasped strongly in the bill. They were killed either by tapping them against a branch and then eaten or by holding them down with a foot and pecking and pulling at them, while the head was simultaneously being worked strenuously from side to side.

Concerning the obtaining of nectar not much has been written on the use and movements of the bill and tongue while feeding from *Metrosideros* and *Sophora* blossoms—the more extensively utilized sources of nectar for *L. virens.* Baldwin (1953: 311) wrote as follows concerning *virens* feeding from these blossoms: "At such times it seemed that nectar was being taken, judging by the manner in which the bird reached into the interior of the flowers and swallowed without wiggling the mandible or submalar feathers as would be expected had insects been eaten." On many occasions I observed this same form take nectar from these blossoms. When feeding upon the typically leguminose *Sophora* blossoms, the bird plunges its bill and whole face into the blossom and keeps it there for about five seconds, or the bill may be inserted down to the nectary through a slit punctured in the side of the corolla by the proddings of the bills of previous visitors. When feeding from the multi-stamened blossoms of the cymes (10–20 blossoms per cyme) of *Metrosideros*, *virens* dips the tip of its bill into the shallow, exposed nectaries through the long, slender stamens either from above the nectary or from the side. A bird may visit a dozen or so cymes without pausing and spend several seconds at every cyme. I never saw any movement of the bill or tongue while watching this bird take nectar; however, twice, while I was observing the Iiwi, *Vestiaria coccinea,* feed from *Metrosideros* and *Sophora* blossoms, the mandible and rostrum were seen to move apart and smack together several times while the bird was feeding from a single cyme. I think that during this gaping the tongue was protruded into the nectary of the blossom, but I could not actually see the tongue.

Perkins (1895: 127; 1903: 409) and Munro (1944: 102) wrote that *virens* obtains nectar from large lobelia blossoms by piercing with the bill the base of the corollas to reach the nectaries; the smaller lobelia blossoms are not pierced according to Perkins. Henshaw (*supra. cit.*) observed this same behavior with respect to nasturtium blossoms.

GREATER AMAKIHI, *Loxops sagittirostris*

To my knowledge the only naturalists who ever saw this species alive in its natural habitat were Henry C. Palmer (Walter Rothschild's field collector) who discovered it in 1892, R. C. L. Perkins who independently found it in 1895, H. W. Henshaw who observed it on several occasions in the middle 1890's, and a person named A. M. Walcott whose name appears as the collector on the tag of a Bishop Museum alcoholic specimen taken in 1901. Both Baldwin and I (Richards and Baldwin, 1953: 222) attempted to locate this species in the late 1940's and in 1950 but without success.

Perkins (1903: 412–413) wrote that the forest crickets of the genus *Paratrigonidium* formed a large part of the stomach contents of eight specimens of this bird which he dissected; he wrote as follows:

> "Some of these crickets are specially attached to the Ieie [,*Freycinetia arborea*, which grows attached to the trunks of *Metrosideros* trees] and some live beneath the loose bark of large Ohias, while others are only found on certain ferns, which on more than one occasion I notice. . . [*Loxops sagittirostris*] visiting, no doubt in search of these insects. Caterpillars and spiders were also taken from the bird's stomach as well as a common carabid beetle, which lives at the base of the Ieie leaves, where these are closely attached to the stem. For obtaining the latter and the crickets [*Paratrigonidium freycinetiae* according to Zimmerman (1948: 160)] which live in the same situation, the strong beak of . . . [*Loxops sagittirostris*] is well adapted. Once only I saw one feeding at the flower of the Ohia, and although I was unable to procure this for examination, I have little doubt that it was feeding on nectar, since its tongue is still unchanged from the form exhibited by that of the most persistent nectar-eaters. As in some [other] species of [Drepanididae] the habit of feeding on nectar probably survives as a rare occurrence, the typical form of the tongue being fully perserved, since it assists in obtaining some of these insects which form a large part of the bird's food, and not because nectar is of much importance as an article of diet."

Henshaw (1902: 43) wrote that *sagittirostris* "seems to live chiefly upon insects which it gleans from the foliage of the ohias, to which tree it it seems to confine its attention chiefly."

HAWAII CREEPER, *Loxops maculata mana*

Types of Food Taken: Perkins (1895: 122; 1901: 570; 1903: 416) reported that *L. maculata* is almost entirely insectivorous, feeding chiefly on exposed caterpillars, spiders and small moths; larger moths, myriapods, slugs and beetles are also taken. Perkins (1901: 570), Henshaw (1902: 47) and I never saw *mana* take nectar. Henshaw (*loc. cit.*) reported this form to feed mostly upon beetle larvae. Munro (1944: 106) found insects, "grubs" and insect eggs in the stomachs of specimens of this race. On five different occasions I observed it to eat unidentified insect and lepidopterous larvae and adult insects.

Methods of Feeding: Perkins (1895: 122; 1903: 415–416) observed the several subspecies of *maculata* hunting their arthropod prey on the trunks and branches of forest trees and bushes and sometimes going down to the bases of the trunks and, rarely, even to the ground. He reported them climbing either up or down the trunks and on the upper and lower surfaces of horizontal limbs. He noted that the species searches dead wood and beneath tree bark for caterpillars. Those exposed on foliage are also caught. Henshaw (1902: 47) reported that the Hawaii subspecies creeps along tree trunks and branches taking insects from the interstices of bark, mosses and lichens. Perkins (1903: 415) noted this same race to be partial to large Koa trees and also to *Myoporum* and *Sophora* trees. I found that, out of seventeen observations of feeding on the part of *mana*, eight were on *Acacia Koa*, five on *Sophora*, two on *Metrosideros*, one on a dead *Myoporum*, and one on an Olapa tree, *Cheirodendron* sp. (Araliaceae). I noticed in all cases that the birds were creeping on the branches or trunks. *L. m. mana* seems to be just as adept at creeping right side up or upside down along horizontal branches as it is at creeping straight up or straight down on vertical branches and trunks. My field notes indicate almost the same number of observations made on the birds in all four of these categories. They were also observed to creep in a rough spiral around vertical branches or trunks. While creeping in any position the bird's body is held close to the bark and its legs close to its belly; the bird advances jerkily, about one-half to one inch every few seconds, by either stepping forward, one foot at a time, or by hopping forward, both feet moving at the same time. The wings are flicked now and then, presumably in the maintenance of balance during advancement or in the event of slippage of the claws. This creeping ability appears to me to be a highly evolved behavioral adaptation which allows this species to position its body so that its jaw and tongue mechanisms can be made use of rapidly and efficiently.

While the animal creeps, it continuously peers from side to side interrupting this only when it probes, pecks and pries with the bill into crevices in and under the edges of sheets of bark or into mounds of hair-like lichen or into moss. Out of twenty-five descriptions in my field notes twelve of these probings were at the bark of branches and trunks, seven were into hair-like lichens, two onto exposed twigs, two into moss on branches, one in rotten wood, and one underneath a flat lichen growing on a branch. I saw one ply so hard at Koa bark that pieces of bark about three quarters of an inch across were falling from the site.

Perkins (1895: 122; 1903: 416) mentioned that when *maculata* catches large moths, it holds them down with its claws and tears off the wings before eating them. Bryan (1908: 165) wrote of the Molokai Creeper, *L. m. flammea*, that sometimes "moths are taken of such size that . . . [the birds] are compelled to hold them under their feet and pull them to pieces so as to devour them piecemeal." He noted that this form seldom, if ever, takes insects on the wing. I, likewise, never saw the Hawaii Creeper, *mana*, either perched or in flight, catch any insects on the wing. Twice I observed *mana* capture large insect larvae and beat them against a limb before eating them; one was an inch-long caterpillar which was removed from the bark of a Koa limb only after vigorous pecking. On other occasions smaller insects were captured from the bark or lichens and immediately devoured.

MAUI CREEPER, *Loxops maculata newtoni*

Types of Food Taken: The mainly arthropod diet of the species noted by Perkins (*supra, loc. cit.*) would apply to this race also. Henshaw (1902: 50) saw this creeper feed its young small green caterpillars. In addition to this animal food, on rare occasions *Metrosideros* nectar is also taken by the Maui Creeper (Perkins, *supra, loc. cit.*; Henshaw, 1902: 50). The only other Creepers which take nectar, and only rarely from *Metrosideros*, are the Lanai Creeper, *L. m. montana*, (Perkins, *supra, loc. cit.*) and the Kauai Creeper, *L. m. bairdi*, (Munro, 1944: 105).

Methods of Feeding: Again, the remarks of Perkins (*supra, loc. cit.*) on the creeping and feeding behavior of the species would apply to the Maui form. He noted that the Maui form abounds in large Koa trees, but that it is also found in forests devoid of this tree. Henshaw (1902: 49–50) observed *newtoni* take small green caterpillars from Koa and *Metrosideros*. He noted that this form hunts not only on tree trunks and branches but also spends much time in the undergrowth and "not rarely descends even to the ground in its hunting excursions." He went so far as to say that it is "far more an inhabitant of the scrub than the trees." I observed this subspecies only on two different days, but the first one I saw was in the three- to four-foot heather-like Pukeawe shrub, *Cyathodes* sp. (Epacridaceae), about 100 feet from the edge of a low forest. On a number of occasions during these two days I saw *newtoni* feeding along the small branches, which were covered with flat lichens, and among the twigs and leaves of the following trees: *Metrosideros*; *Cheirodendron* sp.; the Alani, *Pelea* sp., (Rutaceae), and *Myrsine* sp. I presumed that the birds were hunting insects, for their heads were constantly moving, the bills being probed under lichens and among the leaves. The creeping ability of this race seems as good as that of the Hawaii Creeper, but it was noted that the Maui race spent much time among the leaves of the trees, whereas I never observed the Hawaii Creeper in this situation.

HAWAII AKEPA, *Loxops coccinea coccinea*

Types of Food Taken: Perkins (1895: 121; 1903: 418–419) reported that *coccinea* feeds mostly upon caterpillars and the smaller spiders, the former consisting both of the exposed span-worms or loopers and also smaller forms concealed inside of leaf buds or between leaves fastened together by the larvae. Henshaw (1902: 58, 62) observed the form from Hawaii and the Maui Akepa to feed mostly upon soft, small insects, caterpillars and very small spiders. Munro (1944: 109–110, 112) wrote that Akepas take scale insects, that the Hawaii race feeds mostly upon insects, caterpillars and spiders and that the Kauai subspecies, *L. c. caeruleirostris*, takes caterpillars, spider eggs, coccids and other insects. Perkins (*loc. cit.*) observed *L. c. ochracea* and *L. c. caeruleirostris* taking nectar on rare occasions from *Metrosideros* blossoms; this was proven by the fact that nectar was dripping from the bills of freshly shot specimens. I never observed *coccinea* to take nectar.

Methods of Feeding: According to Perkins (1895: 121; 1901: 569; 1903: 418–419) the species seeks its arthropod prey chiefly from the foliage and leaf buds, and more rarely on the branches, of certain forest trees where wood-feeding larvae are obtained. *L. c. coccinea* is partial to Koa forests but also occurs in forest devoid of this acacia (1903: 417). In the Koas, which act as host plants to many species of Lepidoptera, the Hawaiian race obtains its food mainly amongst the Koa phyllodes, but in forest of Ohia it searches mainly the terminal leaf buds of this tree for the lepidopteran larvae concealed within the buds. In the dryer upland forests it hunts not only on the Koas but also in the smaller Naio; Aalii, *Dodonaea* sp. (Sapindaceae); and other lesser trees (1903: 417–418). Henshaw (1902: 58–59), also, noted that this race is partial to the Koa forests, where it searches for its food among the phyllodes, small outer twigs and flowers of this tree, but that its food is also taken on the Naio, *Myoporum*, and Mamani, *Sophora*. I found the Hawaii Akepa feeding only in *Acacia Koa* and *Metrosideros*. Observations on the feeding of twelve of these birds were made in a forest of mixed Koa, Ohia, Naio, Mamani and other trees. Seven were feeding in the Ohias and five in the Koas; all appeared to be searching for insects. Different individuals of these twelve birds were seen to search Ohia leaves four times, Ohia leaf buds three times, the long green crescent-shaped Koa phyllodes five times and the dry pods of the Koa five times. These crude data may aid in giving an idea of the food niche of this race.

I noted that while hunting in these situations the birds could maneuver their bodies into almost any imaginable position with respect to the vertical and horizontal; this of course allows the bird to place its body in the most satisfactory position for using its jaw and tongue mechanisms in the capture of its prey—be it exposed or concealed. Taking exposed insects from the Koa phyllodes and Ohia leaves undoubtedly is the simpler and easier method. To do this the bird merely has to perch on an Ohia twig or climb amongst the Koa phyllodes and pick off the caterpillars and spiders from the bases and surfaces of the leaves or phyllodes. However, to capture insects or larvae living inside the Ohia leaf buds or dry Koa pods (Fig. 3) more strenuous effort must be exerted. On one occasion I observed (field notes) an Hawaii Akepa feeding in an Ohia tree "climb about near the ends of the twigs, bending its neck back, & praying into the Ohia buds. . . . It kept this up for about 4 min." At another time I observed (field notes) one of these birds in an Ohia, and it "moved from one bunch of leaf buds to the next, poking into the buds from above with its short bill. The neck was often bent so that the chin rested almost on the anterior part of the neck." I observed (field notes) on another occasion an Akepa, feeding above me in a Koa about forty feet tall, catch onto a dry pod hanging vertically downward. "This it clung to with both legs while it attempted to open the bottom of the pod with its bill. A cracking noise could be heard. The bird & pod swing around crazily during this operation. At times the bird's head was doubled up almost under its breast." At another time (field notes) an Akepa "was seen to hang upside down on a Koa pod & pry at it with the bill."

The Akepas, like the Holarctic Crossbill, *Loxia curvirostra*, have asymmetrical mandibular and maxillary (or rostral) rhamphothecae which cross at their tips. Parts of the skeleton and some of the muscles of the jaw apparatus are also asymmetrically arranged. It was the opinion of Perkins (1903: 418–420) that the mandibular rhamphothecal asymmetry was of definite use to the species in some of its feeding habits: "The abnormal structure of the mandible [rhamphotheca] is clearly connected with the habit of seeking food in the closely imbricated buds of some of the forest trees." He adds:

> "The essential use of the distorted mandible of . . . [*Loxops coccinea*] is without the least doubt for the extraction of insects living hidden in the leaf-buds of certain forest trees. These buds may not inaptly be compared to the pine cones from which . . . [*Loxia curvirostra*] procures its food, although their much softer substance by no means requires the more powerful implements of the crossbill. As has been already mentioned the bill of *Loxops* [*coccinea*] is also useful in opening out the koa phyllodes, when fastened together by certain caterpillars, or by some spiders (of which it is extremely fond) which thus conceal their nests."

Here Perkins neatly hit upon what we think is the essential use to which the asymmetrical rhamphothecae are put, but we do not think he was aware of the skeletal and muscular asymmetries or understood the method by which the whole muscular, skeletal and horny bill apparatus is used.

Even the avian anatomist Gadow did not mention (1899: 246) any skeletal or muscular asymmetries, or the method by which such an asymmetrical apparatus could be used. However, he did recognize a parallelism between the Akepa and the crossbills and, concerning the former, mentioned (*loc. cit.*)

> "the under jaws of these . . . birds are not symmetrical—the distal half of the under jaw is twisted either to the right or to the left. . . .There is not the slightest doubt that this asymmetry is acquired individually by their twisting open husks or seeds, or cracks of bark, in search of their food."

He was of course guessing when he used the terms "husks or seeds, or cracks of bark"; however, the principle of twisting probably does apply, but on the other hand we think he (Gadow, 1891: 495–496) incorrectly understood the method by which the crossbills open pine cones and was not cognizant of the principles involved in the jaw apparatus employed by either the crossbills or the Akepa.

Henshaw (1902: 58–59) appreciated the parallelism between the Akepa and the crossbills in respect to the asymmetry of the mandibular rhamphothecae and that the asymmetry in *coccinea* undoubtedly somehow is correlated with its feeding habits. Although he had observed thirty or forty individuals of the Akepa feeding, he did not visualize the analogy between an Ohia leaf bud or Koa pod and a pine cone, and therefore, could not offer any explanation for the use of this rhamphothecal asymmetry in the feeding habits of the Akepa. He was further misled by Gadow's erroneous mention of "husks and seeds, or crack of bark," for he knew the species well enough to realize that it is not granivorous and that it does not hunt its prey by twisting open crevices in the bark. He was seemingly unaware of any internal anatomical asymmetries and stated that he did not know of any opinions of Perkins on the matter.

Munro (1944: 109) suggested that the crossed mandibular sheath is useful for removing scale insects from leaves, for he found scale insects in the stomachs of some specimens. It may be used this way; however, since Coccidae are not native to the Hawaiian Islands (Baldwin, 1952: 315), it seems impossible that the presence of these insects for only 100 years or less in the niche of the Akepa could have acted as a selective force for such drastic changes (from the presumed ancestral condtion) in feeding behavior and concomitant ontogenetically variable morphological asymmetry. Furthermore, the removal of scale insects from a leaf or stem, even by a twisting method, would not involve exerting enough force to develop asymmetrically the jaw musculature and skeleton of an individual bird in its lifetime.

Concerning the use of the tongue in the feeding of this species, Perkins (1903: 419) has this to say:

> "The thin, long, honey-sucking form of tongue is fully preserved in all [the races], in spite of the small attention paid to . . . [nectar], but with the distorted mandible it is obviously a very efficient help in procuring the larvae which feed in the terminal buds of trees as well as those which live between leaves fastened together, which I have seen them extracting."

SUMMARY OF FOODS AND METHODS OF FEEDING

L. v. virens: The order of preference of food for this form seems to be soft-bodied insects and spiders, nectar, and juices of fruits and fruit pulp. The arthropod prey is hunted mostly among leaves, twigs, blossoms and smaller barnches and, to a lesser extent, upon larger branches and trunks of *Metrosideros*, *Acacia Koa* and *Sophora.* The larger insects are grasped with the bill. Possibly very small ones are brushed up with the tongue. Nectar is taken mainly from *Metrosideros* and *Sophora* and sometimes from the campanulate blossoms of the native lobelias (Campanulaceae) and from other plants. This species hunts its prey more amongst the leaves and twigs and less upon the large branches and trunks of trees than the other species of *Loxops* except for *coccinea* which spends almost all of its time hunting amongst the leaves. *L. v. virens* takes much more nectar than any of the other species of *Loxops.*

L. sagittirostris: The Greater Amakihi fed mostly upon certain crickets and a carabid beetle which live at the bases of the stout leaves of *Freycinetia.* Caterpillars and spiders were also taken and these possibly from the foliage of *Metrosideros* and ferns. Large prey undoubtedly was grasped with the bill. The tongue probably was also used for capturing smaller insects in crevices at the bases of *Freycinetia* leaves, and on rare occasions the tongue was probably used in taking nectar from *Metrosideros* blossoms.

L. m. mana: The Hawaii Creeper is almost completely insectivorous, feeding mostly on exposed caterpillars, spiders, and moths, although myriapods, slugs and beetles are also taken. The bird creeps over the larger branches and trunks of *Acacia Koa*, *Myoporum* and *Metrosideros* trees probing and prying at and also under bark, lichens and moss to obtain these animals. The larger moths and larvae are held down with the claws and torn apart with the bill.

L. m. newtoni: The animal food of the Maui Creeper is practically the same as that of the Hawaii race. On rare occasions *newtoni* also takes nectar from *Metrosideros* blossoms. Like *mana* it hunts its prey by creeping over the large branches and trunks of trees such as *Acacia Koa* and *Metrosideros*, but it also spends much time searching the leaves of trees and underbrush which *mana* does not do.

L. c. coccinea: The Akepas, like the Creepers, are almost entirely insectivorous, feeding mostly upon soft, small insects, caterpillars and small spiders obtained chiefly from the foliage of *Acacia Koa* and *Metrosideros*. Only rarely do they hunt their prey on the branches of the trees. Ohia leaf buds and dry Koa pods containing caterpillars, and Koa phyllodes sewn together by spiders or lepidopterous larvae, are opened by these crossbilled forms in a manner probably very similar to that used by *Loxia* in opening pine cones. It is probable that the tongue of the Akepa is used to remove larvae from these opened plant structures. Although the Maui and Kauai Akepas take nectar from Ohia blossoms on rare occasions, the Hawaii race, as far as I know, has never been observed to do so.

RHAMPHOTHECAE OF THE BEAK

Description: The horny sheaths, or rhamphothecae of the maxilla and the mandible of the several species of *Loxops* differ from one another mostly in general external shape and curvature, and in the relative size of the opercula covering the nostrils (Pls. 1 and 2). Differences in the structure of the floor and roof of the mouth within the bill proper also occur. Many of these features can be seen in the excellent drawings of the bills of *Loxops* and other drepanidids found in Rothschild's monograph (1893–1900: pl. 82, figs. 8, 11, 15, 18, 25).

Examination of alcoholic specimens (except for *sagittirostris*) and of study skins of all species and many subspecies of *Loxops* revealed that the rhamphothecae of both the maxilla and the mandible of *virens* are more decurved than those of the other forms. Curvature of all parts of the rhamphothecae is judged relative to the longitudinal axis along the length of the jugal bar. In lateral view of the bill, this curvature is obvious both in the dorsal surface and ventral edge of the maxillary rhamphotheca and in the dorsal edge and ventral surface of the mandibular rhamphotheca.

Closer comparison of some of the taxa in the subgenus *Viridonia* shows some interesting cases of character displacement. Sympatry exists between *v. stejnegeri* and *parva* on Kauai, and between *v. virens* and *sagittirostris* on Hawaii; in each case, the bills of these sympatric forms have become markedly different. *L. parva* is the smallest species in the genus and in bill shape is much like *v. virens* except that its bill is somewhat straighter. Presumably it was an early geographic representative of the *virens* group on Kauai (Amadon, 1950: 165). With subsequent reinvasion of this island by another population of *Loxops virens*, competition between the ancestor of *parva* and the more recently arriving progenitor of *stejnegeri* was presumably responsible for divergent evolution of their bills, resulting in a smaller straighter bill in *parva* and a larger, strongly decurved bill in *stejnegeri*. This latter form has the most strongly decurved bill in the genus and in size is second only to *sagittirostris*. These forms differ markedly in feeding habits (Amadon, 1950: 245–246), *parva* being very similar to other races of *virens* and *virens stejnegeri* being specialized for obtaining insects from beneath bark (a creeper-like feeding habit, but presumably different from that utilized by *maculata*). The interactions between the species of *Loxops* on Kauai is extremely interesting because of the double invasion in the subgenus *Viridonia* and the double development of creeper habits in two species of different subgenera; it deserves to be studied further in greater detail.

In similar fashion, *v. virens* may have been the original form on Hawaii with a second population of *virens*, the progenitor of *sagittirostris*, invading this island at a later time. Competition between the ancestors of *v. virens* and of *sagittirostris* was again responsible for the divergent evolution of their bills, resulting in the very large, straight bill in *sagittirostris* which is the largest species in the genus possessing the most robust bill. From the little we know about the feeding habits of this species, we can correlate the difference in bill morphology between it and *v. virens* with differences in their feeding habits.

Thus, members of the subgenus *Viridonia* display two excellent examples of the classical pattern of insular reinvasion with subsequent divergence of the sympatric forms into different niche relationships with respect to their feeding habits and the resultant divergence of their morphological features (see also Amadon, 1950: 246–247; Bock, 1970).

Members of the subgenus *Paroreomyza* have a straighter and more ruggedly constructed bill than *virens*, and also display considerable geographic variation. The Malokai subspecies, *maculata flammea* has the most decurved bill, one that is almost as curved as that of *virens* but stouter. In degrees of curvature, *newtoni* comes next; its bill is so much straighter that it can hardly be called decurved at all. The bill of *mana* is even straighter still with the tips of both rhamphothecae extending straight out to end in an extremely acute angle. Moreover, its bill is more ruggedly constructed than that of either *virens* or *newtoni*. Its strong build is especially noticeable in the greater height and width of the horny ridge between the dorsal nasal operculae of *mana*. The cline of increasing straighter, stronger bills in the races of *L. maculata* from Molokai to Hawaii should be noted, although it is not known whether this represents a pattern of gene flow or is strictly coincidental.

The symmetry of the bill in these species is shown in their dorsal aspect (Pl. 2). Some differences exist in the attenuation of the bill, those of *v. virens* and *parva* are thinner than the others, but the differences are considerably less than differences in curvature as seen in lateral view.

The bill of *coccinea* is shortest of all and the most finch-like or siskin-like in appearance except for a definite curvature of the dorsal surface of the rostal rhamphotheca. Some geographic variation in size exists as that shown between *c. coccinea* and *c. caeruleirostris*. The tips of both the maxillary and mandibular rhamphothecae are asymmetrical as seen in dorsal view. Because of these asymmetries in the rhamphothecae and those in several skeletal structures (Pls. 6 and 9) and jaw muscles (Pls. 16, 17, and 18), individuals of *coccinea* can be referred to as either "right-billed" or "left-billed." A right-billed individual is one in which the mandibular rhamphotheca protrudes or crosses to the right from beneath the maxillary rhamphotheca which crosses to the left (*e.g., c. coccinea*, Pl. 2f and g; and *c. caeruleirostris*, Pl. 2i and j). A left-billed bird is one in which the opposite relationships exist (*e.g., c. coccinea*, Pl. 2h). In a right-billed individual, the right, or cutting, edge of the tip of the mandibular horny sheath is wider, flatter, and usually higher than the left edge. The left, or cutting, edge of the tip of the rostral rhamphotheca of a right-billed bird is likewise wider, flatter, but lower than the right. These cutting edges are, hence, knife-like and are able to slice through plant material, as will be discussed below. In a few specimens, both mandibular and maxillary cutting edges are gouged out where they had been worn away through use (*e.g.*, Pl. 2i and j). Most of the description of the cranial elements and jaw muscles and discussion of the jaw muscles will be for right-billed birds.

In the four species for which alcoholic specimens were available, and probably also in *sagittirostris*, the edges of the maxillary rhamphotheca are knife-like and overlap the similarly sharp edges of the mandibular rhamphotheca when the bill is closed, except at the tips of the crossed bill of *coccinea*.

A medial trough or slot exists on the ventral surface of the maxilla in the four forms for which specimens were available and presumably also in *sagittirostris*. This slot is of an inverted U-shape in cross section and is narrower at the tip of the rostrum than at its posterior end. From about the middle of the maxilla, two parallel ridges extend posteriorly on either side forming the lateral walls of the trough. These parallel ridges are most evident in *newtoni* and *virens* and less evident in *mana* and *coccinea*. In *newtoni* a low, sharp median ridge extends the length of the trough to an anteriorly-pointing, wedge-shaped mound of tissue in the posterior end of the trough. These structures (*i.e.*, the median ridge and wedge-shaped mound) exist in the other forms studied but to a much lesser degree of development. Beecher (1953: 312–313; fig. 15) describes the structure of the horny palate in *Psittirostris cantans* which is similar to that found in *Loxops*. The tongue of all forms fits into this dorsal, maxillary slot, the closest fit being in *virens* and *newtoni*.

On the dorsal surface of the mandibular part of the bill there is another trough or slot which is also U-shaped in cross section. In *virens* the dorsal edges of this trough overhang its lumen. In *newtoni* the walls are practically vertical with an almost imperceptible amount of overhang. In *mana* and *coccinea* the walls of this trough are less steep (*i.e.*, they are neither overhanging nor vertical but diverge laterally). In the two creepers studied there is a low, sharp median ridge in the floor of this mandibular slot; it is more pronounced in the Maui race. It is barely perceptible in *virens* and *coccinea*. When the tongue is depressed, this ridge fits into a narrow, median slit in the horny undercoating of the tongue proper.

All of the forms examined have both dorsal and ventral nasal opercula. The dorsal operculum is a flap of corneous skin more or less covering the opening of the external naris from above. The ventral operculum is a similar flap of skin, but smaller in area, which is overlapped by the dorsal operculum and which extends partway into the opening of the external naris from the ventral margin of this opening (Gadow, 1891 and 1899: 223, 224, 229, 230, 231, 234, 245–247, figs. 11, 17, 36, 37, 42, 49; Amadon, 1950: 226–227). Two bilaterally placed preconchae hang within the vestibule of the nasal cavity (Stresemann, 1927–1934: 120–121, cited in Amadon, 1950: 227). The figures in Rothschild's monograph (*loc. cit.*) indicate in *sagittirostris* the presence of a rather large dorsal operculum if not also a ventral one. Furthermore, he states (*op. cit.*: 107) that the "nostrils are protected by an upper operculum. . . ." We found the dorsal and ventral opercula in *virens* larger than in the other forms examined. Those of *newtoni* are only slightly smaller, and those of *mana* and *coccinea* are developed still less, those of *coccinea* being the smallest. In *virens* and *newtoni* the ventral opercula hide from view the cartilaginous bilateral preconchae hanging in the vestibule of the nasal cavity; in the *mana* and *coccinea* these structures can be seen in lateral aspect.

Functional interpretation: The structure of the horny parts of the bill may be correlated to some extent with the type of food taken by the bird and the methods by which it is obtained. These correlations between the rhamphothecal morphology and feeding observations are largely hypotheses to be tested by further observations, not proven facts.

The knife-like edges of both rhamphothecae are not only useful to the species of this primarily insectivorous genus for grasping and killing of their prey, but the close fit of the one against the other while the bill is closed also serves to keep desiccation of the interior of the mouth at a minimum.

The decurved bill of *virens* is probably an adaptation for obtaining nectar from curved lobelia blossoms and secondarily from *Metrosideros*, *Sophora* and other blossoms. Although bill shape in *virens* presumably evolved in connection with feeding on nectar from lobelia blossoms, this species now obtains most of its nectar from the shallow flowers of *Metrosideros*, *Sophora* and other plants.

It is Perkins' hypothesis (1903: 384–385) that the nectar-feeding drepanidids obtained their principal supply of food from the blossoms of the specialized and ecologically restricted lobelias (Campanulaceae) before the relatively recent invasion of the Hawaiian Islands by the South Pacific *Metrosideros* tree (we might add *Sophora* and perhaps others). The nectar-feeding species of the Drepanidinae originally fed on nectar from the deep, curved blossoms of lobelias; their decurved bills are an adaptation for feeding on these flowers. Although sources of nectar are abundant in *Metrosideros* and *Sophora* blossoms, observations of earlier naturalists (Baldwin, 1953: 310; Perkins, 1903: 401, 422–424) suggest that *Drepanis*, *Vestiaria*, *Hemignathus obscurus* and *Hemignathus procerus* preferred the nectar of lobelias over that of *Metrosideros.*

L. virens has been observed to take nectar from lobelias although it feeds more frequently from *Metrosideros* and *Sophora.* This species is often considered to be the most primitive member of the genus *Loxops* which is, in turn, regarded as the most primitive genus in the Psittirostrinae and by some as the most primitive genus in the entire family (Amadon, 1950: 231). If *virens* evolved from the Drepanidinae, it would have a decurved bill inherited from these forms as an adaptation for feeding on deep, curved lobelia blossoms. If *Loxops* is the primitive genus in the family from which both the Drepanidinae and the Psittirostrinae evolved, then it would have fed originally on lobelia blossoms if Perkins' hypothesis is correct, and the bill would have become decurved as an adaptation for feeding on these deep curved flowers. Whatever the evolution of *Loxops* has been, its decurved bill corresponds in shape to the curved campanulate blossoms of lobelias, and a straight bill would be of significantly less advantage to a bird feeding on these flowers.

The decurved bill of the *virens* would thus be preadapted to taking nectar from the shallow nectarines of the long-stamened *Metrosideros* cymes, from *Sophora* blossoms and from flowers of other more recently invading trees. The curved bill of a short-billed form like *virens* would be more suitable for obtaining nectar from shallow *Metrosideros* nectaries than would a straight one, because the bird could obtain nectar by shoving the tip of its curved bill among the stamens from the side of the cyme rather than down from the top. The tip of the decurved bill would then dip into the nectaries without having the long upright stamens of the blossoms poke into the bird's eyes, which of necessity should be kept open to locate the nectaries. A straight-billed species would have to plunge its whole face from above into the mass of stamens in order to reach the nectaries effectively. Nor would it be able to reach efficiently all nectaries of a cyme from the side because the tip of the bill is not bent downwards allowing easy entry into those nectaries toward the center of the cyme. Richards has observed both *virens* and *Himatione s. sanguinea* obtaining nectar from *Metrosideros* blossoms by shoving the bill among the stamens from the side of the cyme, but, on the other hand, he has seen them also plunge the whole bill and face into the stamens from above the cyme.

Although the decurved bill of *virens* probably did not evolve as a primary adaptation for insect-feeding, it is presumably reasonably suited for those feeding habits. Many insectivorous birds have slightly decurved bills, and it is not obvious whether a slightly decurved bill or a straight bill is better suited for insect feeding. One advantage to a slightly decurved bill is that the tips are anterior and ventral to the eye so that the bird may be able to see its prey between the tips easier than in a straight billed species.

The straight bills of the creepers, *mana* and *newtoni* and of *sagittirostris* are probably adaptations to their insectivorous habits. Many of the arthropods eaten by these birds are exposed on limbs or foliage. Others living beneath bark, lichens, moss, or at the bases of leaves are exposed by the actions of the birds. Some of these animals move rapidly and must be snatched up quickly. The problem lies in whether a straight bill is better adapted than a curved one for quick capture of insects. It seems reasonable to assume that a straight bill is better because once the tip of a straight bill is aimed accurately at an insect, the axis of the bill can be more easily maintained than can the axis of a curved bill during the subsequent rapid forward extension of the neck, opening of the bill and seizure of the prey. Certainly an extremely curved-billed form would have to execute separate, more difficult compensatory movements of the mandible and rostrum, and perhaps of the head, in order that the tips of the bill arrive accurately on the target at the end of a rapid thrusting and snatching maneuver. But the difference in the curvature of *virens* and of *mana*, *newtoni* and *sagittirostris* is not extreme. And it may be questioned whether a slightly decurved bill may not be more advantageous than a straight one as mentioned above. In any case, it is not definite that the straight bill of these insectivorous forms of *Loxops* is an adaptation for quick capture of their prey.

A straight bill is a stronger structure than a curved one for certain types of forces acting upon it, but it is not inherently stronger than curved ones with respect to all forces (see Bock, 1966, for a discussion of bill shapes and forces acting on them). The almost completely insectivorous *mana* has a very straight bill which is effectively used as a pry and wedge under bark and lichens or to grasp actively and tear off pieces of bark. These actions would place forces on the tip of the bill, directed posteriorly or laterally. A straight bill would be stronger with respect to such forces; as seen in the straight bill of woodpeckers (Bock, 1966). *L. m. newtoni* feeds more among the foliage and even rarely takes nectar; its bill is more decurved and less robust than that of *mana* as might be expected because of less posteriorly and laterally directed forces on the tips of the bill, and because of the advantages of a curved bill in nectar feeding.

L. sagittirostris captures much of its prey in the deep crevices at the bases of *Freycinetia* leaves. Judging from the attenuated, wedge-like shape of the bill and the relatively large size of the mandibular depressor muscle of this species, we presume that this bird first forces its bill between the base of the leaf and the stalk of the plant and then gapes widely which involves strong depression of the mandible. The forces on the mandible would be partly posteriorly directed ones on its tip when the bill is wedged into the space between the leaf base and stem, and partly dorsoventral ones when the bird gapes. Moreover, a decurved bill may not be well suited for gaping because the curved dorsal surface of the rostrum would tend to slip and push the bill backwards out of the crevice as the bill opened instead of the bill remaining in position and widening the size of the hole. Once the bird has widened the space between the leaf and stem and disturbed this area by its movements, the crickets and beetles living there may scramble about, thus placing themselves in positions more vulnerable to the now gaped beak of the predator than if they remained in a resting, or "crouched," position deep in the crevice.

The short, siskin-like bill of *coccinea* is no doubt an adaptation allowing greater leverage in the opening of leaf buds and Koa pods. The short, relatively wide bill is well suited to resist the laterally directed forces on the tips of the mandible and rostrum when they are rotated in the leaf buds and Koa pods, as well as the ventrodorsal forces on the tips when the bird gapes and spreads the cut material apart to expose insects within the leaf bud or Koa pod. The cutting edges of the two rhamphothecae (the right edge of the mandibular and left of the rostral of a right-billed individual), being wider and flatter, serve as better cutting edges than those of the opposite sides. Furthermore, being wider, they possess a greater potential of viable horny material which can be expended in wear before the actual bony tissue of the dentary and premaxillary bones is exposed. The mandibular cutting edge is kept sharp by its rubbing against the rostral rhamphothecal edge directly dorsal to it, and the rostal cutting edge is sharpened by its grinding against the mandibular rhamphothecal edge directly beneath it. This process is analogous to the method involved in the maintenance of sharp edges on the mandibular tusks of pigs in which the flat surface of the blunt dorsal tusk is ground against the sharp, beveled, ventral one.

That the mandibular cutting edge is usually higher than the opposite one and that the rostral cutting edge is lower than the opposite one of *coccinea* suggests an adaptation which facilitates cutting of leaf tissue or springing apart halves of dry Koa pods during strong adduction of the lower jaw and simultaneous depression of the upper jaw. Because the cutting edges are situated in this way they tend to guide the tips of the rhamphothecae towards the frontal plane rather than away from it during closing of the bill, allowing the muscles involved to perform at maximum efficiency. Furthermore, during depression of the mandible and simultaneous elevation of the maxilla, these edges would not be involved in cutting; instead the rhamphothecal surfaces immediately ventral to the mandibular cutting edge and immediately dorsal to the maxillary cutting edge would be pushed broadside into the bud tissue or against the pod margin and would act, therefore, as spreaders.

The rostal and mandibular slots or troughs, found in the bills of the species of *Loxops* studied, serve to house and guide the tongue. It also seems plausible that in the forms which feed on nectar, *virens*, *sagittirostris* and *newtoni* (occasionally), these slots, when moistened with saliva and nectar, would act as a sealed tube facilitating the conduction of nectar or water up the tube-like or trough-like tongue. It should be noted that the closest fit between slots and tongue is to be found in *virens* and *newtoni*, both of which are partly nectarivorous.

The low median ridge in the roof of the maxillary slot of *newtoni* and in the floor of the mandibular slot of both creepers possibly aid further in guiding the tongue by means of the narrow median slot along the ventral surface of the anterior end of the tongue.

The anteriorly-pointing wedge-shaped mound of tissue in the posterior part of the rostral trough, most noticeable in the *newtoni* but also present in the other forms, may act as a "bumper" against which the tongue is held snugly by muscular contraction when not in use.

The dorsal and ventral nasal opercula, which are better developed in the nectar-feeding *virens*, *newtoni* and presumably *sagittirostris*, together with the nasal preconchae, undoubtedly function as baffles which help to keep pollen grains from entering and plugging the vestibule of the nasal cavity and may be regarded as adaptations for nectar-feeding (Amadon, 1950: 227).

CRANIAL OSTEOLOGY

INTRODUCTION

The skull and mandible of *L. v. virens* will be described in detail first, after which the crania of the four taxa will be compared. The general description will emphasize the features of the skull characteristic of the genus *Loxops*, or at least of the family Drepanididae. Special attention is given to those cranial features essential for understanding a description of the jaw musculature and the functional properties of the feeding apparatus. Because a detailed description and terminology of the passerine skull is not available, decision on the names to be used for many of the finer features of the skull was difficult. We followed as far as possible the general terminology being used in the recent literature without strict regard for priority of the terms or exact homology of the features with those in other vertebrate groups (see Bock, 1960b: 367 footnote). Some arbitrary decisions had to be made, and in these instances we chose those names allowing greatest clarity in understanding the functional properties of the skull.

Comparison of the skulls will stress the differences observable among the four taxa under consideration. These differences will be correlated with the jaw musculature and observations on feeding behavior as the basis on which cranial adaptations for feeding can be analyzed.

Particular attention will be given to those morphological features involved in cranial kinesis in the description of both the skull and the jaw muscles (see Bock, 1964, for a review of avian cranial kinesis). It is our opinion that the morphology, function and adaptation of the feeding apparatus in birds can be understood only with respect to the property of cranial kinesis.

SKULL OF *L. v. virens*

The general appearance of the skull of *virens* (Pls. 3, 7, 8, and Figs. 4, 5, 6) is that of a typical small passerine bird of insectivorous or omnivorous feeding habits. It is not dissimilar to the skull expected in a very thin-billed finch; the general appearance of the skull in *coccinea* is reminiscent of that in a small unspecialized finch or a heavy-billed insect-eater. No unique or specialized passerine features are found in the skull of *Loxops*. The *bony rostrum* (r) (upper jaw, u j, or maxilla, mx) is about 80 per cent of the length of the *braincase* (b c) plus the *orbit* (o). Its longitudinal axis (along the *bony tomium*, b t) bends downward at an angle of almost 45° relative to the longitudinal axis of the braincase (along the jugal bar or the sphenoidal rostrum). The plane of the *occipital plate* (o p) is angled about 60° above the longitudinal axis of the braincase. The braincase is large, about one-third the total length of the skull with its height slightly greater than its length. The length of the orbit

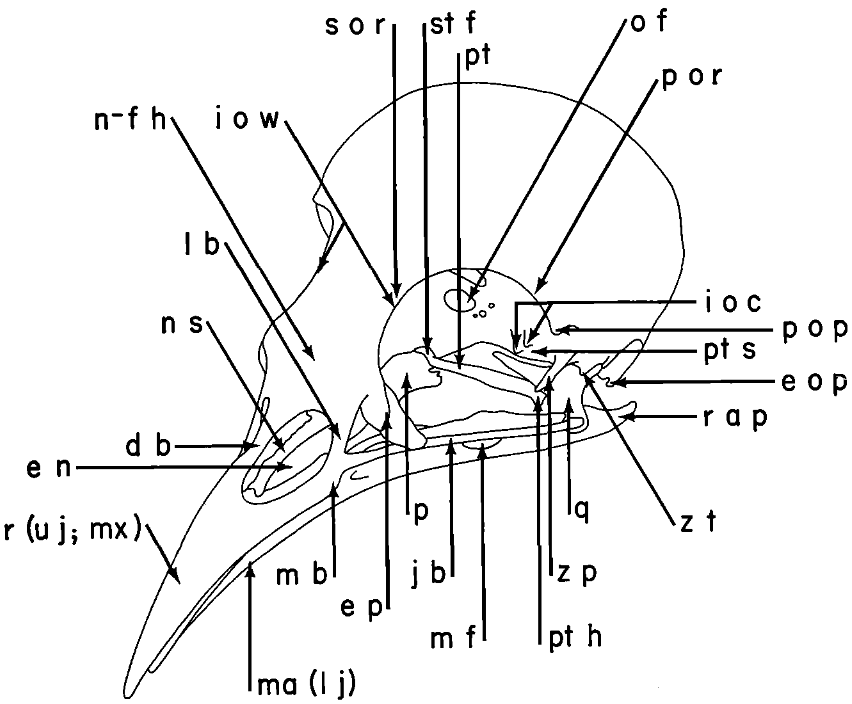


Figure 4. Skull of *L. v. virens* in oblique view labelled as a guide to identification of the osteological features in Plates 3–6.

is about two-thirds the length of the braincase with its height about equal to its length. In ventral view, the maximum braincase width is slightly less than half the skull length; the skull with its bill tapers gradually and evenly from its maximum width across the quadrates to the tip of the rostrum.

The cranial features of *Loxops* can be grouped into the four major mechanical units (Gans, 1969)—braincase, upper jaw, bony palate (including quadrate and jugal bar) and mandible—that comprise the avian kinetic skull (Bock, 1964: 4; and ms.) with a *prokinetic nasofrontal hinge* (n-f h) formed by a thin flexible sheet of bone. This hinge is very broad, being over 80 per cent of the maximum width of the base of the upper jaw and about one-fourth of the maximum width of the skull.

The *braincase* (b c), with its anterior extension comprised of the *supraorbital rims* (s o r; frontal region), *interorbital septum* (i o s) and *sphenoidal rostrum* (s r), forms a single rigid unit. The slightly winged and laterally notched *ectethmoid plate* (e p) is large (Pl. 8) and separates the *orbit* (o) almost completely from the *antorbital space* (a o s). Its *ecteth-*

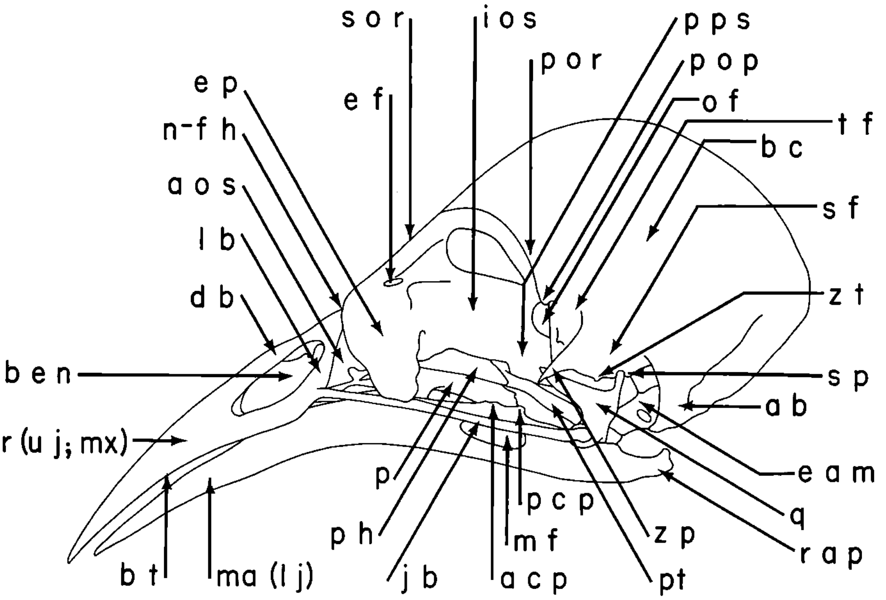


Figure 5. Skull of *Loxops v. virens* in lateral view labelled as a guide to identification of the osteological features in Plates 3–6.

moid foramen (e f) has a single posterior opening and two (sometimes one) anterior openings as a result of division of the ectethmoid canal. The broad externoventral edge of the ectethmoid lies on the dorsal edge of the jugal bar. No trace of the *lacrimal bone* (l) remains in the adult skull (although a small vestige may exist but is lost during cleaning).

The *interorbital width* (i o w) across the frontal region lying between the supraorbital rims is narrow, being less than one-fourth the maximum width of the braincase. Its dorsal surface just posterior to the nasofrontal hinge is concave, but becomes flat toward the braincase roof. Most of the ventral half of the interorbital septum is ossified but a large unossified window leading into the cranial interior exists on each side at the medioposterodorsal corner of the orbit. The sphenoidal rostrum, forming the hollow, beam-like ventral edge of the interorbital septum, is swollen along its entire length with the anterior half of this swelling extending slightly further dorsally than the posterior half. The large *protractor pterygoid scar* (p p s) lying between the *optic foramen* (o f) and the sphenoidal rostrum reduces the height of the swelling in the posterior half of the sphenoidal rostrum. The pterygoid foot and palatine hasp articulate against the anterior half of the swollen sphenoidal rostrum in a sliding joint.

The braincase is bulbous and quite smooth; muscle scars and the limits

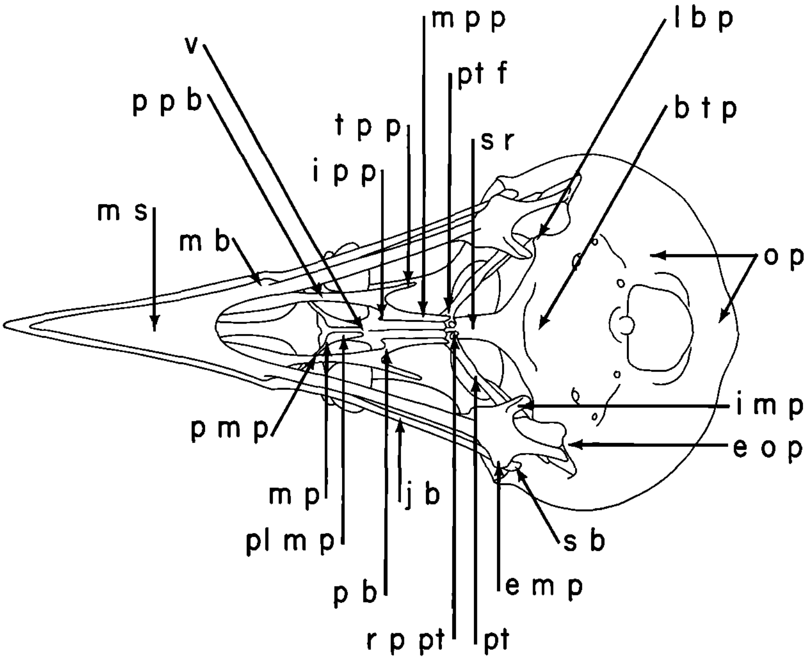


Figure 6. Skull of *L. v. virens* in ventral view labelled as a guide to identification of osteological features in Plates 3–6.

of fossae are scarcely evident. The *postorbital process* (p o p) is a small nubbin, scarcely distinct from the rest of the *postorbital rim* (p o r). The *zygomatic process* (z p) is the most distinct process on the lateral surface of the braincase, but it is only of moderate size in comparison with that in many other passerine birds. It is slightly flattened anteroposteriorly and has a sharp lateral edge. A small *zygomatic tubercle* (z t) is located posterior to the zygomatic process near the ventroposterior corner of the suprameatic fossa. A small, indistinct *temporal fossa* (t f) lies between the postorbital and zygomatic processes, and a slightly larger but still indistinct *subtemporal fossa* (s f) lies between the zygomatic process and the *suprameatic processes* (s p) plus its seemingly anterior extension, the zygomatic tubercle. One or two *intraorbital cristae* (i o c) are found on a bulbous *pseudotemporal swelling* (p t s) of the postorbital wall just medial to the zygomatic process; a depression exists on the medial side of the swelling, corresponding in general shape to the orbital process of the quadrate. The *auditory bulla* (a b) (Dilger, 1956; Bock, 1960a: 38) is not swollen, but its anterior edge extends far forward so that the *external auditory meatus* (e a m) is somewhat narrowed. Only a narrow notch separates the *exoccipital process* (e o p) and lateral basitemporal process of the auditory bulla. Two low ridge-like cristae are located posterior to, and converge at the posteroventral corner of, the exoccipital process; they bound the periphery of the area of origin of the m. depressor mandibulae. The exoccipital process forms the ventrolateral portion of the *occipital plate* (o p); only its ventralmost tip may be distinct from the rest of the occipital plate. The *basitemporal plate* (b t p) is slightly bulbous with a distinct *lateral basitemporal process* (l bt p) extending ventrally from its lateral corners. The distal end of the lateral process of the basitemporal plate bears two small facets (Pl. 7). An obvious, more ventral facet faces ventrolaterally and a less obvious (hidden by the quadrate) more anterodorsal one faces anterolaterally. The former facet functions as a base or prop for a tiny pneumatized tubular bone (this structure may possibly be a cylinder of collagenous fibrous connective tissue) extending between the anteroventral corner of the bony external auditory meatus and the pneumatic foramen in the dorsal surface of the internal mandibular process. The latter facet may abut against the medial edge of the lower half of the otic process of the quadrate and thus may function as a medial brace or guide for the quadrate as it rocks back and forth, but the exact relationships of these bones are difficult to determine in dried skulls and must be checked further before the bracing function of this process is definitely established.

The *rostrum*, *maxilla*, or *bony upper jaw*, (r, mx, or u j) is slender and curves gradually downward from its base to its tip. The cutting edge of the *bony tomium* (b t) projects slightly below the ventral surface of the rostrum, starting abruptly at the junction between the jugal bar and rostrum. The *bony external naris* (b e n) is large, in length about one-third the rostral length, oval, and almost completely unossified; neither the membranes in the external naris nor the medial *nasal septum* (n s) are ossified except for a bit around the edges of the septum. The *lateral bar* (l b) lying between the external naris and the antorbital space is narrow but relatively stout as is the *dorsal bar* (d b) lying along the dorsal edge of the maxilla above the external naris. The jugal bar and prepalatine bar join the upper jaw at the same level as does the maxillopalatine, the base of which is hidden (when viewed ventrally but not dorsally) by the prepalatine bar. The *palatine process of the premaxilla* (p p pm) is completely fused with the prepalatine bar (Pl. 7). A slight expansion of the base of the prepalatine bar exists and appears as an early rudimentary stage in the evolution (or as a late vestigial stage in the loss) of the *lateral flange condition* (l f c) of the palatine process of the premaxilla (Bock, 1960b: 380–381). Only the anterior two-thirds of the rostrum floor are completely ossified; the area between the bases of the prepalatine bars (floor of the nasal cavity) is unossified.

Lying at the junction between the braincase, bony palate and mandible, the *quadrate* (q) has a central role in all kinetic movements (Pl. 8). Hence the exact details of its articulations with surrounding bones are most important. All processes may be considered as extensions from a central mass—the *body of the quadrate* (b q). The *otic process of the quadrate* (ot p q) extends posterodorsally to articulate with the braincase at its ventrolateral corner below the suprameatic process and anterior to the external auditory meatus. The quadrate-squamosal articulation is elongated with its longitudinal axis inclined anterolaterad at an angle of about 75° to the longitudinal axis of the skull; the quadrate rotates about this articulation as it rocks back and forth during kinetic cranial movement. This articulation is two-headed with a very shallow saddle between the *lateral condyle of the otic process* (l c ot p) and the *medial condyle of the otic process* (m c ot p); no clear break appears to exist between the articulating surfaces of these condyles. The lateral condyle of the otic process lies anterodorsal to the medial condyle of this process. The suprameatic process lies posterior to the lateral condyle of the otic process and apparently assists in its support. A large, sharply defined fossa covers most of the posteroventral surface of the otic process. At the level of the ventral end of this fossa, the medial edge of the otic process may rest against the more dorsal facet at the tip of the lateral basitemporal process. If these structures do not touch in the living bird, they approach each other very closely. The *orbital process of the quadrate* (ob p q) projects anterodorsomedially from the medial surface of the quadrate body; it is long and slender with a tapered tip. A short ridge-like *rugosity of the orbital process of the quadrate* (r ob p) exists on the dorsolateral edge of the distal tip of the process. A small *tubercle of the orbital process of the quadrate* (t ob p) lies on its dorsolateral surface about one-third of the distance from the base of the process. The distal half of the orbital process lies close to the bulbous swelling of the postorbital wall on which the intraorbital cristae are found. An elongated depression exists on the medial edge of the pseudotemporal swelling which corresponds approximately to the orbital process in size and shape. This swelling may act as a bony stop that limits dorsoposterior movement of the orbital process; hence anterodorsal rotation of the quadrate and elevation of the upper jaw might be restricted. The groove may be a phenotypic modification during the life of an individual bird resulting from frequent, intermittent pressure of the orbital process of the quadrate on the postorbital wall. The *mandibular process of the quadrate* (m p q) extends ventrally on the medial side of the bone, while the *jugal process of the quadrate* (j p q) extends lateroventrally from the lateral side of the bone. A distinct saddle separates these processes; this is most evident in posterior view. The mandibular process bears the large knob-like *medial condyle of the quadrate* (m c q) on its ventral tip and the smaller *pterygoid condyle of the quadrate* (pt p q) on its medial surface. The lateral tip of the jugal process has a cup-like socket into which the jugal bar articulates and bears the *lateral condyle of the quadrate* (l c q) on its ventral surface. The *posterior condyle of the quadrate* (p c q) extends back from the lateral condyle along the posterior edge of the jugal process and ends in the posterior edge of the saddle between the two ventral processes. The lateral condyle is considerably smaller and lies further dorsally than the large knob-like medial condyle. The posterior condyle exists mainly as an extension of the lateral condyle. The posterior end of the *jugal bar* (j b), which is slightly compressed laterally along most of its length, has a distinct lateral bend around the distal tip of the jugal process of the quadrate. Its posterior tip then bends medially at a right angle and articulates into the concavity on the lateral face of the jugal process of the quadrate in a ball and socket joint. The jugal bar is thin and relatively straight along most of its length. At its junction with the posterolateral base of the rostrum, it is slightly flattened dorsoventrally.

The *pterygoid* (pt) is a nearly straight bar of bone from the quadrate to the palatine and sphenoidal rostrum (Pls. 7, 8); it meets the sphenoidal rostrum at an angle of about 45°. The *pterygoid head* (pt h) is expanded slightly and articulates with the rounded pterygoid condyle of the quadrate. On the dorsal surface of the pterygoid head is the stout *protractor pterygoid tubercle* (p pt t). It is slightly curved so that its free tip points toward the origin of the m. protractor pterygoidei et quadrati at the protractor pterygoid scar. The anterior end of the pterygoid is expanded into a dorsolateral *pterygoid foot* (pt f) and a ventromedial *retractor process of the pterygoid* (r p pt); these expansions curve around the swollen sphenoidal rostrum; the retractor processes of the paired pterygoids meet midventrally. Each retractor process has on its posterior surface a small, low depression which serves as part of the origin of the m. pterygoideus retractor. The pterygoid foot articulates with the palatine hasp along a flexible suture line.

The *palatine* (p) is, morphologically and functionally, a bony bar extending from the pterygoid to the posteroventral base of the upper jaw, with several processes jutting out in different directions; the bony strut transmits force between the pterygoid and the rostrum, and the several processes serve as sites of muscle attachment and supports for closely associated structures (Pl. 7). Its elongated dorsal extension forms half of the *palatine hasp* (p h). The right and left halves of the palatine hasp embrace the sphenoidal rostrum, meeting midventrally beneath it, and articulate with it in a long sliding hemicylindrical diarthrosis. From the ventral edge of the palatine hasp, the palatine extends ventrally as the plate-like *wall of the palatine trough* (w p t). The paired walls of the palatine trough meet along the midline of the skull below the sphenoidal rostrum to form the hemicylindrical *palatine trough* (p t) which opens ventrally. The wall of the palatine trough includes the mediopalatine process posteriorly and the interpalatine process anteriorly. In cross-section, the palatine hasp and palatine trough form a figure 8 with its base and top cut off. The palatine trough contains the *posterior nasal canal* (p n c) that extends from the internal nares to open ventrally on the roof of the pharynx. The ventral edges of the palatine trough support the edge of the opening of the posterior nasal canal into the pharynx. The posterior half of the wall of the palatine trough forms the *mediopalatine process* (m p p) which extends beneath the retractor process of the pterygoid (*i.e.*, partially covers the retractor process in ventral view). The free posterior tip of the mediopalatine process is frequently broken during preparation of the skeleton so that the process appears shorter than its actual length.

The *interpalatine process* (i p p) extends forward from the anteroventral tip of the wall of the palatine trough and points toward the maxillopalatine. The interpalatine process and maxillopalatine are connected by a collagenous fibered band which supports the anterior end of the posterior nasal canal.

The *palatine blade* (p b) extends ventrolaterally from the lateral surface of the palatine trough. As compared to its degree of development in other oscines (*e.g.*, *Corvus*), it is relatively narrow anteroposteriorly but stout. The elongated, thin *transpalatine process* (t p p) extends back from the lateral edge of the palatine blade; the distal tip of this process is slightly bifurcated. The stout *prepalatine bar* (p p b) connects the palatine blade to the base of the upper jaw. A narrow lateral flange exists at the anterior end of the prepalatine bar. Although the palatine appears to be thin, fragile and ramified, it is essentially a stout, straight bar of bone extending from the pterygoid foot to the base of the rostrum.

The bilateral pair of pterygoid feet and the two halves of the palatine hasp grasp the sphenoidal rostrum in a long sliding articulation. The bones on the two sides meet or almost meet on the midventral line, but are nowhere fused together. The *vomer* (v) extends anteriad from the anteroventral edges of the bilateral halves of the palatine hasp as a pair of thin bars that terminate in a broad triangular anteromedial plate (Pl. 7). The *maxillopalatine* (m p) arises from the dorsal surface of the rostral floor at its junction with the jugal bar, and passes dorsally above the prepalatine bar. The *pedicel of the maxillopalatine* (p m p) extends medioposteriorly at an angle of about 45° to the longitudinal axis of the skull. The terminal *plate of the maxillopalatine* (pl m p) is an elongated, narrow pneumatized tube with laterally flattened edges, and lies ventrad to the medial plate of the vomer.

The *mandible or lower jaw* (ma, l j) is thin and decurved, following the curvature of the upper jaw; the total angle of curvature is at least 45° (Pl. 3). Both rami are fused together at their anterior tip to form the *mandibular symphysis* (m s) that is about one-fourth the total length of the mandible. A low, but distinct bony *mandibular boss* (m b) is present on the dorsolateral rim of the ramus just posterior to the mandibular symphysis. This boss fits into the space medial to the posterior end of the bony tomial ridge of the upper jaw so that it abuts and presses against the ventral end of the lateral bar of the upper jaw. This arrangement of the mandibular boss and the tomial ridge reinforced by the lateral bar forms the bony support for what may be cutting and/or crushing rhampothecial surfaces correlated with insect-eating. The *mandibular foramen* (m f) is small and lies directly below the low coronoid processes. It lies in the posterior end of a large *external* and a large *internal mandibular fossa* (e m f and i m f), each of which extends forward to the level of the mandibular boss. The ventral edge of the internal mandibular fossa is bounded by the *medial mandibular ledge* (m m l).

A pair of low *anterior* and *posterior coronoid processes* (a c p and p c p) extend from the dorsal edge of the ramus above the mandibular fossa (Pl. 8). On the medial surface of the ramus just anterior to the internal mandibular process lie the *tubercle of the posterior mandibular adductor* (t p m a) and the *tubercle of the pseudotemporalis* (t pt), both of which are small and indistinct in *virens*. The tubercle of the posterior mandibular adductor is a tiny rounded tubercle and in height is about twice the width of the anterior coronoid process, both measured when viewing the ramus directly from above. It lies immediately lateral and slightly dorsal to the anterior margin of the groove in the dorsal surface of the internal mandibular process, into which the medial condyle of the quadrate articulates. The tubercle of the pseudotemporalis is of about the same size, but its anterodorsal surface is flat. It lies slightly anteroventral and also medial to the tubercle of the posterior mandibular adductor.

The *internal mandibular process* (i m p) extends dorsally more than medially and is thin with a slightly expanded tip that is laterally compressed and anteriorly beaked. Each side of this tip contains a muscle scar. A large pneumatic foramen opens on its lateral surface just distal to the articular surface at the base of the process. The area or shelf at the corner formed by the mandibular ramus and internal process is the *internomandibular flange* (i m f); it is best seen in ventral aspect, and its ventral surface functions as the insertion for certain musculature. The dorsal surface of this flange has a deep elongated *articular groove* (a g) limited medially by the internal mandibular process and laterally by the mandibular ramus; this groove forms the mandibular articulating surface for the large medial condyle of the quadrate (Pl. 8). On the laterodorsal edge of the ramus opposite the internal mandibular process is the elongated low *external mandibular process* (e m p). Its dorsal surface forms the articulating surface for the lateral condyle and the small posterior condyle of the quadrate. The ridge-like external mandibular process fits into the deep saddle between the medial and lateral condyles of the quadrate. The quadrate-mandibular articulation is, hence, one that would permit considerable anteroposterior sliding in addition to dorsoventral rotation of the mandible but only limited lateral rotation of the mandible. The mandible terminates in a long *retroarticular process* (r a p) which appears in dorsal view as a posterior extension of the external process. An obvious, knobby, dorsally projecting tubercle on the dorsal edge of its distal tip functions as part of the insertion for the m. depressor mandibulae. A shallow depression on the medial surface of the retroarticular process is continuous with the articular groove for the medial condyle of the quadrate. Transversely across the dorsal edge of the retroarticular process and immediately posterior to the external mandibular process is a tiny *retroarticular notch* (r a n) into which the small posterior condyle of the quadrate slips when the mandible, either in its closed or its depressed position, is pushed forward. This notch may serve as a bony stop or support for the mandible when it is depressed.

One or two *sesamoid bones* (s b) are found in the internal jugomandibular ligament where it passes along the posterior edge of the quadrate-mandibular articulation (see Fiedler, 1951: 268–270 for a review of these sesamoids). Moreover, a short tubular bone or cylinder of heavy collagenous fiber extends dorsally from the pneumatic foramen in the internal mandibular process. It runs along the posterior surface of the otic process of the quadrate, lying between the quadrate and the lateral basitemporal process. This tube is sometimes still attached to the mandible or to the base of the brain case.

CRANIAL KINESIS

Basic to understanding the form, function and adaptive significance of the cranium and jaw musculature of *Loxops*, a clear comprehension of the mechanism of avian cranial kinesis, particularly of the passerine skull, is necessary (Fig. 7). This mechanism has been described among others by Lakjer (1926: 96–101), Moller (1931: 138–147), Engels (1940: 364–365), Beecher (1951a: 412–415; 1962) and has been reviewed recently by Bock (1964; and ms). We refer the reader to Bock (1964 and ms) for a discussion of the basic properties of cranial kinesis.

Cranial kinesis has adaptive significance in both dynamic and static conditions (Bock, 1966); in *Loxops* the basic significance of kinesis apears to be associated mainly with movement of the upper jaw. The number of degrees of arc through which the tip of the maxilla moves from the retracted to the protracted position is referred to as the degree of kinetics of the skull. In *Loxops*, this degree of kinetics in a cleaned, water-soaked skull appears to be about 27°. Certainly such movement could be put to good use by all forms both during protraction and retraction of the rostrum while gaping or grasping with the bill during feeding. In *virens*, kinesis is important while presumably gaping in campanulate blossoms, foliage, mounds of lichen or in the pulp of fruit. The creeper *newtoni* probably gapes in lichens and foliage to expose insects, while its relative *mana* uses its kinetic upper jaw presumably to gape with the bill beneath sheets of bark or in lichens and to grasp pieces of bark or large struggling insects. Similarly, *coccinea* may gape while widening and cutting holes in leaf buds or springing open Koa pods, and may clamp down on the leafy material while removing wads cut from leaf buds. The higher degree of flexibility in the nasofrontal hinge (34°) and the relatively long bill of *newtoni* are perhaps correlated with its almost purely insectivorous diet and its hunting in foliage rather than on bark. It can be surmised that the majority of arthropods living in foliage depend upon rapid scrambling movements or aerial flight by jumping, flying or suspension by silk threads for escape from predators rather than hiding beneath tough sheets of bark as do many of the insects living on trunks or large branches of trees. To capture such nimble, foliage-inhabiting prey, a bird must be able to expose and seize them quickly before they can escape. To hunt in a dense maze of overlapping, flexible and obscuring leaves, a bird would be better adapted if it could spread these leaves widely apart by gaping its bill than if it could spread them apart to only a lesser extent with little movement of the maxilla. The bird could thus see the prey more easily, and, moveover, its beak would be widely opened and ready to grab the prey quickly. Furthermore, movement of both jaws during opening the bill would decrease considerably shifts in orientation of the line of sight with respect to the longitudinal axis of the bill between the two jaws (Moller, 1931: 146; Bock, 1964: 28) which is of particular value to a bird peering quickly between the tips of its jaws for insects. The fact that the bill of *newtoni* is relatively longer than that of *mana*, for example, gives the former a further advantage for spreading leaves widely apart, etc., because the same degree of kinetics for both a long-billed and a short-billed form will allow the tip of the rostrum during protraction to travel through a greater distance in the former than in the latter.

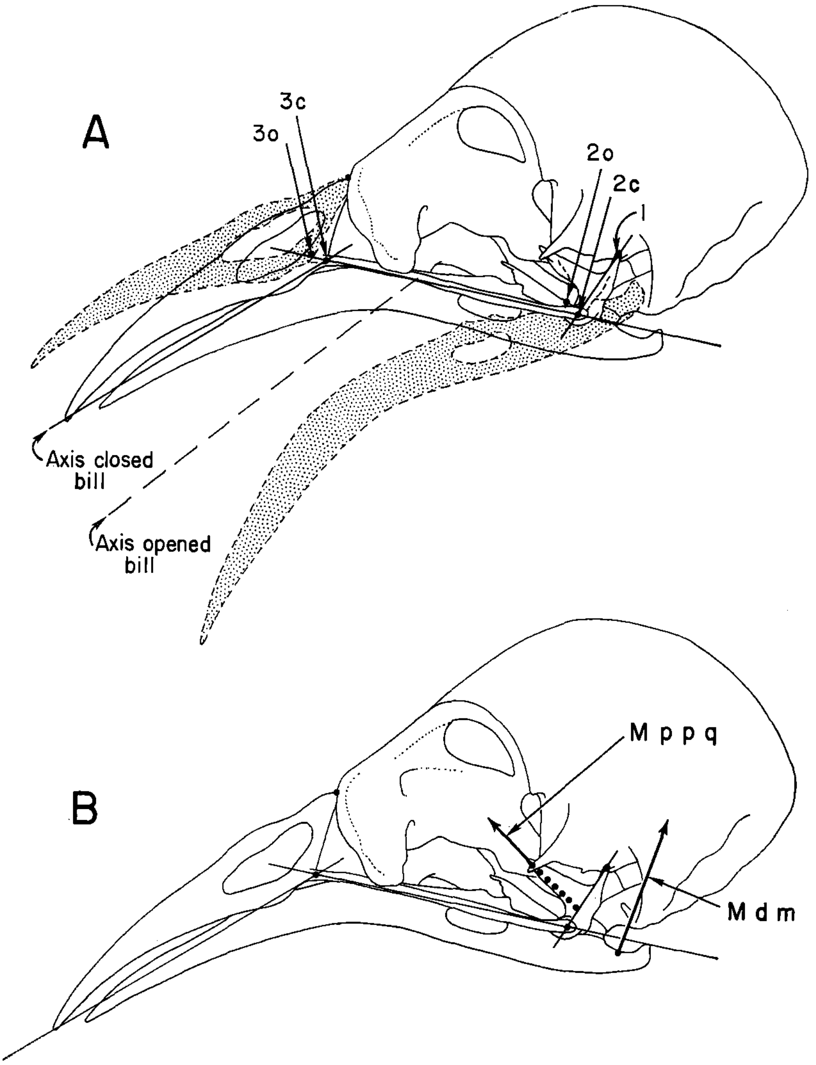
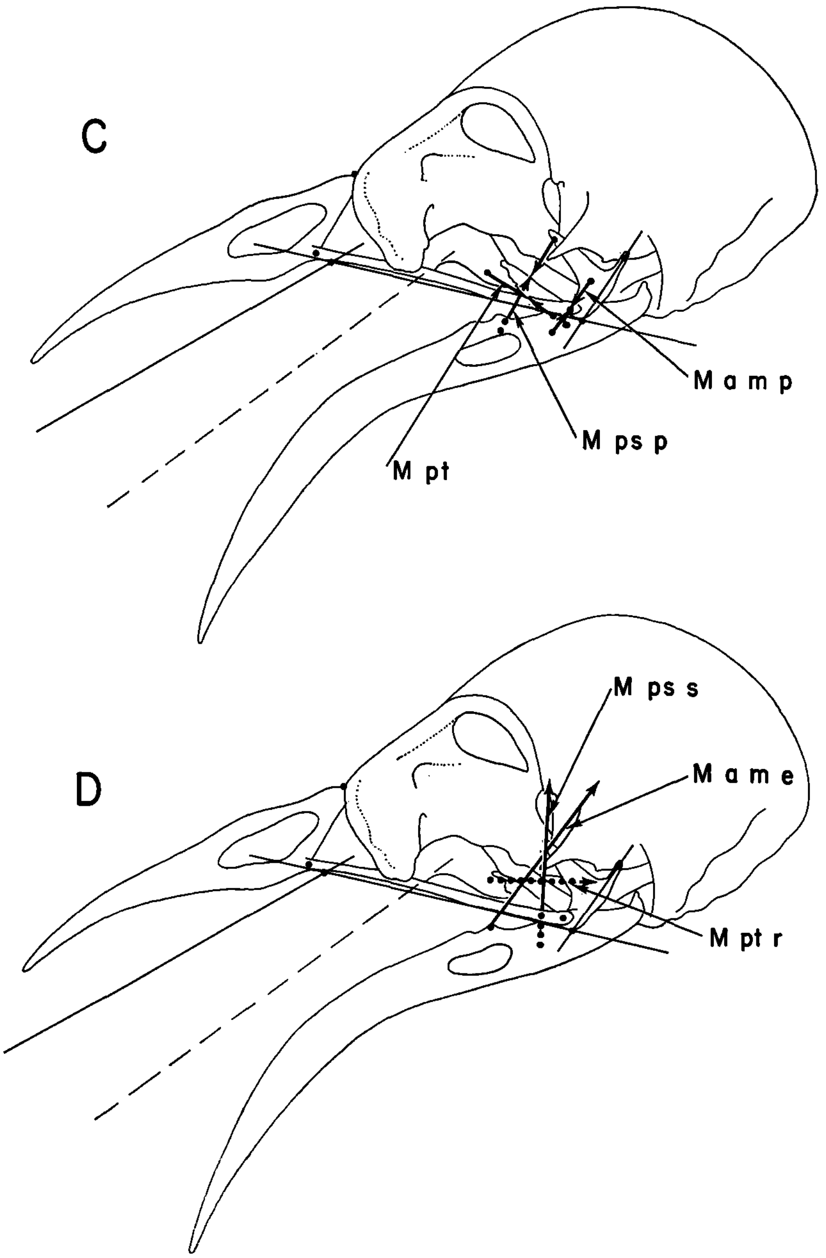


Figure 7. Schematic model of *L. v. virens* to show movements of the maxilla and the mandible during opening and closing of the bill. A) Solid lines indicate the position of the jaws in closed position while the dashed lines and stippling shows them in the fully opened position. The solid lines connecting the heavy dots indicate the longitudinal axis of the quadrate, jugal bar and beak in the closed position. The long dashed line indicates the longitudinal axis of the beak when the jaws are opened. The heavy dots indicate: (1) the squamosal articulation of the quadrate; (2) the quadrate-mandibular articulation in the closed (2c) and opened (2o) positions; and (3) the posteroventral corner of the maxilla in the closed (3c) and opened (3o) positions. B) Force vectors of the two muscles, m d m and m p p q, that serve to open the jaws; the heavy dotted line indicates the part of a force vector lying behind a bone.



C) Force vectors of the three muscles, m a m p, m ps p and m pt, that serve to close the jaws without being able to retract the whole jaw apparatus relative to the brain case. D) Force vectors of the three muscles, m a m e; m ps s and m pt r, that serve to close the jaws and retract the whole jaw apparatus relative to the brain case.

GAPING ADAPTATIONS

In addition to the importance of cranial kinesis for gaping, modifications of several other features of the head are probably correlated with this feeding method. One of these osteological adaptations is in the shape of the ectethmoid plate. In *Loxops* and many other passerine birds, the ectethmoid flares out laterally at its dorsal and ventral ends. Between these dorsal and ventral alae is an in-cut saddle or notch as illustrated by Beecher (1953: 275, fig. 1) who refers to this condition as the "winged" ectethmoid plate. This ectethmoid notch is well developed in starlings (Sturnidae) and meadowlarks and blackbirds (Icteridae) in which the jugal bars bend medially (are pinched in) at their junction with the base of the upper jaw. Although it has been reported that most birds have little or no capability of rotating the eyeball which fits tightly into its socket (Walls, 1940: 307), the European Starling, *Sturnus vulgaris*, and meadowlarks, *Sturnella* spp., can turn their eyes forward while the birds are gaping among grass roots, soil, etc. That these birds look forward for their food items between the upper and lower jaws as they are gaped apart is well described by Lorenz (1949). Forward rotation of the eyes to bring the central foveae into position for forward binocular vision would be of great advantage to such gaping insectivorous birds as has been demonstrated by Oehme (1962). Beecher (1951a: 423–424; 1953: 275) also describes this mechanism for meadowlarks and other birds.

In *Loxops* the interectethmoid width measured between the troughs of the notches is narrowest in *newtoni.* It is somewhat less narrow in *mana* and widest in *virens* and *coccinea.* These conditions fit the observations that *mana* and *newtoni*, especially the former, feed more on highly active arthropod prey which must be exposed quickly by gaping movements and snatched-up before it has a chance to escape. The narrowness of the interectethmoid width would allow a greater uninhibited view of the prey through the gaped beak.

COMPARISON OF THE SKULL IN *Loxops*

Certain peculiar differences in shapes and relative sizes of parts of the skulls and jaws exist in each form which allow relatively easy differentiation between them. The summary of these differences in Table 1 taken together with the figures of the skulls (Plates 3 to 9) will aid in comprehending these differences which are more apparent in the actual specimens. Because the crania of these four forms are all about the same height (11 to 12 mm.), direct comparisons can be made between these congeneric taxa without the need of compensating for any effects of relative size.

The maxillary, premaxillary, nasal, and dentary bones serve as the foundations for the rhamphothecae; in curvature and relative length the

TABLE 1

COMPARISON OF OSTEOLOGY OF SKULLS AND MANDIBLES: GROSS FEATURES

Structure or Feature	*L. v. virens*	*L. m. mana*	*L. m. newtoni*	*L. c. coccinea*
General Shape:				
1. Mandible:				
a. Length	long	shorter	long	shortest
b. Intercondylar width	wide	wide	narrow	wide
c. Curvature along dorsal edges	decurved	straight	slightly decurved	straight
2. Rostrum:				
a. Length	long	shorter	long	shortest
b. Curvature	decurved	straight	slightly decurved	decurved
3. Cranium:				
a. Bulbousness	not bulbous	bulbous	not bulbous	not bulbous
b. Mean height (mm.)[1]	11.3 (25)	11.8 (2)	11.6 (2)	10.9 (1)
Relative Strength	frail	robust	most frail	most robust
Relative Sizes:				
1. Interorbital width	wide	wide	narrow	widest
2. Interorbital septum	thin, or with small performation	small perforation	large perforation	solid; no perforation
3. Nasofrontal hinge: kinetics[1, 2]	26.7° (4)	25.0° (2)	34.4° (1)	*ca.* 25° (1)
4. Sphenoidal rostrum thickness	thick	thick	thin	thickest
5. Nasal arch: thickness	wide	wider	narrow	widest
6. Pterygoid: thickness	thin	thick	thinnest	thick
7. Jugal bar: thickness	thin	thin	thin	thinnest
8. Prepalatine bar: width	narrowest	wide	narrow	wide
9. Palatine hasp: ventral surface	divided	divided	divided	divided at posterior end only
10. Mandibular foramen: size	medium to large	medium	large	small
11. Mandibular ramus: thickness	thick	thicker	thin	thicker
Interectethmoidal Width:[3]	widest	narrow	narrowest	wide

[1] Number in parentheses is sample size.
[2] Arithmetic means of degrees of kinetics.
[3] As seen from in front and measured from troughs of notches.

underlying bones parallel the rhamphothecae, for which the functions and adaptations have already been discussed. The intercondylar distance between the mandibular rami in *newtoni* is definitely narrower than that of the other forms, thus giving to this race a relatively narrower and more acutely pointed bill. The cranial width of all forms except *mana* is about the same. The cranium of the latter, however, is noticeably more bulbous than in the rest; its functional significance is not known. In some way this bulbousness may be correlated with obtaining prey by strenuous prying into bark crevices. An extremely bulbous cranium also occurs in the psittirostrine, *Hemignathus wilsoni*, which pounds and prys in dead wood and bark in search of its insect prey much as does a woodpecker. It is interesting to note that Burt (1930: 471, 472, 474, 521) found that those woodpeckers which obtain most of their food by actively pecking in wood have relatively larger brain cavities than those which pluck their prey from surfaces of branches or from other sites. He offers no explanation for this phenomenon.

The skull of *coccinea* appears the strongest in structure and that of *newtoni* the frailest. The skull of *mana* appears slightly frailer than that of *coccinea* but sturdier than that of *virens*. These differences (see Table 1) are most evident in the interorbital septum (checked in as many specimens as possible); degree of kinetics of the upper jaw, and thus flexibility of the nasofrontal hinge; amount of division ventrally between the two halves of the palatine hasp; thickness of the sphenoidal rostrum, nasal arch between the external nares, mandibular rami, pterygoids and prepalatine bars; and size of mandibular foramen. Seemingly incongruous is the fact that the jugal bars of *coccinea* are the smallest in diameter of the four forms. These may not be relatively smaller than the jugal bars in other forms of *Loxops* because *coccinea* is the smallest of the four forms under study, and its cranial height is also slightly lower than that of the others.

It seems reasonable that these aspects of general sturdiness or frailty of the skull are of adaptational significance in feeding methods. Certainly, *coccinea* and *mana* would need a skeletal structure of stronger architecture for strenuous opening of closely imbricated leaf buds or tightly closed bean pods and for prying in crevices of hard bark, than would *virens* and *newtoni* for obtaining insects from foliage and lichens or nectar from blossoms.

The skulls also exhibit differences in sizes and shapes of sites of muscle attachment. These are not so obvious as the general differences in shapes, relative sizes, degrees of sturdiness of skull architecture or flexibility of the skulls described above; however, they are real and discernible and have functional significance. These are seen as differences in size and shape of a number of small bony processes and tubercles on the cranium, palate and jaws; as variations in sizes, shapes, and depths of muscle scars and fossae; and as variations in sizes of surface areas for attachment of certain muscles. Many of these differences are discernible in Plates 3–9 showing the skulls, and they are tabulated in Table 2. Because their functional significances are closely correlated with the jaw muscles, they will be discussed in the following section on the anatomy and function of these muscles.

TABLE 2
COMPARISON OF OSTEOLOGY OF SKULLS AND MANDIBLES: MINUTE FEATURES

Structure	*L. v. virens*	*L. m. mana*	*L. m. newtoni*	*L. c. coccinea*[1]
intmand. flange: width	narrow	wide	narrower; bulges ventrally	left: widest right: wide
pal. blade: lateral area[2]	narrower	broad	narrowest	left: broadest right: broad
prepal. bar: width	narrowest	wide	narrow	left: widest right: wide
proc. art. ext.: width	wide[3]	wide	narrow	left: wide right: narrow
proc. art. int.: length	shortest	shorter	long	shorter
proc. corn. ant.: size	low; thin	low; thin	low; thick	low; thicker
proc. corn. post.: size	high; thin	high; thicker	low; thick	low; thicker
proc. intraorb.: size	long; thin	long, thicker	shortest; thin	medial: shorter; thick. lateral: abbreviated
proc. orb. quad.: size	long; thick; narrow	shorter; thick; narrower	shortest; thin; narrow	long; thick; wide
proc. postorb.: truncation	truncated	truncated	sharply pointed	truncated
proc. postpal.: length and lateral area	long; narrow	short; wide	longest; narrow	short; wide
proc. retroart.: length[4]	long	shorter	shortest	long
proc. ptery. ret.: size and degree of concavity	medium; concave	large; most concave	small; convex	large; convex
proc. transpal.: length and diameter	longest; slender	shorter; thicker	long; slender	left: shortest; thickest right: shorter; thicker
proc. zyg. dors.: size	long; narrow thicker	long; wide thicker	shortest; narrow thin	left: shorter; wide; thicker right: long; wider; thickest
proc. zyg. vent.: size	large	small	small; thin	smallest
protr. pter. scar: size	long; shallow to deep	long; deep	short; shallow	longest; deepest
rug. proc. orb. quad.: size	small	absent	absent	left: larger right: large
tub. add. post.: size	larger?	large	smaller	smaller
tub. proc. orb. quad.: size	large	small	large	smallest
tub. protr. pter.: size	long; thinner	shorter; thick	long; thin	longest; thinner

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[1] Right-billed specimens.
[2] Not shown well in Plates 3–6.
[3] Not shown well in Plate 3.
[4] Longest and deep in *L. sagittirostris*.

CRANIAL ASYMMETRY IN *L. c. coccinea*

As would be expected, the asymmetrically crossed rhamphotheceal tips of *coccinea* are reflected further in bilateral asymmetry in its skull, but far fewer features are affected than one might anticipate. The bony maxilla and mandible are symmetrical as are the braincase (including ectethmoid plates, supraorbital rims and basitemporal plate), jugal bars and palate except for small details. The only differences in the palate appear to be a straighter, less laterally flaring transpalatine process (in a right-billed bird which will be described herein) and a slightly larger pterygoid foot on the left side. The temporal and subtemporal fossae are larger on the right side of the braincase with a sharply defined dorsoposterior border and a larger zygomatic process separating them. These differences are correlated with bilateral differences in jaw muscles as described below.

The major cranial asymmetries occur in the quadrate-mandibular articulations (Pl. 9) which are associated with lateral rotation of the mandible as the bill tips slide laterally in a slicing movement. On the right side of the skull, the medial condyle of the quadrate is slightly larger so that the pterygoid condyle appears to be shorter. The saddle between the mandibular and jugal processes of the quadrate is slightly deeper with a sharply defined ridge along its lateral edge. This ridge forms the medial edge of the small lateral condyle of the quadrate. A large articular surface lines the lateral wall of the saddle below the lateral condyle; this articular facet extends to the bottom of the saddle and backward to a distinct, and large for *Loxops*, posterior condyle of the quadrate. On the corresponding side of the mandible, the internal process has an extended tip, and the internomandibular flange appears a bit broader. Its articular groove is broader and less distinct with the articular facet restricted to the center of the groove. Most notable is the very small (low) external process of the mandible, and the elongated articular surface along the dorsal edge of the ramus (corresponding to the large articular surface in the saddle of the quadrate) that extends onto the retroarticular process and ends in a distinct ridge. Because this articular surface covers the base of the retroarticular process, this process appears to be shorter than that on the left side, but the two retroarticular processes are of equal length.

On the left side of the skull, the medial condyle of the quadrate is shorter, the lateral condyle is broader and flatter and the posterior condyle is almost absent. No distinct articular surface is present on the saddle between the jugal and mandibular processes. On the mandible, the external process is large with an extensive articular facet (for the large lateral condyle of the quadrate) covering its entire dorsal surface. The articular groove is narrower and better defined with an articular facet extending along its entire length. The retroarticular process has a more definite concavity on its medial surface. The posterior mandibular adductor tubercle and the pseudotemporalis tubercle are both larger on the left side of the mandible.

JAW MUSCULATURE

INTRODUCTION

The currently accepted system of identifications and homologies of avian jaw muscles with those of other vertebrates has its foundations in the now classic study of Lakjer (1926) and subsequent works of Hofer (1950), Fiedler (1951) and Starck (1959 and others). In this study we have followed the system of identification and terminology for passerine jaw muscles and their parts advocated by Bock (ms). This system follows that of Fiedler (1951) very closely and hence stems from the earlier works of Lakjer (1926), Moller (1930, 1931) and Hofer (1950). No attempt will be made to summarize the synonymies of the names used by these authors and others such as Beecher (1951a, 1951b, 1953) and Bowman (1961); the reader is referred to Bock's (ms) study for this information.

The functional properties (Fig. 7) of the individual jaw muscles, sets of these muscles, the entire musculature and the jaw apparatus were analyzed and correlated with the field observations of feeding behavior made by Richards. All conclusions reached in this phase of the study are speculations and must be treated as hypotheses to be tested, not as demonstrated facts. Discussions of the actions of these muscles follow the general analysis of Bock and Morioka (ms) and include consideration of fiber arrangement, whether parallel-fibered or pinnate (see Gans and Bock, 1965), of the position of the muscles relative to the articulations in the skeletal level system, whether one-joint or two-joint (see Bock, 1968), and most importantly, of the consequences of cranial kinesis in birds (reviewed by Bock, 1964, 1966). These several factors underlying the functional properties of the jaw muscles are closely interrelated with one another and must be considered simultaneously as demonstrated for the m. pseudotemporalis superficialis and m. pseudotemporalis profundus (Bock, 1967; Bock and Shear, ms a).

The innervations of the jaw muscles were not included in the dissections made by Richards as he found that he could homologize the muscles observed in *Loxops* with those described in other passerine birds by Lakjer, Moller, Fiedler and most of those illustrated by Beecher. Moreover, Bock (ms) also concluded that the homologies of the jaw muscles and their major parts in passerine birds could be established without considering their innervations.

The jaw ligaments were examined only superficially during the original dissection and will be excluded from the description. However, the absence of the postorbital ligament as a functional structure (it may be present as an extremely thin vestige) was ascertained specially in dissections made in the summer of 1963 by Richards and Bock. *Loxops* agrees with the cardueline and other finches in lacking this ligament and hence possesses uncoupled cranial kinesis (Bock, 1964).

The following description and comparison of the jaw muscles is based upon dissection of the four taxa of *Loxops* under consideration. All statements referring to left or right sides of *coccinea* are based upon observations made on right-billed specimens. The opposite configuration would be found in left-billed specimens. The figures illustrating the jaw muscles of each species are grouped together into composite plates; thus the musculature of *virens* is illustrated on Plates 10 and 11, of *mana* on Plates 12 and 13, of *newtoni* on Plates 14 and 15, of *coccinea* on Plates 16, 17 and 18, and of *sagittirostris* on Plate 18. Reference to these figures will not be repeated in the descriptions of individual muscles as this would be overly redundant and of little use to the reader because the plates illustrate the whole musculature, not individual muscles.

DESCRIPTION OF INDIVIDUAL MUSCLES

A) *M. protractor pterygoidei et quadrati* (m. protr. pter. quad., m p p q): The protractor of the bony palate is frequently divided into two distinct muscles, the m. protractor pterygoidei (*sensu stricto*) that inserts on the pterygoid and the m. protractor quadrati that inserts on the quadrate. However, separation of these parts is nebulous as we were never certain whether the cleft between these muscles made by an inserted probe during dissection was a natural division or an artificial extension of the slight gap at the pterygoid-quadrate articulation in the insertion of this muscle. Because the two parts of the protractor muscle were recorded and described separately during dissection, they will be so discussed herein without any commitment as to whether they constitute discrete parts.

The m. protr. pter. quad. is a blade-shaped muscle lying along the ventral edge of the posterior wall of the orbit. Hence it is one of the deepest jaw muscles and can be observed clearly only when most of the other muscles have been removed. The fibers are unipinnate and insert on a tendon running along the ventrolateral edge of the muscle. Those fibers inserting on the protractor tubercle of the pterygoid are designated as the m. protr. pter. s. str. and those that pass posteriorly to insert on the quadrate as the m. protr. quad.

1) *M. protractor pterygoidei sensu stricto* (m. protr. pter. s. str.; m p p): This is the largest portion of the protractor of the palate and the only part visible in a lateral or oblique view without removal of the overlying muscles.

Origin: A long fleshy origin from the sides and base of the sphenoidal rostrum and from an oblong depression, the protractor pterygoid scar on the interorbital septum anteroventral to the optic foramen and dorsal to the palatine hasp. In *coccinea,* also from the ventral rim of the optic foramen.

Insertion: By means of a heavy tendon running along the ventrolateral edge of the muscle to insert on the protractor tubercle of the pterygoid.

Comparison: The m. protr. pter. quad. is a unipinnate muscle with many relatively short fibers that run ventrolaterally from their origin on the brain case to the tendon of insertion. This muscle is relatively deep which belies its appearance as a small and consequently weak muscle when only its superficial aspect is examined. The fibers of the medial part of this muscle, those of the m. protr. pter. s. str., are shorter and insert onto the tendon of insertion at a smaller angle. The fibers in the lateral end of the muscle, the m. protr. quad., are longer and insert onto this tendon at a large angle if at all. Most of these lateral fibers attach directly to the quadrate, onto the mandibular process, so that the m. protr. quad. is closer to a parallel-fibered muscle than a unipinnate muscle.

This muscle is shorter, thicker and more truncated at its anterior end in *newtoni* than in the other forms of *Loxops*, but may still be stronger than that of *virens*. A faint line of demarcation was seen in ventral view between this muscle and the m. protr. quad. in *newtoni*, more distinct than in the other forms. The m. protr. pter. s. str. is larger and stronger in appearance in *mana* than in either *virens* or *newtoni*, and almost approaches the maximum size of this muscle seen in *coccinea* in which the tendon of insertion is extremely strong. Moreover, in *coccinea*, this muscle is larger by an estimated 5 to 10 per cent on the left side than on the right (not visible in the figures).

The differences in size and shape of the protractor pterygoid scars and tubercles are summarized in Table 3. The tubercle is longest and thinnest in *coccinea* and shortest but thickest in *mana*, being intermediate in *newtoni* and *virens*. The scar is deepest in *coccinea*, shortest, widest and shallow in *newtoni*, and intermediate in *mana* and *virens*. Thus, great length but not necessarily thickness of the tubercle and greater length and depth of the scar seem to correlate with larger size of the muscle.

Action: Bilateral contraction of this muscle pulls (protracts) the pterygoids forward and medially and rocks the quadrates forward and upward, pivoting them around their squamosal articulations. Because the m. protr. pter. quad. inserts on the medio-posterior side of the pterygoid and quadrate, and because of the orientation of the axis of the quadrate-squamosal hinge with respect to the longitudinal axis of the skull, the head of the pterygoid rotates slightly medially around the pterygoid-palatine articulation as this bone slides forward. Forward motion of the pterygoid foot is transmitted to the palatine hasp and hence to the posteroventral base of the rostrum via the prepalatine bars. The force of the m. protr. pter. quad. pushes on the posteroventral base of the rostrum and hence rotates it upwards (elevates or protracts it) around the nasofrontal hinge. Anterior rotation of the quadrate also carries the mandible forward.

The m. protr. pter. quad. is the prime protractor of the palate and with probable assistance from the m. depr. mand.: the amount of force contributed by the m. depr. mand. to protraction is difficult to estimate.

2) *M. protractor quadrati* (m. protr. quad.; m p q): A short muscle extending between the base of the sphenoidal rostrum and quadrate, that lies deep below other jaw muscles and is visible only when most other muscles are removed (as in the deep dissection of the ventral view).

Origin: Fleshy from the lateral part of the sphenoidal rostrum, posterior to the origin of the m. protr. pter. s. str., and from the ventrolateral surface of the braincase below the trigeminal foramen.

Insertion: Fleshy to the medial surface of the base of the orbital process of the quadrate, but mainly to the mandibular process of the quadrate adjacent the pterygoid condyle. The main part of the insertion may be weakly tendinous.

Comparison: The m. protr. quad. is mainly parallel-fibered with longer fibers than found in the m. protr. pter. s. str. No apparent differences could be detected among the forms dissected.

Action: See above under m. protr. pter. s. str.

B) *M. adductor mandibulae externus* (m. add. mand. ext.): This large dorsal, superficial adductor of the mandible may be divided into three parts that are reasonably distinct from one another although some merging of fibers occurs between these parts. These subdivisions of the m. add. mand. ext.—the rostralis, ventralis and caudalis—have somewhat different actions and are differentially developed in the several species of *Loxops.*

1) *M. adductor mandibulae externus rostralis* (m. add. mand. ext. rost.; mamer): The large m. add. mand. ext. rost. may be subdivided further into three smaller portions—the temporalis, lateralis and medialis. In spite of the somewhat greater degree of merging between these subunits, and the awkward terminology for these muscles, these parts can be recognized as discrete features, homologized in different passerine birds, and exhibit differential development in various groups of perching birds. The tendons of insertion of the three parts join just before or at their insertion on the mandible.

a) *M. adductor mandibulae externus rostralis temporalis* (m. add. mand. ext. rost. temp.; mamert): This portion of the m. add. mand. ext. rost. occupies a central position in this muscle, lying between the medialis and lateralis portions and dorsal to the mm. add. mand. ext. ventralis and caudalis.

Origin: Fleshy from the whole of the temporal fossa dorsal to the zygomatic process and the m. add. mand. ext. caudalis, from the medioanterior surface of the zygomatic process, from the tip and orbital margin of the postorbital process, from tendons arising from the tips of these processes, and in *mana* and *coccinea* from the anterodorsal edge of the m. add. mand. ext. caudalis "b".

Insertion: By a central tendon starting with the fibers originating in the temporal fossa, passing deep beneath the postorbital process and running along the medial edge of the muscle to insert on the anterior coronoid process. Part of the tendon lies close to the lateral edge of the m. add. mand. ext. rost. medialis. The fibers of the m. add. mand. ext. rost. temp. insert on the dorsal, ventral and medial sides of the central tendon depending upon their site of origin.

Comparison: Basically the m. add. mand. ext. rost. temp. is a bipinnate muscle with numerous short fibers; however, the somewhat bent course of the muscle and complex origin of the fibers result in a more complicated appearance. It is a very strong muscle as indicated by the large number of fibers contained within it, but can displace only over a limited distance as indicated by its short fibers.

In regard to relative size, the rank from largest to smallest goes from *coccinea* right side, left side, *newtoni, mana, virens*; the muscle on the right side of *coccinea* is by far the largest in the series. It is only slightly larger in *mana* than in *virens.* This muscle inserts on the mandible farthest forward in *coccinea,* thus attaching farthest away from the center of rotation of the mandible at its quadrate articulation which results in the longest moment arm of the muscle force vector in this species. The large force development of the m. add. mand. ext. rost. temp. and its long moment arm means that its torque development is the largest in this species. *L. m. newtoni* has the second farthest insertion and hence moment arm, and *virens* and *mana* are similar, having the shortest insertion of this muscle.

The postorbital process is short and truncated in all forms studied except in *newtoni* in which it is sharply pointed; length of this process may be correlated with the size of the m. add. mand. ext. rost. temp. but the relationship is not clear. In all taxa, the anterior coronoid process is low in height.

Action: Bilateral contraction of the m. add. mand. ext. rost. temp. simultaneously adducts and retracts the mandible. Retraction of the mandible results in a backward rocking of the quadrate about its squamosal articulation and hence retraction of the palate and depression of the rostrum. Hence this muscle can close the bill via movement of both the mandible and rostrum, not only by raising the mandible. Unilateral contraction of the muscle would adduct and retract the mandible on that side more than on the opposite side, and would still lower the upper jaw. Moreover, unilateral contraction would twist the mandible (rotate it laterally) toward that side of the head, thereby bringing about a crossing of the tip of the mandible under the tip of the rostrum toward the side at which contraction takes place. In the asymmetrically muscled *coccinea,* bilateral contraction of the m. add. mand. ext. rost. temp. would result in an action similar to unilateral contraction in the other symmetrical forms of this genus, i.e., a crossing of the tip of the mandible beneath the rostrum toward the side of the stronger adductor.

b) *M. adductor mandibulae externus rostralis lateralis* (m. add. mand. ext. rost. lat.; mamerl): This portion of the m. add. mand. ext. rost. is the lateralmost part of the whole jaw musculature and often projects beyond the jugal bar which lies along the ventral edge of the m. add. mand. ext. rost. lat. Although it lies on the lateral surface of the m. add. mand. ext. ventralis and is frequently included as part of that muscle, the fibers of the m. add. mand. ext. rost. lat. are sharply distinct from those of the ventralis.

Origin: Tendinous along the entire length of the lateral edge of the zygomatic process and from a tendon arising from the distal tip of this process, from the lateral surface (its surface aponeurosis) of the m. add. mand. ext. vent., and from the anterior surface of the m. add. mand. ext. caud. "b" near the zygomatic process.

Insertion: By a tendon to the lateral surface of the mandible anterior to the insertion of the m. add. mand. ext. rost. temp. and dorsal to the anterior tip of the insertion of the m. add. mand. ext. vent. The tendon of the m. add mand. ext. rost. lat. may join that of the m. add. mand. ext. rost. temp. just before their attachment onto the mandible.

Comparison: Basically the m. add. mand. ext. rost. lat. is a unipinnate muscle with relatively short fibers. In *newtoni,* it tends towards a bipinnate condition. This part of the rostralis is decidedly weaker than the m. add. mand. ext. rost. temp. since the total number of contained muscle fibers is far smaller.

In relative size from largest to smallest, and presumably with larger size reflecting greater force, the order is *coccinea,* right side, left side, *newtoni, virens,* and *mana.* Further, this muscle inserts farthest forward on the mandible in *coccinea,* thereby having the longest moment arm which, in combination with the greatest strength, would produce the largest torque. *L. m. newtoni* has the next farthest insertion followed by *virens* and *mana* which are similar with the insertion closest to the articulation. The torques produced by this muscle in these forms would be progressively smaller.

The size and shape of the zygomatic process varies among the taxa of *Loxops* studied, giving further indication of the strength of some of the mandibular adductors attaching to it. It is sturdiest in build in *coccinea* (right side more so than the left side) and in *mana,* less sturdy in *virens* and highly abbreviated in *newtoni.* Hence, the build of the zygomatic process does not correlate simply with the relative sizes of the muscle.

Action: The action of the m. add. mand. ext. rost. lat. is similar to that described for the temporalis portion.

c) *M. adductor mandibularis externus rostralis medialis* (m. add. mand. ex. rost. med.; mamerm): This portion of the m. add. mand. ext. rost. is the medial-most part of the external adductor, lying just lateral to the m. pseudot. superf. and m. pseudot. prof. It can be seen only when the muscles are viewed obliquely through the orbit or when most of the lateral parts of the m. add. mand. ext. are removed.

Origin: Fleshy and tendinous from the lateral edge of the posterior wall of the orbit and medial edge of the temporal fossa medial to the origins of the m. add. mand. ext. rost. temp. and m. add. mand. ext. vent. The origin of this muscle varies slightly in the taxa of *Loxops* as follows:

i) *virens* and *mana*: Fleshy and deep (medial) to the origin of the m. add. mand. ext. rost. temp., from the lateral edge of the posterior orbital wall, the medial (ventral) edge of the temporal fossa, the anterodorsal surface of the zygomatic process and the medial surface of the origin of the m. add. mand. ext. rost. temp., and tendinous from several tendons arising from these areas of origin especially on the medial side of the muscle.

ii) *newtoni*: Same as in *virens* and, in addition from part of the anterior edge of the m. add. mand. ext. caud. "b" dorsal to the origin of the m. add. mand. ext. rost. lat.

iii) *coccinea*: Same as in *virens* and in addition from the anterior edge of the fascia forming the edge of the m. add. mand. ext. vent.

Insertion: Tendinous to the anterior coronoid process just posterior to the tendon of insertion of the m. add. mand. ext. rost. temp. In *mana*, also posterior to the anterior coronoid process along the dorsal edge of the mandibular ramus in a laterally fleshy slip medial to the belly of the m. add. mand. ext. vent. and anterior to the insertion of the m. add. mand. ext. caud. "b".

Comparison: The m. add. mand. ext. rost. med. is a unipinnate to bipinnate muscle with lateral and medial fibers inserting on a central tendon. The muscle contains a very large number of quite short fibers; hence it is a very strong muscle comparable in strength to the m. add. mand. rost. temp. although it appear smaller than this latter muscle.

In relative size from largest to smallest, the order is *coccinea* right side, left side, *newtoni*, *mana* and *virens*. The relative sizes and shapes of the zygomatic process and the anterior coronoid process have been discussed above under the mm. add. mand. ext. rost. temp. and lat. The relative sizes of the muscle do not correspond perfectly with the relative sizes of the zygomatic process as, for example, in *newtoni*.

Action: The m. add. mand. ext. rost. med. has an action similar to that of the m. add. mand. ext. rost. temp.

2) *M. adductor mandibularis externus ventralis* (m. add. mand. ext. vent.; mamev): This large fan-shaped muscle is located in the anterolateral part of the cheek region and lies lateral and ventral to most of the m. add. mand. ext. rost. and anterior to the m. add. mand. ext. caud., but its dorsolateral surface is covered by the superficial m. add. mand. ext. rost. lat. The ventral half of the m. add. mand. ext. vent. spreads out to cover a large area of the lateral surface of the ramus around the mandibular fossa. Although most of this muscle is sharply distinct from surrounding parts of the m. add. mand. ext., some merging of fibers may occur with

the m. add. mand. ext. rost. lat. (anterior), m. add. mand. ext. rost. med. (a few, medial) and m. add. mand. ext. rost. caud. (a few, posterior).

Origin: The origin of this muscle varies somewhat in the taxa studied, as follows:

i) *virens*: By a heavy flat tendon from the ventromedial edge and tip of the zygomatic process.

ii) *mana*: By a heavy tendon from the anteromedial surface tip and distal part of the lateral edge (beneath the origin of the m. add. mand. ext. rost. lat.) of the zygomatic process.

iii) *newtoni*: By a rather narrow flattish tendon from the anteroventral tip of the zygomatic process.

iv) *coccinea*: Strongly tendinous (stronger than in other forms) from the anteromedial surface and tip of the zygomatic process, and partially fleshy from the anterior margin of this process.

Insertion: This, too, varies among the several forms studied, as follows:

i) *virens*: In a fleshy manner, covering the mandibular foramen, the lateral surface of the mandible surrounding this foramen and on the dorsolateral edge of the mandible between the insertions of the m. add. mand. ext. rost. med. and the m. add. mand. ext. caud. "b".

ii) *mana* and *newtoni*: Same as in *virens*, except not on the dorsolateral edge of the mandible.

iii) *coccinea*: Same as in *virens*, but, in addition, the part originating from the anteromedial surface of the zygomatic process inserts between the two coronoid processes, between the insertions of the m. add. mand. ext. rost. med. and the m. add. mand. ext. caud. "b".

Comparison: The fibers of this fan-shaped muscle are unipinnate, but relatively long so that the total number of fibers is small compared to the two other parts of the m. add. mand. ext. It is definitely the weakest portion of this external adductor. In relative size from the largest to the smallest, the ranking is *newtoni*, *coccinea* right side, left side, *mana*, *virens*. Relative size, however, may not give an accurate indication of strength for this muscle because its origin in *newtoni* seems weakest even though its area of insertion appears largest. The m. add. mand. ext. vent. is probably the strongest among these forms on the right side of *coccinea* which is indicated by the size of the zygomatic process in this form.

Action: The action of the m. add. mand ext. vent. is very similar to that of the m. add. mand. ext. rost. med.

3) *M. adductor mandibulae externus caudalis* (m. add. mand. ext. caud.; mamec): This portion of the external adductor is located in the rear part of the cheek region posterior to the mm. add. mand. ext. rost. and vent. and anterior to the external auditory meatus and the m. depressor mandibulae. It can be divided into two parts, "a" and "b", which are not always easily separable so that the division of these parts is purely arbitrary in some cases. Part "a" lies anterodorsally to part "b". This separation of the m. add. mand. ext. caud. into two parts is very reminiscent of that found in the cardueline finches (Fiedler, 1951). These two parts will be described separately.

a) *M. adductor mandibularis externus caudalis "a"* (m. add. mand. ext. caud. "a"; mameca): This more ventral and posterior part of the m. add. mand. ext. caud. extends from the ventral part of the subtemporal area to the mandible.

Origin: Fleshy from most of the ventral subtemporal fossa, suprameatic process and from the anterior surface of the otic process of the quadrate. Tendinous from the ventral zygomatic tubercle and suprameatic process. In *newtoni* also by a deeper slender head from the anterior part of the skull base medial and ventral to the ventral zygomatic tubercle.

Insertion: On the dorsal rim of the mandibular ramus posterior to the insertion of the m. add. mand. ext. rost., but varies somewhat among the forms studied as follows:

i) *virens*: By a stout tendon on the posterior coronoid process posterior to the insertion of the m. add. mand. ext. caud. "b".

ii) *mana*: By a short, thick, partially fleshy tendon to the posterior coronoid process, posterior and lateral to the insertion of the m. add. mand. caud. "b". Also, by a small, fleshy slip over the lateral surface of the mandible across the posterior corner of the mandibular foramen and on the surface of the m. pseudot. prof.

iii) *newtoni*: By two tendons to the posterior coronoid process just behind the insertion of the m. add. mand. caud. "b"; the deeper, slender head (mentioned above) inserts posterior to the larger one.

iv) *coccinea*: Semitendinously on the posterior coronoid process immediately posterior to the insertion of the m. add. mand. post., and by a narrow fanlike slip which inserts directly over (lateral to) the mandibular foramen and that part of the m. pseudot. prof. adjacent medially. The central tendon of m. add. mand. caud. "a" dissipates itself in this slip.

Comparison: The m. add. mand. ext. caud. "a" is a simple bipinnate muscle with the fibers inserting on a central tendon. The fibers appear to be somewhat longer than other pinnate dorsal adductors of the mandible.

In relative size from largest to smallest, the ranking is *virens, coccinea* right side, *mana, coccinea* left side, and *newtoni.* In the size of the ventral zygomatic tubercle, *virens* is largest, *mana* and *newtoni* are smaller, but of equal size, and *coccinea* is the smallest. The posterior coronoid process of *mana* is tall and thick; of *virens*, tall and thinnest; of *coccinea*, low and thick; and of *newtoni*, low and thinner. The variation of these processes may reflect in part the relative sizes of this muscle in the four taxa.

Action: Bilateral contraction of this muscle would adduct the mandible and also depress the rostrum via retraction of the mandible, which rotates the quadrates posteriorly about their squamosal articulations and hence retracts the bony palate. Only the portion of the m. add. mand. ext. caud. "a" that originates from the braincase can retract the mandible; those fibers arising from the otic process of the quadrate are unable to retract the mandible. Unilateral contraction of this muscle would probably assist in swinging the tip of the mandible toward the side of contraction. In the asymmetrical *coccinea*, the action brought about by bilateral contraction of the m. add. mand. caud. would simulate the consequences of unilateral contraction in the symmetrical forms.

b) *M. adductor mandibulae externus caudalis "b"* (m. add. mand. ext. caud. "b"; mamecb): This more dorsal and anterior portion of the m. add. mand. ext. caud. extends from the dorsal part of the subtemporal fossa to the dorsal rim, being bounded anterodorsally by subdivisions of the m. add. mand. ext. rost., especially by the temp. portion of that muscle. The anterior fibers of this muscle may merge slightly with fibers of the m. add. mand. ext. rost. and perhaps with some of the m. add. mand. ext. rost. lat.

Origin: Fleshy from the posteroventral surface of the zygomatic process, from the dorsal part of the subtemporal fossa and side of the cranium to a point dorsal and posterior to the ventral zygomatic tubercle. The posterior end of the m. add. mand.

ext. caud. "b" at its origin is covered by the anterior tip of the origin of the m. depr. mand. "b" in *virens, mana* and on the left side of *coccinea,* but not in *newtoni.* On the right side of *coccinea,* the anterior tips of the m. depr. mand. "a" and "b" are covered by the posterior tip of the m. add. mand. ext. caud. "b".

Insertion: Tendinously (partly fleshy in *newtoni*) on the posterior coronoid process just anterior and slightly medial to the m. add. mand. ext. caud. "a" and posterior to the fleshy slip of the m. add. mand. ext. vent. (*virens* and *coccinea*) or of the m. add. mand. ext. rost. med. (*mana*; no such slip exists in *newtoni*). In *mana* this insertion is by a short, flat tendon into a tiny dorsoventrally directed groove on the lateral surface on the posterior coronoid process.

Comparison: The m. add. mand. ext. caud. "b" is a bipinnate muscle (possibly only unipinnate in *mana*) with a large number of short fibers inserting onto a strong central tendon. The numerous short fibers make this a very strong muscle for its mass, similar to the m. add. mand. ext. rost. temp. or med., or to the m. pseudot. superf. In relative size from largest to smallest, the ranking is *coccinea* right side, left side, *mana, newtoni, virens.* Note the heavy triangle of fascia on the lateral surface of this muscle on the right side of *coccinea.* The muscle fibers bulge out above this fascia, as can be seen in Plate 16.

The posteroventral surface of the zygomatic process is largest in *coccinea* (right side), second in *mana,* third in *virens* and *coccinea* (left side), and smallest in *newtoni.* This series corresponds rather well with the relative sizes of the muscle in these taxa. The differences in details of the posterior coronoid process are described above under the m. add. mand. ext. caud. "a"; these size differences probably are related in part to differences in relative sizes of the muscle.

Action: The action of part "b" of the m. add. mand. ext. caud. is similar to that of part "a", but it exerts a greater pull on the mandible because of its larger number of fibers and slightly longer moment arm. And because all parts of this muscle originate from the braincase, it retracts the mandible more than does the m. add. mand. ext. caud. "a".

C) *M. adductor mandibulae posterior* (m. add. mand. post.; m a m p): This muscle is located deep in the posteroventral cheek region so that only a small part of the muscle at its insertion can be seen without removal of the overlying m. add. mand. ext. It extends between the quadrate and the mandible, lying posteriorly and medially to the m. add. mand. ext. and laterally to the m. pseudot. superf.

Origin: Fleshy from the lateral surface of the proximal part of the orbital process of the quadrate posterior to the origin of the m. pseudot. prof., from the body of the quadrate, and tendinous from the tubercle of the orbital process of the quadrate.

Insertion: Fleshy to the dorsal edge and the medial and lateral surfaces of the mandibular ramus, posterior to the posterior coronoid process and the insertion of the m. pseudot. superf., and anterior to the external and internal processes of the mandible. That part of the insertion on the medial surface of the mandible includes the tubercle of the posterior mandibular adductor.

Comparison: The m. add. mand. post. is bipinnate in *Loxops,* an unusual condition in passerine birds but which may also exist in cardueline finches (Fiedler, 1951: 261). The larger number of fibers increases the force developed by the muscle. This muscle is symmetrical in *coccinea.*

The m. add. mand. post. is largest in *virens* and *mana,* intermediate in size in *newtoni* and smallest in *coccinea.* The surface area of the base of the orbital process of the quadrate appears to be about the same size in all forms. The tubercle of the posterior mandibular adductor is slightly larger in *virens* and *mana* than in the other two forms, thus corresponding with muscle size. The tubercle of the orbital process of the quadrate is largest in *virens*, and *newtoni*, smaller in *mana* and much smaller in *coccinea*, reflecting size differences in this muscle.

Action: Bilateral contraction of this muscle adducts the mandible and depresses the upper jaw, but does not retract the mandible relative to the brain case. Its main function may be protection of the jaw articulation against strong lateral forces on the mandible.

M. adductor mandibulae internus (m. add. mand. int.): The remaining mandibular adductors are sometimes grouped together as a single muscle under this name. We include mention of this term only for ease of reference to other studies, but do not advocate its continued use because it is not practical in functional discussions (three or four quite distinct actions occur in the included muscles) nor is it certain that all of the included parts have a common evolutionary origin or are homologous with the m. add. mand. int. of reptiles.

D) *M. pseudotemporalis superficialis* (m. pseudot. superf.; m ps s): The complexly pinnate m. pseudot. superf. is located in the posteroventral part of the orbit, lying between the m. pseudot. prof. and the mm. add. mand. ext. and post. If the overlying m. add. mand. ext. has not been removed, the m. pseudot. superf. can be seen only in an oblique view into the orbit. In lateral view after removal of the m. add. mand. ext., most of the m. pseudot. superf. is visible except for its ventral end which is covered by the m. add. mand. post. The anterior slip of this muscle is similar to that seen in the cardueline finches (Fiedler, 1951: 251–252; Beecher, 1953: 310–312, who illustrates and discusses this anterior slip of the m. pseudot. superf.).

Origin: Fleshy from the posterior wall of the orbit around the intraorbital cristae, and tendinous from these cristae.

Insertion: By one or two laterally compressed slips—one in *coccinea*, one or two in *virens*, and two in *mana* and *newtoni*. The anterior slip is present in one of the four specimens of *virens* dissected. The posterior slip is always present in all forms and inserts mainly tendinously on the tubercle of the pseudotemporalis on the medial surface of the mandibular ramus.

The anterior slip inserts mainly in a fleshy manner on the medial side of the dorsal edge of the mandible from the anterior to the posterior coronoid process (in *mana* and *newtoni*) or just on the medial edge of the posterior coronoid process (*virens*). Furthermore, in *newtoni* a posterior part of the anterior slip inserts on a supernumerary tubercle of the pseudotemporalis located immediately anterior to the main tubercle.

Comparison: The m. pseudot. superf. is a tripartite muscle with each part either unipinnate or bipinnate. The individual muscle fibers are very short with the total number of fibers in the whole muscle being extremely large. Hence, this muscle develops great force but shortens very little, if at all, during its contraction.

In size, the range from largest to smallest is: *coccinea*, both sides, and *newtoni* are similar, followed by *mana* and then *virens*. The anterior slip is most obvious in *newtoni*, and in this form it inserts further anterior than in *mana* and *virens*. The m. pseudot. superf. is symmetrical in *coccinea*. The large size of this muscle in *newtoni* seems incongruous when considered with the fact that the intraorbital cristae are smallest in this taxon. These cristae are large and thick in *mana* and *coccinea*, although in the latter the lateral process is sometimes much abbreviated. In *virens*, they are longer and narrower. Although these cristae in these three forms relate well to the relative sizes of the m. pseudot. superf., other factors may influence the development of these bony plates. The tubercle of the pseudotemporalis is about the same size in all forms; *newtoni* has an accessory one.

Action: Bilateral contraction aids in adduction of the mandible. Because of the vertical orientation of the pull (force vector) of this muscle with respect to the mandible and quadrate, the m. pseudot. superf. may contribute little to retraction of the mandible and quadrate. However, the anterior slip of this muscle may retract the mandible somewhat.

E) *M. pseudotemporalis profundus* (m. pseudot. prof.; m ps p): This bulky muscle is located in the posteroventral part of the orbit medial to the m. add. mand. ext. and the m. pseudot. superf. and laterodorsal to the m. pter. dors. It is visible only in an oblique view into the orbit or when the other dorsal mandibular adductors are removed. The m. pseudot. prof. extends from the orbital process of the quadrate to the medial surface of the mandible.

Origin: Fleshy from the lateroventral and medioventral surfaces of the distal three-fourths of the orbital process of the quadrate. The distal-most part of the origin is from the rugosity of the orbital process. Some fibers arise from a tendon attaching to this rugosity.

Insertion: Fleshy to the medial surface of the mandibular ramus, along the medial ledge of the mandible dorsal to the insertion of the m. pter. dors. lat., along the medial side of the dorsal edge of the ramus and from the dorsal and ventral margins of the mandibular foramen and surrounding bony surface. The insertion covers the mandibular foramen, and extends back to the anterior edge of the internomandibular flange.

Comparison: The m. pseudot. prof. is a bulky, essentially parallel-fibered muscle with long fibers and consequently relatively few fibers for the bulk of the muscle. The dorsal portion of the muscle is partly pinnate or fan-shaped with some of the fibers arising from a tendon attaching to the tip of the orbital process of the quadrate. This muscle is asymmetrical in *coccinea*, being slightly larger on the left side.

In relative size, the rank order from largest to smallest is *coccinea*, left side, right side, *mana*, *virens*, *newtoni*. It appears longest in *virens* but is stronger in its appearance in *coccinea* and *mana*. The muscle is shortest in *newtoni*. Its insertion extends relatively farther anterior in *coccinea* and *virens*. The orbital process of the quadrate, corresponding well with the relative size and length of the muscle, is long, thick and wide in *coccinea*; thick and narrower in *virens*; shorter than that of *virens* in *mana*; and shortest, thinner and narrowest in *newtoni*. The rugosity on the orbital process is largest on the left side of *coccinea*, slightly smaller on its right side, and small in *virens*. It is absent in *mana* and *newtoni*. Its size appears to correlate somewhat with probable differences in force except for its incongruous absence in *mana*.

Action: Bilateral contraction of the m. pseudot. prof. elevates the mandible and lowers the rostrum by pulling the orbital process of the quadrate ventral (i.e., rotating the quadrate ventrally about its mandibular hinge) with the force transmitted to the base of the upper jaw through the bony palate and jugal bars. The m. pseudot. prof. probably also aids in keeping the bill closed in the resting position. Its relatively low force development is compensated for by its long moment arm.

F) *M. pterygoideus* (m. pter.; m pt): The m. pter. constitutes the ventral adductor of the mandible and depressor of the rostrum. It lies more or less in a frontal plane, arising from the palatine and pterygoid and inserts on the mandible except for a small portion that inserts on the basitemporal plate. The m. pter. is a large muscle, either the largest or the second largest following the m. add. mand. ext., and is divided into five major parts—the ventralis lateralis, ventralis medialis, dorsalis lateralis, dorsalis medialis and retractor. The m. pterygoideus dorsalis medialis is divided further into an anterior and a posterior part. A few small subdivisions of the m. pterygoideus ventralis medialis can be recognized. Some of these portions of the m. pterygoideus are sharply separated from other parts and readily recognized, while the separation between other subunits such as between the m. pterygoideus ventralis lateralis and medialis are difficult to ascertain with certainty. An initial division of the muscle into a dorsal and a ventral portion is not justified (see Bock, ms; Morioka, ms).

Identification of the parts of the m. pter. has been badly confused in the earlier literature on passerine jaw muscle. We follow the scheme advocated by Bock (ms) which is very close to that used by Richards in his thesis.

The whole m. pterygoideus, as well as its constituent parts, is asymmetrical in *coccinea*, being larger on the left side. It should be noted that the ventral adductor—the m. pterygoideus—is largest on the left side of the head in a right-billed individual of *coccinea* while the asymmetrical dorsal adductors are stronger on the right side of the head.

1) *M. pterygoideus ventralis lateralis* (m. pter. vent. lat.; m pt v l): The lateral and ventral part of the m. pter. that arises from the transpalatine process and prepalatine bar and extends to the mandible. It cannot be seen in a dorsal oblique view into the orbit unless the m. pter. dor. lat. is removed, but is fully visible in a ventral view of the jaw musculature.

Origin: Partly fleshy, but mainly tendinous from the ventral and lateral surfaces of the transpalatine process and the prepalatine bar. It is closely pressed to the ventral surface of the m. pter. dor. lat., and indeed a common aponeurosis of origin separates these two muscles for some distance behind the distal tip of the transpalatine process. In *newtoni* the origin is weakly tendinous only along the distal half of the transpalatine process. The same is true in *coccinea* on the left side but with some fleshy insertion; its right side is strongly tendinous.

Insertion: Fleshy to the ventrolateral, and to a slight extent the ventromedial surface and ventral edge of the mandible from a point approximately below the anterior edge of the mandibular foramen almost to the base of the retroarticular process; those fibers inserting on the lateral surface of the mandible curve around its ventral edge and may be seen in a lateral view of the head. Also fleshy to the anterior part of the insertion of the m. depr. mand. "a" located on the medial side of the retroarticular process and from the ventral surface of the internomandibular flange. Tendinous on a sheet of fascia comprising the ventrolateral edge of the m. pter. vent. med., and tendinous on a bony tubercle near the posteromedial corner of the confluence of the internal mandibular and retroarticular process. The following variation in the insertion has been noted:

i) *newtoni*: Fleshy to the ventromedial surface of the mandible from a point approximately below the midpoint of the mandibular foramen to the anterior side of the base of the internal mandibular process. Also fleshy to the ventral surface of the proximal two thirds of the internal mandibular process and to the internomandibular flange.

ii) *coccinea*: The insertion on the left side is the same as in the general description and, in addition, fleshy from most of the ventral edge of the retroarticular process. Also, on the ventrolateral edge of the mandible, fleshy to as far forward as two lengths of the mandibular foramen beyond the anterior end of this foramen. Moreover, about 75 per cent of the anterior end of the insertion of the m. depr. mand. "a" medial to the retroarticular process is overlapped by that of the m. pter. vent. lat.

The insertion on the right side is the same as described for the left side, but less of the ventral edge of the retroarticular process is covered by the muscle and the insertion on the ventrolateral edge of the mandible does not extend so far forward. Less of the insertion of the m. depr. mand. "a" is overlapped. The tendinous part of the insertion on the tubercle at the confluence of the internal mandibular and retroarticular processes is weaker than on the left side.

Comparison: Although the m. pter. vent. lat. appears as a parallel fibered muscle, the fibers are probably unipinnate throughout most of the length of the muscle. They are relatively long, however, compared to other pinnate jaw muscles. This part is one of the strongest segments, second only to the m. pter. dors. lat., of the m. pterygoideus and contributes most to closing the bill. The demarcation between this muscle and the m. pter. vent. med. is difficult to fix with certainty, and it is not absolutely definite whether the division used in the dissections and descriptions of the musculature in *Loxops* corresponds exactly to those advocated for *Corvus* (Bock, ms). We have attempted to be consistent within *Loxops* even if our decision as to what constitutes the division between these muscle parts may be partly arbitrary.

In relative size, the ranking from largest to smallest is *coccinea,* left side, right side, *mana, virens, newtoni.* Of this series, the muscle on the left side of *coccinea* is by far the largest, being an estimated 85 to 100 per cent larger than even the second largest in the series, which is the same muscle on the right side of this species. The greater area of overlap in *coccinea* onto the lateral surface of the mandible, the retroarticular process and the insertion of the m. depr. mand. "a" should be noted. This muscle in *newtoni* is probably by far the weakest, as it does not overlap even onto the ventral surface of the mandible.

The ventral surface of the internomandibular flange is flat or concave and widest in *coccinea* and *mana,* of intermediate area in *virens* and narrowest and even convex in *newtoni.* The flange on the left side of *coccinea* perhaps has a greater surface area and is more concave and rugose than that on the right. The size and shape of this flange corresponds well with the relative sizes of the muscle.

The transpalatine process is shortest and thickest on the left side of *coccinea,* a little longer and slenderer on its right side, slightly longer and slenderer in *mana,* and longest and slenderest in *newtoni* and especially so in *virens.* A short, thick transpalatine process is a more efficient point of origin for the stronger muscles in this series.

The prepalatine bar is widest in *coccinea* and *mana,* slightly narrower in *newtoni* and narrowest in *virens.* It is widest of all on the left side of *coccinea.* This situation in general reflects the relative sizes of this muscle in the four taxa as well as the relative sizes and forces of the sets of muscles acting through the palate to elevate and depress the rostrum.

Action: The main function of this muscle is retraction of the palate, relative to the mandible (not necessarily to the braincase), and hence depression of the upper jaw. Unilateral contraction of this muscle aids in crossing of the mandible under the rostrum in a direction away from the side on which contraction takes place (toward the contralateral side). This probably takes place to a slight degree in the symmetrical forms of *Loxops.* Crossing of the tips of the bill is possible because the medial condyle of the quadrate can experience a certain amount of fore-and-aft movement and a slight amount of pivoting in the groove into which it fits on the dorsal surface of the internomandibular flange. In *coccinea* lateral rotation of the mandible and crossing of the bill tips (by way of bilateral contraction) is the usual rather than the unusual action. The quadrate condyles, mandibular grooves and other articulations are so modified that during bilateral contraction of the asymmetrical m. pterygoideus, the stronger muscles on the left side cause the whole mandible to swing toward the right, pivoting on the articulation between the medial condyle of the quadrate and the corresponding mandibular groove on the left side of the lower jaw. Thus the tip of the mandible crosses toward the right and the right ramus "backs up" as it were, its internomandibular flange sliding beneath the medial condyle of the right quadrate.

2) *M. pterygoideus ventralis medialis* (m. pter. vent. med.; m pt v m): The medioventral part of the m. pterygoideus consists usually of two and sometimes three (*virens*) parts: a main belly adjacent to the m. pter. vent. lat. and lateral to the palatine salivary gland; a more medial part located dorsal to the posterior end of the palatine salivary gland and termed the m. pter. vent. med. "fan" because of its resemblance to a fan; and, in some specimens of *virens*, an anteromedial part termed the m. pter. vent. med. "scapularis" because of its resemblance to a mammalian scapula. The m. pter. vent. med. "fan" probably is homologous with a small part of the m. pter. vent. med. described but not named by Fiedler (1951: 251, 255), and the superficial fibers of this muscle described by Bock (ms) which attach on the fascia of the m. pter. retr. and on the connective tissue around the openings of the eustachian tubes. The m. pter. vent. med. "'scap." may be homologous with the muscle part described by Moller (1930: 688 1931: 128) as the m. pter. vent. internus.

This part of the m. pter. runs from the transpalatine and mediopalatine processes of the palatine to the mandible; the divisions of it are separated only in *virens*. Only a small part of the medial portion is visible in an oblique view through the orbit in *virens*; in this and the other taxa, it can be seen fully only in a ventral view of the musculature.

Origin: The origins of the several subdivisions of the m. pter. vent. med. will be described separately, as follows:

Main belly: Partly tendinous from the ventromedial edge of the transpalatine process, anteriorly to a point adjacent to the prepalatine blade, from the ventromedial surface of the originating end of the m. pter. dors. lat. and from the lateral surface and posterior end of the palatine salivary gland. In *newtoni*, the thinned-out medial part of the main belly originates weakly from the lateral surface of the anterior base of the mediopalatine process.

"Fan"-like part: Fleshy from connective tissue around the oral opening of the eustachian tubes, from the ventral surface of the posterior end of the m. pter. retr., and from the dorsal surface and posterior end of the palatine salivary gland.

"Scapular" part of *virens*: By three small fleshy slips, together in a group, on the lateral surface of the posterior end of the palatine hasp immediately anterior to the pterygoid foot and origin of the m. pter. dors. med. ant., and dorsal to the palatine salivary gland. Visible through the orbital in an oblique view and barely in a lateral view.

Insertion: The insertion of the three subdivisions will be described separately, as follows:

Main belly: Fleshy to the ventral surface of the distal (medial) quarter to two-thirds of the internal mandibular process and to the dorsomedial surface of the m. pter. vent. lat.

"Fan"-like part: By a tiny cordlike tendon to the medial tip of the internal mandibular process in *virens*. In other forms by such a tendon and also to a thinned-out medial extenson of the main belly of the m. pter. vent. med.

"Scapular" part of *virens*: Fleshy to the ventral surface of the m. pter. dors. med. ant. and the dorsal surface of the palatine salivary gland. (Note: Plate 11A is erroneous in that it shows the "scapular" part ventral to the anterolateral end of the m. pter. retr. and dorsal to the m. pter. dors. med. ant.; it should be ventral to the m. pter. dors. med. ant.)

Comparison: The main belly of the m. pter. vent. med. is probably unipinnate throughout most of its length, with relatively long fibers. Its size is comparable to that of the m. pter. vent. lat. in *mana*, *newtoni*, and *coccinea*, but is much smaller in *virens*.

The main belly of this muscle is largest on the left side of *coccinea* where it is an estimated 50 per cent larger than on the right side. The right main belly of *coccinea* and main belly of *mana* are about equal and rank second in size. The muscle is smaller in *virens* and smallest in *newtoni*.

The relative sizes and shapes of the transpalatine process, which is short and thick in *coccinea* and *mana* and long and slender in the other two forms, may reflect the relative strength of the main belly of the m. pter. vent. med.

The fan-like part is about the same size throughout, being a relatively thin muscle. In all forms, except *virens*, it blends laterally with the thin medial portion of the main belly of the m. pter. vent. med. This is especially true in *newtoni*.

Action: The action of the main belly of the m. pter. vent. med. is very similar to that described above for the m. pter. vent. lat.

Contraction of the m. pter. vent. med. "fan" may act to open the common aperture of the eustachian tubes in the roof of the pharynx by pulling posterolateral on the surrounding connective tissue. Thus it may function to equalize air pressures on both sides of the ear drum during changes in altitude in flight. Relaxation of the fan-like part would allow this orifice to close since its lips do not normally appear to hold it open. The automatic closure of this opening would be advantageous during feeding in that it would prevent food particles or fluids from entering the eustachian tubes.

3) *M. pterygoideus dorsalis lateralis* (m. pter. dors. lat.; m pt d l): This part of the m. pterygoideus consists of the large dorsolateral portion running from the transpalatine process and palatine blade to the medial surface of the mandibular ramus. No fibers of this part attaches to the pterygoid; these fibers are all part of the m. pter. dors. med. The m. pter. dors. lat. can be seen, in part, in an oblique view through the orbit, or ventrally after removal of the ventral portions of the m. pter.

Origin: Slightly different in the four taxa studied, as follows:

i) *virens*: Fleshy from the dorsal surface of the transpalatine process and palatine blade, from the aponeurosis on the dorsolateral surface of the originating end of the m. pter. vent. lat., and of the dorsomedial surface of the originating end of the m. pter. vent. med. (Note: These three origins are separable by careful probing. See note under the description of the origin of the m. pter. vent. lat.)

ii) *mana*: Fleshy from the dorsal surface of the transpalatine process and the palatine blade, from the aponeurosis on the dorsolateral surface of the originating end of the m. pter. vent. lat. and from the side of the palatine between the mediopalatine process and palatine blade, dorsal to the ventral head of origin of the m. pter. retr.

iii) *newtoni*: Fleshy from the dorsal surface of the transpalatine process and palatine blade, from the ventral surface of the palatine blade and from the side of the palatine between the mediopalatine process and the palatine blade, ventral to the anteriormost part of the origin of the m. pter. dors. med. post.

iv) *coccinea*: On the left side, fleshy from the dorsal surface of the transpalatine process and palatine blade, from the ventral surface of the palatine blade to the dorsolateral and dorsomedial surfaces of the aponeurosis of the originating end of the m. pter. vent. lat., from much of the dorsal surface of the prepalatine bar and from the mediopalatine process anterior to the ventral head of origin of the m. pter. retr.

On the right side the origin is less extensive than on the left; it does not extend as far medially nor posteriorly on the ventral surface of the palatine blade, and not as far anteriorly on the prepalatine bar.

Insertion: As for the origin, the insertion of the m. pter. dors. lat. varies slightly in the four taxa of *Loxops*, as follows:

i) *virens*: Fleshy to the medial surface of the mandibular ramus, dorsal to the insertion of the m. pter. vent. lat. and ventral to the insertion of the m. pseudot. prof., along the medial ledge of the mandible anteriorly from a point opposite the anterior margin of the mandibular foramen and posteriorly to the anterolateral corner of the internomandibular flange immediately in front of the insertion of the m. pter. dors. med. ant. Tendinous along the medial mandibular ledge by an aponeurosis on the ventral surface of this muscle.

ii) *mana*: Same as in *virens* and, in addition, tendinously by a tendon comprising the posteromedial border of this muscle and attaching to a bony tubercle dorsal to the anterolateral corner of the internomandibular flange.

iii) *newtoni*: Thinly tendinous to the anterior edge and dorsal surface of the internomandibular flange.

iv) *coccinea*: On the left side, the same as in *virens* and, in addition, strongly fleshy from the dorsal corner of the anterior end of the internomandibular flange. Also strongly tendinous on a tendon comprising the posteromedial edge of this muscle and attaching onto the anterior edge of the internomandibular flange.

On the right side, the insertion is about the same as found on the left side but not extended as far anteriorly.

Comparison: The m. pter. dors. lat. is probably unipinnate throughout most of its length, with relatively long fibers. Its fibers run ventrally-dorsally from origin to insertion while those of the m. pter. vent. lat. run dorsally-ventrally. Together, the fibers of the two muscles simulate a bipinnate muscle. In size, it is equal to or usually considerably larger than the m. pter. vent. lat. and is usually the largest and presumably strongest part of the m. pterygoideus. It contributes greatly to closing the bill. This muscle part is asymmetrical in *coccinea*, being largest on the left side.

In relative size from largest to smallest, the rank order is *coccinea* left side, right side, *mana*, *newtoni*, *virens*. In *virens* it appears as though the medial part of the origin of the m. pter. dors. lat. has been crowded out by the palatine salivary gland and has left no vestige.

It should be noted that the posteromedial edge of the m. pter. dors. lat. and the anterolateral edge of the m. pter. dors. med. ant. do not meet along a common boundary in *virens* and *newtoni* but are separated by a wide gap. This is a common condition in many thin-billed passerine birds and shows clearly the separation between the m. pter. dors. lat. and m. pter. dors. med. (Fiedler, 1951:259; Bock, ms). In *mana* and *coccinea*, the edges of these muscles come into close contact with one another giving the impression of a single bipinnate muscle. However, the tendon on the posteromedial edge of the m. pter. dors. lat. and the tendon on the anterolateral edge of the

m. pter. dors. med. ant. are always clearly separated from each other and a probe can be inserted between them without creating an artificial tear. This is the common condition in heavy-billed birds such as finches (Fielder, 1951) and crows (Bock, ms).

In *coccinea*, the m. pter. dors. lat. is larger on the left than on the right. This is obvious not only in the differences in the extent of the origins and insertions, but also in the width of the belly of the muscle and in the size of its originating end. On the left side, the origin on the dorsal surface of the palatine hasp is robust; on the right side, it is band-like. On the ventral surface of the palatine blade, and on the side of the palatine proximal to the mediopalatine process, and medial to the transpalatine process, the origin on the left side is a bulging ridge of muscle; on the right, the muscle is flat at its origin.

The palatine blade is broadest on the left side of *coccinea*, slightly less so on the right, a little less broad in *mana* than on the right side of *coccinea*, narrower than this in *virens*, and narrowest in *newtoni*. These differences are more noticeable in dorsal view than in ventral. This situation parallels rather well the relative size of the m. pter. dors. lat.

Action: The action of the m. pter. dors. lat. is very similar in general to that described above for the m. pter. vent. lat. This muscle is a very strong depressor of the upper jaw because of its large size and contained number of fibers. Indeed, most of the force for retracting the palate relative to the mandible and hence depressing the rostrum comes from the contraction of these two lateral parts of the m. pterygoideus.

4) *M. pterygoideus dorsalis medialis* (m. pter. dors. med.; m pt d m): This dorsomedial part of the m. pterygoideus is divided into two quite distinct divisions, one originating from the anterolateral surface of the pterygoid and the other from the posteromedial surface and pterygoid head. They will be distinguished as the anterior (m. pter. dors. med. ant.; m pt d m a) and the posterior (m. pter. dors. med. post.; m pt d m p) divisions of this muscle part, but will be described together under the same heading. The m. pter. dors. med. lies in the medioventral corner of the orbit, running from the pterygoid to the internal mandibular process. It can be seen partly in an oblique view into the orbit and ventrally after removal of the underlying superficial layer of ventral pterygoid muscles.

Origin: The origin of these parts of the m. pter. dors. med. differ slightly in the four taxa, as follows:

i) *virens*: The m. pter. dors. med. ant. has a fleshy origin along the anterolateral surface of the anterior two-thirds of the pterygoid up to the joint between the pterygoid foot and palatine hasp. The origin of the m. pter. dors. med. post. is fleshy from the posterior third of the anterolateral surface of the pterygoid, around the ventral surface of the pterygoid head, from the anterior half of the ventral surface and the whole of the medial surface of the pterygoid, and from the dorsal part of the pterygoid foot between the origins of the m. pter. retr. (dorsally) and the m. pter. dors. med. ant. (ventrally). The anterior part of the origin is not forked about the pterygoid at the pterygoid foot, but the muscle passes dorsal to this bone and into the orbit to be "squeezed" between the originating heads of the m. pter. retr. and m. pter. dors. med. ant.

ii) *mana*: The fleshy origin of the m. pter. dors. med. ant. covers the anterolateral surface of the anterior two-thirds of the pterygoid, extending from the anteriormost origin of the m. pter. dors. med. post. to a small half moon-shaped depression at the base of the mediopalatine process immediately ventral to the pterygoid foot. The m. pter. dors. med. post. has a fleshy origin from the posterior third of the anterolateral surface of the pterygoid, around the pterygoid head, and from the whole of the dorsal and medial surfaces of the pterygoid. The anterior end of the muscle is forked around (dorsal and ventral) the pterygoid foot. The ventral head originates from a small depression at the base of the mediopalatine process, deep to and hidden by the origin of the m. pter. dors. med. ant. The dorsal head originates from the pterygoid foot immediately ventral to the dorsal head of the m. pter. retr. and dorsal to the originating head of the m. pter. dors. med. ant.

iii) *newtoni*: The fleshy origin of the m. pter. dors. med. ant. extends from the anterior three-fourths of the anterolateral surface of the pterygoid anterior to the tip of the origin of the m. pter. dors. med. post. The anterior end is compressed between the two halves of the m. pter. dors. med. post. as the latter forks around the pterygoid. It is not visible through the orbit in lateral view. The m. pter. dors. med. post. has a fleshy origin from the posterior fourth of the anterolateral surface of the pterygoid, around the head of the pterygoid, and from the ventral and posteromedial surface of the pterygoid. The anterior end of the muscle is forked around the pterygoid with the ventral head originating from the lateral surface of the mediopalatine process anterodorsal to the origin of the m. pter. retr. and ventral to the pterygoid foot and the head of the dorsal fork. The dorsal head originates from the whole surface of the pterygoid foot ventral to the origin of the m. protr. pter. quad. and dorsal to the origin of the ventral head of the fork. Both heads are visible in side view through the orbit.

iv) *coccinea*: The origin of the m. pter. dors. med. ant. is a fleshy attachment from the anterolateral surface of the anterior two-thirds of the pterygoid anterior to the tip of the m. pter. dors. med. post., lateral side of the mediopalatine process and ventral part of the palatine hasp just ventral to the origin of the m. pter. dors. med. post. The m. pter. dors. med. post. possesses a fleshy origin from the posterior third of the anterolateral surface of the pterygoid, around the pterygoid head, and from the whole length of the ventral and posteromedial surfaces of the pterygoid. The anterior end is forked around the pterygoid with a narrow ventral head originating from the mediopalatine process just dorsal to the origin of the ventral head of the m. pter. retr.; it is not visible in side view. The dorsal head extends over (dorsal to) the anterior end of the pterygoid to originate from the pterygoid foot and from a small depression on the lateral surface of the palatine hasp ventral to the origin of the dorsal head of the m. pter. retr. and dorsal to the origin of the m. pter. dors. med. ant.

Insertion: The insertion of the m. pter. dors. med. on the mandible varies slightly in the four taxa of *Loxops*, as follows:

i) *virens*: The m. pter. dors. med. ant. has a fleshy insertion on the dorsal surface and anterior edge of the anteromedial corner of the internomandibular flange and a tendinous attachment to a small tubercle projecting medially immediately anterior to the internomandibular flange; this tendon runs along the anterolateral edge of the muscle. The fleshy attachment of the m. pter. dors. med. post. inserts on the anteromedial edge of the dorsal surface of the internomandibular flange posterior to the insertion of the m. pter. dors. med. ant., and from the distal three-fourths of the anterodorsal edge of the internal mandibular process dorsal to the insertion of the main belly of the m. pter. vent. med.

ii) *mana*: The fleshy insertion of the m. pter. dors. med. ant. covers the dorsal surface and anterior edge of the anterolateral corner of the internomandibular flange; the remaining fibers insert tendinously posterior to the insertion of the tendon of the m. pter. dors. lat.; the tendon of insertion runs along the anterolateral edge of the muscle very close to the tendon of the m. pter. dors. lat. The m. pter. dors. med. post. has a fleshy insertion on the anteromedial edge of the dorsal surface of the internomandibular flange posterior to the insertion of the main belly of the m. pter.

vent. med. Also, a very small part inserts on the medial side of the pterygoid condyle of the quadrate.

iii) *newtoni*: The entire insertion of the m. pter. dors. med. ant. is fleshy on the anteromedial edge and end of the dorsal surface of the internomandibular flange. The fleshy insertion of the m. pter. dors. med. post. covers the distal seven-eighths of the anteromedial edge of the internal mandibular process, with an especially strong component on the distal tip of this process dorsal to the origin of the main belly of the m. pter. vent. med. and m. pter. vent. med. "fan."

iv) *coccinea*: The strong fleshy insertion of the m. pter. dors. med. ant. covers the dorsal surface of the anterior end of the internomandibular flange immediately posterior to the insertion of the m. pter. dors. lat. The m. pter. dors. med. post. has a fleshy insertion on the anteromedial edge of the dorsal surface of the internomandibular flange posterior to the insertion of the m. pter. dors. med. ant., with a strong portion from the distal three-fourths of the dorsal surface of the internal mandibular process; on the left side, also from the posterior edge of the tip of this process.

Comparison: Both parts of the m. pter. dors. med. are mainly unipinnate for most of their length; the posterior part of the m. pter. dors. med. is fan-shaped where it spreads beneath the pterygoid head. The fibers are moderately long in comparison with other pinnate jaw muscles and are moderately numerous. The two parts of the m. pter. dors. med. are relatively small muscles and presumably develop little force.

In relative size, the rank order of the m. pter. dors. med. ant. from largest to smallest is *coccinea,* left side (slightly larger than right), right side, *virens, newtoni, mana.*

Little if any difference in size exists among the four taxa studied in the fan-like posterior part in the m. pter. dors. med. post.; it may be slightly larger in *newtoni* than in other forms. For the rest of this muscle, the rank order from largest to smallest is *newtoni, coccinea* left side, smallest and similar in *coccinea* right side, *mana, virens.*

The internal mandibular process is longest in *newtoni,* shorter in *mana* and *coccinea,* and shortest in *virens.* The greater length in *newtoni* may correlate in part with the larger size of the m. pter. dors. med. in this taxon.

Action: It is doubtful from their positions and attachments that the two parts of the m. pter. dors. med. contribute to adducting the mandible or depressing the upper jaw as do the other parts of the m. pterygoideus. Their importance appears to lie in rotating the pterygoid around its articulation with the quadrate (or controlling this rotation) during kinetic movement. The m. pter. dors. med. ant. can rotate the pterygoid foot anterolaterally around the pterygoid-quadrate articulate, while the m. pter. dors. med. post. can rotate the pterygoid foot posteromedially about this articulation. The latter movement is essential in depression of the rostrum especially in its extreme depression when the palate must be retracted back beyond its resting position when the bill is closed. Anterolateral rotation would occur when the rostrum is elevated, and it is possible that this part of the m. pter. dors. med. acts during opening of the bill. The posterior fan-shaped part of the m. pter. dors. med. post. may serve to protect the pterygoid-quadrate joint against excessive tension; no ligaments appear to be present around this articulation.

5) *M. pterygoideus retractor* (m. pter. retr.; m pt r): This small part of the m. pterygoideus runs from the pterygoid foot and mediopalatine process to the basitemporal plate; it is the only part of this muscle to insert on the braincase and hence functions quite differently from the rest of the m. pterygoideus. A small bit of its anterior end may be visible in an oblique view through the orbit; it is visible in ventral view when the covering parts of the m. pter. vent. med. are removed.

Origin: The origin of this retractor portion varies slightly in the four taxa of *Loxops* studied, as follows:

i) *virens*: The anterior end of the m. pter. retr. is forked around the anterior end of the pterygoid. The fleshy ventral head originates from the ventrolateral surface of the mediopalatine process ventral to the pterygoid foot and deep to the originating end of the m. pter. vent. med. "scap." The fleshy dorsal head originates from the posterior surface of the anterior third of the pterygoid, from the retractor process of the pterygoid foot, and from the lateral surface of the pterygoid foot ventral to the origin of the m. protr. pter. quad. and dorsal to the origin of the m. pter. dors. med. post.

ii) *mana*: The anterior end of the muscle is forked around the anterior end of the pterygoid with two fleshy heads of origin. The ventral head arises from the ventrolateral surface of the mediopalatine process as far anterior as the posterior margin of the palatine blade, and from the retractor process; it is not visible in lateral view because it is obstructed from view by the origins of the m. pter. dors. lat. and m. pter. dors. med. ant. The dorsal head originates from the distal end of the pterygoid foot ventral to the origin of the m. protr. pter. quad. and dorsal to the origin of the dorsal head of the m. pter. dors. med. post.

iii) *newtoni*: The originating head of this muscle is not forked around the pterygoid; it originates tendinously from the mediopalatine process and retractor process (dorsalmost part of originating head); a small fleshy head originates from the connective tissue walls of the opening of the eustachian tubes.

iv) *coccinea*: The anterior end of this muscle is forked around the anterior end of the pterygoid with two fleshy heads of origin. The ventral head arises from the ventral edge of the mediopalatine process and from the retractor process just ventral to a small ventral head of the m. pter. dors. med. post. (the latter not visible in lateral view) and immediately posterior to the originating head of the m. pter. dors. lat. The ventral head of the m. pter. retr. is visible in side view on the right but not on the left side. The dorsal head of the fork arises from the pterygoid foot and in slight degree from the posterior part of the palatine hasp ventral to the origin of the m. protr. pter. quad. and dorsal to the dorsal head of the m. pter. dors. med. post.

Insertion: Fleshy onto the base of the brain case (basitemporal plate) in a triangular depression to the side of the sphenoidal rostrum immediately anterior to the anterior margin of the inserting cervical muscles, the m. rectus captis ventralis, and immediately ventral to part of the belly of the m. protr. pter. quad.

Comparison: The fibers of the m. pter. retr. are parallel to one another and are relatively long for the mass of the muscle. This muscle may be slightly asymmetrical in *coccinea*, perhaps larger on the left side.

The relative size of this muscle in rank order from largest to smallest is *mana*, *coccinea*, both sides similar, *virens*, *newtoni*. It is interesting to note that this muscle in *newtoni* is noticeably much smaller than in the other forms, but on the other hand the m. pter. dors. med. post. is much larger in this creeper than in the others and may compensate for the smallness of the m. pter. retr.

The retractor process at the posteroventral tip of the pterygoid foot is largest and most deeply concave in *mana*. It ranks second in size, but is concave in *coccinea*. It is third in size and concave in *virens*, and is smallest and convex in *newtoni*. Larger size and greater concavity possibly can be associated with larger size of the muscle.

Action: The major function of this muscle is to retract the palatine relative to the brain case, and hence depress the upper jaw. This is the only part of the m. pterygoideus that can retract the whole jaw apparatus relative to the brain case. It may also function to keep the bill closed by maintaining a retracting force on the palate.

G) *M. depressor mandibulae* (m. depr. mand.; m d m): The m. depr. mand. extends from the occipital region of the cranium to the retroarticular and internal processes of the mandible. It is clearly visible in lateral and ventral view. The m. depr. mand. is strongly asymmetrical in *coccinea,* being larger on the right. This is the only jaw muscle that could be studied in *sagittirostris.*

Origin: The origins of the three parts of the m. depr. mand. will be discussed separately, as follows:

Part "a": Partly anterior and deep to part "b." Fleshy from the ventral part of the occipital area of the cranium, from most of the exoccipital process, and from the anteromedial surface of part "b." Tendinous from the anterodorsal edge of the auditory bullae; this tendon comprises part of the anterior edge of part "a."

Part "b": Broadly fleshy from the side of the cranium, from the posterolateral surface of part "a," and from the anterolateral surface of part "c."

Part "c": Fleshy from the posteromedial surface of part "b," from a narrow strip of the occipital region of the skull posterior to part "b" and anterior to the insertion of part of the m. complexus of the cervical musculature, and from the surface of the inserting end of this neck muscle.

Insertion: Again, the descriptions of the three parts will be separate, as follows:

Part "a": Fleshy on the lateral surface, dorsal edge and medial surface (not on this surface in *sagittirostris*) of most of the length of the retroarticular process anterior to the insertion of part "b," and on the posterior edge of the internal mandibular process (not known if the insertion of part "a" in *sagittirostris* includes this process, but it presumably does). Tendinously by a tendon forming the anterior edge of part "a" to the anterolateralmost part of the insertion.

Part "b": Tendinous to the dorsolateral and dorsomedial sides and top of the tip of the retroarticular process anterior to the insertion of part "c" and posterior to that of part "a."

Part "c": Tendinous to posteromedial tip of the retroarticular process. In *sagittirostris,* the same and, in addition, fleshy to most of the medial surface of this process.

Comparison: The fibers of part "a" are relatively short and arranged in a series of pinnate patterns; this part is essentially a complex bipinnate muscle. Parts "b" and "c" are long, parallel-fibered muscles. The differences in fiber length in these several parts of the m. depr. mand. are probably correlated with the differences in the distance these fibers must shorten; those of parts "b" and "c" must shorten much more than those of part "a." Because it contains a large number of fibers, part "a" develops much force, perhaps as much as parts "b" and "c" combined. But it inserts much closer to the center of rotation of the mandible and hence has a shorter moment arm than either parts "b" or "c." Hence, these last two parts may develop a greater torque than "a" and contribute more to opening the jaws.

The rank order of relative size of the whole muscle, from largest to smallest, is *sagittirostris, mana, coccinea* right side, *virens, coccinea* left side, *newtoni.* Although *sagittirostris* is a larger species than the other forms of *Loxops* studied and has a mandibular depressor an estimated 50 to 75 per cent larger in absolute size than in the other forms, this muscle is still relatively larger by some 25 to 50 per cent. Part of this large size is probably due to the relatively larger part "c" in *sagittirostris.*

The m. depr. mand. on the right side of *coccinea* is possibly 30 to 40 per cent larger on this side than on the left. This asymmetrical bulkiness is more noticeable in ventral than in lateral view. Furthermore, the lateral surface of the muscle on the right side is covered with an extremely tough casing of fascia not found on the left side, and the whole dorsal margin of the muscle on the right side bulges laterally dorsal to this aponeurosis. This robust, longitudinal ridge of muscle is not found on the left.

Part "b" in *coccinea, mana,* and *sagittirostris* appears subdivided by vertical raphes to form portions similar in shape, superficially only, to the narrow, sickle-like part "c." Thus, part "b" is subdivided into three parts in *mana*—a large, broad, anterior section and two slender posterior ones—into two parts of about equal size in *sagittirostris,* and into six slender parts in *coccinea.* (Note: Plates 16 and 17 do not show the small raphe between the two most anterior subdivisions.) Such subdivision of a muscle may increase its force, especially if the muscle becomes pinnate with more included fibers as seen in the third and fourth subdivisions (counting back from the anterior edge) on the left side of *coccinea*; these two subdivisions are unipinnate. Pinnateness could not be found, however, in the larger right muscle of *coccinea,* nor in *mana* or *sagittirostris.*

The retroarticular process is probably relatively longest in *sagittirostris,* although this is a supposition because this process is incomplete in all specimens. But even in the incomplete specimens, it is long and dorsoventrally deep. It is long and straight in *coccinea* and long and dorsally hooked in *virens,* but is somewhat shorter in *mana* and short and blunt in *newtoni.* These observations correlate rather well with the relative sizes of the whole muscle.

Action: Bilateral contraction of the whole muscle brings about depression of the mandible. At the same time, the resultant force vector at the mandible-quadrate articulation may act to rotate the quadrate anterodorsally about its squamosal hinge and raise the upper jaw (see Bock, 1968; Bock and Morioka, ms), but this cannot be stated definitely without analyzing all of the forces acting on the mandible.

Unilateral contraction in symmetrically-muscled birds probably allows, during depression of the mandible, a certain amount of crossing of the mandible under the rostrum in a direction toward the side on which contraction takes place (the ipsilateral side). The m. depr. mand. would draw the retroarticular process medially which would rotate the mandible on the medial condyle of the quadrate, and hence the tip of the mandible would move out laterally beyond the tip of the rostrum on that side.

In the asymmetrical *coccinea,* however, bilateral contraction of the m. depr. mand. depresses the mandible, of course, but at the same time (in a right-billed individual) the more robust caudal parts ("b" and "c") on the right side force the retroarticular process more strongly toward the midline. Since the joint between the medial condyle of the quadrate and groove on the mandible is a pivot joint, the mandible can pivot on the joint on one side and slide along on the joint on the other side, so that the anterior part of the mandible rotates toward the side of more forceful contraction (the right) and its tip crosses to the right under the tip of the rostrum as the mandible is depressed.

SUMMARY OF COMPARISONS OF JAW MUSCLES

With reservations, as noted in the paragraphs above in the section on materials and methods, the data presented in Table 3 may aid in summarizing the lengthy descriptions and comparisons of the jaw muscles. In this table, the muscles are ranked only in relative size with the largest muscle given the rank of "1"; no quantitative values are assigned to the differences in any of these rankings. Larger muscles are assumed to be stronger, i.e., develop a greater maximum force. The only valid comparisons that can be made in these tables are horizontal ones within the homologous muscle or possibly within a set of muscles in the several taxa. Comparisons *must not* be made

TABLE 3

COMPARISON OF RELATIVE SIZES OF JAW MUSCLES OF *Loxops*[1]

Jaw Muscle[2]	*L. v. virens*	*L. m. mana*	*L. m. newtoni*	*L. c. coccinea*[3]			
				Left	Right	Weak[4]	Strong[5]
m. p. p. ss	5[6]	3	4	1	2	2	1
m. p. q.	3	3	3	3	3	3	3
m. d. m.	3	1	5	4	2	4	2
m. a. m. e. r. t.	5	3	4	2	1	2	1
m. a. m. e. r. l.	4	5	3	2	1	2	1
m. a. m. e. r. m.	5	4	3	2	1	2	1
m. a. m. e. v.	5	4	1	3	2	3	2
m. a. m. e. c. "a"	1	3	5	4	2	4	2
m. a. m. e. c. "b"	5	3	4	2	1	2	1
m. a. m. p.	1	1	3	4	4	4	4
m. ps. s.	5	4	1	1	1	1	1
m. ps. p.	4	3	5	1	2	2	1
m. pt. v. l.	4	3	5	1	2	2	1
m. pt. v. m.	4	2	5	1	2	2	1
m. pt. d. l.	5	3	4	1	2	2	1
m. pt. d. m. a.	3	5	4	1	2	2	1
m. pt. d. m. p.	3	3	1	2	3	3	2
m. pt. r.	4	1	5	2	2	2	2
Totals[8]							
Whole musculature	69(5)	54(3)	65(4)	37(2)	35(1)	44(2)	29(1)
Adductors (all)	50(5)	46(3)	48(4)	27(2)	26(1)	33(2)	20(1)
Dorsal adductors[7]	35(5)	30(4)	29(3)	21(2)	15(1)	22(2)	14(1)
Jaw openers	11(4)	7(1)	12(5)	8(2)	8(2)	8(2)	8(2)
M. pterygoideus	23(4)	17(3)	25(5)	8(1)	13(2)	13(2)	8(1)
Protractors	8(5)	6(3)	7(4)	4(1)	5(2)	5(2)	4(1)

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[1] Comparisons can be made only across the horizontal rows, not up and down the vertical columns.

[2] See text or appendix I for abbreviations.

[3] Right-billed individuals.

[4] The set of weaker muscles regardless of the morphological side. Includes the right m. p. p. ss, m. p. q., m. ps. p. and all parts of the m. pt., the left m. d. m. and all parts of the m. a. m. e. The m. a. m. p., m. ps. s. and m. pt. r. are symmetrical.

[5] The set of stronger muscles regardless of the morphological side. Includes the opposite muscles from those listed under footnote 4.

[6] See text (pp. 74–5) for explanation of index; lowest number indicates the strongest muscle.

[7] Dorsal adductors are the mandibular adductors minus the m. pterygoideus.

[8] The smallest totals indicate the strongest set of muscles with the ranking of the species given in parentheses. Two rankings are given for *L. c. coccinea*, one for the morphological sides and one for the strong-weak composite sides.

vertically along the columns between different muscles or different sets of muscles because the same rank, e.g., 1, in several different muscles does not imply equal size or force development. The muscles on the two sides of *coccinea* were arranged in two ways. In the paired columns marked "right" and "left," the ratings for these muscles in a right-billed individual are given; these would be reversed for a left-billed bird. In the columns marked "weak" and "strong," the muscles were arranged with respect to the size, and hence strength, of the muscles without regard to the morphological side of the animal. Thus for a right-billed individual, the hypertrophied muscles on the right side of the head would be the m. depr. mand. and m. add. mand. ext., and those on the left side of the head would be the m. pseudot. prof., the m. pter. and the m. prot. pter. (slightly); these would be reversed in a left-billed bird. A comparative examination of these two systems for expressing the asymmetry of the musculature in *coccinea* should reveal clearly the morphological and functional arrangement of these muscles in providing strength to the mandible and upper jaw for resisting the opposing lateral forces acting on their tips when the bird is working on a leaf bud or Koa pod.

The data summarized in Table 3 suggest that, among the four forms thoroughly studied, *coccinea* has jaw muscles which are relatively larger, and presumably stronger, than those of the other three taxa. Second largest is *mana*, followed by *newtoni* and *virens* which are about equal, although *newtoni* may have slightly larger jaw muscles of the two. The strong side of *coccinea* is considerably larger than the weak side of this species which is still larger and presumably stronger than *mana*, the next larger species.

The rankings for the openers of the bill, the m. protr. pter. quad. and m. depr. mand., is *mana* having the largest muscles, followed by *coccinea* both sides, *virens*, and *newtoni* with little difference between the overall size of the musculature in the first two species and in the last two. The protractors of the rostrum show the same approximate order with *coccinea* having the largest muscles with little difference between the other species. The m. depr. mand. is largest by far in *sagittirostris*, followed by *mana*, *coccinea* right side, *virens*, *coccinea* left side, and *newtoni*. However, this muscle may be stronger than its relatively small size would indicate in *coccinea*, because part "b" is subdivided into six sections, four of which are pinnate on the weak side. Because the m. depr. mand. also protracts the rostrum, its relative size should be included in any considerations of rostral protractors. Basically, *sagittirostris* and *mana* have the strongest openers of the bill, followed closely or equaled by *coccinea*, with those of *virens* and *newtoni* being about equal in size and weaker than in the first three species. This ranking agrees well with the feeding habits of these species.

The rankings of the complete set of mandibular adductors starting with the largest is *coccinea* right side, left side, *mana*, *newtoni*, and *virens*. The considerably stronger mandibular adductors in *coccinea* as compared to the other forms of *Loxops* is readily apparent when examined on the simple basis of right-left morphological sides. The magnitude of the bilateral asymmetry and the great strength of these adductors on the "strong" side is obvious in the summary of the weak and strong sides of the jaw musculature in *coccinea*. The difference in the total mandibular adductors between the weak and strong sides in this species indicates the size of the lateral component of force on the mandible, and to a lesser extent on the maxilla, when the bird closes its jaws. The direction of this lateral force component is toward the side of the bill possessing the lateral cutting edge. The rankings of the dorsal adductors alone and of the m. pterygoideus shows the same general sequence from the largest in *coccinea* to intermediate size in the creepers *mana* and *newtoni* to the smallest in *virens*. Some variations exist such as *newtoni* being slightly larger than *mana* in its dorsal adductors and *virens* being slightly larger than *newtoni* in its m. pterygoideus. These variations are of little importance because of the small size of the differences compared to the crude system of comparisons. The comparisons between the bilateral sides of the dorsal adductors and m. pterygoideus in *coccinea* is especially interesting. Again, separation of the musculature into weak and strong sides reflects the same large asymmetry indicated by the complete set of mandibular adductors. The comparison of these muscles by right versus left morphological sides clearly demonstrates the hypertrophy of the dorsal adductors on the right side and of the m. pterygoideus on the left side in a right-billed individual. Thus the dorsal adductors place a laterally directed force component (to the right) on the right ramus and the m. pterygoideus places a medially directed force component (to the right) on the left ramus. Moreover, the m. pterygoideus places a force component to the left on the palate and hence the maxilla. These laterally directed components are in the direction of the lateral cutting edges of the mandible and maxilla respectively.

The rankings of the adductor muscles and the m. pterygoideus agrees with the general food habits of these species. The weakest set of jaw closers is found in *virens* which is a twig and leaf gleaner, taking smaller, soft-bodied insects. Moreover it feeds more on nectar than do the other forms. Both feeding habits require a small amount of muscular force for closing the jaws. The creepers, *newtoni* and *mana* are mostly insectivorous, taking their food from the surface of and from crevices in the bark of larger branches and trunks of trees. Although *newtoni* takes some nectar, this is a minor part of its diet. Insects eaten by these creepers are slightly larger than those taken by *virens*, and the method of capture employed by these creepers may require somewhat more force but the magnitude of these differences in the strength of bill-closing in *virens*, *newtoni* and *mana* appear to be small. The spread of the values for these forms for the total adductors (46–50), for the dorsal adductors (29–35) and for the m. pterygoideus (17–25) is in general small when compared to the difference between the strongest set of these muscles in these three forms and the weakest morphological side in *coccinea*. These are namely 46 in *mana* to 27 in *coccinea* for the total adductors, 29 in *newtoni* to 21 in *coccinea* for the dorsal adductors and 17 in *mana* to 13 in *coccinea* for the m. pterygoideus. These differences are greater if the average for the two sides in *coccinea* is used instead of the weakest side.

Maximum size and strength of the jaw closing muscles in *coccinea* are correlated with the feeding habits of this species. Use of the bill to open leaf buds and Koa seed pods would require large adducting forces during various phases of opening these plant structures (see below). Moreover the asymmetry of these muscles agrees exactly with the asymmetrical placement of lateral cutting edges on the mandible and maxilla and the presumed asymmetrical lateral forces exerted on both jaws when the bird is attempting to open these plant structures to obtain its insect prey. It should be emphasized that the considerably larger adductor muscles in *coccinea* are not correlated with feeding on larger insect prey (the insect prey of these species appear to be similar in size) but with a radically different method of obtaining food.

Although information about the size of the adductor muscles in *sagittirostris* is not available, we suspect that this species possessed the largest mandibular adductors in *Loxops*, even larger than those in *coccinea*, judging from the size of its skull. Evolutionary increase in size and strength of these muscles in *sagittirostris* has been, most likely, associated more with a change in prey items (larger sized insects) than with its particular feeding habits of probing into the base of leaves. The observed large m. depr. mand. and presumed large m. protr. pter. quad. of *sagittirostris* would be correlated with its probing method of feeding.

FUNCTIONAL INTERPRETATION OF THE SKELETAL AND MUSCULAR MECHANISM OF THE JAWS

The morphology of the skeletal elements of the jaw apparatus and of the musculature that move and strengthen these bones will be correlated, as far as possible, with the observations on feeding habits of these birds. We are clearly cognizant of the lack of essential information on the exact movements of the jaws during feeding, on the exact forces, musculature and otherwise, acting on the jaw apparatus, on the exact food preferences of each species and other equally important factors, so that these conclusions are offered only as hypotheses for further consideration and testing. In spite of their inadequate basis, these conclusions form a valuable basis for further study and we offer them without apology. The functions of the jaw muscles are summarized in Table 4.

The crude data on relative muscle size summarized in Table 3 does correlate with the general architecture of the skull and with the types of food taken and the general feeding methods. A more detailed comparison of the structure of the jaw musculature, size of the muscles, degree of pinnation, sites of attachment, together with the structure of the skull is required to ascertain whether these morphological features are adaptations for the different feeding methods observed in these species.

As noted above in the section on cranial osteology, *coccinea* has the

TABLE 4

FUNCTIONS OF THE JAW MUSCLES[1]

Muscle[2]	Function						
				Retraction			
	Abduction	Adduction	Pro-traction	Palate[3]	Whole jaw apparatus[3]	Right lateral pull[4]	Special
m. p. p. ss			x				
m. p. q.			x				
m. d. m.	x		x				
m. a. m. e. r. t.		x			x	right	
m. a. m. e. r. l.		x			x	right	
m. a. m. e. r. m.		x			x	right	
m. a. m. e. v.		x			x	right	
m. a. m. e. c. "a"		x		?[5]	?[5]	right	
m. a. m. e. c. "b"		x			x	right	
m. a. m. p.		x		x			
m. ps. s.		x			?[6]		
m. ps. p.		x		x		left	
m. pt. v. l.		x?[7]		x		left	
m. pt. v. m.		x?[7]		x		left	
m. pt. d. l.		x?[7]		x		left	
m. pt. d. m. a.							x[8]
m. pt. d. m. p.							x[8]
m. pt. r.					x		

[1] See text for complete statements of functions of these muscles in *Loxops*.

[2] See text or appendix 1 for abbreviations.

[3] Muscles running from the braincase to the mandible or palate can retract the whole jaw apparatus, while those running from one part of the jaw apparatus to another pull the mandible forward while retracting the palate with the whole jaw apparatus not moving relative to the skull.

[4] For right-billed *L. c. coccinea*, combined action of these muscles of the right or left sides pulls the mandible to the right.

[5] The ability of this muscle to retract the whole jaw apparatus or only the palate depends upon whether it originates from the braincase or quadrate or both.

[6] Depending upon the direction of its force vector relative to the quadrate, but probably it does not contribute to retracting either the whole jaw apparatus or the palate.

[7] Adduction of the mandible by these muscles depends upon the position of their force vectors relative to the center of rotation of the mandible. Probably contributes slightly to mandibular adduction by these muscles.

[8] Rotates the pterygoid about its quadrate articulation during protraction and retraction of the palate.

sturdiest skull followed by *mana*, then *virens* and last *newtoni*, which has the frailest skull of all. These observations seem to correlate rather well with those on the overall relative size of the jaw musculature of these forms, the only possible discrepancy being that *newtoni* ranks third rather than fourth in musculature size. However, the difference in musculature between *virens* and *newtoni* is probably insignificantly small. What is important is that the species which use their jaws least strenuously in obtaining food—*virens* and *newtoni*—are the ones with frailer skulls and weaker jaw musculature. The slightly larger jaw muscles in *newtoni* compared to *virens* in spite of the somewhat frailer skull in the former may be associated with the possibility that *newtoni* works more strenuously at bark and lichens to obtain some of its food.

Similar correlations can be made for the large mandibular depressors and rostral protractors in *coccinea* and *mana* which probe and gape strongly in their feeding operations on tight leaf buds and Koa pods, and on bark and lichens, respectively. These activities require more force in opening the jaws, and these species have the largest and presumably strongest m. depr. mand. and m. protr. pter. quad. The species which gape mostly in foliage and blossoms and to a much lesser degree than others between pieces of bark and lichen—*virens* and *newtoni*—require less force to open their jaws and hence have smaller, weaker muscles to open the jaws. *L. sagittirostris* obtains much of its food by gaping in the crevices at the bases of stout *Freycinetia* leaves which would involve considerable gaping force. This species has the largest m. depr. mand. observed in the genus and presumably has a relatively huge m. protr. pter. quad.

Capture of insect prey would be relatively similar in the four taxa as this action involves rapid movement of both jaws against little resistance until the prey item is grasped between the jaws. The size of insect and other prey is similar in the four forms of *Loxops* and should require approximately equal amounts of adductor force for capture (closure of the jaws) and subsequent crushing. It is not possible to distinguish between those adductor muscles primarily responsible for closing the jaws and those that provide mainly crushing forces on insects and other food objects held in the mouth. The basic size of adductor muscles in *Loxops* would correlate with this minimum requirement of closing force.

Gleaning of insects from the surface of foliage and small twigs by *virens* requires little crushing force and the small size of the mandibular adductors in this species is an adaptation to the food habits of this species.

Grasping and pulling bits of bark and lichens by the two creepers, *mana* and *newtoni*, as they probe for insects on the bark surface and in the crevices of large branches and tree trunks would require somewhat more adductor force. The slightly larger total adductor musculature and sturdier skull in these forms appear to be adaptations for their probing methods of feeding. The extra amount of adductor force required by the probers over that needed by the surface gleaner *virens* is small as indicated by the minor increase in the adductor muscles in the creepers compared to those in *virens*.

Considerably more adductor force would be needed by *coccinea* for opening leaf buds and Koa pods which is reflected in the sturdier skull and larger adductor muscles (including the m. pterygoideus) in this species. Increased development of the mandibular adductor in *coccinea,* as shown in Table 3, provides force over and above that required to capture and crush its insect prey. A considerable part of this increase in adductor force arose because of the requirement for a laterally directed force component (see below). However, at least some of the increase in mandibular adductors in *coccinea* developed because of the need for greater bilateral force for closing the jaws during opening plant structures to expose its insect prey.

Nectar feeding in *virens*, *coccinea* and *newtoni* (rarely) does not require any special development of the jaw muscles. Presumably the actions of the jaw muscles required for this feeding method fall with the capabilities of these muscles for the other feeding methods employed by each species.

THE ASYMMETRICAL JAW APPARATUS OF *L. coccinea*

In the section on the methods of feeding of the *coccinea* we suggested that this species probably opens the imbricated leaf buds of *Metrosideros* by using methods almost analogous and very similar to the methods used by Holarctic crossbills of the genus *Loxia* in opening pine cones to obtain pine nuts.

A number of natural historians and anatomists have investigated the method of feeding and the jaw and tongue mechanisms of the crossbills. Among those whose observations on the feeding behavior have been published are Townson (1799? *in* Yarrell, 1829:462–463), Gadow (1891:495–496), Duerst (1909:284–287), Böker (1922:88–89), and Robbins (1932: 161–164); it is our opinion that the accounts of Robbins and Duerst are the most complete and logical, and probably the most accurate.

Many of the asymmetrical structures in the crossbill (Huber, 1933) are similarly so in *coccinea*. Some of the structures have already been described in the sections on the rhamphotheca and the jaw musculature. Others have not. Before describing these, it may be instructive to outline briefly the asymmetries already mentioned. Descriptions are for right-billed specimens as are all discussions on possible feeding methods.

The tips of both rhamphothecae are asymmetrical; the bony skeletal elements deep to the horny parts are not. The mandibular rhamphotheca is bent or crossed to the right under the rostral rhamphotheca, which is bent or crossed over the former to the left (see Plate 2). The right or cutting edge of the tip of the mandibular sheath is wider and flatter (though it may also be gouged out through use) and usually higher than the left edge. The left or cutting edge of the tip of the maxillary rhamphotheca is likewise wider and flatter (it too may be gouged out), but in contrast to the mandibular rhamphotheca, the left edge is lower than the right edge.

Several jaw muscles are asymmetrical with the muscle on one side of the head hypertrophied beyond the expected size of that muscle in *coccinea*. In addition, the fiber arrangement has modified in some of these muscles to provide increased force. In listing the hypertrophied jaw muscles, the numbers in parentheses are estimates in per cent of the amount of increase in size of the hypertrophied muscle against the unhypertrophied muscles of the opposite side and the asterisk indicates those muscles believed to be the more important for providing lateral force. The muscles enlarged on the right side of the head include all parts of the m. add. mand. ext.* (30–40) and m. depr. mand. "b"* (30–40). The muscles hypertrophied on the left are the m. protr. pter. s. str. (5–10), m. pseudot. prof. (slight), m. pter. vent. lat.* (85–100), m. pter. vent. med.* (50), m. pter. dors. lat.* (60–70), m. pter. dors. med. ant. (slight), m. pter. dors. med. post.* (20–30), and m. pter. retr. (slight). Those muscles whose pull is in or close to the plane of rotation of the mandible about its quadrate hinges, e.g., the m. pseudot. superf. and m. add. mand. post., are symmetrical in size.

It could not be determined whether m. complexus of the back of the neck is asymmetrically developed because of destruction of this area during collection and dissection of the specimens before realization of the importance of this muscle in the feeding method of *coccinea.* We suspect this muscle to be hypertrophied on the left as in *Loxia* because of the similar twisting action of the head in the two genera.

Certain features of the bony skeleton of the head of the *coccinea* are developed asymmetrically. Some of these have already been described briefly in the section on the description of the musculature. On the right side the zygomatic process extends farther posteriorly onto the lateral surface of the cranium and has wider anterodorsal and posteroventral surfaces than on the left. This asymmetry reflects the hypertrophy of mm. add. mand. ext. rost. temp., add. mand. ext. rost. med., and add. mand. ext. vent. on the right side of the head. The sturdier build of the prepalatine bar and transpalatine process and the larger and more rugose surface area of the ventral surface of the internomandibular flange on the left side of the head correlate well with the enlarged left m. pter. vent. lat. And the large left palatine blade corresponds well with m. pter. dors. lat. which is larger on this side than on the right.

The quadratomandibular joints (Plate 9) of *coccinea* are similar in basic design and function to those of the crossbills although not quite as highly perfected as those of the latter. In *coccinea* the joint on the right is much looser than the one on the left and allows a lot more fore and aft sliding of the medial condyle of the quadrate in the trough-like depression in the dorsal surface of the internomandibular flange. The left joint acts pretty much like a ball and socket joint although not perfectly so, for a small amount of anteroposterior movement is permitted. The reasons for such movements can be seen in the bony structures of these joints, namely, the internomandibular flange, mandibular and jugal processes of the quadrate, and external process of the mandible.

The trough or slot in the dorsal surface of the right internomandibular flange is wide and open, providing a relatively large space in which the longer right medial condyle of the quadrate on the mandibular process can slide backwards and forwards. The anterior end of this trough is wider than the same area in the left slot. The ventral surfaces of the medial condyle are smooth, rounded articular surfaces. The articular surface of the right side extends farther posteriorly than the left one, providing a longer surface for maintenance of articulation with the wider anterior part of the slot in the right internomandibular flange during retraction of the right mandibular ramus at the time of closure of the bill. The trough in the left internomandibular flange is narrower than that in the right; this is especially noticeable at the anterior end of the slot and may represent the incipient stage of the evolution of a shortened, eventually round, socket in this flange similar to that of *Loxia.* The shorter and rounder left medial condyle of the quadrate fits more snugly into its trough than does that on the right. Little anteroposterior movement is permitted by this tight fit, but pivoting of the mandible to the right is allowed, along with the normal dorsoventral movements.

The jugal processes of the quadrate and the external mandibular processes are also asymmetrical. The ventral surface of the right jugal process of the quadrate is more deeply grooved than that of the left. This greatly facilitates fore and aft movement of the external mandibular process over the narrow, flattened dorsal edge of the right mandibular ramus in this region, and aids in preventing disarticulation. The articulating surface of the lateral condyle of the left quadrate on the jugal process is much flatter than that of the right and, therefore, facilitates rotary pivoting of this process on the wide, flat left external mandibular process. This left mandibular process projects laterally from the mandibular ramus like a shelf and is much more extensive in area than the one on the right.

It is our opinion that the left external mandibular process is used in maintaining the articulation between the lateral condyle of the left quadrate and the left ramus during retraction of the mandible on the right and lateral rotation of the mandible towards the right during both opening and closing of the bill. The left external mandibular process is placed so that, at the time of depression of the rostrum, adduction of the mandible, and rotation of the mandible towards the right, the lateral condyle of the left quadrate maintains its contact with the flat, dorsal articulation surface of the left external mandibular process, thus aiding in insuring smooth articulation. In order that this coincidence of articulating surfaces can take place, it is noticeable to the eye that the left quadrate must be in its resting position because these articulating surfaces do not meet when the left quadrate is in an extreme retracted position. This is probably brought about on the left through the strong contractions of the hypertrophied pterygoid muscles which place the left quadrate in the resting position by overpowering the tendency of the small left m. add. mand. ext. and the symmetrical m. pseudot. superf. to retract the mandible and hence the left quadrate. Simultaneously on the right side of the head, the hypertrophied m. add. mand. ext. aids in retracting the mandible and quadrate on the right, and rotating the mandible to the right. Thus, on the left side of the head, mandibular ramus and quadrate are in approximately the resting position, and on the right, the mandibular ramus and quadrate are in the retracted position, with smooth, strong articulation preserved on both sides. Such a maneuver could take place probably only in birds with an asymmetrical jaw apparatus such as is possessed by *Loxia* and *Loxops coccinea.*

The left external mandibular process is placed, also, so that at the time of protraction of the rostrum (when the quadrate is swung forward and when the mandible is depressed, retracted on the right, and swung to the right) the left jugal process of the quadrate again perfectly coincides with it, thus maintaining smooth articulation. If the left external mandibular process were not situated as it is, there would be no articulation at this time between it and the left jugal process of the quadrate, and at such a time, the chances of disarticulation between mandible and quadrate would be great.

In the section on methods of feeding, we outlined the presumed basic method used by *coccinea* to open Ohia leaf buds and Koa pods. This description is hypothetical because close, accurate observations were impossible to make in the field. It is based upon superficial observations of feeding behavior on the part of Perkins (1903:418–420) and Richards, and upon a careful study of the anatomy of the jaw apparatus including considerations of the feasible functional properties of these structures. The several methods to be described were reached on the basis of a careful reconsideration of all available evidence by Richards and Bock at the time the final draft of this manuscript was readied for publication; although the basic ideas are the same these methods differ somewhat from those advocated earlier by Richards (1957) in his thesis. In these descriptions, we shall emphasize important aspects that should be watched for whenever the feeding behavior of *coccinea* can be observed by other ornithologists. The diagrams in Text Figures 8, 9, 10 and 11 are semi-schematic attempts to show the relationships between the positions and movements of the bird and the tips of its jaws with respect to the leaf bud or Koa pod.

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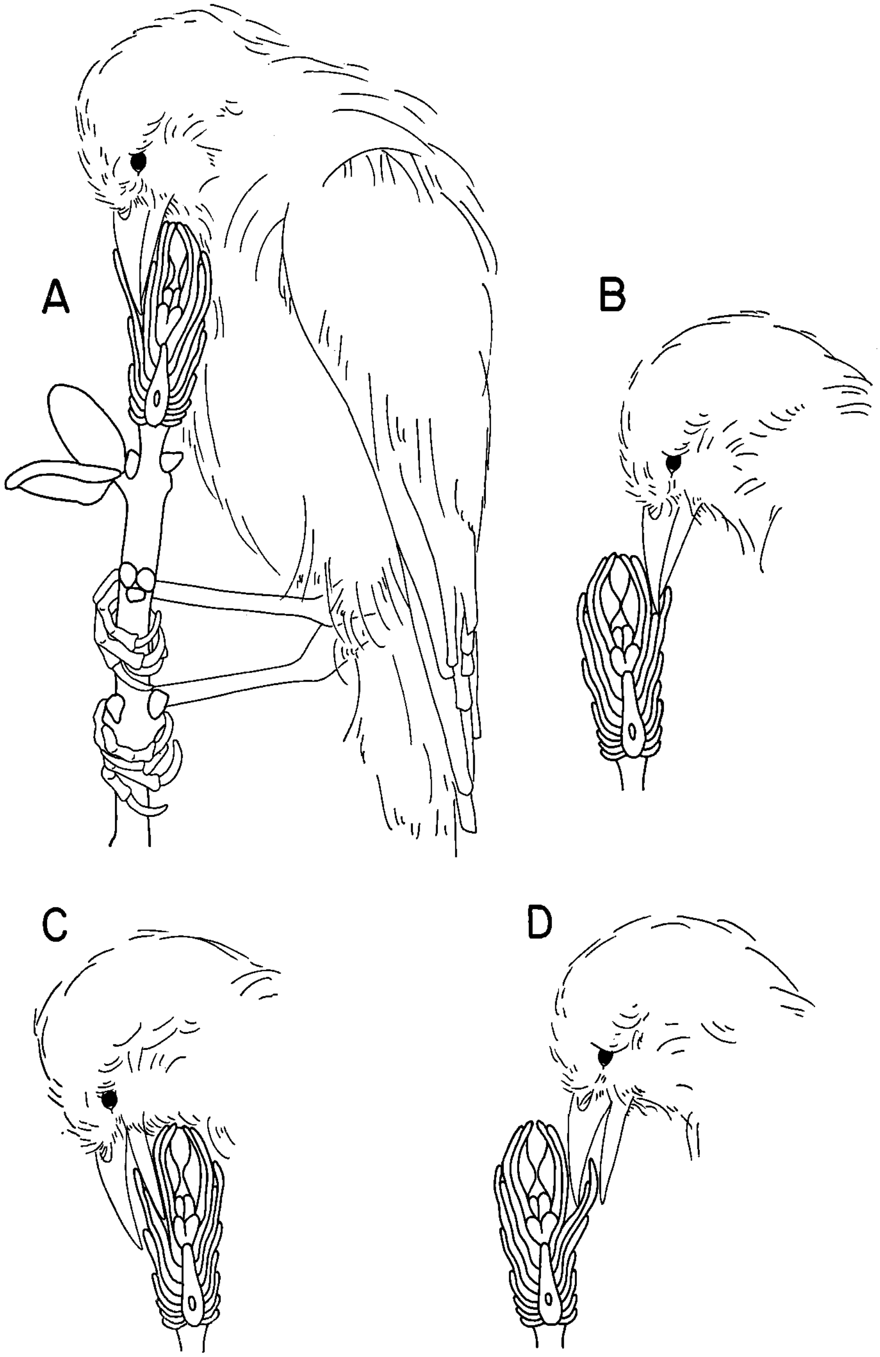
Figure 8. Schematic drawings showing the position of *L. c. coccinea* relative to a leaf bud while opening it and several possible methods of inserting the bill into the bud. A) Closed bill method with bill inserted into far side (from body) of leaf bud, this being the most probable approach. B) Closed bill method with bill inserted into near side of leaf bud. C) Opened bill method with bill inserted into far side of leaf bud. D) Opened bill method with bill inserted into near side of leaf bud; the approaches shown in B and D are probably used rarely if at all.


A
B
C
D

Three basic methods will be considered, two for opening leaf buds and one for Koa pods; we have excluded minor variations of these methods.

When working on an Ohia leaf bud, the bird would grasp the twig firmly with its feet just below the bud; the bird's body and many of its movements were usually obscured by the large leaves just below the bud. The bird was observed to bend its head downward so that its chin seemed to rest against its neck. Presumably the bird may hold the leaf bud against its body (Fig. 8) so that the force exerted by the tip of the bill on the leaf bud as the tip penetrates into the bud is resisted by force exerted on the opposite side of the bud by the body of the bird. If the bud was not braced against the body of the bird, it would move when the bill is inserted into it and thus reduce the effective force of penetration. The position of the bud relative to the body of the bird is an important point and should be noted by field observers.

The second point is whether the bird bends its head over the tip of the bud and inserts its bill into it on the side opposite to the body of the bird or whether the bird inserts its bill on the same side as its body (Fig. 8). We have assumed that the bird bends over the bud and penetrates the bud on the opposite side. This has two clear advantages. First, the force of the bill on the bud is resisted by the force of the body on the bud which would not be possible if the bill is inserted on the same side as the body; otherwise the force of the bill would tend to push the bud away from the bird (bend it on its stem) and thus reduce the force of penetration. Second, the curvature of the jaws corresponds closer to the curvature of the leaf scales with the bill either closed or opened at the time of penetration. If the bird inserts its bill into the bud on the same side as the body, then the curvature of the jaws do not coincide to the curvature of the leaf scales. Consequently, the bird would require more force when insinuating its bill, and the bill probably could not be inserted into the bud as far as the bases of the leaf scales. It is possible that the bird insinuates its bill into the apex of the bud from above. The shape of the jaws corresponds reasonably well to the curvature of the distal leaf scales, but the bud would probably bend somewhat under the force of penetration.

It is possible that the bird attacks the bud directly from the side and forces its bill through the surfaces of the leaf scales rather than insinuating it between adjacent scales. However, we doubt that this occurs as a regular method and shall not consider it further.

The field observer should note the side of the bud penetrated by the bill as the bird starts to open it, to determine if the bird approaches the bud from above, on the same side as the body, or on the opposite side, and, if possible to ascertain whether the bird insinuates its bill between adjacent scales or pushes it through the flat surface of leaf scales. We assume that the bird inserts its bill between leaf scales on the opposite side of the bud.

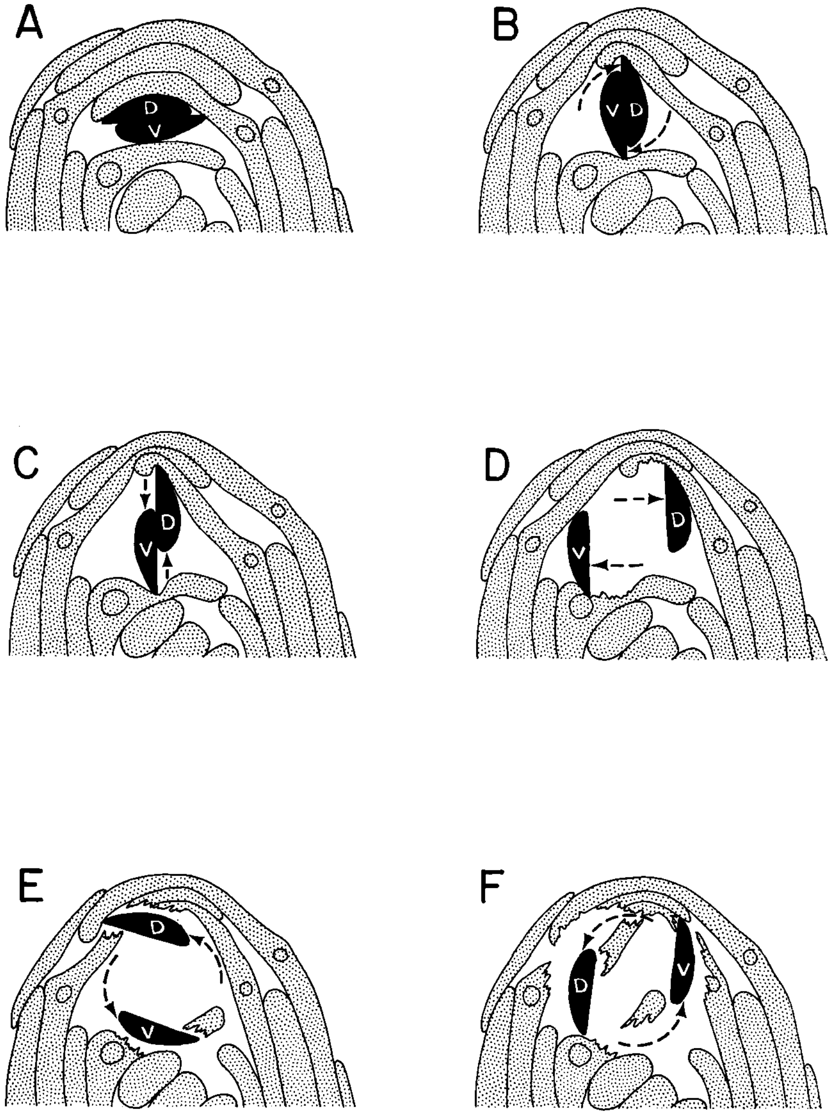


Figure 9. Cross-section through leaf bud and tips of the maxilla (D) and mandible (V) of a right bill *L. c. coccinea* with its bill inserted in a leaf bud as shown in Figure 8A to show the sequence of movements of the bill in opening the leaf bud. The series of movements are: A) Insertion of bill into leaf bud; B) Rotation of head and bill 90° to the right; C) Lateral movement of mandible to the right; D) Gaping of bill; E) Rotation of gaped bill to the left to the original inserted position; F) And continued rotation 90° to the left of the original inserted position. As a result of these movements the leaf bud is damaged and a wad of material is cut and may be removed to exposed hidden insects.

Further, the field observer should note, if possible, whether the bill is closed or gaped slightly at the time of penetration. Both methods are feasible and we shall describe the probable sequence of actions associated with each type of penetration.

In the *closed-bill method* (Figs. 8 and 9), the bird would insinuate its closed bill between two adjacent leaf scales with the frontal plane of the bill held parallel to the flat surfaces of the leaves; the tip of bill is slightly flattened dorsoventrally which reduces the force required to insert it into the leaf bud. The two adjacent scales are forced apart as the bill is pushed toward the axis of the bud. When the bill has penetrated fully, several actions take place probably, but not necessarily, in the following sequence. Also, the bird may repeat one or more of these actions, again not necessarily in the order described.

The first step (Fig. 9) may be a rotation of the head and bill approximately 90° to the right, that is, opposite to the direction of the final cutting motion. Some, but relatively little resistance from the leafy material will be met by the bill. The lateral cutting edges of the jaws would push the adjacent leaf scales further apart and may have cut or torn the surfaces of the leaves. The cutting edges of the jaws are perpendicular to the surfaces of the leaves and hence are in position to penetrate and cut them. Moreover, the left m. complexus of the neck is stretched prior to the turning of the head toward the left during the cutting action which is soon to follow. Such stretching permits the muscle to remain in the high force portion of the tension-length curve when it contracts and shortens to rotate the head during the cutting phase of this sequence. This rotation of the head to the right is important and should be noted by field naturalists.

A lateral movement of each jaw in opposite directions forcing their lateral cutting edges into the proximal and distal leaves may follow next. This action may take place prior to gaping, simultaneously with gaping, or following it. The extent and significance of lateral movement of the jaws is difficult to ascertain. In any case, the maximum lateral displacement of the rhamphothecal tips is small as compared to their movement during gaping.

A gaping action would follow in which the mandible and maxilla are opened with an asymmetrical lateral movement of the jaws if this has not occurred already. The lateral rhamphothecal cutting edges possibly scour, cut into or otherwise damage the adjacent surfaces of the proximal and distal bud leaves. The jaws would now be in final position prior to the rotary cutting action. Gaping is essential for increasing the size of the wad of leafy material to be cut from the bud.

The head and bill would now twist to the left by action of the m. complexus and other cervical muscles. The cutting edges of both jaws, having been placed perpendicular to the surfaces of adjacent leaves, damage and turn back, or cut through the bud leaves. The cut presumably continues until the head has rotated through approximately 180°, and the mandible and maxilla reaching the position occupied by the other at the start of the rotary cut.

During this rotary motion, a large asymmetrical lateral force would act on the edge of each jaw—a force directed toward the right acts on the maxilla and one directed toward the left acts on the mandible. These forces must be resisted or counteracted by laterally directed muscular forces. The asymmetrical jaw muscles can provide the necessary lateral forces. The hyptertrophied dorsal adductors on the right side of the head provide a lateral force component on the right mandibular ramus directed to the right as do the hypertrophied left m. pseudot. prof. and m. pter. on the left mandibular ramus. The hypertrophied left m. pseudot, prof. and m. pter. provide a lateral force component on the maxilla via the bony palate directed to the left. The asymmetrical muscular forces prevent rotation of the mandible to the left and reduce stress on the nasofrontal hinge of the maxilla. Although the maxilla cannot rotate laterally, the lateral force on its tip would place a lateral torque on the maxilla about the nasofrontal hinge; hence the bony material of the hinge would be stressed, and this stress can be reduced by the opposite asymmetrical muscular force of the m. pseudot. prof. and m. pter. via the bony palate.

Finally, the jaws would close on the wad of cut and damaged leaves which is grasped firmly and pulled out of the leaf bud by withdrawing the head. The wad is then discarded, and any caterpillars or other insects exposed inside the bud are seized quickly and eaten.

A subtle but important point concerning the asymmetrically developed jaw muscles must be made. The laterally directed force component of these muscles can rotate the mandible to the right. We have assumed that such rotation occurs because of the structure of the quadrate-mandibular hinges and because slight lateral rotation of the mandible would allow the jaws to absorb excessively large shocks that may disarticulate the mandible if it was rigid in the horizontal (frontal) plane. Further, we have assumed that the mandible is crossed toward the right beneath the maxilla before the start of rotary cutting; its tip may be forced back to the left as the bill cuts through the leaf bud. However, lateral movement of the mandible is not essential for the method of cutting wads in leaf buds. And asymmetrical development of the jaw muscles and associated skeletal elements can occur without the possibility of lateral movement of the mandible. The asymmetrical lateral forces produced by these muscles could serve only as a counterbalance to the asymmetrical lateral external forces acting on the bill as it cuts through

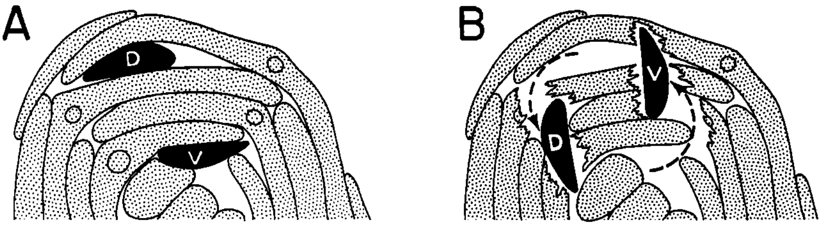


Figure 10. Cross-section through leaf bud and tips of the maxilla (D) and mandible (V) of a right-bill *L. c. coccinea* with its bill inserted in a leaf bud as shown in Figure 8C. In this method the bird uses the following sequence. A) The opened bill is inserted with the result that several leaves separate the two jaws. B) The bill is rotated about 90° to the left until a wad of material is cut and can be removed to expose hidden insects.

the leaf bud. Consequently, while we believe that crossing of the mandible to the right occurs as a normal part of cutting wads out of leaf buds, this is not an absolutely essential part of this feeding method.

A second possible method of cutting wads from leaf buds is the *opened-billed method* in which the bird would gape prior to insinuation of the bill into the leaf bud. In this case, the maxilla and mandible would be inserted between different leaf scales so that several leaves lie between the two jaws (Fig. 10). When the jaws have penetrated fully into the bud, they are already gaped and displaced laterally. In this case, rotation of the head to the right probably does not occur as this would force the blunt edge of the jaws against the bud leaves. Rather the head would be rotated only to the left with the cutting edges of the jaws cutting through leaf material. Presumably the head must be rotated only 90° or slightly more to cut a wad from the bud; part of the circumference of the wad is formed by the gap between different sets of adjacent leaves which has been enlarged when the jaws are insinuated into the bud. The wad is then grasped, pulled out and any exposed insects seized and eaten.

During the cutting of wads by either method, the bird may gape, cut laterally and grasp the wad repeatedly to further weaken the bud. It is unlikely that the bird cuts a neat wad from the leaf bud every time. No matter what variations exist in the cutting methods, a twisting of the head seems to be

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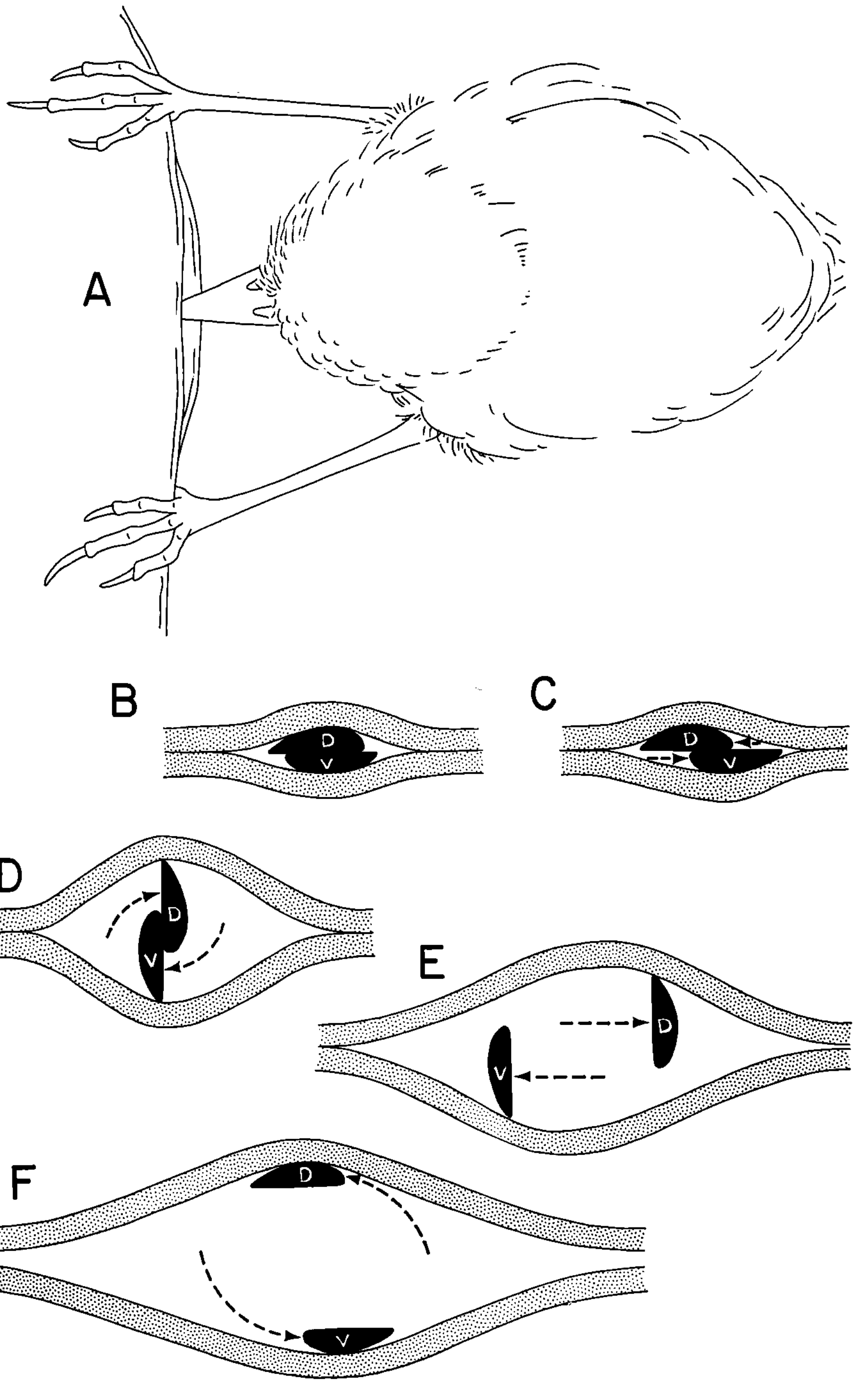
Figure 11. Schematic drawings showing A) the position of *L. c. coccinea* relative to a koa seed pod while prying apart the two valves and B to F) the sequence of movements of the jaws during this action showing the edges of the seed pod valves and bill tips in section. In this sequence the bird: B) Inserts the tip of its bill between the free edges of the valves; C) Rotates the mandible to the right, and/or moves its head and bill from side to side; D) Rotates its entire head and bill 90° to the right; E) Gapes its jaws with the bill held in the rotated position; F) Rotates its gaped bill 90° to the left back to its original inserted position. The result of this action is to spring open the seed pod and expose any hidden insects.


A
B
D
V
C
D
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D
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E
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V

an essential movement. Were this not to occur, the functional and evolutionary bases for the asymmetrical development of jaw muscles would be difficult, if not impossible to explain.

Little evidence or reasoning exists on which any decision can be made about the frequency with which the closed-bill or opened-bill method is used or whether one or the other is not used at all. The size of the wads cut is about the same although their shapes differ slightly. Insinuation of the bill may be easier and require less force in the closed-bill method than in the opened-bill method. But the opened-bill method requires fewer movements after the bill has penetrated into the leaf bud and perhaps requires less expenditure of energy than the closed-bill method. It seems feasible to assume that the bird can generate sufficient force for all steps in each method, and no step in either method appears to require considerably more force than the maximum force required in the other method. At this time we can conclude only that each method is possible and that field observations are needed for further resolution.

Opening the long, slender, thin Koa pods can be accomplished by similar movements of the jaws and head. The bird clings to the pods and inserts its bill between the slightly opened slit between the two shells of the pod (Fig. 11). In this case, the bird clings to the pod so that the force required to wedge the bill between the pod halves is resisted by transmission of force via the feet and hind limbs of the bird. The bird's head is bent downward in a position similar to that used in cutting leaf buds.

The first step is forcing the bill into the slit between the halves of the pod. The bill is probably held so that its frontal plane is parallel to the edges of the slit, allowing the slightly flattened tip of the bill to be wedged between the pod halves (Fig. 11). Presumably the bill is inserted only a slight distance, probably only enough to allow the tips to obtain a hold on the margins of the pod walls.

The second step would be lateral movement of the mandible without any gaping until the tips of the jaws are crossed to a maximum amount. During this movement the lateral cutting edges would cut any material connecting the edges of the two pod shells. Possibly the bird also swings its head from side to side to cut through more connecting material.

With the tips of the bill crossed maximally, the bird would rotate its head about 90° to the left so that the smooth curved surfaces of the jaws slide along the edges of the pod. Rotation of the jaws would force the pod halves apart as the lateral distance of the crossed mandibular tips is greater than their vertical dimension. The gouges in the lateral cutting edges of the jaws probably hook on the edge of the pod shells.

Presumably the initial twisting of the mandible is not sufficient to spring open the pod. The bird would then gape with the jaws held in the crossed position. As the jaws open, they would slide along the edges of the pod; the gouges would maintain the position of the jaws and prevent them from slipping out of the pods.

With the jaws held opened, the bird would twist its head back to the original position, thereby spreading the halves of the pod further open. The bird may have to repeat the entire sequence at several points along the pod before it is sufficiently open or springs open by elastic recoil of its drying walls to expose insects that may be living inside the pod. The insects would then be seized quickly and eaten.

In opening Koa pods, lateral crossing of the tips of the jaws is an important component. Actual movement of the mandible is involved to increase the distance between the two cutting edges and hence the distance the pod halves can be forced apart during the initial rotation of the bill. Once maximum crossing of the jaws is reached, the muscles must continue to provide lateral force to hold the jaws in their crossed position as the bill turns against the resistance of the pod halves. Consequently, when opening Koa pods, both lateral movement and large lateral muscle force component to counter external forces appear to be essential. The gouges observed in the rhamphothecae of the cutting edges are presumably the result of wear as the bird gapes its bill in the semi-opened pod. The gouges are adaptations in that they maintain the position of the jaws and prevent their slipping out of the pod while the bill is gaped.

A comparison of the methods used to cut wads from leaf buds and to open Koa pods suggests that the morphological features of the head in *coccinea* are adaptations for both types of feeding. Most interesting is that neither feeding method involves structural modifications that are disadvantageous for the other method. The asymmetry of the jaw muscles in *coccinea* would permit an automatic sidewise cutting by the rhamphothecal tips or asymmetrical resistance of force by these tips when the muscles contract. Compared to a bird with symmetrical jaw muscles, like the creepers, *coccinea* has a tremendous advantage at such times when these lateral movements or resistance to force are used in feeding. Presumably the creepers can use their jaws asymmetrically on occasion when feeding. In order to bring about a sidewise cutting and spreading movement of the jaws simulating *coccinea*, the creepers would have to relax part of the mm. add. mand. ext. and depr. mand. "b" and "c" on the left and the mm. pter. vent. and dors. on the right (that is, the bird would have to contract the muscles differentially and not achieve maximum force of these muscles on one side of the head). Thus, the creepers would not be using their muscles fully, while *coccinea* could counteract its muscles maximally and still achieve lateral movements or lateral force development. Further, *coccinea* can achieve symmetrical actions of its jaws by not contracting the hypertrophied muscles fully and hence developing equal force on each side without having to sacrifice any force that could be attained.

The asymmetries of the head and the functioning of the asymmetrical jaw apparatus in the crossbills of the genus *Loxia* and in *coccinea* are similar in that they both depend upon a very similar quadrate-mandibular articulation and similar asymmetries in the individual muscles. In both cases, the mandible can be rotated laterally on the crossed side, but not the other, and the head is rotated during cutting action. In both cases, strong and opposite lateral muscular force components are needed to resist the asymmetrical lateral forces on the tips of both jaws. And in both cases, the bird "drills" its bill into the plant material. The major differences are in the shape of the crossed rhamphothecal tips which necessitate a different sequence of movements in the two forms. Consequently, the cross-billed condition and asymmetrical morphology of the head in the genera *Loxia* and *Loxops* and associated feeding methods are not homologous, having evolved independently from different ancestors with symmetrical cranial features. But it is quite possible that they are close parallel developments dependent upon the possession of a similar quadrate-mandibular hinge in the common ancestor that permitted lateral swinging of the mandible.

THE TONGUE APPARATUS

Introduction

The morphology of the tongue, or hyoid apparatus as it is often called, will be described in three sections, the corneous part of the tongue, the skeleton of the tongue and the tongue musculature, which are followed by a consideration of the functional properties and adaptations of the tongue. We prefer the terms tongue skeleton and the tongue musculature rather than hyoid skeleton and hyoid musculature for several reasons. First, skeletal elements from the first branchial arch are included in addition to elements from the hyomandibular arch; the "hyoid" horns are formed from parts of the first branchial arch. Second, muscles derived from mandibular arch muscles, branchial muscle plates and the hypobranchial spinal muscle series are included in the set of muscles often called the hyoid muscles in addition to those from the hyomandibular arch. And lastly, the whole morphological complex is associated mainly or only with the mechanism of the tongue; hence in analogy to the jaw apparatus, the tongue apparatus is a more apt term than the hyoid apparatus.

The Corneous Tongue

The corneous tongue might be called the tongue proper and is that part visible in an examination of the external morphology of a bird. It consists of a resilient corneous sheath supported from within by the paraglossal bones of the hyoid skeleton. The sheath, presumably continuous with the stratum corneum of the epidermis of the skin, is bound by fibrous connective tissue to these bones. Other than some small blood vessels, nerves and glands, and perhaps some skeletal muscle, the paraglossal bones and surrounding corneous sheath constitute the major histological components of the tongue (Moller, 1931:121, Fig. 10).

In the genus *Loxops* the tongues are of two general shapes (Pls. 19 and 20). Those species in the subgenus *Viridonia* (*virens* and *sagittirostris*) have tongues which are long, slender, somewhat decurved and tubular. The tongues of the forms in the subgenus *Paroreomyza* (*mana* and *newtoni*) are shorter, broader, rather straight, and shallowly trough-like rather than tubular. The tongue of *coccinea* of the subgenus *Loxops* is structurally somewhat intermediate between the tongues of the two other subgenera. It is broad in its posterior half in a manner similar to the tongues of *Paroreomyza*, but it is tubular in its anterior half like those of *Viridonia.* It is not as decurved as the tongue of *virens* but is more so than those of *Paroreomyza.*

In decurved, tubular tongues such as those of *Viridonia* the lateral edges are curled upwards and medially. As the tongue narrows anteriorly, the edge of one side curls over that of the other side. These edges are rather thick proximally, but distally they are thin and transparent and somewhat shredded into laciniae (fringes) so that they have the appearance of the edges of the vane of a partially unpreened feather. At the tip of the tongue these laciniae are long, slender, and finely bristle-like and sometimes even forked at their tips, *e.g.*, in *sagittirostris*, so that the tip of the tongue looks like a minute brush. Such a tongue no doubt makes a good conduit for nectar, water, and probably juice from fruits in the partially nectarivorous forms such as *virens* and probably also *sagittirostris.* The brush-like tip possibly allows these birds to take advantage of the physical principle of capillary action when they ingest these liquid foods. Amadon (1950:223) noted that the dried tubular tongues of drepaniids collected fifty years earlier "when placed in alcohol . . . still suck up the fluid by capillary attraction." The decurved shape of the tongue probably is an adaptation, concomitant with the decurved bill, to the taking of nectar from the curved blossoms of the endemic lobelias. It was noted in the section on methods of feeding that the Maui and Kauai races of *coccinea* also take nectar on rare occasions. This species, too, has a tubular and decurved tongue, although the tubular part is relatively shorter than in *Viridonia.* It was Perkins' opinion that these tubular tongues of *virens*, *sagittirostris* and *coccinea* are of use to the species in procuring small insects from small crevices between leaves or in lichens, at the bases of *Freycinetia* leaves, or in *Metrosideros* leaf buds, respectively. Although the fringed tip of the tongues in these species would be useful in picking up insects especially if it is covered with sticky mucus, the tubular configuration of the tongue would not possess any value in insect feeding; we presume that Perkins was alluding to the fringed tip of the tongue in his statement.

In the shallow, trough-like tongues of *Paroreomyza*, the edges curl upward and inward only near the tip, and only here are laciniae and bristles present. The edges do not overlap to form a tube. The tip of the tongue is stiff and forked. It may be that this forked type of tongue is better adapted to picking up insects, perhaps larger ones, than the brush-tipped, tubular tongues of *Viridonia*, and that the tongues of the latter are primarily adapted to taking nectar and secondarily adapted for ensnaring tiny insects. Nevertheless, the trough-like tongues of *newtoni*, and also of the Lanai and Kauai forms, must be capable of conducting nectar into the mouth, as we have no reasons to doubt the observations of Perkins and Munro of these forms taking nectar.

It would seem that the backwardly-projecting spines at the proximal ends of all of these tongues and on the roof of the mouth are adaptations common to many passerine birds, aiding in the retention of highly active arthropod prey in the mouth.

Osteology of the Tongue

The tongue skeleton (Pls. 21 and 22; Fig. 12) which supports the corneous tongue and its musculature is derived from the combined hyoid (second) and third visceral arches of primitive piscine vertebrates. We follow the terminology advocated in Bock and Shear (ms. b) which follows closely that of Engels (1938).

The tongue apparatus lies for the most part ventral to the skull between the mandibular rami except for the epibranchialia which curl upward around the back of the skull in a slot or pocket in the superficial fascia outside the musculature, posterior to m. depr. mand. "c" and lateral to m. complexus of the neck. The apparatus is attached to the mandible and skull by five paired muscles. Anteriorly the m. genioglossus attaches the tongue to the mandibular symphysis; laterally the m. branchiomandibularis and m. mylohyoideus attach it to the medial surface of the mandibular ramus; and posteriorly the m. serpihyoideus connects it to the basal part of the cranium, and the m. stylohyoideus attaches it to the retroarticular process of the mandible. Furthermore, at the distal tip of the ceratobranchialia, tufts of fascia attached to the surface of m. branchiomandibularis blend in with the superficial fascia and the thin periostial sheath which covers the whole skull, thus attaching the hyoid skeleton to the skull in this area, too.

The whole apparatus is flexible by reason of its three sets of joints and the thin, flexible bones comprising the horns. Anteriorly, the paraglossal-

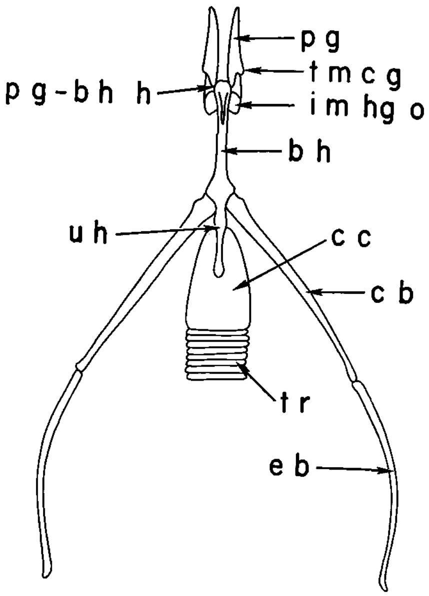

Figure 12. Tongue skeleton of *L. v. virens* in ventral view labelled as a guide to identification of the osteological features in Plates 21 and 22.

basihyal hinge allows the two paraglossalia to be depressed as a unit. They pivot on the lateral and anterior surfaces of the tip of the basihyale when the tendon of m. ceratoglossus, inserting on the tubercle on the lateral surface of the paraglossale, is under tension. This same hinge allows the two paraglossalia to be turned as a unit to either side. It is thus close to a universal joint. The anterior ends of the paired ceratobranchialia articulate with the posterolateral corners of the basihyale in ball and socket joints. These joints allow the ceratobranchialia to move upward, downward and mediad, and laterad. Between the ceratobranchiale and the epibranchiale is a single joint allowing the latter to bend dorsad. The urohyale is fused onto the posterior tip of the basihyale.

As stated in the section on methods and materials, the combined lengths of basihyale plus urohyale were held constant in the drawings of the tongue skeletons for all forms because it was reasoned that the length of this composite bone probably would change less during evolution than the lengths of the paraglossale or the hyoid horn (ceratobranchiale and epibranchiale). The drawings made in this manner point out two features (see Pls. 21 and 22). The first is that the epibranchiale is relatively longer in *virens* and *sagittirostris* than in any of the other forms. The second is that the paraglossalia of the two creepers (*mana* and *newtoni*) are relatively longer than in the other species.

The first feature appears to be found then in the birds with long, tubular tongues; it may be noted that the epibranchialia of *coccinea*, a species whose tongue is tubular in its distal half, are shorter than those of the subgenus *Viridonia* but are no shorter than those of *mana* and are longer than those of *newtoni*. The extra length of these bones, especially in *Viridonia*, perhaps is correlated with nectar feeding since it would allow the tongue to be protracted further (a longer horn allows a longer m. branchiomandibularis which allows further shortening and hence protraction of the tongue). Greater protraction is a useful adaptation to birds which take, or whose progenitors took, nectar from lobelia blossoms with deep corollas. It may also be useful in capturing small insects from deep crevices. The fact that the paraglossalia are relatively shorter in these subgenera, *Viridonia* and *Loxops*, than in *Paroreomyza* perhaps also may be correlated with present day or ancestral nectarivorous feeding behavior. Short paraglossalia would give less support, and thus more flexibility, to the attenuated, resilient distal end of a tubular tongue, hence perhaps facilitating the insinuation of such a tongue into the farthest corners of a lobelia nectary.

The second feature, long paraglossalia, is found in the subgenus *Paroreomyza* which has a relatively shorter, open, forked tongue, presumably more useful in snaring insects than a brush-tipped tubular one. These relatively longer bones would give to this tongue more support and hence stiffness, a feature seemingly advantageous to the capture of some of its prey with the tongue.

The lateral surface of the anterior end of the ceratobranchiale has an elongated, shallow concavity in all species of *Loxops*. A similar, but more pronounced cavity is found in the ceratobranchiale of carduelines and in some other groups of finches (Eber, 1956).

Other differences in shapes and sizes of tubercles and muscle scars are discussed in the section on the tongue musculature.

Musculature of the Tongue

The studies of Moller (1931:116–120, 131–134), Edgeworth (1935:58–60, 97, 107, 109, 158, 203–205, 274–288), Engels (1938:642–649), and Bock and Shear (ms.) were used as guides to the identification and analysis of the tongue musculature. The nomenclature of Bock and Shear (ms. b) has been followed; their system follows that of Engels (1938) and of George (1962) quite closely which in turn is based largely on the studies of Gadow (1891–1893). Arrangement of muscles into groups is based upon the system of Engels who classified these muscles into sets according to their ontogenetic development as shown by Edgeworth (1935). The descriptions of the tongue muscles use the same system as for the jaw muscles with the abbreviations given in parentheses following the name of the muscle. Note that the name m. thyreohyoideus has been retained and used even though a thyroid cartilage does not exist in birds.

Innervations of the tongue muscles were not traced in this study because the homologies between the tongue muscles in *Loxops* and those in other passerine birds could be established easily on other comparative morphological criteria.

The general pattern and identification of tongue muscles are presented in text Figure 13. Details of the skeletal elements and musculature of the tongue are illustrated in Plate 22 for *sagittirostris*; Plate 23 for *virens*; Plate 24 for *mana*; Plate 25 for *newtoni*; and Plate 26 for *coccinea*. As for the jaw muscles, reference to these plates will not be repeated in the descriptions of the individual muscles as it would be overly redundant and of little advantage to the reader.

A) M. mylohyoideus (m. mylohy.; m m h): A transverse, thin, sheet-like muscle layer that extends between the mandibular rami with a raphe along the median line between the two halves. It lies immediately deep to the skin of the throat region except laterally where it is covered by the m. branchiomand. It is thin and translucent posteriorly where it covers (lies ventral to) the medioanterior tip of the m. serpihy. Some variation may exist at this point in that the m. serpihy. may cover (lie ventral to) the medioposterior tip of the m. mylohy.

Origin: Fleshy along a long, thin line from the medial surface of the mandible, deep (dorsal) to the origin of the m. branchiomand., from a point near the mandibular symphysis posteriorly to the area of origin of the m. branchiomand. (posterior head).

Insertion: On a medial raphe between the two halves of the muscle.

Comparison: The m. mylohy. is a parallel-fibered muscular sheet. It is very thin and contains relatively few fibers (one should not be fooled by the apparent large size of this muscle when viewed from below); hence it is a rather weak muscle. Its fibers are quite long, their effective length being the distance between the mandibular rami or twice the length of the muscle from origin to insertion.

In both *coccinea* and *newtoni*, this muscle extends further posteriorly and superficially to the ventral surface of the m. serpihy. than in *virens* and *mana*. It appears to be a thicker sheet in *coccinea* and *mana* than in the other two forms. Unfortunately, it was destroyed in the available specimens of *sagittirostris*.

Action: Contraction of the two halves of this muscle would aid in constricting the lumen of the buccal cavity by elevating the floor of the mouth, and thereby providing a firm base along which the tongue can move back and forth.

B) M. ceratohyoideus (m. ceratohy.; m c h): A ribbon-like muscle with the two halves forming a "V" with its apex pointing anteriad. It lies deep (dorsal) to the m. serpihy.

Origin: Fleshy from a tiny concavity in the medial surface of the distal tip of the ceratobranchiale, immediately anterior to its articulation with the epibranchiale. The origin of the m. ceratohy. is encased by the m. branchiomand. and is covered dorsally by the originating end of the m. ceratoglos.

Insertion: Each half of the muscle inserts on the median line with its contralateral mate. This line of insertion is attached to the medial line of the dorsal surface of the m. serpihy. and of the m. mylohy.

Comparison: The m. ceratohy. is a parallel-fibered, strap-like muscle. Again, the two halves constitute morphologically and functionally a single muscle more than forming two separate muscles. The m. ceratohy. is a thin muscle, hence it contains few fibers and is relatively weak. Its fibers are long, extending the length of the muscle as required for the relatively great displacement undergone as it contracts.

Little difference exists in the structure of this muscle among the forms studied.

Action: Contraction of the two halves of this muscle would prevent the two hyoid horns from separating when the tongue is protruded by the pull of the m. branchiomand.; its medially directed force component opposes the laterally directed force component of the m. branchiomand.

C) M. stylohyoideus (m. styloh.; m st h): A long, thin, flat, tapering muscle that extends from the retroarticular process to the basihyale. It lies anterior to the m. serpihy. and superficial to the m. branchiomand., with its posteromedial edge bound to the anterolateral edge of the m. serpihy. At its origin, fibers of the m. stylohy. may blend with fibers of the inserting end of the m. depr. mand. "b" and "c."

Origin: By a tough aponeurosis over the lateral surface and ventral edge of the retroarticular process and a flat tendon immediately anterior to the insertion of the m. depr. mand. In *sagittirostris, mana,* and *newtoni,* the inserting end of the m. depr. mand. is also covered by an aponeurosis.

Insertion: Fleshy on a small area on the lateral surface of the basihyale near its dorsal edge and halfway between its anterior and posterior tips; this insertion lies anterior to the insertion of the m. tracheohy. and dorsal to the insertion of the m. hypoglos. obl.

Comparison: The m. stylohy. is a strap-like, parallel-fibered muscle with quite long fibers. Because of the small total number of fibers, the m. stylohy. is a relatively weak muscle, but one that can be stretched over a long distance and can shorten a relatively large absolute length.

This muscle is approximately the same in all forms except for the more extensive origins noted for *sagittirostris, mana* and *newtoni.*

Action: Bilateral contraction of this muscle would aid in retracting the tongue by pulling backward on the basihyale, this being its major function. The m. stylohy. is the major retractor of the tongue. If the tongue is held in place by the m. branchiomand., the m. stylohy. would aid in enlarging the lumen of the buccal cavity by depressing the floor of the mouth. Unilateral contraction would deflect the corneous tongue to the ipsilateral side when the paraglossal-basihyal articulation is stabilized.

D) M. serpihyoideus (m. serpihy.; m s h): A broad, flat, ribbon-like muscle, forming with its mate a "V" with the apex pointing forward. It lies posterior to the m. mylohy. with its anterior end dorsal to the posterior tip of the m. mylohy. The tips of these muscles lie in close contact and their fibers may be blended with one another. The anterolateral edge of the m. serpihy. is strongly appressed to the posteromedial edge of the m. stylohy.

Origin: By a small, fleshy head from the base of the cranium immediately medial to the retroarticular process. Although it was not clearly observed, this muscle presumably originates from the anterior edge of the occipital plate (exoccipital process) close to the lateral process of the basitemporal plate.

Insertion: On a medial raphe with its mate; this raphe attaches to that of the m. ceratohy.

Comparison: The m. serpihy. is a strap-like, parallel-fibered muscle with relatively long fibers. Its small physiological cross-section indicates that this muscle can develop only little force, while the long fibers allow the muscle to stretch and shorten over a great distance.

Little describable variation exists in this muscle throughout the series of forms.

Action: The paired mm. serpihy. forms a loop around the pair of hyoid horns; contraction of this muscle would maintain the correct position of the hyoid horns as the tongue is protracted and retracted. In particular, this loop of the mm. serpihy. would prevent the hyoid horns from spreading laterally and ventrally as they are pulled forward by the m. branchiomand. Bilateral contraction of this muscle would aid in constricting the lumen of the buccal cavity by pulling the ceratobranchialia dorsally and by elevating the posterior part of the floor of the mouth.

E) M. branchiomandibularis (m. branchiomand.; m b m): This largest of all tongue muscles is entwined about the epibranchiale and distal part of the ceratobranchiale from which it extends to the mandibular ramus. It lies dorsal to the mm. serpihy. and stylohy., and ventral to the m. mylohy. at the origin of the latter muscle from the mandibular ramus. The m. branchiomand. is divided into two parts, an anterior and a posterior portion, over most of its length; these parts have distinct origins which are separated by a clear gap in several forms, notably *coccinea.*

Origin: By two large fleshy heads from the medial surface of the mandibular ramus ventral in position to the origin of the m. mylohy. The origin extends posteriorly from a point approximately adjacent to the beginning of the rhamphotheca to a point adjacent to the insertion of the m. add. mand. ext. vent. In *newtoni,* the m. branchiomand. post. is attached also by a thin, strap-like aponeurosis under the ventral edge of the mandibular ramus. In *mana* and *coccinea,* this aponeurosis extends even further to cover that part of the inserting end of the m. pter. vent. lat. attached to the ventral edge of the mandibular ramus. The originating portion of this muscle was destroyed in *sagittirostris.*

Insertion: After entwining around the epibranchiale, both parts of this muscle insert along its distal end up to the free tip of the epibranchiale.

Comparison: Although partly distorted by its twisting around the hyoid horn, the m. branchiomand. is essentially a parallel-fibered muscle. It is a large muscle in total mass, but much of this mass is dependent upon the length of the fibers which are perhaps the longest in any of the tongue muscles. However, the number of fibers in this muscle is large and may well be the largest of any of the tongue muscles. The length of the hyoid horns is directly related to the length of the m. branchiomand., and hence to the distance that the tongue can be protruded from the mouth.

The m. branchiomand. is larger and stronger in *mana* and *coccinea* than in *virens* and *newtoni.*

Action: Bilateral contraction of this muscle would protract the tongue by causing the muscle-encased epibranchiale to slide forward in the slippery pocket of superficial fascia located posterior to the m. depr. mand. "c" and lateral to the m. complexus of the neck. Unilateral contraction would bring about protraction of the whole tongue apparatus toward the contralateral side.

F) M. genioglossus (m. genioglos.; m g g): A thin, stringy muscle extending from the mandibular symphysis posterior underneath the mucosa of the mouth and dorsal to the m. mylohy. This muscle divides near its posterior end into two slips of insertion, an anterior one and a posterior one. The m. genioglos. ant. is medial to the m. genioglos. post.

Origin: Fleshy by a small head from the posterior surface of the mandibular symphysis just lateral to the midline.

Insertion: The m. genioglos. post. appears to insert in a fleshy manner underneath the oral mucosa just medial to the internal and medial mandibular salivary(?) glands. Possibly and quite likely, this muscle continues to the tongue skeleton and inserts on the mucosa anterior to the cricoid cartilage. The m. genioglos. ant. inserts in a fleshy manner on the dorsal surface of the posterolateral edge of the paraglossale posterior to the paraglossal-basihyal joint.

Comparison: The m. genioglos. is a parallel-fibered muscle with few, long fibers; hence it is a weak muscle that can shorten over a great distance.

The relative size of the m. genioglos. post. from largest to smallest is *virens*, *mana*, *newtoni* and *sagittirostris* (equal), and *coccinea*. The shriveled appearance of this muscle in *sagittirostris* may be due to shrinkage of the specimen which was obtained in 1901. The range in relative size from largest to smallest of the m. genioglos. ant. is *mana*, *newtoni* and *coccinea* (all equal), *virens*, and *sagittirostris*. Again, this muscle in the last species may have been shrunken.

Action: The action of this very thin muscle is hard to deduce because of its presumed small force development. One suggestion advanced by Bock and Shear (ms) is that this pair of muscles acts as a set of guides along which the tongue slips as it is protruded.

G) M. ceratoglossus (m. ceratoglos.; m c g): This is a long muscle extending from the body of the ceratobranchiale to the paraglossale with a tough, cord-like tendon extending from a large aponeurosis on the belly of the muscle. The belly of the muscle is shaped like the hull of a dugout canoe lying on its side with the cavity opening toward the medial line and the paper-thin "bottom" facing anterolaterally. The ceratobranchiale is encased by the "gunwales" and "bottom" of the canoe.

Origin: Fleshy from the dorsal surface of the ceratobranchiale from its distal tip to its proximal end, and from the lateral and dorsal surfaces of the joint between the ceratobranchiale and basihyale. The ventral "gunwale" attached along the medial edge of the ceratobranchiale, and in *coccinea*, the dorsal "gunwale" also attached to the anterior third of the medial edge of the ceratobranchiale.

Insertion: By a strong tendon to the bony tubercle on the ventrolateral side of the paraglossale anterior to the paraglossal-basihyal hinge.

Comparison: The m. ceratoglos. is an unipinnate muscle with relatively short fibers. Although it is a small muscle in total mass, the m. ceratoglos. contains a large number of fibers so that it may equal or exceed the strength of the m. branchiomand. Certainly it is one of the strongest members of the tongue muscles.

This muscle shows little variation throughout the forms with the exceptions of a stronger origin in *coccinea* and being longer and narrower in *sagittirostris*. The last exception, however, may be due to shrinkage in the specimen.

The tubercles of insertion are relatively largest in *virens* and *mana*, intermediate in size in *sagittirostris* and *coccinea*, and smallest in *newtoni*. These differences may not be significant.

Action: Bilateral contraction of this muscle brings about depression of the tongue since its insertion lies in front of the paraglossal-basihyal joint. Unilateral contraction would cause the tongue to be depressed on the ipsilateral side. This muscle need shorten only slightly to accomplish its action—hence its short fibers. But it may have to depress the tongue against resistance and therefore must develop considerable force—hence the large physiological cross-section.

H) M. hypoglossus anterior (m. hypoglos. ant.; m hg a): This muscle *per se* is absent in all forms of *Loxops* dissected by Richards; however, there appear to be some remaining nonmuscular vestiges. In *virens*, *sagittirostris* and *mana*, there are more or less paired bundles of whitish fibers on the underside of the tongue deep to the corneous layer and to a layer of cartilage-like material. These bundles originate between the ventral edges of the paraglossalia anterior to the paraglossal-basihyal joint and extend anteriorly almost to the tip of the corneous tongue. Skeletal muscle striations were not visible in this tissue when viewed under a compound microscope. These bundles appear to be composed of fibrous connective tissue that may represent the connective tissue stroma of the almost completely vestigial m. hypoglos. ant.

The vestigial nature of the m. hypoglos. ant. in *Loxops* agrees with the condition of this muscle in finches (George, 1962:31) and in the cardueline finch *Hesperiphona* (Bock and Shear, ms), and in the drepanidine *Ciridops* (Bock, 1972).

I) M. hypoglossus obliquus (m. hypoglos. obl.; m hg o): This is a short, chunky muscle extending from each side of the basihyale to the underside of the posterior end of the paraglossale. Its fibers are transverse, running at right angles to the longitudinal axis of the tongue.

Origin: Fleshy from the whole of the flat, lateral surface of the basihyale ventral to the insertions of the mm. stylohy. and thyreohy., and from the anteroventral surface of the bulge in the basihyale just anterior to its joint with the ceratobranchiale. Anteriorly, the ventral edge of the basihyal is crossed by a thin layer of transverse muscle fibers extending from one muscle to its mate.

Insertion: Fleshy into a cup-like (in some forms) depression in the ventral surface of the posterior end of the paraglossale.

Comparison: The m. hypoglos. obl. is a parallel-fibered muscle with a rather large number of fibers that are short for a tongue muscle. Its total number of fibers is relatively large and probably exceeded only by the m. branchiomand. and m. ceratoglos.

There is little describable variation in size and shape of this muscle throughout the series of forms dissected. The muscle is chunkier in *virens* and *mana*, and slenderer in *sagittirostris, coccinea* and *newtoni.*

The lateral surface of the basihyale is relatively largest in area in *sagittirostris* and *virens,* is intermediate in area in *mana,* and is smallest in area in *coccinea* and *newtoni.*

The area of insertion of this muscle is a cup-like, oblong depression in *sagittirostris* and *virens,* is more or less flat and oblong in *coccinea* and *mana,* and is long, narrow and flat in *newtoni.*

These differences in the skeleton are probably not significant.

Action: Bilateral contraction of this muscle depresses the posterior ends of the paraglossalia, thus elevating the anterior end of the tongue. Unilateral contraction would probably elevate and turn the tip of the tongue toward the ipsilateral side.

J) M. tracheohyoideus[1] (m. tracheohy.; m tr h): This muscle lies along the ventrolateral surface of the trachea just lateral to the m. tracheolateralis. Its insertion on the cricoid cartilage lies between and is partly obscured by the two heads of origin

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[1] The medial muscles lying along the trachea and extending from the cricoid cartrilage to the basihyale posed considerable difficulties to Richards during his dissections and the writing of his original thesis description. These difficulties involved the m. tracheolateralis, the m. tracheohyoideus and the m. thyreohyoideus, and arose because of vagueness in the description of these muscles by Engels (1938). Description and discussion of these muscles in Richards' thesis (1957: 181–183) were only partly correct. Fortunately the figures of the tongue muscles drawn by Richards from his dissections are excellent and allow conclusive identification of every muscle based upon comparison with the tongue muscles of other passerine birds (Bock and Shear, ms. b; Bock, 1972). Descriptions of these muscles presented herein are based partly upon information gleaned directly from the thesis and from Richards dissection notes, and partly upon comparative inference from our knowledge of these muscles in other passerine birds.

The m. tracheolateralis (m tr l) is usually grouped with the syringeal muscles and was not included in the dissections of the tongue muscles, but it is shown in the illustrations. It lies along the ventral surface of the trachea, medial to the m. tracheohyoideus and the origin of the ventral head of the m. thyreohyoideus. It appears similar in all respects to the m. tracheolateralis in other passerine birds (Bock and Shear, ms. b).

of the m. thyreohyoideus. Some fibers of the m. tracheohyoideus may continue into the dorsal head of origin of the thyreohyoideus, as is typical for many passerine birds, but this possibility could not be ascertained from the dissection notes.

Origin: The origin of the m. tracheohy. is posterior to the cut by which the head was severed from the body in preparation for dissection. In all passerine birds, and presumably also *Loxops,* this muscle originates from the sternum as the m. sternohyoideus with an intermediate attachment to the skin of the neck close to the midpoint of the muscle (Bock and Shear, ms. b).

Insertion: The major part of this muscle inserts in a fleshy manner on the ventrolateral surface of the cricoid cartilage between the two heads of origin of the m. thyreohyoideus. Presumably a few fibers (5% of the total number) continue into the dorsal head of the m. thyreohyoideus and insert with this muscle onto the basihyale.

Comparison: The m. tracheohy. is a strap-like, parallel-fibered muscle with few, very long fibers. It is, hence, relatively weak but would be able to shorten over a long distance. Little or no variation exists in this muscle between the forms studied.

Action: Bilateral contraction would aid in retracting the tongue by pulling posteriorly on the cricoid cartilage. It would also retract the anterior end of the trachea.

K) M. thyreohyoideus (m. thyreohy.; m th h): A flat muscle extending from the cricoid cartilage, dorsal to the proximal end of the ceratobranchiale, to the basihyale.

Origin: From the cricoid cartilage by two separate heads. The large ventral head arises from the ventral surface of this cartilage between the insertions of the m. tracheohy. and the m. tracheol. The small dorsal head arises from the lateral edge of the cricoid cartilage dorsal to the insertion of the m. tracheohy.; this head receives a small number of fibers from the m. tracheohy.

Insertion: Fleshy onto the lateral surface of the basihyale posterior to the insertion of the m. stylohy. and deep (medial) to the body of the m. hypoglos. obl.

Comparison: The m. thyreohy. is a strap-like, parallel-fibered muscle, having about the same number of fibers as the m. tracheohy., but the fibers are much shorter, being only the length of the gap between the cricoid cartilage and the basihyale (midpoint of each element).

Little or no variation exists between the forms studied.

Action: Bilateral contraction retracts the basihyale and hence the corneous tongue with respect to the cricoid cartilage. Unilateral contraction could bend the corneous tongue slightly toward the ipsilateral side. The main function of this muscle is apparently to retract the tongue and thus close the gap between the tongue and larynx (anterior end of the trachea) that may widen as the tongue is protruded.

FUNCTIONAL INTERACTIONS OF THE TONGUE MUSCULATURE

The above descriptions of the tongue muscles and their actions demonstrates the large number of potential synergistic and antagonistic actions of these muscles regulating normal tongue movements (Fig. 13 and Table 5).

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Figure 13. Schematic drawings of the skull, tongue and tongue muscles of *L. v. virens* in ventral view as a guide to the morphology and functional properties of the tongue muscles. A) The two muscles that serve as slings to maintain the proper position of the tongue apparatus relative to the jaws. B) The four muscles that serve to protract and retract the tongue (indicated by the arrows) relative to the skull. C) The four muscles that serve to move parts of the tongue relative to one another (indicated by the arrows) but not to the skull. D) The two muscles in lateral view that can raise (m hg o) or lower (m c g) the anterior part of the corneous tongue relative to the basihyale and the rest of the tongue apparatus.

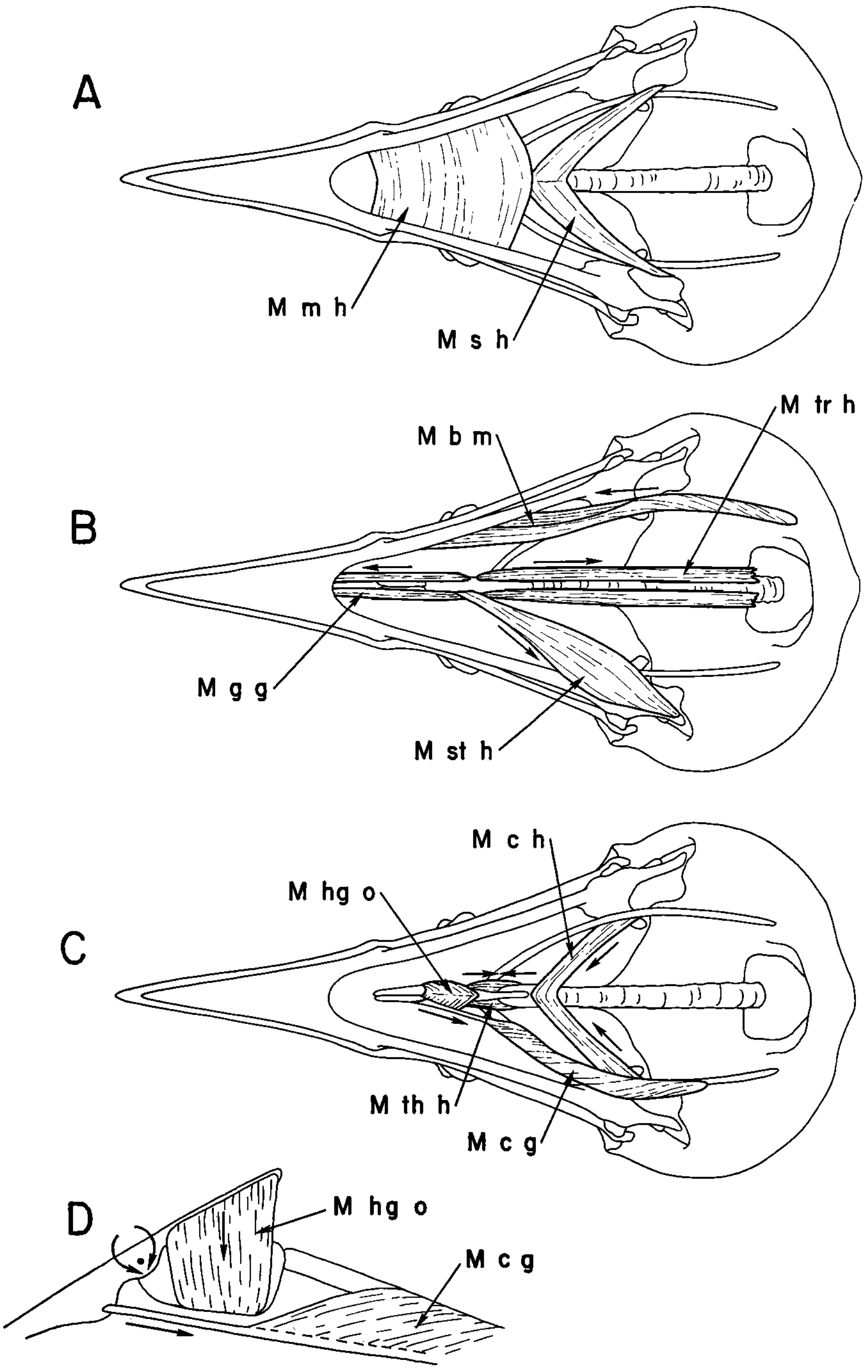
A
M m h
M s h
B
M b m
M tr h
M g g
M st h
C
M c h
M hg o
M th h
M c g
D
M hg o
M c g

TABLE 5
FUNCTIONS OF THE TONGUE MUSCLES[1]

	Functions						
Muscle[2]	Protract tongue	Retract tongue	Lateral rotation tongue	Tilt corneous tongue	Support tongue	Modify oral cavity	Special
m. m. h.					x	x(c)[3]	
m. c. h.							x
m. st. h.		x(w)[4]	x			x(e)[3]	
m. s. h.					x	x(c)[3]	
m. b. m.	x		x			x(e)[3]	
m. g g.							x
m. c. g			x	x(d)[5]			
m. hg. o.			x	x(u)[5]			
m. tr. h.		x(w)[4]					
m. th. h.		x(c t)[4]					

[1] See text for complete statements of functions of these muscles in *Loxops*.
[2] See text or appendix 1 for abbreviations.
[3] Either constricts (c) or expands (e) lumen of mouth; the m. st. h. acting together with m. b. m.
[4] Either retracts the whole tongue apparatus (w) or only the corneous tongue (c t).
[5] Either tilts the corneous tongue up (u) or down (d) about the basihyale.

Considering the rapidity and subtle variation in the contraction of these muscles, the delicate degree of needed control, and the small size of the whole tongue apparatus, it is unlikely that sufficiently accurate studies of the functions and biological roles of these muscles will be made in the immediate future. We would like to outline only the broadest actions of the tongue apparatus and of the underlying muscular control.

The functional properties of the tongue muscles, either acting singly or in sets, can be comprehended with greater ease if the muscles are arranged into three groups (Fig. 13). The first set comprises the muscles extending from one side of the skull to the other and forming a ventral sling for the tongue; these include the m. mylohy. and the m. serpihy. The second group comprises the extrinsic tongue muscles that extend from the skull or other part of the body to the tongue apparatus (including the head of the trachea) and can move the whole tongue relative to surrounding features; these include the m. branchiomand., m. stylohy., m. genioglos. and m. tracheohy. The third set comprises the intrinsic tongue muscles that extend from one part of the tongue apparatus to another and hence can only move parts of the tongue relative to each other; these include m. ceratohy., m. ceratoglos., m. hypoglos. obl., and m. thyreohy. The other intrinsic muscle in the passerine tongue apparatus, the m. hypoglos. ant., is absent in *Loxops*.

When considering diverse actions of the tongue muscles, it is necessary to distinguish between movement of the whole tongue relative to surrounding structures and movement of parts of the tongue apparatus relative to one another. This is done most easily by examining movement of the center of mass of the whole tongue and movement of the separate centers of mass of its individual parts. Only the extrinsic muscles can move the center of mass of the entire tongue apparatus relative to the skull, be it protraction, retraction or lateral bending. Intrinsic muscles can move the corneous tongue, for example, in varied ways, but cannot shift the entire tongue relative to the head. Unless this distinction is kept in mind, incorrect functions are easily ascribed to individual muscles because of the complexity of the whole system.

The following movements and other actions of the tongue apparatus are considered mainly with respect to those of the corneous tongue. All movements of the corneous tongue will be described as the movement of its anterior tip relative to other features. These actions are summarized in Table 5.

a) Protraction of the tongue is achieved by bilateral contraction of the m. branchiomand., which is the only tongue protractor; we doubt that the m. genioglos. contributes any force to protraction. The latter muscle aids protraction by providing a set of guides along which the tongue "runs" as it moves forward. Possibly this muscle also reduces any slack in the mucosa of the mouth floor and the tongue base during protraction.

Unilateral contraction of the m. branchiomand. would protrude the tongue, pull it toward the ipsilateral side and rotate it toward the contralateral side of the head. This rotation is probably a minor component of the total sideward movement of the corneous tongue.

b) Retraction of the tongue is achieved by bilateral contraction of the m. stylohy., an extrinsic muscle which is the main tongue retractor. Unilateral contraction of the m. stylohy. would retract the tongue, pull it to the ipsilateral side and probably rotate it toward the contralateral side. Contraction of the m. tracheohy. would retract the head of the trachea, and in combination with the m. thyreohy. would retract the tongue; the two muscles would act as an extrinsic muscle. Contraction of the m. thyreohy. alone would retract the corneous tongue toward the head of the trachea, i.e., reduce the gap between these structures.

c) Lateral rotation of the tongue is under the control of several muscles; this rotation may be of the entire tongue apparatus or only of the corneous tongue via movement of the supporting paraglossalia and in some cases also of the basihyale. Unilateral contraction of the m. branchiomand. and of the m. stylohy. would rotate the whole tongue toward the contralateral side, but quite likely these extrinsic muscles have a minor role in lateral movement of the corneous tongue. Such movements are probably under the control of several intrinsic muscles for the most part. The m. thyreohy. could rotate the corneous tongue toward the ipsilateral side by unilateral contraction without elevation or depression of the tongue tip. Likewise, unilateral contraction of either the m. ceratoglos. or the m. hypoglos. obl. will rotate the tongue toward the ipsilateral side but with depression or elevation, respectively, of the tongue tip. Simultaneous unilateral contraction of these muscles will rotate the corneous tongue toward the ipsilateral side in a horizontal plane. Varying the forces produced by these muscles would alter the degree of elevation or depression of the tongue tip accompanying lateral rotation.

d) The whole tongue apparatus may be raised somewhat while it is being protracted by the m. branchiomand. Elevation of the tongue tip is achieved by bilateral contraction of the m. hypoglos. obl.

e) Depression of the whole tongue would occur while it is being retracted by bilateral contraction of the m. stylohy. Combined action of the m. tracheohy. and the m. thyreohy. may also depress the tongue. Passive depression would be caused by the weight of food and other objects held within the mouth cavity. The tip of the corneous tongue is depressed relative to the rest of the tongue by bilateral contraction of the m. ceratoglos.

f) The corneous tongue (and its foundation of the paraglossalia) can be stabilized in the sagittal plane by simultaneous bilateral contraction of the m. ceratoglos. and the m. hypoglos. obl.; this action fixes the basihyal-paraglossal joint. Stability of the basihyale may be achieved by contraction of the m. ceratohy. and possibly of the m. serpihy. which would hold the posterior (free) end of the urohyale against the ventral surface of the tracheal head. This action might be aided by the m. thyreohy. Fixation of the basihyale might be essential for fine movements of the tongue tip which appear to be controlled mainly by the m. ceratoglos. and the m. hypoglos. obl. which move the paraglossalia relative to the basihyale.

g) The floor of the buccal cavity can be depressed actively, thereby enlarging the lumen of the mouth, by bilateral contraction of the m. stylohy. when it retracts the tongue and possibly by contraction of the m. branchiomand. which would force the hyoid horns against the mouth floor; however, such action is probably limited in extent and weak. Strong simultaneous bilateral contraction of the m. branchiomand. and the m. stylohy. would presumably arch the hyoid horns strongly against the buccal floor as the main active method of enlarging the mouth cavity. Passive depression of the buccal floor would be achieved by the weight of food or other objects held in the mouth.

h) The buccal floor can be raised, decreasing the lumen of the mouth by bilateral contraction of the m. mylohy. and the m. serpihy. These transverse muscles form slings beneath the whole tongue apparatus, supporting it or raising it along with the floor of the mouth.

FUNCTIONAL AND ADAPTIVE SIGNIFICANCE OF THE TONGUE

Although the avian bill is frequently regarded as the primary food-obtaining organ, the tongue is equally important especially in the final stages of handling or conveying food particles into the mouth and esophagus. In *Loxops*, this is especially true when the bird is ingesting liquid foods, including water, nectar or fruit juices, or is capturing and ingesting small arthropod prey from crevices in plant structures. We shall consider the probable method of taking up nectar from a lobelia blossom by *virens* since such a maneuver probably would make use of all of the functions of the tongue musculature just described. Capture of small arthropods presumably would involve most of the same movements of the tongue but not the utilization of capillary action of liquids in the terminal bristles of the tongue or the creation of a partial vacuum in the buccal cavity.

The bird approaches a lobelia blossom and probes its closed bill through the slit in the upper surface of the corolla base, and then forces it through the tissues of the base of the staminal column into the partly covered spacious nectary. The bill is opened—probably just enough to emit the tongue—and the tip of the tongue is protruded out of the mouth into the nectary by means of bilateral contraction of the m. branchiomand. The position of the brush tip of the tongue within the nectary can be minutely and accurately adjusted by the bird to insure that nectar from all parts of the nectary is taken up and that the nectary is thus emptied efficiently at the first visit to that particular blossom. These movements are achieved by the complex interactions of the tongue muscle functions described above which need not be repeated here.

At this time, the tip of the tongue is swishing around in the nectar and is thoroughly wetted with nectar and possibly also with saliva. The mechanism by which nectar moves through the tubular tongue and into the mouth is still unclear. Several workers (Gadow, 1883:69; Amadon, 1950:223) have suggested that capillary action allows nectar to ascend the tubular tongue; the bristles of the brush-like tip and the laciniae of the tube may be essential to the capillary mechanism. Water will rise to the posterior posterior end of a tubular drepanidid tongue when it is held vertically and its tip inserted into the fluid. But capillary action alone appears to be too slow a process for the bird to rely upon exclusively for the efficient, rapid obtaining of nectar. Presumably the nectar is either sucked into the mouth through the tubular tongue in much the same way that a person sucks fluids through a straw, or is drawn into the mouth by a rapid series of protractions and retractions of the tongue analogous to the lapping of water by a cat or dog. Sucking actions would depend upon the creation of a partial vacuum in the buccal cavity. The bird could create a vacuum by depressing the mouth floor, but a partial vacuum would be formed only if all openings into the mouth were sealed. Unfortunately, no mechanisms, either a flap or a muscular value, are known which could seal the internal nares. Nor is it known how the space between the corneous tongue and the horny bill can be closed.

Another possible mechanism may exist to create the necessary partial vacuum. A slight concavity is often seen in the flat dorsal surface at the posterior end of the corneous tongue just behind the posterior opening of the tubular portion. The lateral edges of this flat area are supported by the posterior processes of the paraglossalia. A vacuum could be formed if the bird pressed this flat surface of the corneous tongue against the roof of the mouth and increased the size of the central depression. Enlargement of this cavity could be achieved by elevating the posterior processes of the paraglossalia relative to the basihyale which is a function of the M. ceratoglos. Possibly, the basihyale could be lowered, but the necessary muscular action is difficult to comprehend. Lateral spreading of the posterior ends of the paraglossalia would also serve to increase the size of the central cavity. With the creation of a vacuum in this small space, nectar would be pulled up through the tubular tongue and would fill this cavity. Release of the vacuum by depression of the posterior processes of the paraglossalia via contraction of the M. hypoglos. obl. would allow the nectar to flow into the mouth cavity and be swallowed. This mechanism does not require sealing the entire mouth cavity and yet may provide enough suction to empty a single nectary of its nectar.

Nectar could be obtained by repeated protractions—retractions of the corneous tongue which would draw a small amount of nectar into the mouth in each cycle. Such a mechanism would not, however, depend upon a tubular tongue and might be more effective with a different configuration of the corneous tongue. Available knowledge of the structure of the tongue and surrounding features is inadequate to permit further analysis of the mechanisms whereby these birds convey nectar into their mouth cavity. Equally little is known about other nectarivorous passerine birds.

Nectar collected in the mouth cavity is presumably swallowed by tilting the head backward as a bird does when swallowing water. The bird may collect nectar from several flowers before swallowing the accumulated amount.

It should be remembered that all of these complicated actions take place extremely rapidly. Probably these actions account for the observations by Baldwin (1953: 311), mentioned above, of swallowing movements in *virens*, of the smacking together of the rhamphotheca of *Vestiaria* while feeding from Ohia blossoms noted by Richards, and of the rapid darting in and out of the tongue from the bill in *Drepanis funerea* while taking water from wet moss as noted by Perkins (1895: 126–127).

In summary, then, it can be said that the corneous tongue in the members of this genus are of two general types with that of the subgenus *Loxops* being intermediate in shape. In *Viridonia*, of which *virens* at least is nectar-feeding, the tongue is long, slender, decurved and tubular with a thickly tufted tip and laciniated edges to the halves of the tube. In the insect-eating creepers of the subgenus *Paroreomyza*, it is shorter, broader, straighter and shallowly trough-like. The tip is forked and bristly, and laciniae are present only near the tip. In the skeleton, the epibranchialia are relatively longer in *Viridonia* than in *Paroreomyza* and more or less intermediate in length in the subgenus *Loxops*; the m. branchiomand. would be correspondingly longer in *Viridonia.* This feature gives "added reach" to the tongue apparatus so that the corneous tongue can be protruded further in *Viridonia.* The paraglossalia are shorter in *Viridonia* and *Loxops* than in *Paroreomyza*, thus giving less support but more flexibility to the corneous tongue. The tongue of the creepers (*Paroreomyza*), being used to capture larger insects from crevices, would have to be more rigid with a firmer basal support.

These differences in the shape of the corneous tongue and relative sizes of segments of the tongue skeleton probably are correlated, for reasons discussed above, with presumed ancestral nectarivorous feeding behavior or continued partial nectar-feeding in the subgenera *Viridonia* and *Loxops* (and in the ancestor of the entire genus), and with insectivorous feeding behavior in *Paroreomyza.* The tongue musculature appears to vary little throughout the genus; presumably it is adapted to either type of feeding behavior as the needed motions of the tongue are similar and required forces are much the same. The major differences may be in the length of the m. branchiomand. and possibly in the m. stylohy. The major evolutionary changes, therefore, were in the corneous tongue, the tongue skeleton and the feeding behavior of the several species.

DISCUSSION

FEEDING ADAPTATIONS

In the several previous chapters, a comparative summary of the functional properties and of plausible adaptive significances was given for each of the several morphological systems contributing to the feeding apparatus. The disjointed nature of these summaries does not provide a sufficient basis for understanding the adaptation of the entire feeding apparatus for the feeding habits in each species of *Loxops*, and most importantly, for comprehending the adaptive history of the genus *Loxops.* The latter is essential for any future analysis of the evolution and classification of the Drepanididae, including considerations of its origin from some mainland group within the New World nine-primaried oscines.

Feeding adaptations: The morphological adaptations for feeding observed in the several taxa of *Loxops* cannot be comprehended only in terms of the food objects of these birds because all forms feed upon insects and occasionally upon nectar. Although some size difference exists between the insect prey of the several species of *Loxops*, these differences cannot account for the obvious morphological differences between these birds. Of far greater importance are the location of the insect prey in the environment and the various methods used to obtain these insects by the several taxa of *Loxops* investigated in this study. These feeding methods may be regarded as behavioral adaptations for obtaining insects under different circumstances (surface of leaves, crevices in bark, within leaf buds and koa seed pods, and behind the bases of *Freycinetia* leaves), and the morphological adaptations evolved in conjunction with the different feeding methods. In the terminology advocated by Bock and von Wahlert (1965), the selection forces associated with the evolution of feeding adaptations in *Loxops* depend upon the insect prey plus their exact position in the environment. Feeding on the same insects found on surfaces of leaves, in bark crevices and within leaf buds or koa pods would result in different selection forces. The feeding behaviors used by the several species of *Loxops* to obtain insects found in these several parts of the environment would constitute the biological roles of the feeding apparatus. These biological roles depend upon the forms and functions of the features of the feeding apparatus; in this study we are concerned with the morphological features of the feeding apparatus. Hence the adaptation of these morphological features of the feeding apparatus depends upon the interaction (synerg) between the selection force (the insect prey and its location in the environment) of the environment and the biological roles (feeding methods) of the birds. If any of these factors are modified, then the adaptations would be subject to modification. Even if the birds feed upon the same species of insects, but upon individual animals found in a different part of the environment (e.g., the insects found in crevices in the bark of trees rather than on the surface of leaves), then the selection force would change and could result in the evolution of new morphological adaptations. In this case, the evolutionary change would be discussed in terms of the birds using a new source of food. If the insect prey and its location in the environment remain the same, but with the birds modifying their feeding methods, thus establishing a new relationship (synerg) with the environmental factor, this circumstance could result in different selection forces acting on the birds. For example, we could imagine that instead of prying open leaf buds or koa seed pods by direct thrusts of the bill, the bird might gape and twist its bill to force open plant structures and expose hidden insects. Such evolutionary changes are often discussed in terms of adaptations for greater efficiency. The environmental factors have not changed, but the animal has modified the way in which it interacts with the same environmental factor and in doing so, often modifies the selection force acting upon it. New morphological adaptations could result in response to these new selection forces.

The morphological adaptations for feeding in the several taxa of *Loxops* provide many excellent examples supporting the concepts of evolutionary adaptation and associated notions advocated by Bock and von Wahlert

(1965). Therefore, particular attention is given to exact location of food sources and feeding methods used to obtain food and to correlation of the morphological features to these factors. As far as possible, the individual morphological features will be discussed as part of a larger integrated functional unit.

A) *Loxops virens virens*: The Amakihi possesses the slenderest bill of all species in the genus, and in many ways represents the most generalized member of *Loxops* since it has the broadest range of feeding habits in the genus. Moreover, it may well represent the most primitive species in the genus. The following remarks are based upon the Hawaiian Amakihi (*L. v. virens*) but probably hold true for all other subspecies except for the Kauai Island form, *L. v. stejnegeri,* which has a larger and strongly decurved bill, and almost certainly has a different method of feeding. However, the following analysis of the adaptation of the feeding apparatus in *L. v. virens* possibly holds true for the Kauai Island *L. parva.* The external morphology of the bill of this species is very similar to that seen in most populations of *L. virens.*

The Hawaiian Amakihi feeds mainly on insects and small arthropods, preferring soft-bodied, flightless forms between 1.5 and 10 mm in length. Larger, heavy-bodied insects are not taken. The bird hunts for the insects among leaves, blossoms, twigs and smaller branches, and less frequently (less than one-third) on larger branches and trunks of trees. Insects are taken mainly from the surface of leaves by gleaning, but also from between leaves and masses of lichens by probing. All parts of leaves and twigs are visited with the body held in all possible positions although some positions, such as vertically with head down, were observed infrequently. Nectar is the second item of food but is taken far less frequently than insects. The flat broad blossoms of *Sophora* and *Metrosideros* are visited most frequently with the birds approaching the flower from the side to avoid the long stamens. The long tubular lobelia flowers are pierced near the base of the corollas to reach the nectaries. Because of the rapid movements of the birds while feeding, no useful observations could be made on actions of the tongue. The last and least important food item is the juice of fruits; so infrequently is this food item taken that it is presumed to lack a significant influence on the evolution of feeding adaptations in this species.

The bill of *virens* is of medium length for the genus, but slender and most decurved. The bony jaws are correspondingly frail as is the skull. In all features of the cranial osteology, *virens* is either the most lightly constructed member of the genus or only slightly sturdier than *newtoni.* The light construction of the skull is closely paralleled by its small jaw muscles. For most individual jaw muscles or sets of jaw muscles, *virens* possesses either the weakest or second weakest muscles.

The tongue of *virens* is long, slender, somewhat decurved and tubular with the edges and tip shredded into a fringe. The tongue fits into a well developed medial slot bounded by two parallel ridges in the horny palate of the upper jaw. The epibranchialia are relatively long in this species with a long m. branchiomandibularis and probably a long m. stylohyoideus (although relative lengths of this muscle were difficult to ascertain). The paraglossalia are short, allowing a more flexible tongue.

The slender bill with light skull and weak jaw muscles are all adaptations for gleaning small insects from the surface of leaves. No great amount of muscular force is required to capture the insects, hence small muscles are sufficient, and the skull need not be strengthened. Indeed, it should be noted that larger muscles and stouter bones than required would be a disadvantage for a bird feeding on small insects because of increased weight and increased metabolic energy required to maintain and operate these larger structures. A slightly decurved bill as compared to a straight bill may or may not be an advantage for leaf-gleaners, but it is not a disadvantage. The terminal fringe of the tongue may be advantageous in brushing up small insects.

The slight decurvature of the bill is a definite adaptation for nectar-feeding. The bird can probe into shallow blossoms from the side and thereby avoid the long stamens that would interfere with the bird if it approached these flowers from above. Tubular flowers are pierced from the side near their bases and the tongue inserted between the tips of the gaped jaws. Piercing the thin floral tissues does not require great force, and the strength of the jaws and their musculature is sufficient for these piercing and gaping actions. The slightly decurved bill permits the bird to reach the nectar in nectaries opened at the top while probing into the flower from the side. The length of the bill and of the tongue are likewise advantages for nectar-feeding as are the tubular nature of the tongue and its terminal fringe, and the medial slot in the horny palate. Long epibranchialia and branchiomandibularis muscles permit the tongue to be protruded from the mouth more than in other members of the genus and hence more readily reach the furthest nectaries. The short paraglossalia allow greater flexibility of the tongue.

Thus, the shape of the bill and tongue, the lightly-built skull and weak muscles, long tubular fringed tongue with long epibranchialia and branchiomandibularis muscles are adaptations for gleaning small insects from the surfaces of leaves and twigs and for obtaining nectar from broad, flat blossoms of *Metrosideros* and tubular lobelia flowers.

B) *Loxops sagittirostris*: The food, feeding habits and morphology of the Greater Amakihi are poorly known because of the extinction of this species around 1900, but sufficient information is available to allow some conclusions on the adaptations of its feeding apparatus.

The main food items of the Greater Amakihi are larger insects such as forest crickets of the genus *Paratrigonidium*, caterpillars, spiders and a carabid beetle. Most of these arthropods are taken from their hiding places at the base of Ieie leaves, beneath loose bark of large Ohia trees, ferns and similar hiding places. Their prey is obtained by strong probing and prying with the bill. A few observations were made of this species feeding at blossoms of the Ohia, so that it probably obtained some nectar in its feeding; however, nectar was probably a minor food item.

The long stout bill of *sagittirostris* is adapted to the larger insects that form a major part of its food and to the strong probing and prying required to secure these insects from their hiding places at the bases of leaves. Its straight bill is advantageous in feeding methods that result in large forces acting backwards on the tip of the bill.

The only jaw muscle that could be described in this genus is the m. depressor mandibulae which was much larger than that in other members of the genus. A correspondingly long retroarticular process exists in this species. These features are presumably adaptations for strong gaping, a feeding method that would be expected in a bird that obtains insects from the area between leaf bases and stem, beneath loose pieces of bark and other similar places.

The long, slender, decurved tubular tongue with a terminal fringe that was observed in *sagittirostris* is presumably an adaptation for nectar feeding. So are the long epibranchialia and branchiomandibularis muscles and short paraglossalia. These agree with the few observations of the Greater Amakihi feeding at blossoms and suggest that nectar may have been a more important part of its diet than suspected. Possibly *sagittirostris* relied on nectar in its total diet to the same extent as did *virens*.

Thus, the long, stout, straight bill, large m. depressor mandibulae and long retroarticular process of the Greater Amakihi are adaptations for obtaining larger insects from crevices at the bases of leaves and etc. by strong probing, prying, and presumably gaping. The long tubular tongue with its terminal fringe, long epibranchialia and branchiomandibularis muscles and short paraglossalia are adaptations for feeding on nectar in a manner similar to that used by *virens*.

C) *Loxops maculata mana*: The Hawaiian Creeper feeds mostly on arthropods and other invertebrates, taking caterpillars, spiders and small moths, with larger moths, slugs, and beetles sometimes eaten. These prey items are taken on the trunks and large branches of forest trees, either from the surface or generally from crevices in the bark by vigorous probing, pecking and prying with the bill. The bird climbs up and down the trunk and creeps on the upper and lower surfaces of horizontal limbs, searching dead wood and beneath the bark for caterpillars and other insects. The Hawaiian Creeper thus fills the ecological position of nuthatches (*Sitta*) and even more closely, that of the Black and White Warbler (*Mniotilta varia*, Parulidae) in the Hawaiian forests. Few insects are taken in flight. The Hawaiian Creeper apparently never feeds on nectar.

The skull and jaws of *mana* are stoutly developed with the rhamphotheca of both jaws extending straight out to end in an extremely acute angle. The rugged construction of the bill is shown by the greater height and width of the horny ridge between the nasal operculae. The straight bill is clearly adapted for large posteriorly directed forces acting on the tip of the bill. Not only are the bones of the skull stout, but the braincase is bulbous, a condition similar to that seen in woodpeckers and other pecking birds. The bulbous cranium may serve to protect the brain and/or provide a broad base for the bill which would be advantageous in withstanding lateral forces acting on the tip of the bill. Certainly not all blows would be placed directly on the bark but would glance off, resulting in lateral forces acting on the bill tips. Moreover, prying actions of the bill would place strong lateral forces on the bill tip which could be resisted best if the bill had a broad base at the quadrate articulation and at the nasal-frontal hinge. A bulbous cranium would provide the desired width.

The jaw muscles of *mana* are somewhat stronger than those of *newtoni* and *virens*, but are still considerably weaker than those of *coccinea*. Although individual muscles in *mana* are the smallest or the largest in the genus, no subset of jaw muscles in this species is exceptionally well or poorly developed. Rather the entire musculature is uniformly better developed in comparison to that of *virens* to provide the force it requires in vigorous probing and prying for insect prey.

The short, broad and rather straight tongue with its stiff and forked tip is clearly adapted for insect feeding. The long paraglossalia provides support for the tongue required in strong probing for insects. Although the epibranchialia are short, associated with reduced requirement to probe long distances, the branchiomandibularis muscules are larger than in other members of the genus, which is an adaptation for the larger force needed to probe strongly with the tongue and to spear insects with it. The shallow trough and only slightly curled edges are associated with the lack of nectar feeding (hence lack of any need for a tubular tongue) and with the need for a stiff flattened tongue that can be inserted into crevices for insects.

Thus the strong, straight bill, stout skull with its bulbous braincase, stronger jaw muscles, strong straight tongue with its stiff, forked tip and strong branchiomandibularis muscles are all adaptations for uncovering and capturing insects hidden in crevices in the bark of trunks and larger branches. The absence of nectar in the diet of the Hawaiian Creeper precludes the need for compromise in morphological adaptations for nectar feeding and for insect feeding by probing, especially in the structure of the tongue.

D) *Loxops maculata newtoni*: The food and feeding habits of the Maui Creeper differ little from those of the Hawaiian Creeper; indeed these taxa are far more similar to one another than are any of the other species of *Loxops* included in this study. A few important differences do exist between these creepers. The Maui Creeper spends much time among leaves of trees and lichens although it can creep as well as the Hawaiian Creeper, which was never observed by Richards to feed among leaves. It appears to be more of an inhabitant of scrub and undergrowth, although it still spends much time on the trunks and branches. The food items are almost the same as those taken by *mana*; no reports exist suggesting that *newtoni* takes smaller insects. On rare occasions, the Maui Creeper takes nectar from blossoms of *Metrosideros*, a habit shared with the Lanai Creeper, *montana*, and the Kauai Creeper, *bairdi*; however, nectar is a very minor item in the diet of all of these creepers.

As for the Hawaiian Creeper, the bill of *newtoni* is straight, but it is more decurved and weaker than the bill of *mana*. Associated with its weak bill is its frail skull, the frailest of those studied, and smaller jaw muscles (compared to *mana*), which are about the same size and strength as those in *virens*. Presumably, this creeper cannot probe and pry as vigorously as *mana* and spends more time gleaning its arthropod prey from the surface of leaves and off the bark than probing in crevices. If members of this race are able to obtain sufficient food by gleaning and weak probing, then the frail skull and weak jaw muscles are an adaptation in that they can be lighter in weight and require less energy. Unfortunately, we do not have sufficient observations on the size of the insect prey taken by *newtoni* compared to that eaten by *mana* or of the exact feeding methods, both of which would be essential to judge the adaptiveness of the frail skull and weak muscles.

The slightly curved bill may be associated with greater gleaning rather than vigorous probing and prying.

The short, straight tongue with its stiff, forked tip and lack of curled edges are adaptations for insect eating as in *mana*. As in the Hawaiian Creeper, the epibranchialia are shorter and the paraglossalia longer, for increased support of the tongue, and the m. branchiomandibularis strong, but smaller in *newtoni* than in *mana*. A medial slot with parallel lateral ridges is found in the horny palate; the tongue fits into this groove which is an adaptation for the rare taking of nectar. This arrangement would permit formation of a tube for transportation of nectar without compromising the adaptations of the tongue for insect feeding.

Thus the straight, pointed bill and straight tongue with a stiff tip of the Maui Creeper are adaptations for capturing insects by probing and prying. The frail skull and weak jaw muscles appear to be adaptations for weak probing, greater gleaning of insects from leaves and bark and taking smaller insects. The medial groove of the horny palate is an adaptation for feeding on nectar without modification of the tongue, which would have reduced its degree of adaptation for insect-feeding by probing. The major aspects in the adaptation of the feeding apparatus of *newtoni* are associated with weaker probing and greater amount of surface gleaning in its feeding methods.

E) *Loxops c. coccinea*: The Hawaiian Akepa, which may be quite accurately called the Hawaiian crossbill, is the most specialized member of the genus with most of the morphological adaptations of the feeding apparatus closely associated with the twisting motions of its head and beak during feeding.

The food of the Hawaiian Akepa is mainly caterpillars, other insects and small spiders. These arthropods are taken either from the surface of leaves and bark, or from within leaf buds, leaves fastened together by the larval insects or koa seed pods. Richards observed the Akepa feeding only in Ohias (*Metrosideros*) and koas (*Acacia Koa*), and other workers report that this species is very partial to these trees. The birds were observed feeding chiefly in the foliage and leaf buds or on the koa pods and more rarely on branches. While feeding, the bird held its body in almost every imagineable position and could be observed with its head bent so that the bird's chin rested against the anterior part of its neck and upper breast. Unfortunately details of its feeding methods could not be observed.

The Akepa has been reported to feed on nectar rarely, although this was not observed by Richards.

Because of the observed morphology of the feeding apparatus, we presume that the feeding methods used by *coccinea* involve a twisting motion of the head and beak while the tips of both jaws are inserted into the plant material, either in leaf buds or koa seed pods. The essential consequence of these twisting actions is a pair of laterally directed forces acting in opposite directions on the tips of the upper and lower jaws. However, we must stress that the details of the feeding methods presumably used by the Akepa as presented above are deductions based upon the morphology of the feeding apparatus and are not based upon observed facts. The major justification that may be offered is that the entire hypothesis is plausible and internally consistent.

The Akepa is a small species with a short bill resembling that seen in many small unspecialized finches such as siskins with no unusual feature noticeable in lateral view. However, in dorsal or ventral views, the tips of the two rhamphotheca can be seen to cross one another, the degree of crossing being minor as compared to that seen in crossbills (*Loxia*). Both right-billed and left-billed individuals are found; our descriptions will be for the more common right-billed individuals. The lateral edge of both the maxillary and mandibular rhamphothecae on the crossed side forms a sharp cutting edge while the opposite edge is rounded. These cutting edges of the lower and upper jaws are forced against the plant tissue as the bird twists its head; the sharp edge is an adaptation to increase the force with which the rhamphothecae cut into the plant tissue.

In overall shape, the jaws are short and relatively wide, providing greater leverage for the jaw muscles and strengthening the bill against the strong lateral forces acting on the tips of the mandible.

The skull of *coccinea* is short and is the strongest of those in all the taxa studied as are its jaw muscles; both the strength of the bone and of the large muscles are direct adaptations to the strong forces acting on the jaws. However, the most important aspect of these forces is that they act laterally and asymmetrically on the tips of the jaws. A force directed toward the bird's left acts on the right lateral edge of the mandibular tip in a right-billed bird, while a force directed toward the bird's right acts on the left lateral edge of the maxillary tip; these forces are equal in magnitude. Hence, the mandible is pushed toward the left and the maxilla toward the right. The forces developed by the jaw muscles must oppose these external forces and their consequences.

Most of the braincase, jaws and bony palate are symmetrical in *coccinea* with no hint of the asymmetrical rhamphothecae reflected in the bony jaws. Some differences exist in the size and shape of the temporal and subtemporal fossa, in the zygomatic process between them and in the transpalatine process; these differences are associated with asymmetries in the jaw muscles. The most important asymmetries exist in the configuration of the jaw articulations. These features are adaptations to permit a slight lateral rotation of the mandible to the right with the mandibular halves of the jaw articulation sliding and rotating laterally around the quadrate condyles. A slight degree of lateral rotation is an adaptation in the suggested method for opening koa pods in which actual movement of the mandible is an advantage and in all feeding methods as a means of reducing undesirable strong shocks. Reduction of these shocks can be achieved by small lateral rotation of the mandible which could lengthen impact time. A mandible rigid in terms of lateral rotation would be subjected to shorter impacts and larger shocks.

The jaw muscles of the Akepa are not only larger, both absolutely and relatively, than in the other species of *Loxops* included in this study, but asymmetrically developed. The degree of asymmetry in the muscles is considerably greater than in the rhamphotheca or in the skull and is readily apparent even in a quick superficial examination of the head. Moreover, the pattern of asymmetry in the jaw muscles is a clear adaptation to the pattern of external forces placed on the tips of both jaws. Examination of the relative sizes of the muscles on the right and left sides of the head reveals that those muscles with a direct dorsal pull on the mandible—the

m. pseudotemporalis superficialis and m. adductor mandibulae posterior—are symmetrical. Those dorsal muscles which have a laterally directed force component pulling the mandible to the right while adducting it—most of the parts of the m. adductor mandibulae externus—are larger on the right side of the head. Lastly, ventral muscles such as the m. pseudotemporalis profundus and most of the m. pterygoideus which have a medially directed force component pulling the mandible to the right while adducting it are larger on the left side of the head. Hence all of the enlarged jaw muscles have horizontal force components, which would rotate the tip of the mandible laterally to the right or would resist a strong lateral force acting toward the left on the right edge of the mandibular tip. Moreover, the retractors of the palate are on the left side of the head and would result in a stronger posteriorly directed force at the left ventroposterior corner of the upper jaw. This larger force is in a proper position to counteract a lateral force acting to the right on the left edge of the maxilla and hence to reduce part of the stress placed on the nasal-frontal hinge. Lastly, it should be emphasized that the asymmetrical jaw muscles pose no problem when the Akepa wishes to open or close its jaws when no external lateral forces are acting on the jaws. At these times, the bird needs only to contract its muscles differentially so as to develop equal amounts of force on both sides of the head.

The morphology of the tongue in the Akepa does not show any clear adaptations to the feeding methods of this bird on insects hidden within leaf buds or koa seed pods with the possible exception of its length and frilled tip which may be used to ensnare small insects. Rather, the length of the tongue, tubular configuration, frilled tip and large m. branchiomandibularis are all adaptations for nectar feeding. The importance of these adaptations are difficult to assess. Possibly they may be holdovers from an early stage in the evolution of the genus when nectar was an essential part of the diet and maintained because the Akepa still feeds occasionally upon nectar and because these nectar adapted features of the tongue morphology do not conflict with the particular insectivorous feeding methods of this species. Yet it is possible, and even probable, that nectar-feeding and the associated adaptations of the tongue are essential for the survival of this species. Even if nectar is taken relatively rarely, it may provide an important source of food that could be used when the insects on which the Akepa feeds are in short supply. Although the Akepa has the advantage over other members of the Drepanididae in utilizing a food source that is unavailable to them, it may have a disadvantage if its food supply varies greatly during the year. Both leaf buds of *Metrosideros* and seed pods of *Acacia Koa* would be in variable abundance during the year, although probably reaching their peak supply at different times. The availability of another food source—nectar—and especially one that exists at a different time from either insects in leaf buds or seed pods would be a definite advantage especially if the needed adaptations for nectar feeding and insect eating do not conflict. All of these conditions exist in *coccinea.* (It may be noted, in passing, that these conditions do not hold for the creepers which feed on a source of insects that would be relatively constant during the entire year and which necessitates particular adaptations of the tongue that conflict directly with adaptations required for nectar feeding. Hence the creepers had to abandon or were able to abandon nectar in their evolution for feeding on insects in bark crevices because this food supply was dependable during the entire year.)

Thus, the short bill, with crossed rhamphothecal tips having opposing sharp lateral edges, the asymmetrical jaw articulations and jaw musculature of the Akepa are adaptations associated with strong lateral forces on the jaw tips and slight lateral rotation of the mandible involved in capturing insects hidden in leaf buds and koa pods. The stout skull and strong jaw muscles are adaptations for the large forces needed for these feeding methods. Moreover, it is reasonable to predict that associated adaptations exist in the cervical muscles of this species because of the twisting of the head relative to the body. Features of the tongue such as its tufted tip, tubular anterior half and length are adaptations for nectar feeding.

Adaptation and Extinction

Because of the widespread extinction of many taxa of drepanidids, the question of the degree of adaptation of these birds to their environment is an important question. Adaptation of a species to its environment involves all features of the organism and its entire habitat. Extinction can occur if the adaptive relationship between the organism and its environment breaks down for only one facet of its entire niche, if this factor happens to be essential for the survival of the individual or successful reproduction. In considering the adaptations for feeding in *Loxops*, we are confident that all of the known taxa in this genus are well adapted to their environment and that decrease in their population size or their extinction was not a result of a failure in any aspects of the adaptation of these birds to the food gathering part of their niche. Rather we feel that reduction in the numbers or extinction of the several taxa of *Loxops* was due to a lack of adaptation of these birds to a new factor in their environment, namely the appearance of several diseases (bird pox and malaria), the result, in part, of the introduction by man into the Hawaiian Islands of the necessary insect vectors (Warner, 1968). The birds were unable to adapt to this new factor of their environment and became reduced in numbers or extinct in spite of their continued adaptation to probably all other parts of their niche including food gathering. Although reduction or extinction of any living species of organisms is a tragedy, careful analysis of the factors presumably responsible for the demise of each species is important for a clarification of the important but little understood evolutionary mechanism of extinction.

EVOLUTIONARY HISTORY OF THE GENUS *Loxops*

Any considerations of the origin of and the probable evolutionary trends in the genus *Loxops* depend greatly upon an understanding of the evolutionary history of the entire family. Such a discussion is not possible at this time because of our still inadequate knowledge of the relationships and evolution within the New World nine-primaried oscines and of the possible origin of the Hawaiian honeycreepers from this complex. Even if we had a thorough knowledge of the morphology and evolution of the feeding apparatus in the Drepanididae, the necessary comparative information from the nine-primaried complex is not available. Yet, it seems reasonable to offer some thoughts on the possible evolutionary trends in *Loxops* so that we may present our ideas on the origin and evolution of the Drepanididae (Fig. 14). This presentation will be brief because our ideas are based more on intuition than factual evidence.

Ever since the family Drepanididae was described by Gadow, these birds were believed to be related to the New World nine-primaried oscines. Gadow (1891, 1899) regarded the Coerebidae as the ancestral stock of the Hawaiian honeycreepers. Most workers have accepted this idea or the relatively minor modification that the Hawaiian honeycreepers arose from thin-billed members of the Thraupidae (Amadon, 1950: 231–233, 253; Baldwin, 1953: 386–388; Beecher, 1953: 312–313, 324). Much of the evidence cited as support for this conclusion must be re-evaluated carefully, but to do this would lead too far from the purpose of this discussion. However, one bit of evidence is most important and cannot simply be brushed aside, namely the presence of a tubular, nectar-adapted tongue in most members of the family including those species that apparently never take nectar; Amadon (1950) quite rightly stresses this point. If the Drepanididae evolved from nectar-feeding ancestors (e.g., Coerebidae), then a tubular tongue would be a primitive feature of the family (present in the original stock of birds colonizing the Hawaiian Islands) and hence may still be present in species that no longer drink nectar. If the Drepanididae evolved from some other nine-primaried stock, such as finches, then it is almost mandatory to postulate an early nectar-feeding stage in their evolutionary history with the evolution of a tubular tongue and to argue that all known members of the family descended from this nectar-adapted form possessing a tubular tongue. Hence the tubular tongue would be a primitive feature for the known members of the Drepanididae, but not an ancestral feature inherited from its mainland ancestors.

The second major conclusion on the origin of the Drepanididae stems from

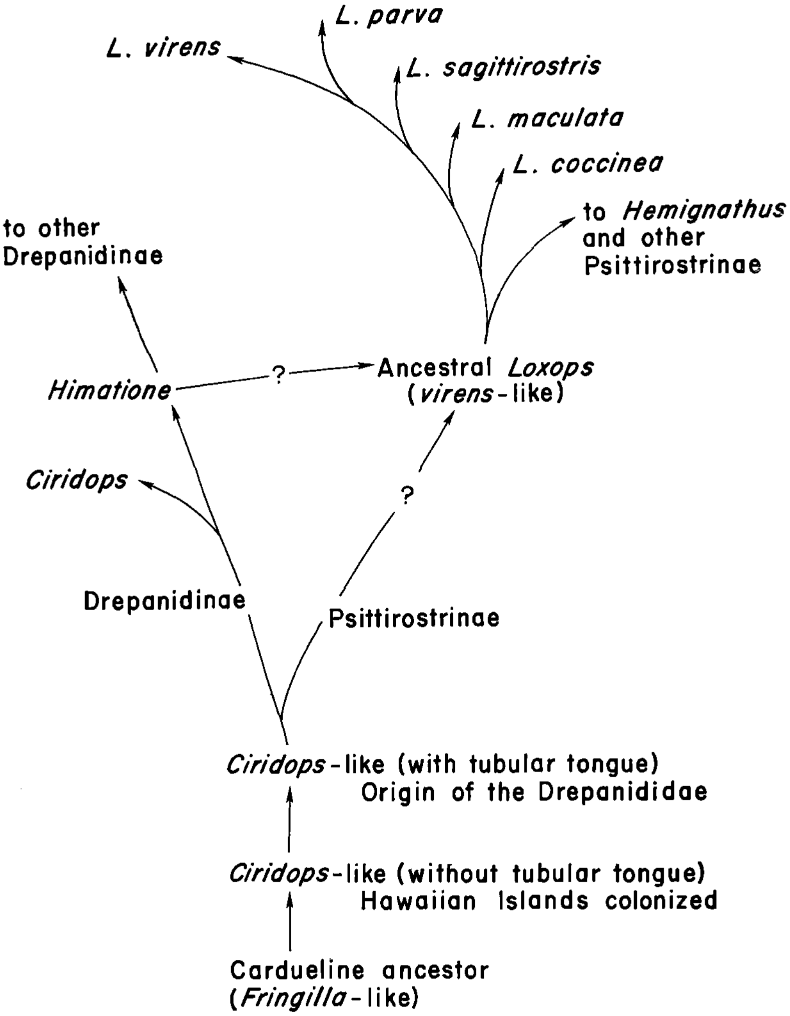

Figure 14. Dendrogram summarizing our ideas of the origin and evolution of the Drepanididae and of the genus *Loxops*. Only the portion involving *Loxops* is supported by the features analyzed in this study. Arrangement of the species within *Loxops* is for convenience only and does not necessarily reflect an evolutionary order.

Sushkin (1929) who suggested that these birds evolved from the cardueline finches. This idea has attracted less attention in the past, but it is becoming more widely accepted. Although we shall base our discussion on the conclusion that the Hawaiian honeycreepers evolved from cardueline finches or from their immediate ancestors, we wish to emphasize the dangers of its wholehearted acceptance. Much of the cited supporting evidence for this idea is really no better than the evidence supporting the Coerebidae-Thraupidae origins of the Drepanididae. Uncritical acceptance of the cardueline origin of the drepanidids has the same serious disadvantages as had the general acceptance of coerebid-thraupid origins of the Drepanididae.

Sushkin's (1929) arguments were based largely upon the close resemblance of the heavy-billed finchlike *Psittirostra* to the cardueline finches. While it is true that *Psittirostra* is very similar to cardueline finches in cranial osteology and jaw musculature, this resemblance could be due to convergence just as many points in the morphology of nectar feeding drepanidids and coerebids could be due to convergence. However, other evidence does support the theory of cardueline origins of the drepanidids which we would like to summarize (see Sibley, 1970, for evidence from the egg-white proteins).

The skull and jaw muscles of *Psittirostra* (Beecher, 1953: 311–313) are very similar to those of cardueline finches including the presence of the lateral flange condition of the palatine process of the premaxillary (Bock, 1960b: 455). Moreover, even the thin-billed *Loxops* shows cardueline-like features. A slight lateral flaring of the palatine process of the premaxilla can be seen in *coccinea,* and an enlarged subtemporal fossa is present in all species of *Loxops.* The postorbital ligament is vestigial in *Loxops* as in carduelines, while it is strongly developed in coerebids (Bock and Morony, unpublished observations). The m. adductor mandibulae externus caudalis is divided into two distinct parts, the anterodorsal one expanding into the enlarged subtemporal fossa. The m. pseudotemporalis superficialis has an anterior slip that is well developed in *Psittirostra* but is also present in *Loxops* in a much less developed condition. Both muscle conditions are characteristic of cardueline finches (including *Fringilla*) but not coerebids and most tanagers. It should be noted that some tanagers such as *Tanagra* and *Chlorophonia* have an anterior slip of the m. pseudotemporalis superficialis as described by Beecher (1951b: 278–279) but obscured in his major work (Beecher, 1953: 310–311) and verified by Bock (unpublished observations), so that the common possession of this feature by carduelines and drepanidids is not such strong evidence as it had once appeared (Bock, 1960b). The position of the two parts of the m. branchiomandibularis in *Loxops* is reminiscent of that found in finches, not coerebids. The configuration of the quadrate-mandibular hinge in *coccinea* is very similar to that in *Loxia,* although this could be the result of convergence.

The plumage of drepanidids is much like that found in many carduelines and also that found in many tanagers. However, we would like to note the especially close similarity between the plumage of the drepanidid genus *Ciridops* and the cardueline genus *Leucosticte.* The latter genus may be a primitive component of the carduelines, being far closer to *Fringilla* than to the more advanced genera.

Unfortunately, little is known about the breeding habits of the Hawaiian honeycreepers. H. B. Tordoff (personal communication) has informed us that his observations of captive *Psittirostra cantans* breeding in his aviaries indicated that these honeycreepers are extremely similar to cardueline finches in courtship and nesting behavior.

Lastly, the chances for any group of songbirds to be successful colonizers of remote oceanic islands would increase if they were birds that wandered in flocks, preferably erratically, over long distances, and bred in the region to which they had wandered (Bock, 1960b: 477; Mayr, 1965). Cardueline finches possess these attributes. The coerebids and thraupids are generally sedentary tropical birds, and as such are less probable colonizers of a remote oceanic island. (This conclusion is not in disagreement with Moynihan's conclusion, 1968, that the "Coerebini" are good colonizers of new areas and habitats and have spread throughout the islands of the Caribbean. He has not considered the problem of crossing large water gaps which is the issue of primary concern here.)

Accepting the cardueline finches as the most likely ancestral stock for the Drepanididae does not automatically solve the question of the probable ancestral genus among the honeycreepers. Indeed, the latter question becomes more difficult. Most likely the typical advanced cardueline finches, such as *Spinus* or *Carpodacus,* did not give rise to the drepanidids. It is far more probable that the honeycreepers arose from either the primitive members of the carduelinae, similar to the present-day *Fringilla* and *Leucosticte* or the birds ancestral to the cardueline group. On the basis of this notion and on the basis of the close similarity in plumage between *Leucosticte* and *Ciridops anna,* we believe that *Ciridops* may well be the closest present-day representative of the primitive stock of the Drepanididae. This conclusion is contrary to Amadon's (1950: 530) conclusion that *Ciridops* is an advanced member of the Drepanidinae. Amadon's placement of *Ciridops* is based upon his conclusion that the Hawaiian honeycreepers evolved from coerebids or thin-billed tanagers. Unfortunately little is known about the morphology and habits of this peculiar and extinct honeycreeper so that it will be difficult, if not impossible, to obtain much support for our conclusion. The morphology of the tongue apparatus has been described recently by Bock (1972).

If the drepanidids arose from primitive cardueline finches and if *Ciridops* is representative of the ancestral stock of honeycreepers, then some speculations can be offered on the early evolutionary history of the Drepanididae. Carduelines of genera, such as *Fringilla,* feed on small seeds and on insects (Eber, 1956) with considerable seasonal variation in their diet. The small seeds on which these birds feed (grasses and beech) may be relatively rare in the habitats available in Hawaiian forests. Hence, after their invasion of the Hawaiian Islands, the original colonizers may have been restricted initially to insects. Exploitation of other food sources would be of definite advantage to these birds especially if no other avian species were using these other food items. If Hawaiian forests at the time of the drepanidid invasion were at all similar to present-day Hawaiian forests, then nectar was in abundant supply at least during certain times of the year. We postulate that the ancestral drepanidids included nectar in their diet and that evolution of a tubular, fringed tongue was one of the earliest, if not the first, important adaptation in the feeding apparatus of this family. Further, it is reasonable to suggest that all known drepanidids descended from birds with a tubular tongue (Fig. 14). Once a tubular tongue evolved in the honeycreepers, further specialization in this direction involves relatively simple evolutionary changes leading to *Himatione* and other members of the subfamily Drepanidinae, which includes the major nectar-feeding members of the Drepanididae.

Evolution from a partly insectivorous, partly nectarivorous *Ciridops*-like bird to present-day *Loxops* involves relatively minor changes. Possibly *Loxops* arose directly from a *Ciridops*-like ancestor or possibly from a *Himatione*-like ancestor. Amadon (1950: 231) regarded *Himatione* as the most primitive member of the Drepanidinae and *Loxops* as the most primitive genus in the Psittirostrinae; we concur except for the placement of *Ciridops*. Further, he emphasizes the closeness of *Himatione* and *Loxops*. On the basis of Amadon's conclusion and our argument (above) we conclude that the ancestor of *Loxops* was a thin-billed bird that fed partly upon nectar and partly upon small insects obtained by gleaning. Evolution in *Loxops* and other genera of the subfamily Psittirostrinae has been in the direction of increasing specialization for insect- and seed-feeding.

Loxops virens is probably closer to the ancestral stock of the genus *Loxops* than the other known members of the genus. It was, as it is now, a generalized nectar-feeder and insect-gleaner and was able to spread to most of the major islands. Certainly some differentiation occurred on some of the islands with double invasions taking place from time to time, although the location of these double invasions is unknown. At present two pairs of such double invasions can still be seen, namely involving *parva* and *v. stejnegeri* on Kauai and *v. virens* and *sagittirostris* on Hawaii. Neither of the divergent forms, *stejnegeri* and *sagittirostris*, spread subsequently to other Hawaiian islands. However, the creepers, *maculata*, and the cross-bills, *coccinea*, which presumably arose from *virens*-like ancestors via double invasions and specialization for different methods of obtaining insects and reducing the importance of nectar in their diet, were both able to spread to most of the major Hawaiian islands.

It is not possible to date the relative times of these double invasions and subsequent spreads with any accuracy. However, on the basis of the degree of morphological changes involved, we would suggest that *coccinea* arose from the *virens*-like ancestor first, followed by *maculata* and last the twin double invasions of *v. virens-sagittirostris* and *v. stejnegeri-parva*. The result of this pattern of double invasions and subsequent spread of the differentiated form is a finer division of the available insect food source by several species of *Loxops* and the presence of three of four species of this genus on the large islands of Kauai, Oaku, Maui and Hawaii (Fig. 1). Moreover, this pattern of double invasions and spread probably extends without a break to the evolution of the genus *Hemignathus* which represents another direction of specialization for insect prey (see Bock, 1970).

Evolutionary changes in the morphology of the feeding apparatus that occurred during the evolution of *v. stejnegeri*, *sagittirostris*, *maculata* and *coccinea* from *virens* can be appreciated by a comparison of the morphological adaptations for feeding habits as given above; these comparisons need not be repated here. We would like to emphasize that these changes in the morphology of the feeding apparatus can be arranged in a series of gradually increasing modifications. *L. v. stejnegeri* is considered to be a geographic representative of *virens*, differing in the size and shape of the bill and presumably osteological and myological features. *L. sagittirostris* is basically a heavy-billed *virens*. *L. maculata* is a straight-billed *virens* which creeps on large branches and trunks and probes for insects more than *virens*. Moreover, the several subspecies of *maculata* differ by becoming increasingly more creeper-like with stronger bills, as shown by the difference between *newtoni* and *mana*. The greatest difference is between *virens* and *mana*. Hence, we believe that the available evidence supports the conclusion that the evolution of the various members of *Loxops* from a *virens*-like ancestor took place by a smooth series of gradual evolutionary changes. The rate of these changes presumably varied greatly in the several phyletic lines and at different times in each of the lineages.

The Drepanididae represent among living vertebrates a remarkable example of adaptive radiation in a short span of geological time. As a part of this radiation, the genus *Loxops* provides a clear example of the beginning of such an adaptive radiation and illustrates the basic evolutionary mechanisms involved in adaptive morphological changes in the feeding apparatus. Although considerable insight into the origin and evolution of the Drepanididae has been gained by this analysis of *Loxops*, these ideas must be verified and furthered by study of the whole family. Unfortunately a completely satisfying study is no longer possible because of the extinction of many important taxa in the Drepanididae and because of widespread destruction of the original Hawaiian environment at the hands of European and Asian man. Enough original environment is still exant on the Hawaiian Islands to permit valid conclusions on the adaptive interrelationships between the drepanidids and their habitat (see Lack, 1965), and populations of most species of honeycreepers still survive, but remain in danger of extinction through disease (Warner, 1968). Hopefully the most significant result of this study of the adaptation in the feeding apparatus of *Loxops* is to provide a stimulus for additional studies on the comparative biology and evolution of the Hawaiian honeycreepers and the eventual understanding of the classical example of adaptive radiation they provide.

SUMMARY

1. The genus *Loxops* was chosen for this initial study of the adaptation and evolution of the feeding apparatus in the Drepanididae because it is a relatively primitive genus and because members of the three subgenera are still extant on the same island, and up to four species, including the now extinct *sagittirostris*, live on the island of Hawaii which was most suitable for field studies.

2. The food and feeding habits of each species could be deduced reasonably well on the basis of information in the literature and field work by Richards. *L. v. virens* feeds on small arthropods obtained by gleaning and upon nectar of *Metrosideros* and lobelias. *L. sagittirostris* feeds on crickets and other large insects obtained by forceful probing into crevices such as the bases of Ieie leaves and less upon nectar. *L. m. mana* feeds upon insects obtained by creeping along trunks and large branches and probing forcefully into crevices, but does not take nectar. *L. m. newtoni* feeds upon insects obtained by creeping and weak probing or gleaning; some nectar is taken. *L. c. coccinea* feeds on insects concealed in *Metrosideros* leaf buds and in koa seed pods which are captured by first opening these plant structures by twisting movements of the head and bill; nectar is taken occasionally.

3. The rhamphotheca of the bill of *virens* is thin, of medium length and slightly decurved, of *sagittirostris*, heavy, long and straight, of *mana*, heavy, of medium length and straight, of *newtoni*, thin, of medium length and very slightly decurved, and of *coccinea*, stout, short and finch-like with the tips slightly crossed. In a right-billed bird, the tip of the mandible crosses to the right and the tip of the maxilla crosses to the left; left-billed birds are the opposite. The lateral edges of both the mandible and maxillary tip are sharp on the crossed side.

4. The skull of *virens* is described in detail and that of each taxon is compared with it. Some noteworthy features are the retroarticular process, a well developed palatal hasp, a reduced lateral flange condition of the palatine process of the premaxillary, and a well developed subtemporal fossa. The asymmetrical features in the skull of *coccinea* are described; the most important of these are the quadrate-mandibular articulation and surrounding bones.

5. The jaw muscles are described and compared in detail in the several taxa of *Loxops* under study. Of interest are the structure of the m. pseudotemporalis superficialis and the m. adductor mandibulae externus caudalis which are similar to these muscles in cardueline finches. Relative strength of the muscles were estimated using a crude index. The functional properties of the jaw muscles in *Loxops* and their correlations with feeding habits are discussed including the correlations between the osteological features of the skull, myological features and feeding methods. The form and functional properties of the asymmetrical jaw muscles of *coccinea* are described and compared to those of *Loxia.*

6. The corneous tongue is long, tubular and with a frilled tip in *virens, sagittirostris* and *coccinea,* and shorter, flat and with a stiff forked tip in *mana* and *newtoni.* The hyoid horns are longer in those species with a tubular tongue while the paraglossalia are longer in those species with a flat tongue. The tongue muscles are described and compared in the several taxa, including *sagittirostris,* of *Loxops* with relatively little interspecific variation found. The functional properties of the tongue apparatus are discussed and their adaptive significance postulated.

7. The morphological adaptations in the feeding apparatus for the food and feeding methods in each species are discussed, the entire feeding apparatus being considered as a single unit. Evolutionary change leading to the particular adaptations in the feeding apparatus of each species is correlated mainly with modifications in their methods of obtaining food with little difference existing in the actual insect prey and other food items in *virens, newtoni, mana* and *coccinea.* Only in *sagittirostris,* does evolutionary change in its feeding apparatus appear to be largely associated with a change in food items, to larger sized insects, and only to a lesser extent with change in feeding habits. Each species is believed to be well adapted to the food gathering part of its niche; reduction in population size or extinction of several taxa has resulted from a failure to adapt to other changes in the habitat of these species. The origin and evolution of *Loxops* are discussed. It is suggested that the evolution of the several speices of *Loxops* with their different feeding methods has resulted from a pattern of double invasion, subsequent divergence and spread of the divergent form throughout the Hawaiian Islands.

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APPENDIX I

GLOSSARY OF ABBREVIATIONS

Skull

Braincase	
a b	auditory bulla
a o s	antoribal space
b c	braincase
b t p	basitemporal plate
e a m	external auditory meatus
e f	ectethmoid foramen
e o p	exoccipital plate
e p	ectethmoid plate
i o c	intraorbital cristae
i o s	interorbital septum
i o w	interorbital width
j b	jugal bar
l	lacrimal
l bt p	lateral basipterygoid process
n-f h	nasal-frontal hinge
o	orbit
o f	optic foramen
o p	occipital plate
p o p	postorbital process
p o r	postorbital rims
p p s	protractor pterygoid scar
p t s	pseudotemporal swelling
s f	subtemporal fossa
s o r	supraorbital rim
s p	suprameatic process
s r	sphenoidal rostrum
t f	temporal fossa
z p	zygomatic process
z t	zygomatic tubercle
Rostrum	
b e n	bony external naris
b t	bony tomium
d b	dorsal bar
l b	lateral bar
l f c	lateral flange condition of the palatine process of the premaxilla
mx	maxilla
n s	nasal septum
p p m	palatine process of the premaxilla
r	rostrum
u j	upper jaw
Quadrate	
b q	body of the quadrate
j b	jugal bar
j p q	jugal process of the quadrate
l c ot p	lateral condyle of the otic process
l c q	lateral condyle of the quadrate

APPENDIX I (*Continued*)

m c ot p	medial condyle of the otic process
m c q	medial condyle of the quadrate
m p q	mandibular process of the quadrate
ob p q	orbital process of the quadrate
ot p q	otic process of the quadrate
p c q	posterior condyle of the quadrate
pt c q	pterygoid condyle of the quadrate
q	quadrate
r ob p	rugosity of the orbital process
t ob p	tubercle of the orbital process
Pterygoid	
p pt t	protractor pterygoid tubercle
pt	pterygoid
pt f	pterygoid foot
pt h	pterygoid head
r p pt	retractor process of the pterygoid
Palatine	
i p p	interpalatine process
m p p	mediopalatine process
p	palatine
p b	palatine blade
p h	palatine hasp
p n c	posterior nasal canal
p p b	prepalatine bar
p t	palatine trough
t p p	transpalatine process
w p t	wall of the palatine trough
Vomer and maxillopalatine	
m p	maxillopalatine
pl m p	plate of the maxillopalatine
p m p	pedicle of the maxillopalatine
v	vomer
Mandible	
a c p	anterior coronoid process
a g	articular groove
e m f	external mandibular fossa
e m p	external mandibular process
i m f	internal mandibular fossa
i m p	internal mandibular process
im f	internomandibular flange
l j	lower jaw
ma	mandible
m b	mandibular boss
m f	mandibular foramen
m m l	medial mandibular ledge
m s	mandibular symphysis
p c p	posterior cornoid process
r a n	retroarticular notch
r a p	retroarticular process
s b	sesamoid bone

APPENDIX I (*Continued*)

t p m a	tubercle of the posterior mandibular adductor
t p t	tubercle of the pseudotemporalis

Tongue Skeleton

b h	basihyale
c b	ceratobranchiale
c c	cricoid cartilage
e b	epibranchiale
i hg o	insertion hypoglossus obliquus
pg	paraglossale
pg-bh h	paraglossal-basihyal hinge
t r	tracheal rings
t m c g	tubercle of the ceratoglossus
u h	urohyale

Jaw Muscles

m a m e c a	m. adductor mandibulae externus caudalis "a"
m a m e c b	m. adductor mandibulae externus caudalis "b"
m a m e r l	m. adductor mandibulae externus rostralis lateralis
m a m e r m	m. adductor mandibulae externus rostralis medialis
m a m e r t	m. adductor mandibulae externus rostralis temporalis
m a m e v	m. adduuctor mandibulae externus ventralis
m a m p	m. adductor mandibulae posterior
m d m	m. depressor mandibulae
m p p q	m. protractor pterygoidei et quadrati
(m p p s s)	(m. protractor pterygoidei sensu stricto)
(m p q)	(m. protractor quadrati)
m ps p	m. pseudotemporalis profundus
m ps s	m. pseudotemporalis superficialis
m pt	m. pterygoideus
m pt d l	m. pterygoideus dorsalis lateralis
m pt d m a	m. pterygoideus dorsalis medialis anterior
m pt d m p	m. pterygoideus dorsalis medialis posterior
m pt r	m. pterygoideus retractor
m pt v l	m. pterygoideus ventralis lateralis
m pt v m	m. pterygoideus ventralis medialis
m pt v m fan	m. pterygoideus ventralis medialis fan
m pt v m scap	m. pterygoideus ventralis medialis scapularis

Tongue Muscles

m b m	m. branchiomandibularis
m c g	m. ceratoglossus
m c h	m. ceratohyoideus
m g g	m. genioglossus
m hg a	m. hypoglossus anterior
m hg o	m. hypoglossus obliquus
m m h	m. mylohyoideus
m s h	m. serpihyoideus
m st h	m. stylohyoideus
m th h	m. thyreohyoideus
m tr h	m. tracheohyoideus
m tr l	m. tracheolateralis

PLATES

Plate 1. Lateral view of the bill of *Loxops.* A) *L. v. virens* (A.M.N.H. 453127). B) *L. v. stejnegeri* (A.M.N.H. 453194). C) *L. m. mana* (A.M.N.H. 453289). D) *L. m. newtoni* (A.M.N.H. 453356). E) *L. m. flammea* (A.M.N.H. 453296). F) *L. c. coccinea* (A.M.N.H. 453403). G) *L. c. caeruleirostris* (A.M.N.H. 193452). H) *L. parva* (A.M.N.H. 453216). I) *L sagittirostris* (A.M.N.H. 453236).

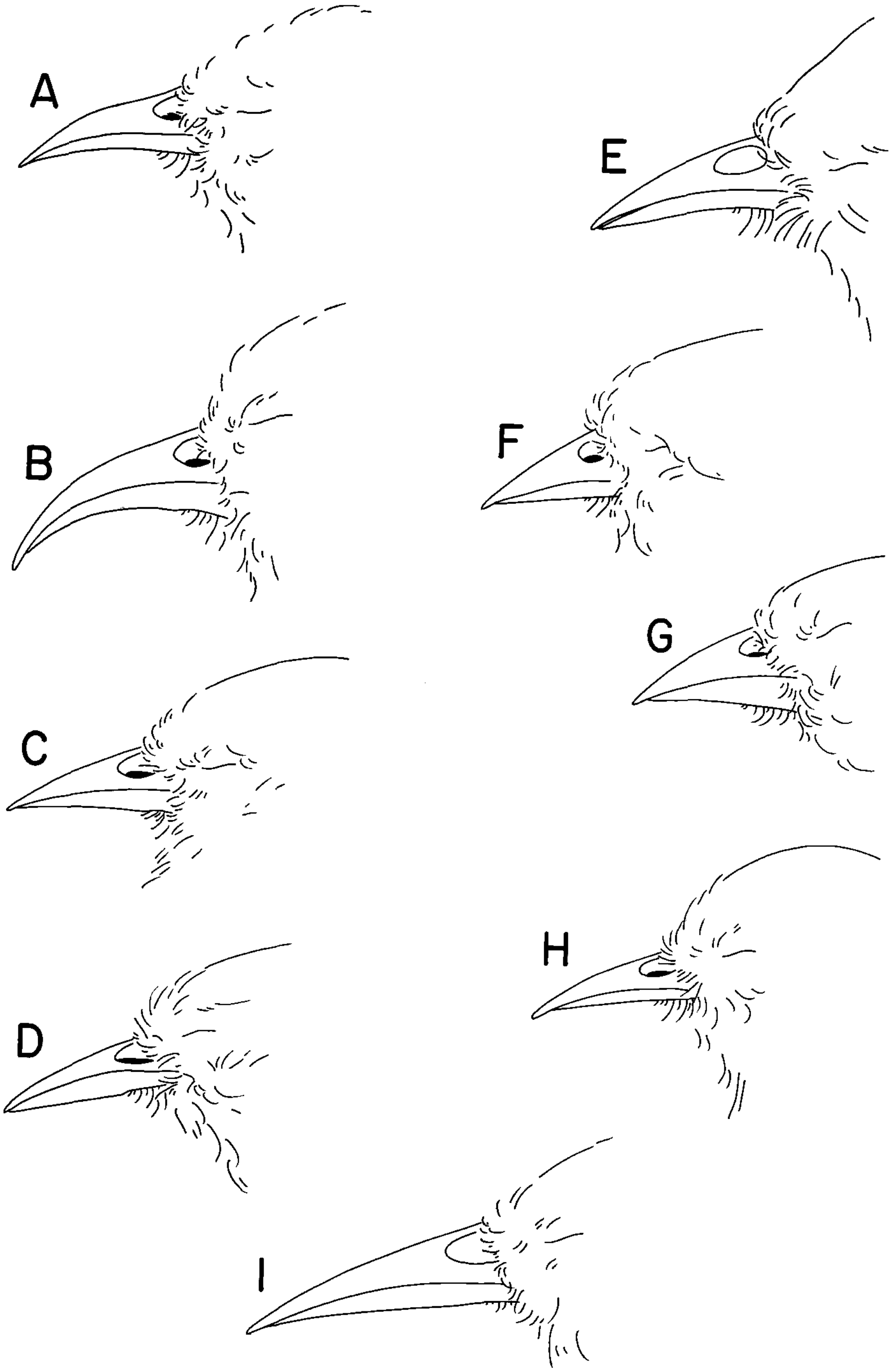

PLATE 1

Plate 2. Dorsal and ventral view of the bill of *Loxops*. A) *L. v. virens*, dorsal (A.M.N.H. 453127). B) *L. v. stejnegeri*, dorsal (A.M.N.H. 453194). C) *L. m. mana*, dorsal (A.M.N.H. 453289). D) *L. m. newtoni*, dorsal (A.M.N.H. 453356). E) *L. parva*, dorsal (A.M.N.H. 453216). F) *L. c. coccinea*, dorsal (A.M.N.H. 453403). G) *L. c. coccinea*, ventral (A.M.N.H. 453403). H) *L. c. coccinea*, ventral (A.M.N.H. 168614). I) *L. c. caeruleirostris*, dorsal (A.M.N.H. 193452). J) *L. c. caeruleirostris*, ventral (A.M.N.H. 193452). K) *L. sagittirostris*, dorsal (A.M.N.H. 453231).

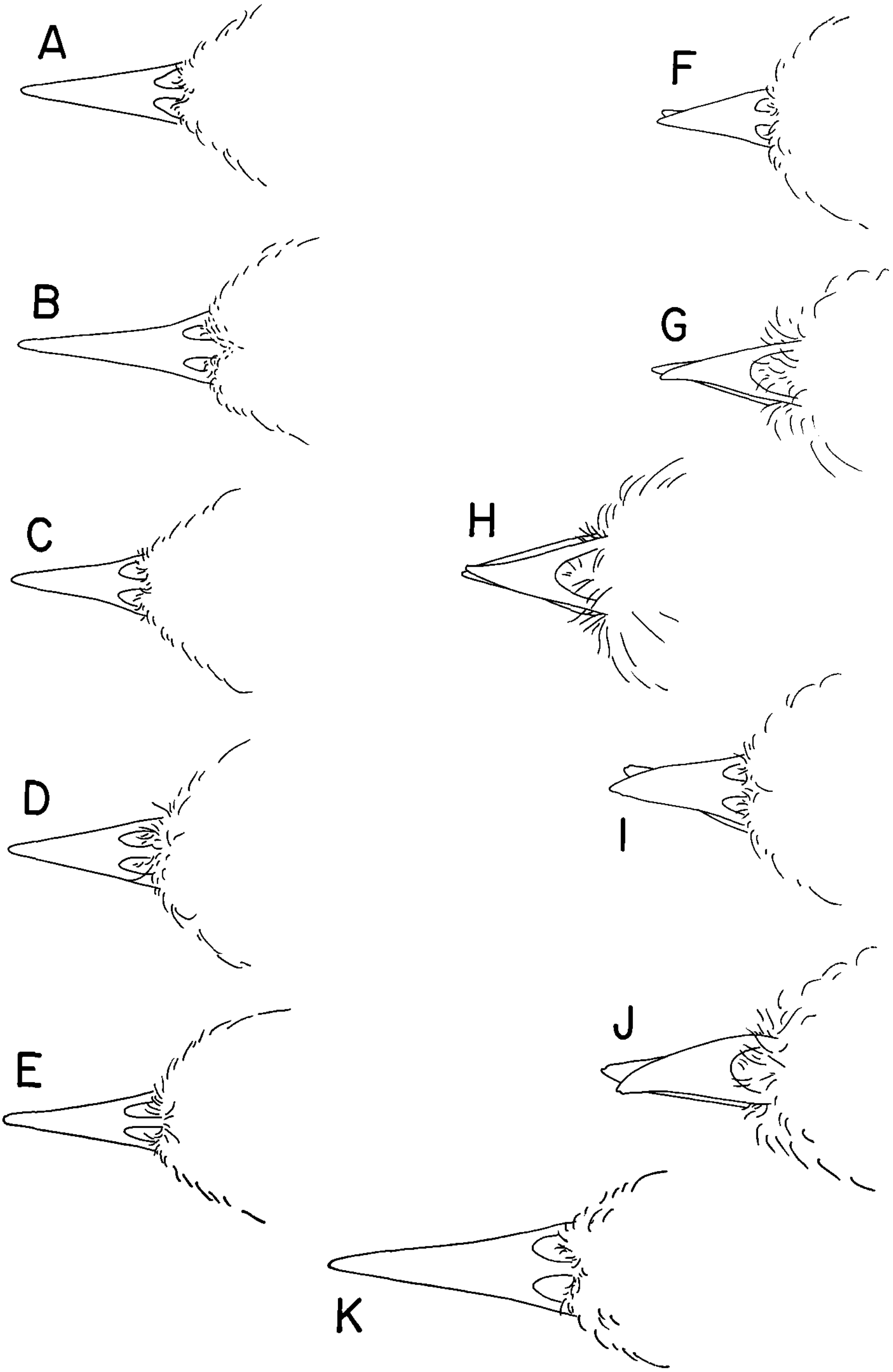

PLATE 2

Plate 3. Skull of *Loxops v. virens.* A) Oblique view. B) Lateral view. C) Ventral view.

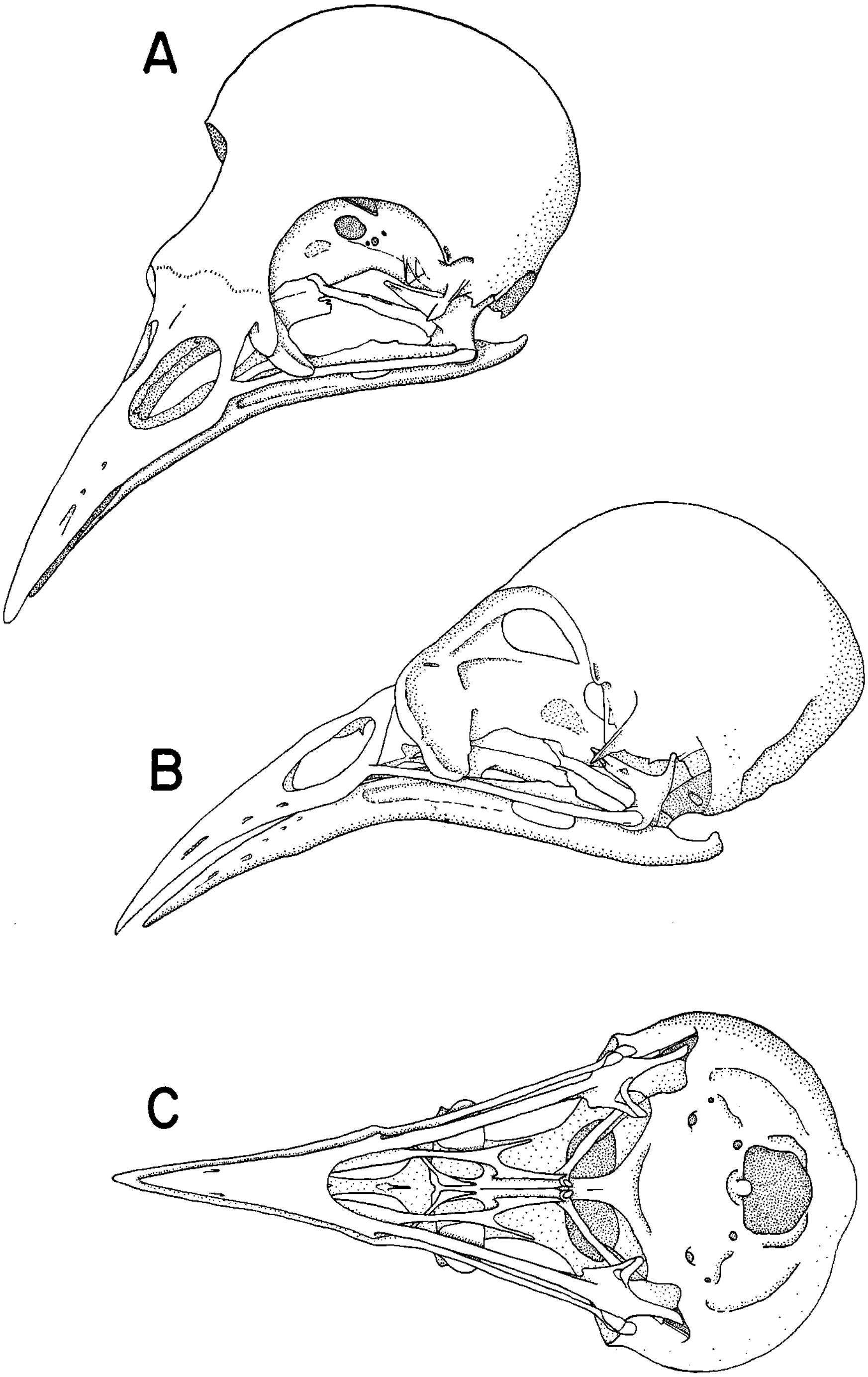

PLATE 3

Plate 4. Skull of *Loxops m. mana.* A) Oblique view. B) Lateral view. C) Ventral view.

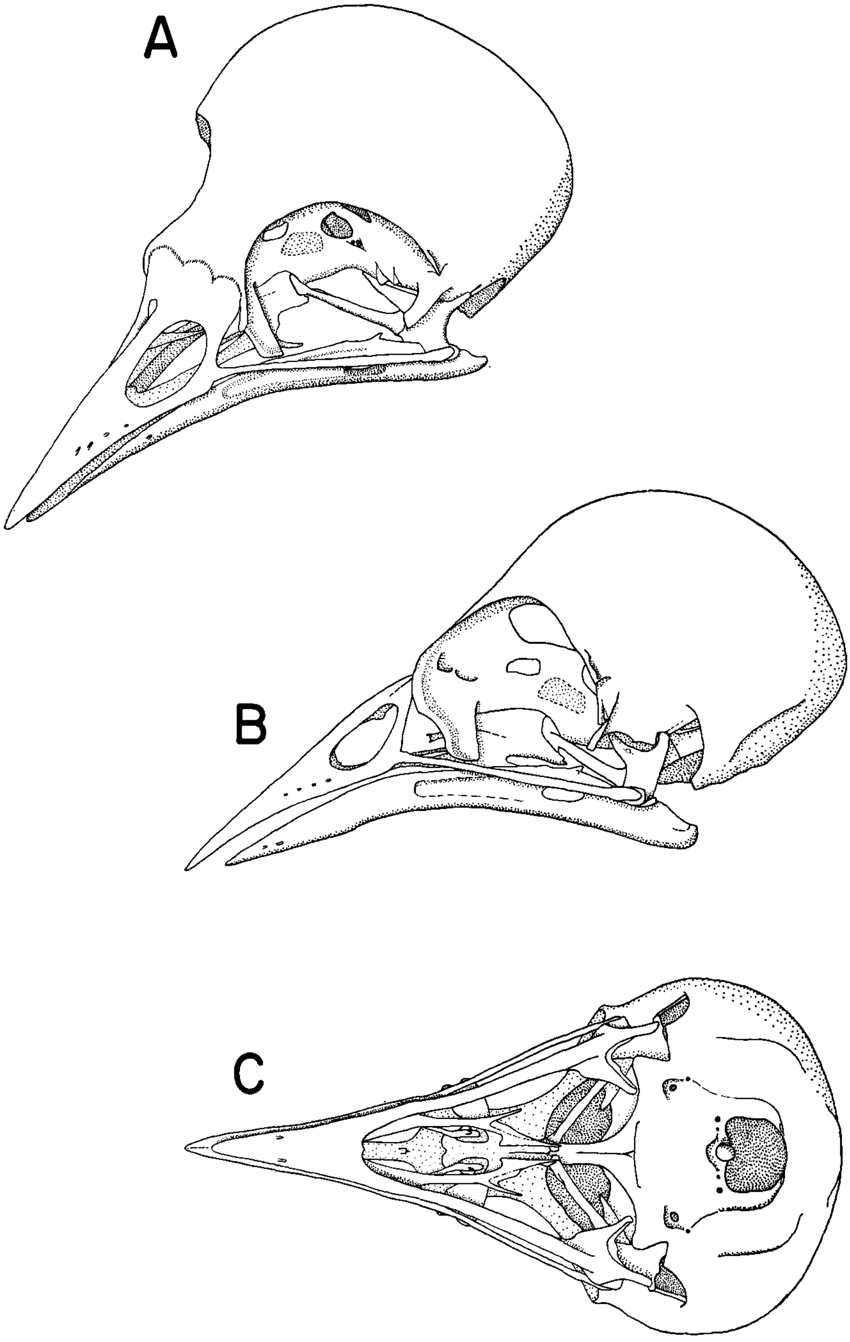

PLATE 4

Plate 5. Skull of *Loxops m. newtoni.* A) Oblique view. B) Lateral view. C) Ventral view.

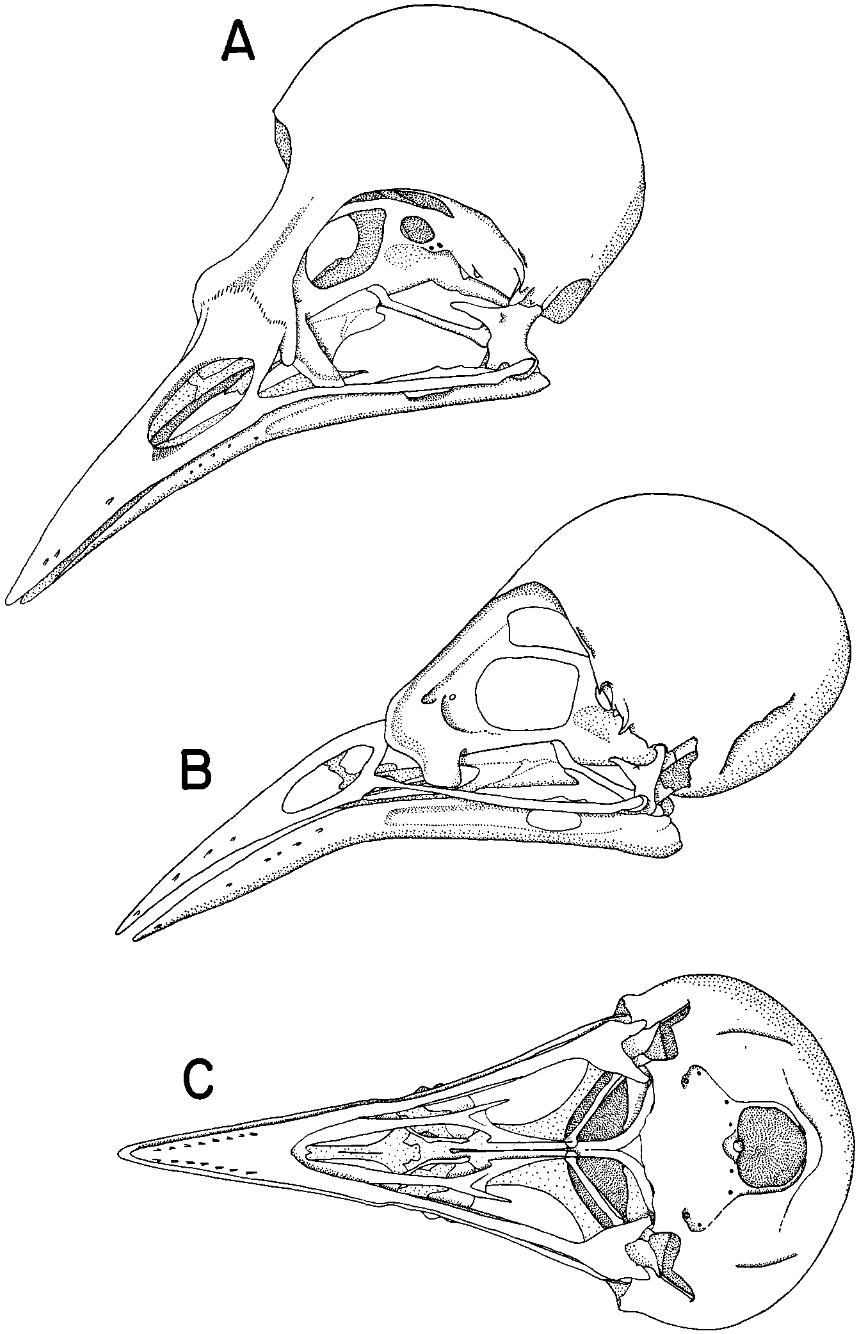

PLATE 5

Plate 6. Skull of *Loxops c. coccinea* (right-billed individual). A) Oblique view. B) Lateral view. C) Ventral view.

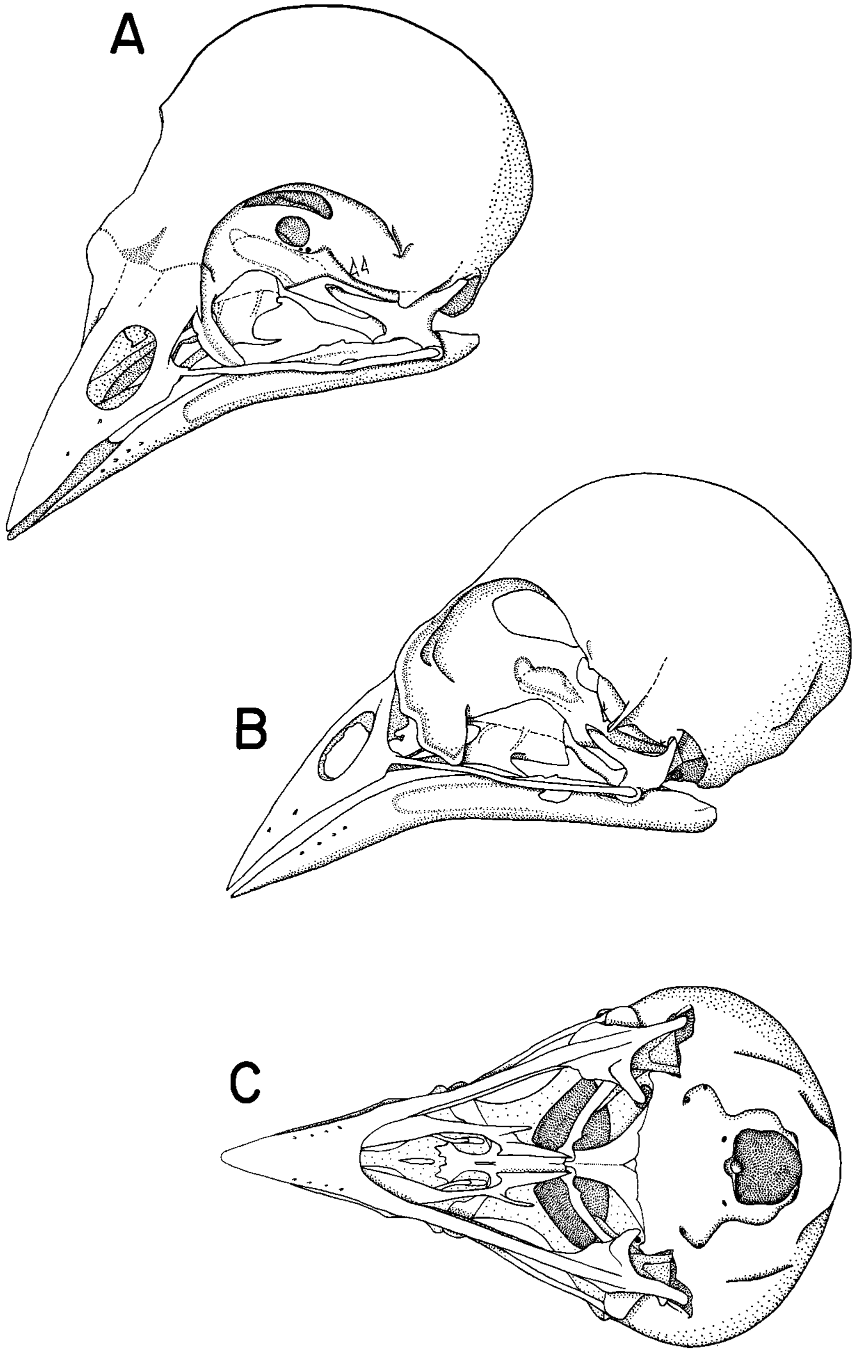

PLATE 6

Plate 7. Details of the skull of *L. v. virens.* A) Ventral view of skull. B) Lateral view of ectethmoid plate. C) Lateral view of palatine. D) Ventral view of palatine. E) Cross-section of palatine hasp and trough.

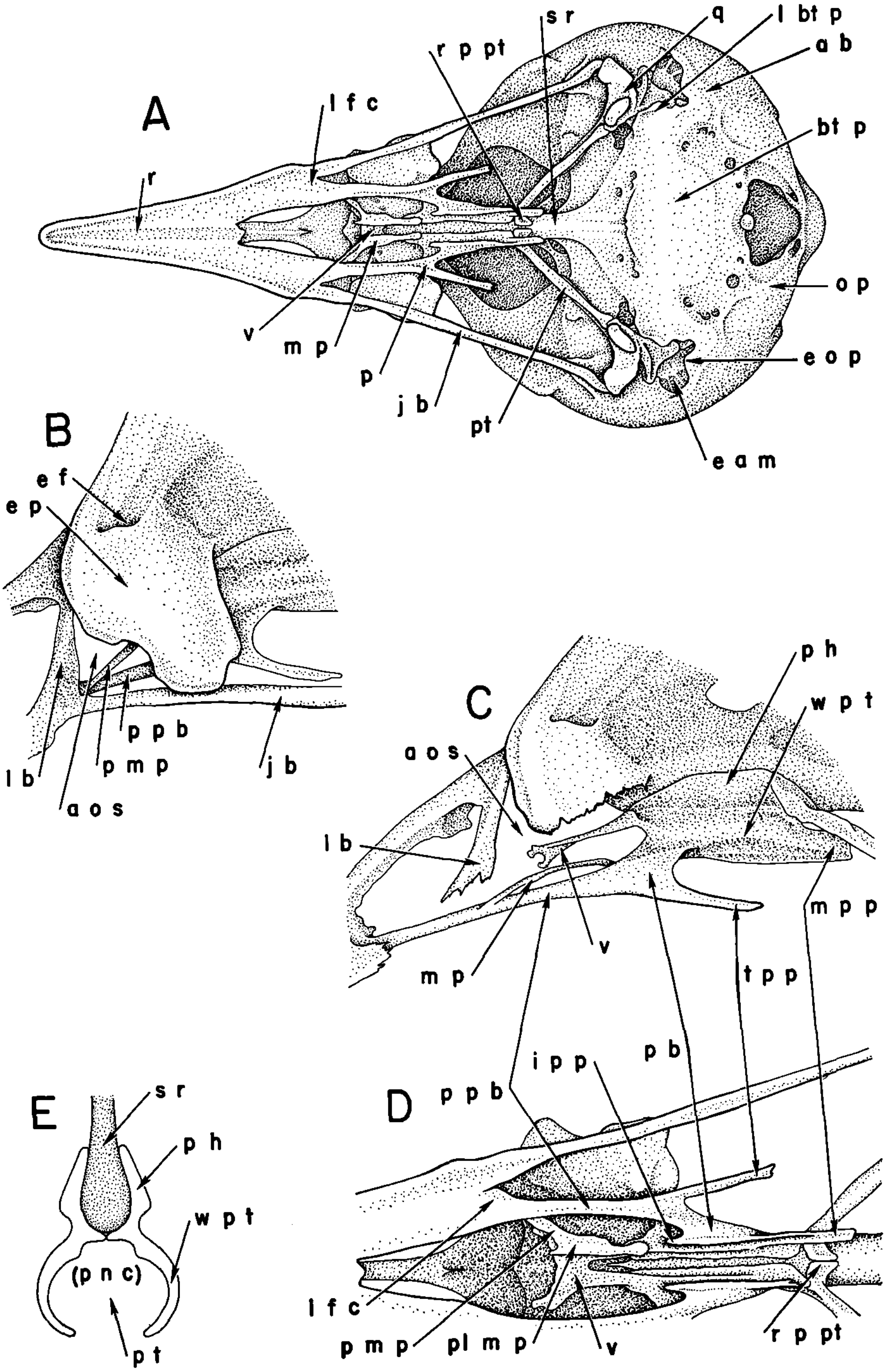
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PLATE 7

Plate 8. Details of the quadrate and mandible of *Loxops.* A) Ventral view of quadrate and surrounding bones of *L. v. virens.* B) Lateral view of quadrate and surrounding bones of *L. v. virens.* C) Dorsal view of posterior end of the mandible of *L. v. virens.* D) Posterior view of quadrate of *L. v. virens.* E) Posterior view of quadrate of *L. m. mana.* F) Posterior view of quadrate of *L. m. newtoni.*

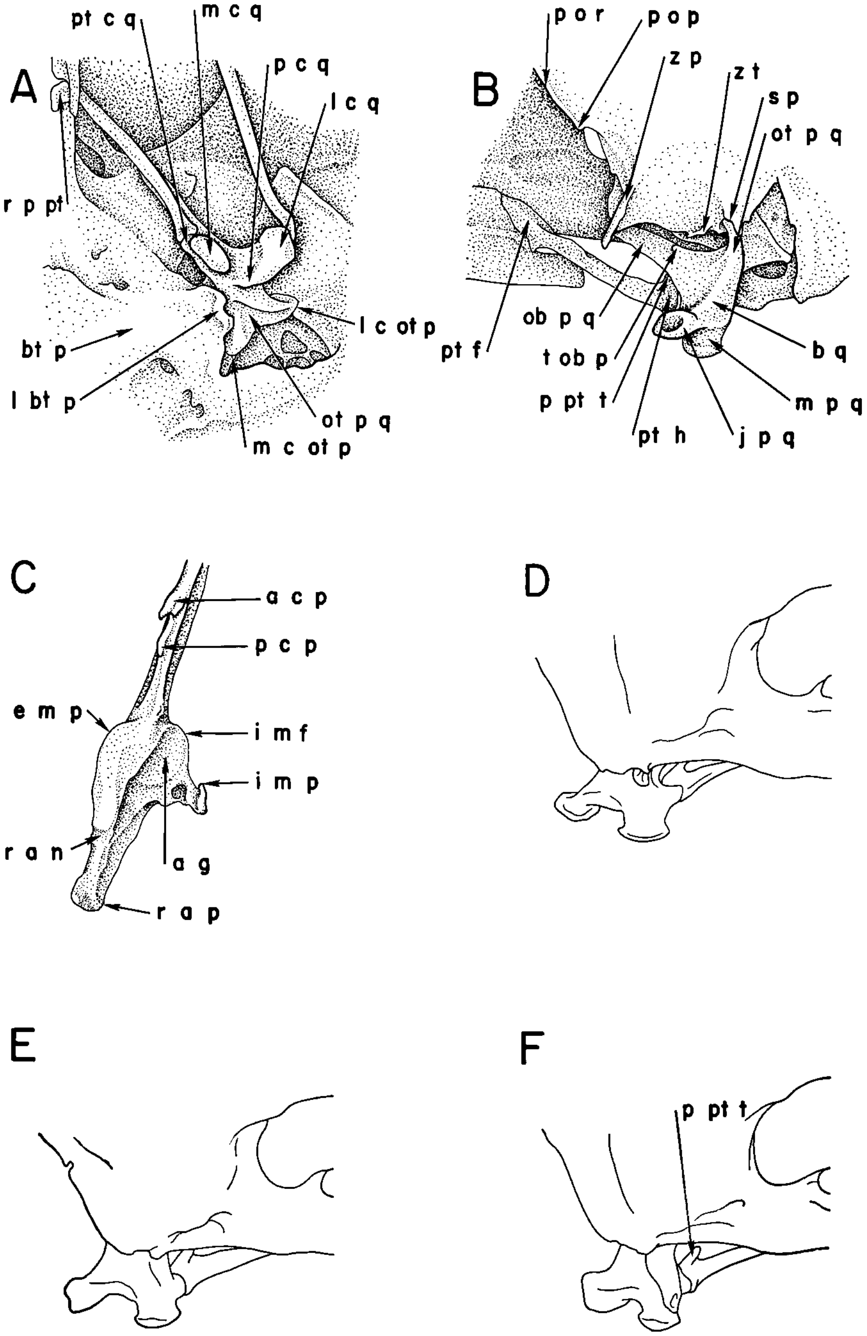
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PLATE 8

Plate 9. Details of quadrate and mandible of *L. c. coccinea* (right-billed individual) to show the asymmetries in these skeletal features. A) Ventral view of posterior end of skull. B) Posterior view of quadrates. C & D) Dorsal view of posterior end of mandibular rami spaced to correspond to the position of the quadrates in B.

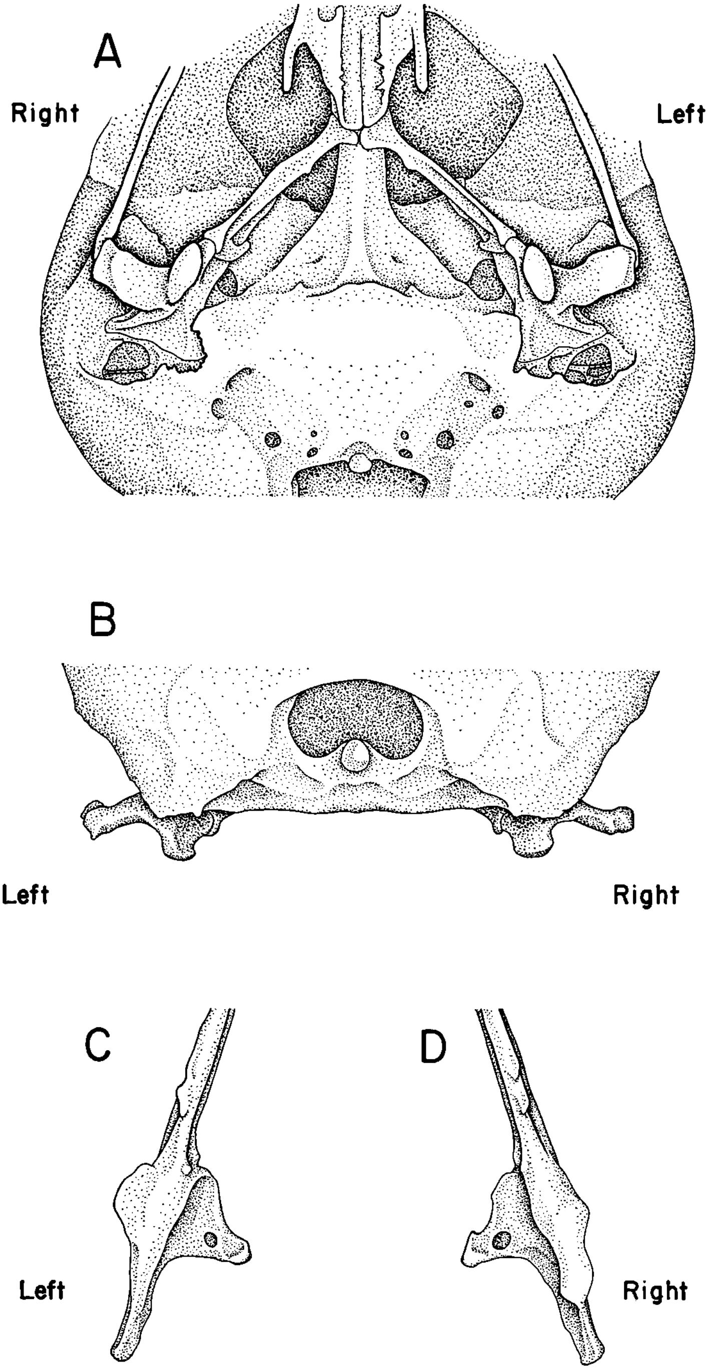

PLATE 9

Plate 10. Jaw muscles of *L. v. virens.* A) Oblique view. B) Lateral view of superficial muscles. C) Lateral view of deeper muscles.

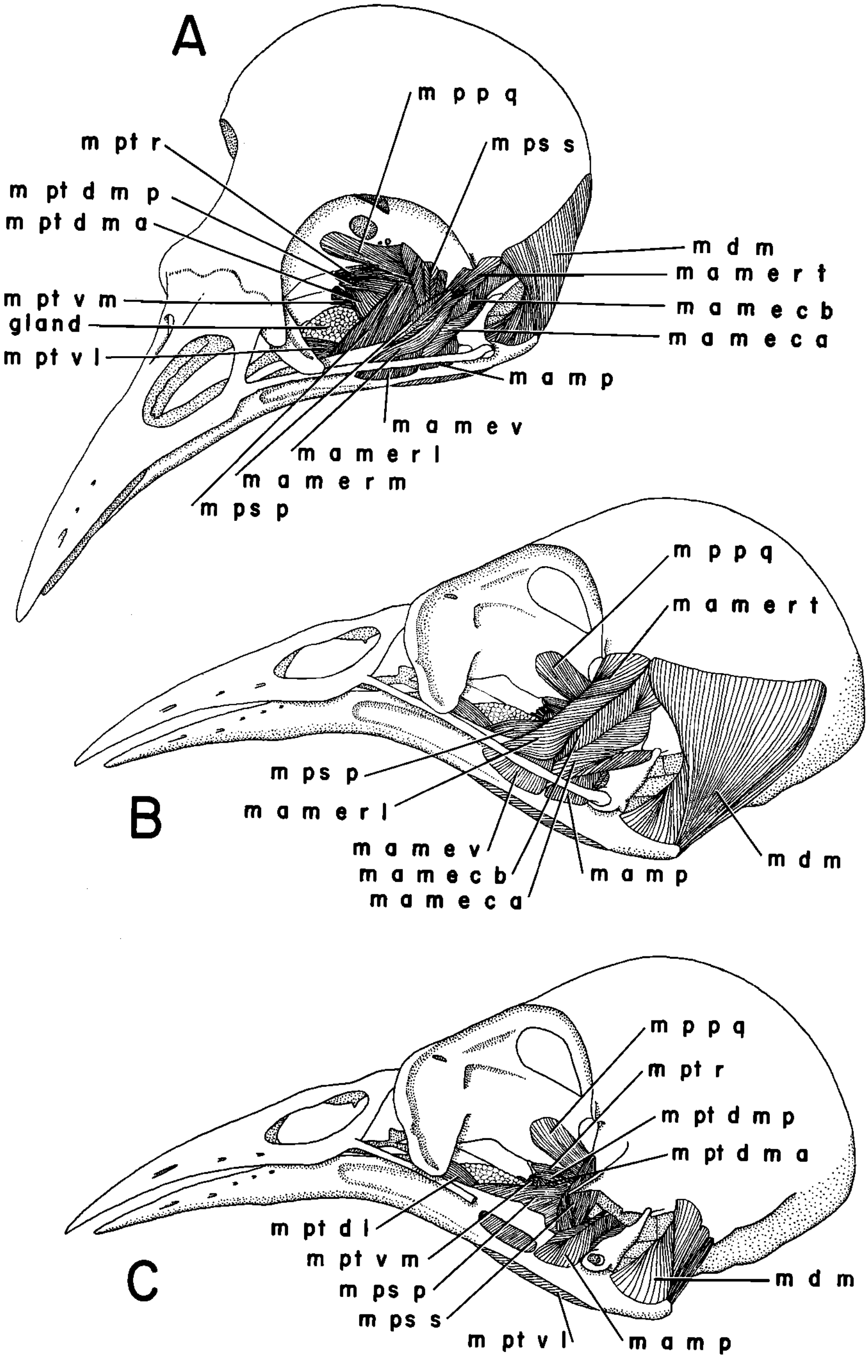
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PLATE 10

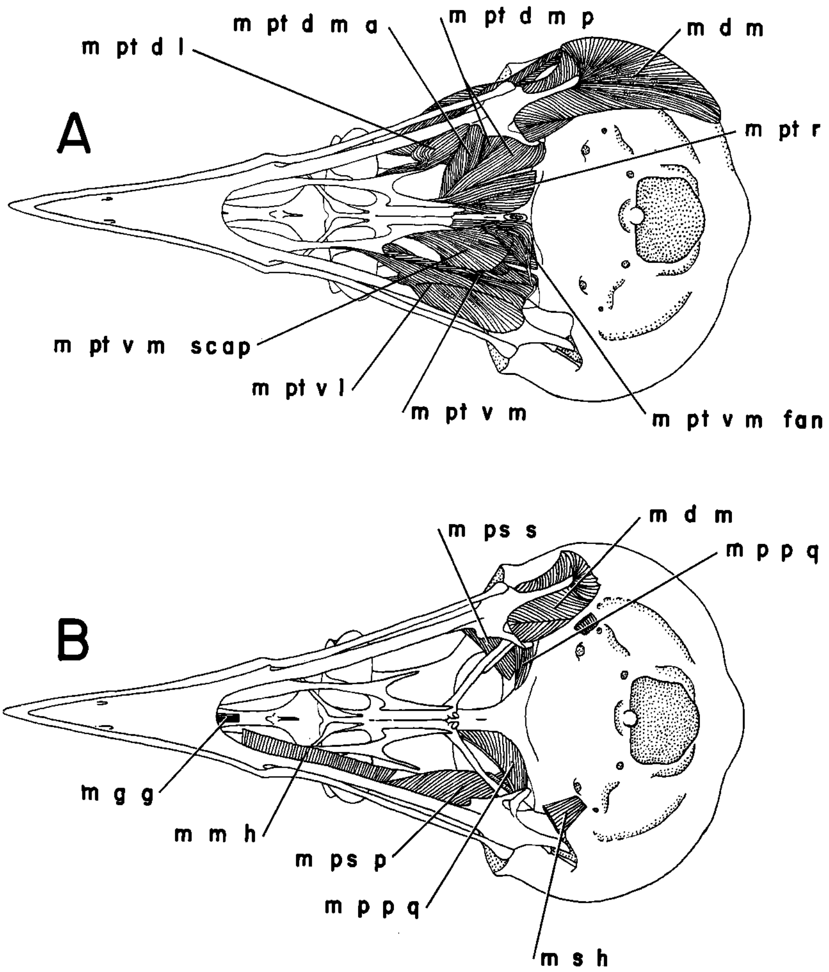

Plate 11. Jaw muscles of *L. v. virens.* A) Ventral view of m. pterygoideus; ventral layer removed on left side of head. B) Ventral view of some tongue muscles and more dorsal jaw muscles.

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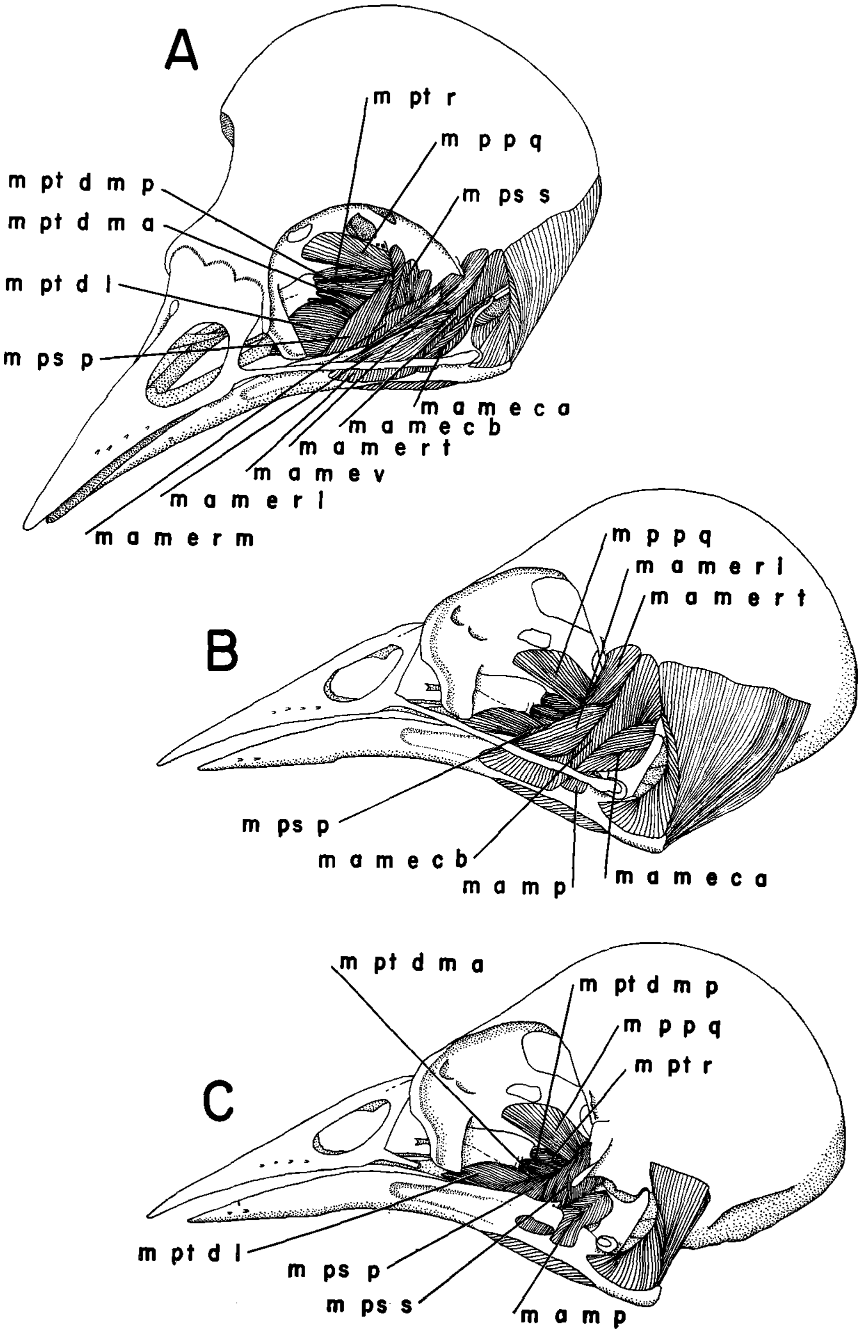
Plate 12. Jaw muscles of *L. m. mana.* A) Oblique view. B) Lateral view of superficial muscles. C) Lateral view of deeper muscles.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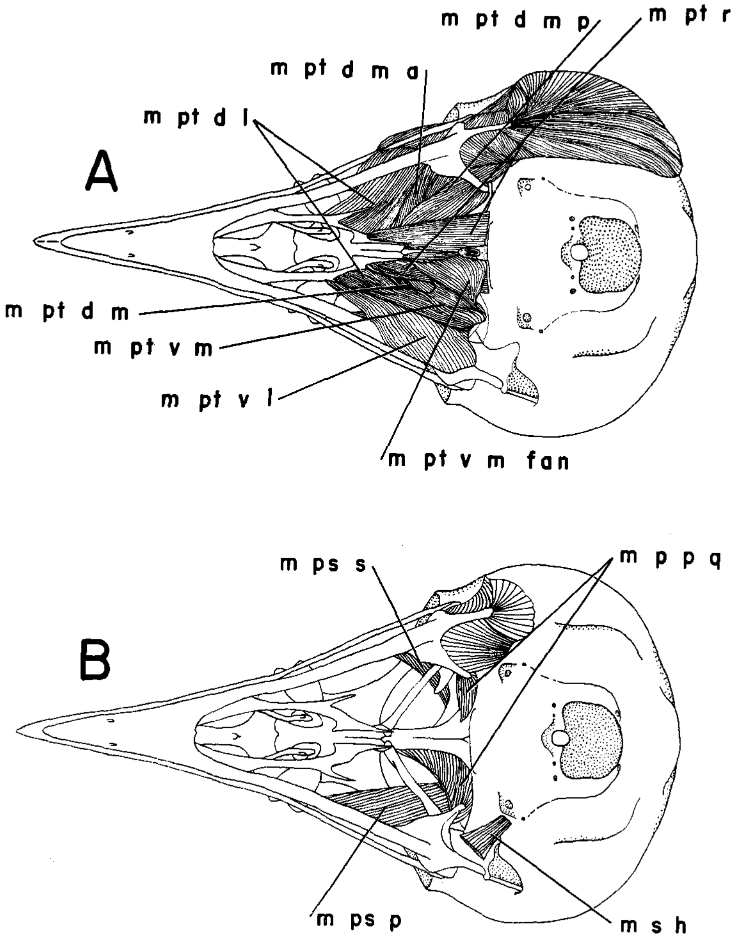

Plate 13. Jaw muscles of *L. m. mana.* A) Ventral view of m. pterygoideus; ventral layer removed on left side of head. B) Ventral view of some tongue muscles and more dorsal jaw muscles.

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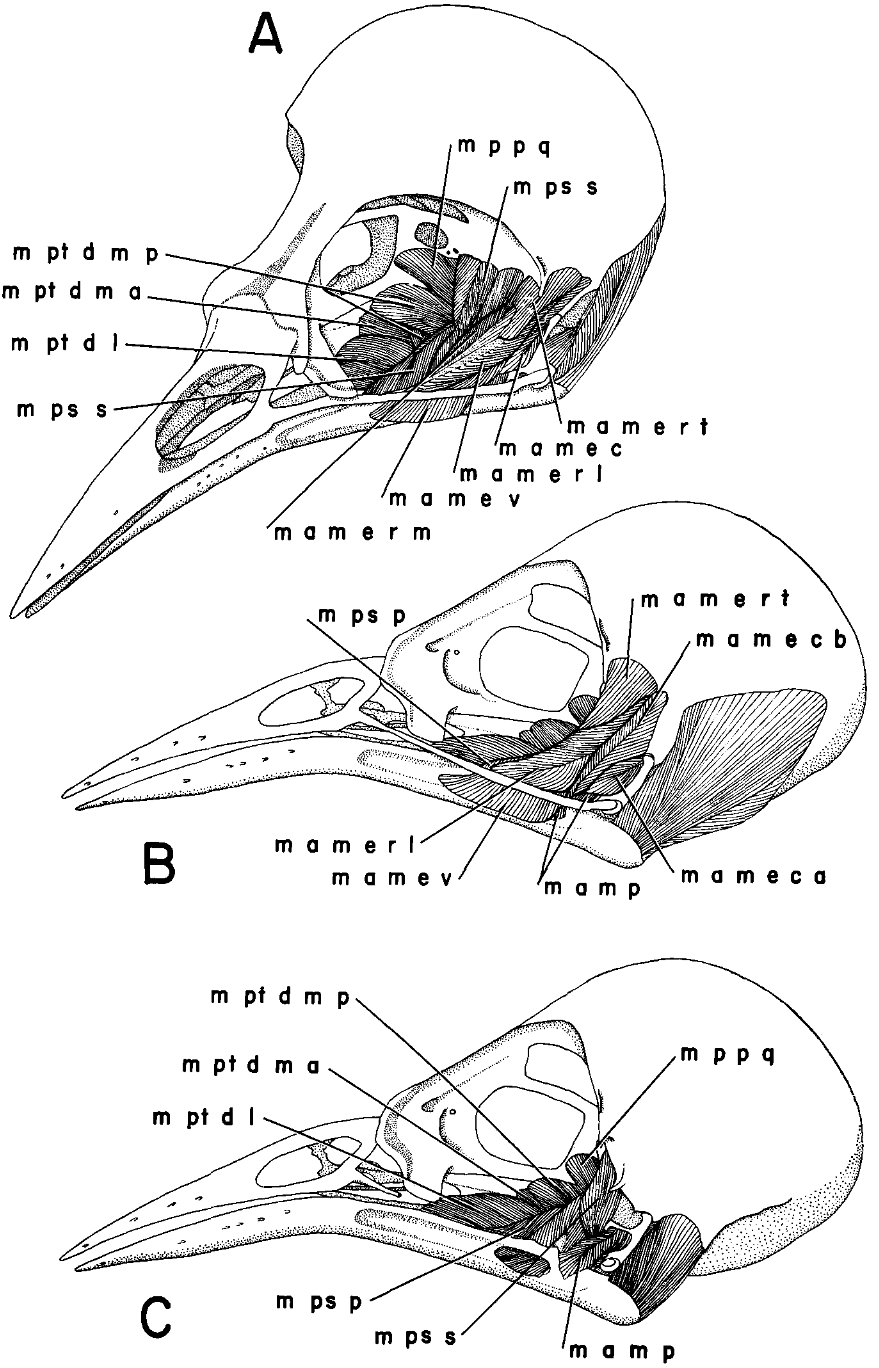
Plate 14. Jaw muscles of *L. m. newtoni.* A) Oblique view. B) Lateral view of superficial muscles. C) Lateral view of deeper muscles.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B
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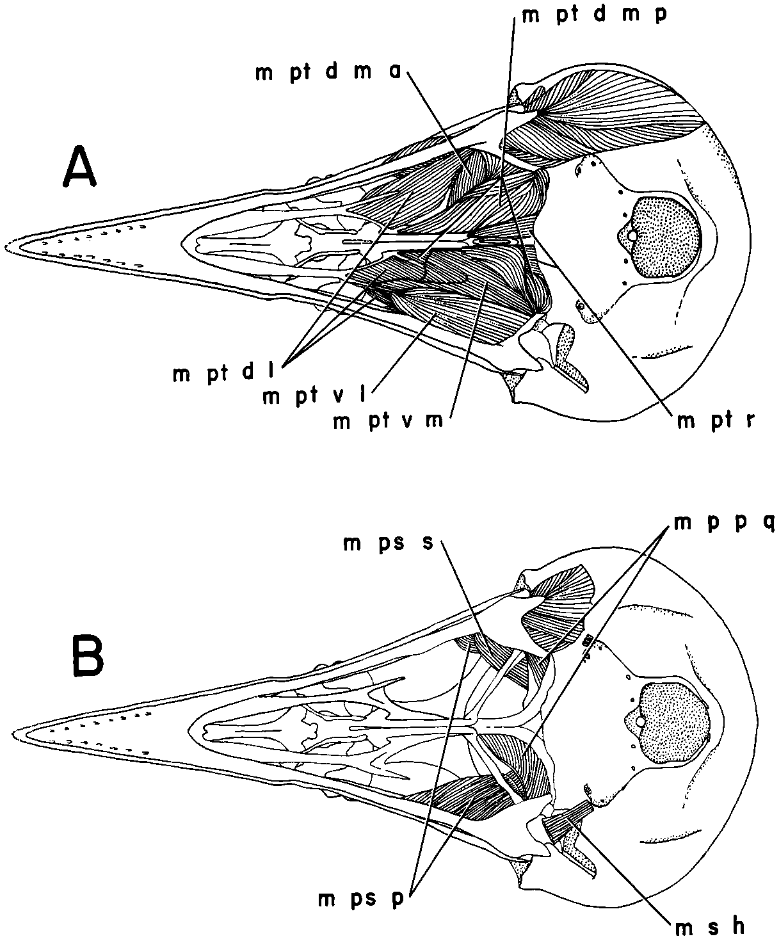

Plate 15. Jaw muscles of *L. m. newtoni.* A) Ventral view of m. pterygoideus; ventral layer removed on left side of head. B) Ventral view of some tongue muscles and more dorsal jaw muscles.

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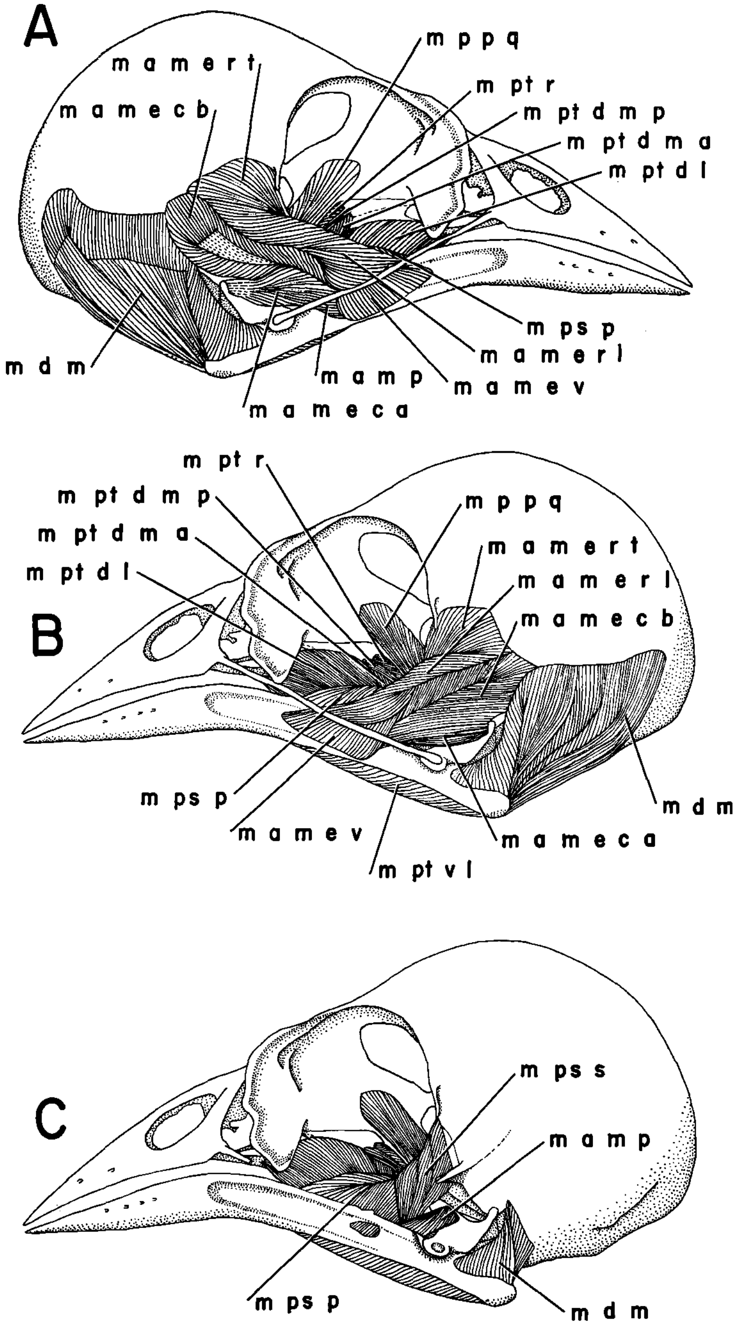
Plate 16. Jaw muscles of *L. c. coccinea* (right-billed individual). A) Lateral view of superficial muscles of the right side. B) Lateral view of superficial muscles of the left side. C) Lateral view of deeper muscles of the left side.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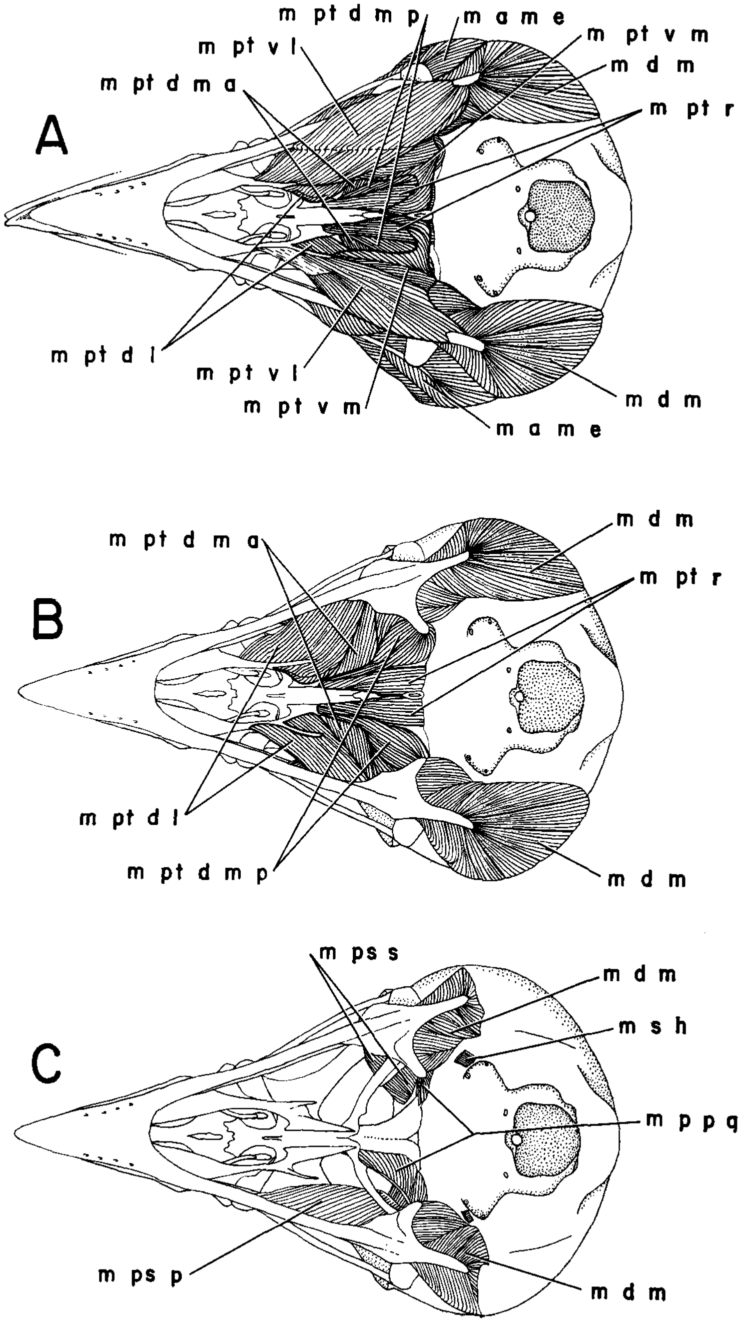
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B
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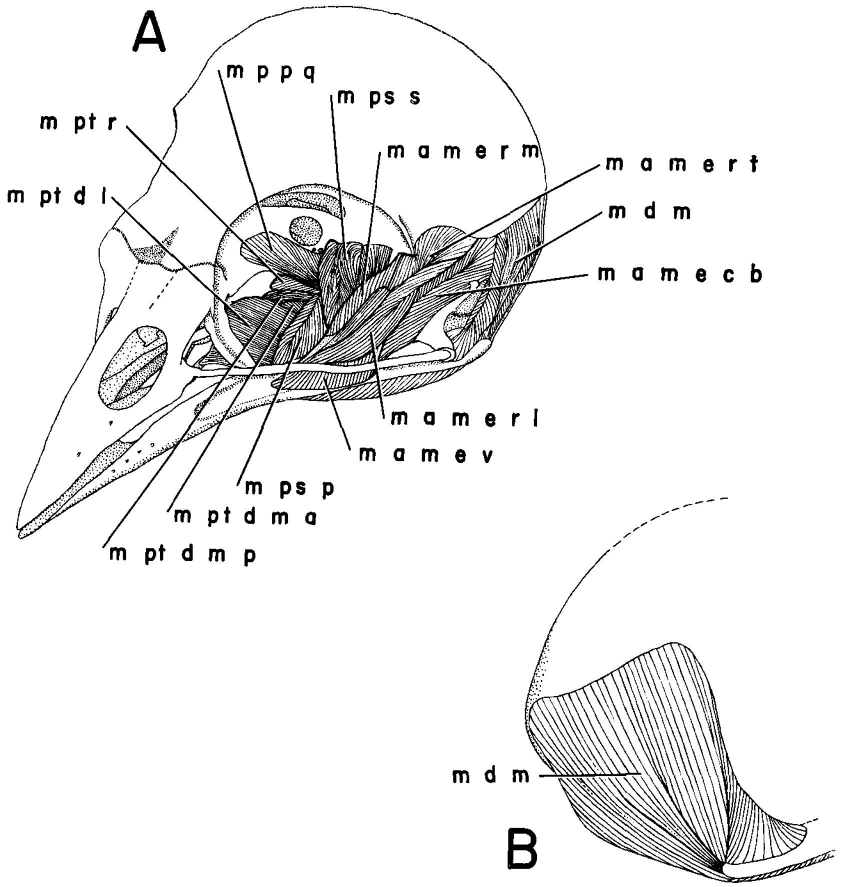

Plate 18. Jaw muscles of *L. c. coccinea* and *L. sagittirostris*. A) Oblique view of the left-side of *L. c. coccinea* (right-billed individual). B) Lateral view of the hind end of the head of *L. sagittirostris* showing the m. depressor mandibulae.

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Plate 17. Jaw muscles of *L. c. coccinea* (right-billed individual). A) Ventral view of the M. pterygoideus and some surrounding muscles (left-side of head uppermost). B) Ventral view of dorsal layer of M. pterygoideus (ventral layer removed on both sides). C) Ventral view of some tongue muscles and more dorsal jaw muscles.

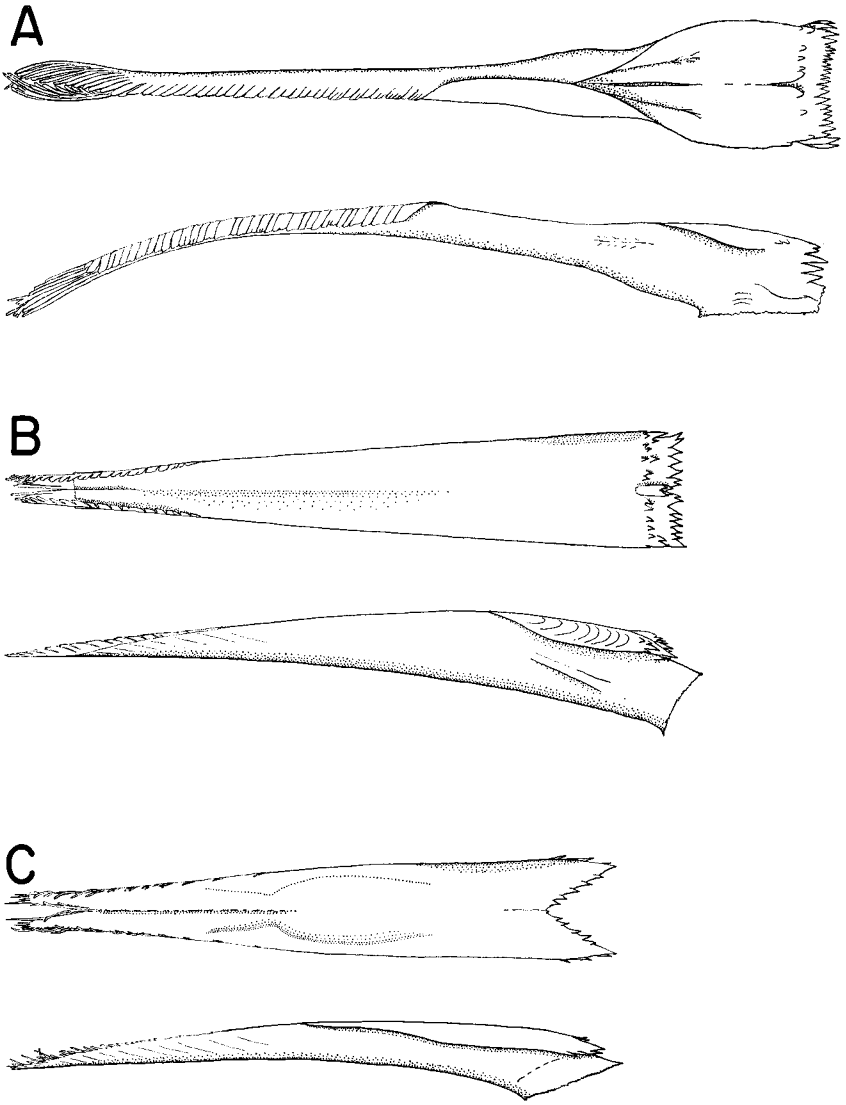

Plate 19. Corneous tongue of *Loxops* in dorsal and lateral views. A) *L. v. virens.* B) *L. m. mana.* C) *L. m. newtoni.*

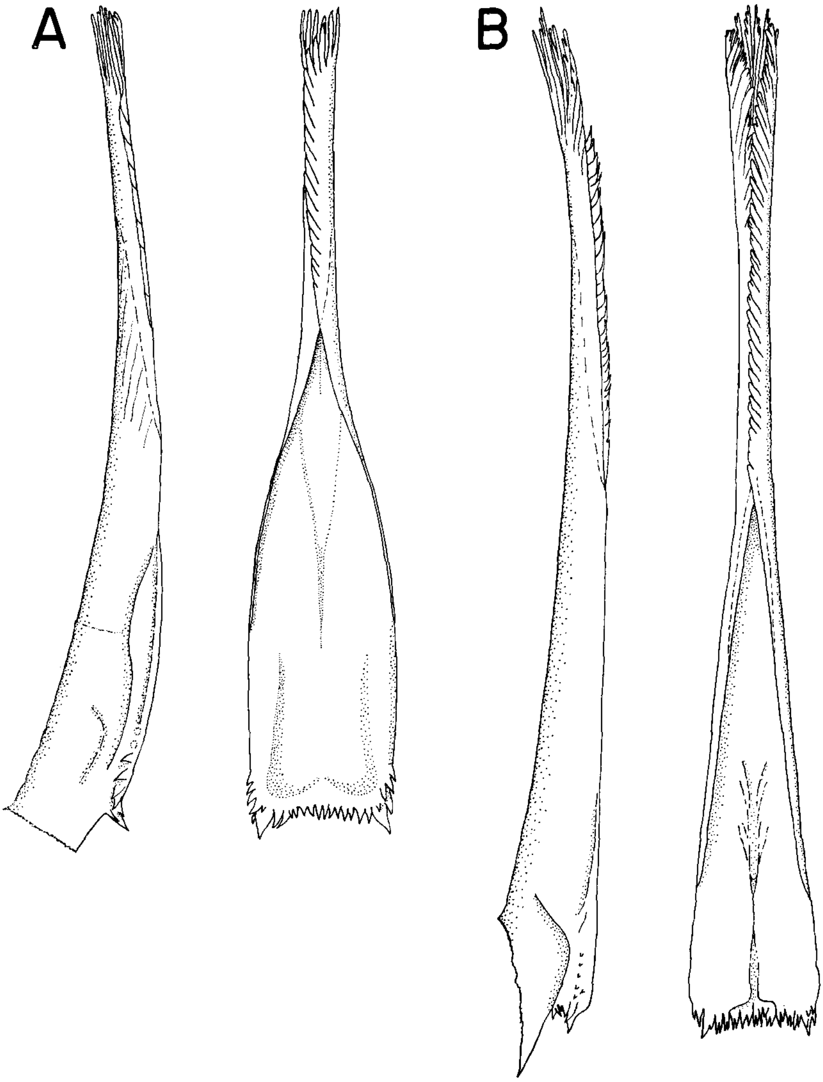

Plate 20. Corneous tongue of *Loxops* in dorsal and lateral views. A) *L. c. coccinea.* B) *L. sagittirostris.*

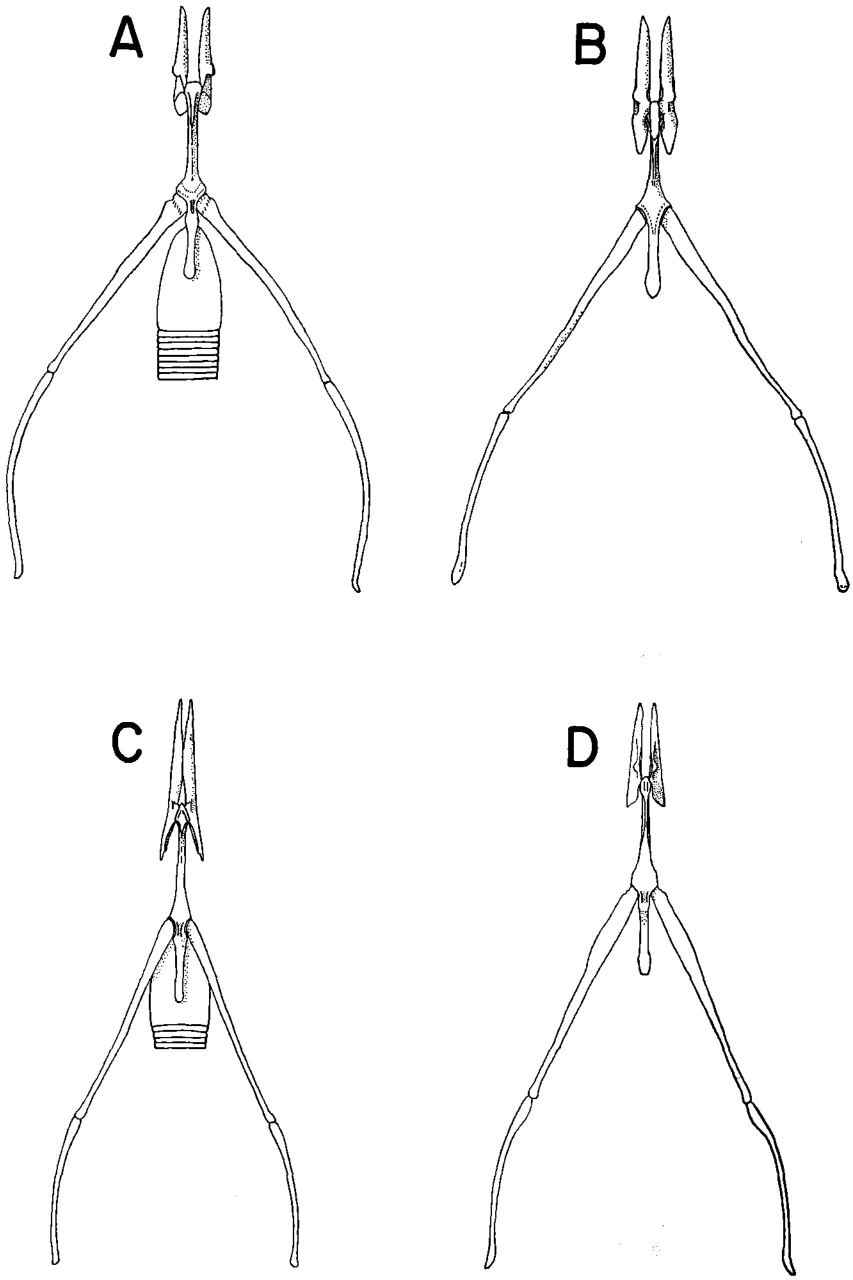

Plate 21. Tongue skeleton of *Loxops* in ventral view. A) *L. v. virens.* B) *L. m. mana.* C) *L. m. newtoni.* D) *L. c. coccinea.*

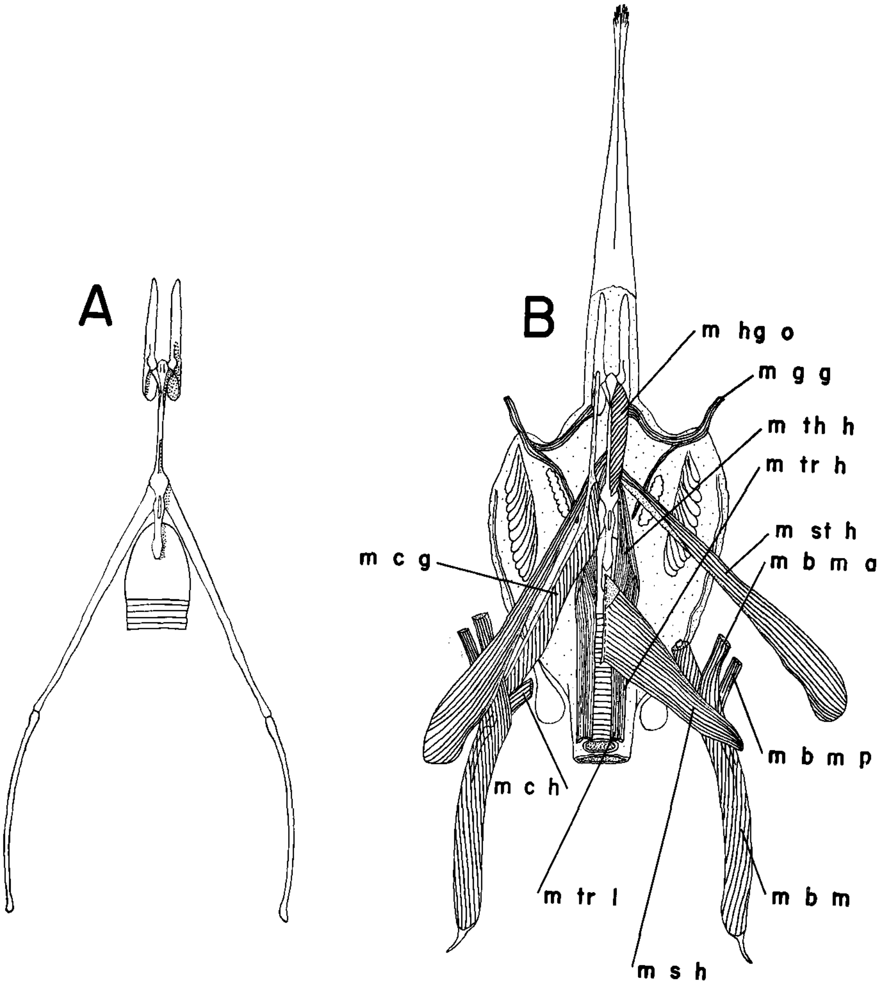

Plate 22. Tongue skeleton and muscles of *L. sagittirostris*. A) Tongue skeleton in ventral view. B) Tongue muscles in ventral view; superficial muscles on right side, deeper muscles on left side.

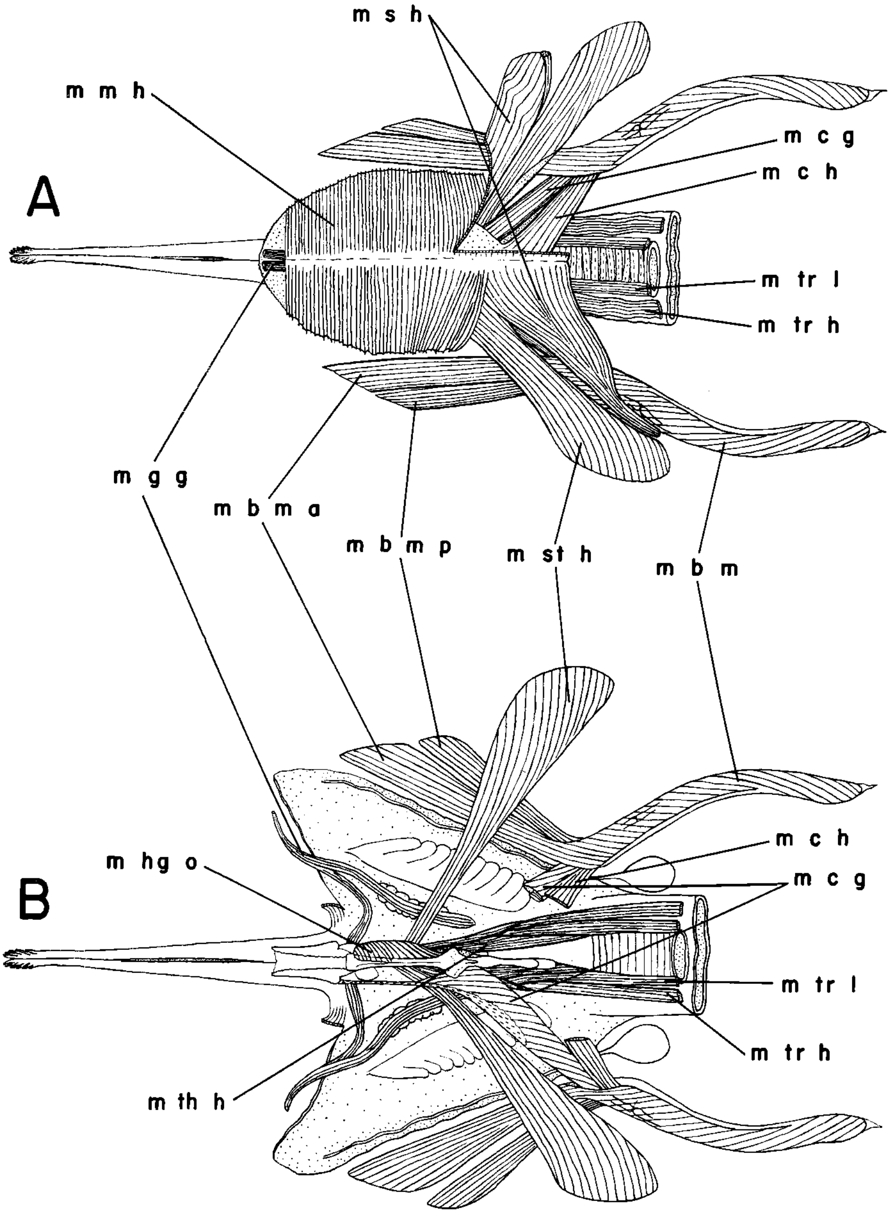

Plate 23. Tongue muscles of *L. v. virens* in ventral view. A) Superficial muscles. B) Deeper muscles.

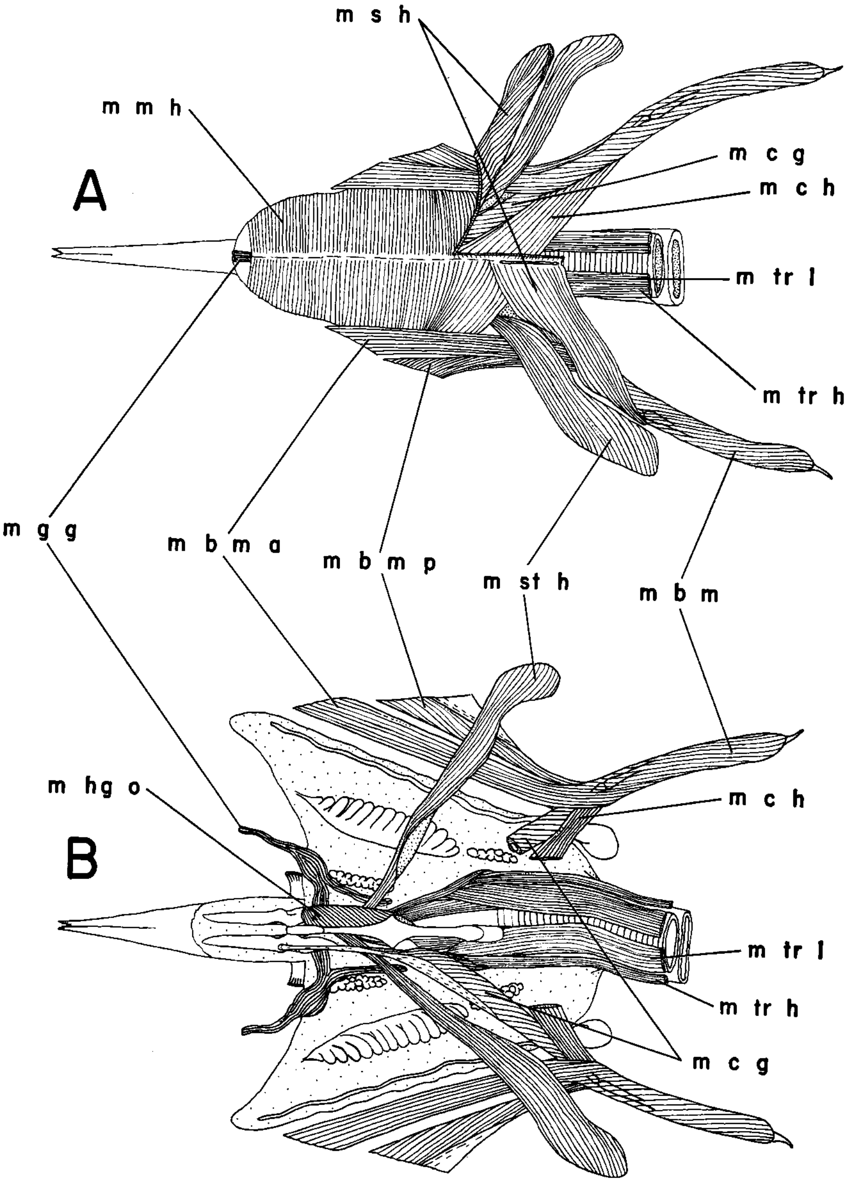

Plate 24. Tongue muscles of *L. m. mana* in ventral view. A) Superficial muscles. B) Deeper muscles.

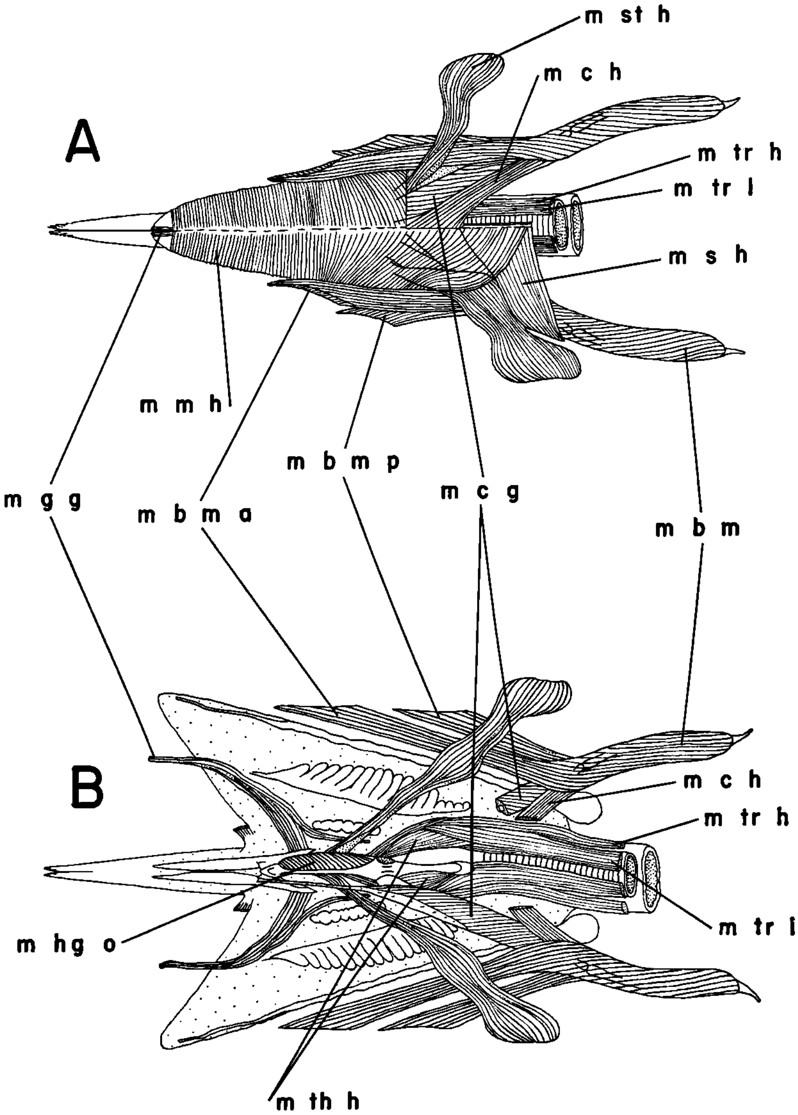

Plate 25. Tongue muscles of *L. m. newtoni* in ventral view. A) Superficial muscles. B) Deeper muscles.

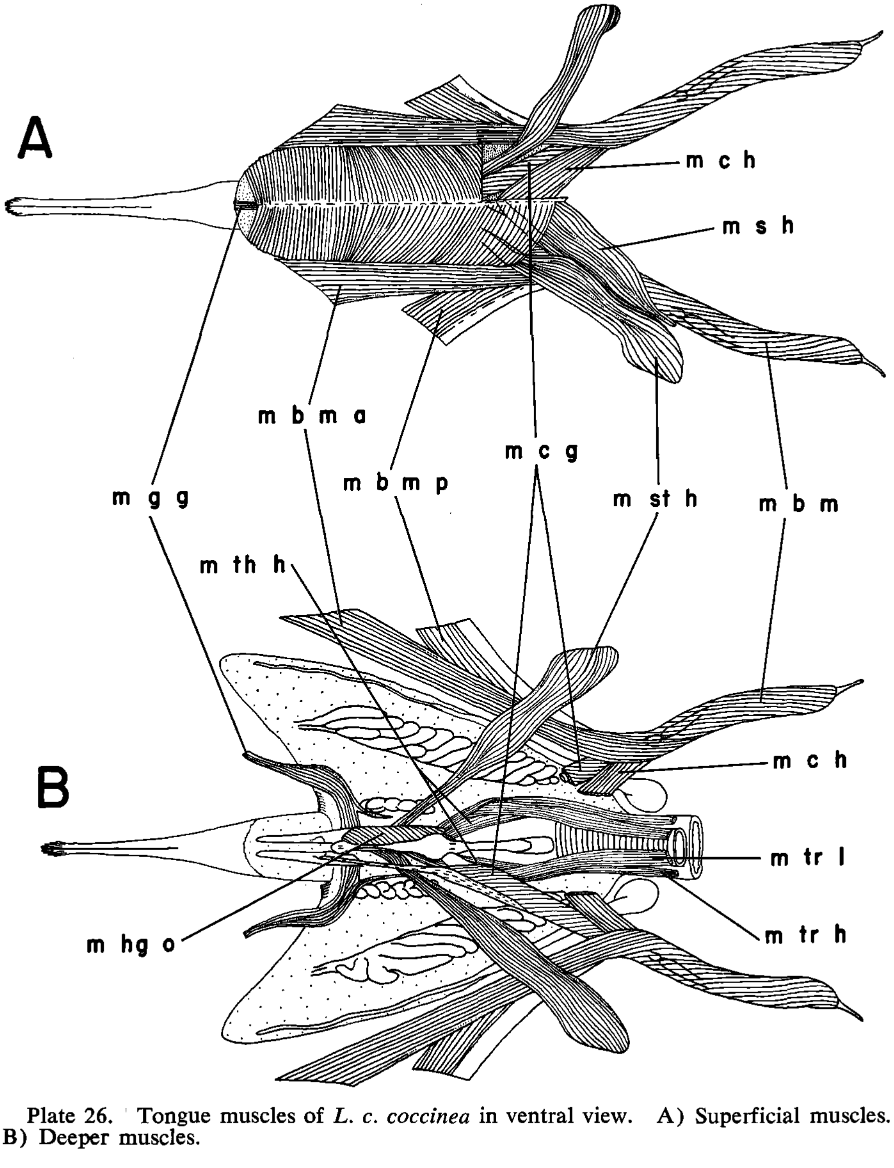

Plate 26. Tongue muscles of *L. c. coccinea* in ventral view. A) Superficial muscles. B) Deeper muscles.

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