ANNALS

OF THE

NEW YORK ACADEMY OF SCIENCES

VOLUME XXVIII

NEW YORK
PUBLISHED BY THE ACADEMY
1918 - 1920

Editor
HERBERT F. SCHWARZ

CONTENTS OF VOLUME XXVIII

DATES OF PUBLICATION AND EDITIONS OF THE BROCHURES

	Edition
Pp. 1– 50, 29 June, 1918	1854 copies
Pp. 51–166, 15 January, 1919	1050 copies
Pp. 167–200, 8 September, 1920	1211 copies

LIST OF ILLUSTRATIONS

Plates

Text Figures

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Vol. XXVIII, pp. 1–50

Editor, Ralph W. Tower

THE SUPERB POSITION OF NEW YORK CITY AS A CENTER FOR PHYSIOGRAPHIC STUDY

BY

A. K. Lobeck

NEW YORK
PUBLISHED BY THE ACADEMY
29 June, 1918

THE NEW YORK ACADEMY OF SCIENCES

(Lyceum of Natural History, 1817–1876)

Officers, 1918

President—Ernest Ellsworth Smith, 50 East 41st Street
Vice-Presidents—George B. Pegram, Frank H. Pike,
Edmund O. Hovey, Pliny E. Goddard
Corresponding Secretary—Henry E. Crampton, American Museum
Recording Secretary—Ralph W. Tower, American Museum
Treasurer—John Tatlock, 37 Wall Street
Librarian—Ralph W. Tower, American Museum
Editor—Ralph W. Tower, American Museum

SECTION OF ASTRONOMY, PHYSICS AND CHEMISTRY

Chairman—George B. Pegram, Columbia University
Secretary—K. George Falk, Harriman Research Laboratory, the Roosevelt Hospital

SECTION OF BIOLOGY

Chairman—Frank H. Pike, College of Physicians and Surgeons
Secretary—William K. Gregory, American Museum

SECTION OF GEOLOGY AND MINERALOGY

Chairman—Edmund O. Hovey, American Museum
Secretary—Charles C. Mook, American Museum

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

Chairman—Pliny E. Goddard, American Museum
Secretary—Robert H. Lowie, American Museum

The sessions of the Academy are held on Monday evenings at 8:15 o'clock from October to May, inclusive, at The American Museum of Natural History, 77th Street and Central Park, West.

[ANNALS N. Y. ACAD. SCI., Vol. XXVIII, pp. 1-50. June 29, 1918]

THE SUPERB POSITION OF NEW YORK CITY AS A CENTER FOR PHYSIOGRAPHIC STUDY

BY A. K. LOBECK

CONTENTS

INTRODUCTION

The commanding position which New York City holds at the meeting place of several distinctly different physiographic provinces (Fig. 2) has occasionally been noted, and it is now the purpose of this paper to bring together in a suggestive way a summary of the opportunities for study thus provided for the teacher and student of physiography. How fortunate are the teachers of physiography in this great city, in having at hand in the near-by out-of-doors such a magnificent laboratory, or one might say such a complete museum of land forms in all their bewildering variety! How fortunate we are in having these things within such easy reach, not only because they invite us to take our classes into the field, classes whose mental pictures of the world are those of city dwellers, but even more because they cry out to us to avail ourselves of these unrivaled opportunities to see things at first hand, to broaden our own conceptions of our chosen subject, to attain the confidence in teaching which comes from this wider outlook, and to be inspired by bringing us face to face with the fascinating problems having to do with the origin of land forms.

There are some cities of the United States situated out upon the plains with miles and miles of undiversified country presenting hardly more than one physiographic problem. How the physiographer must envy us when he looks at a geological map of our area (Fig. 1) and realizes its splendid location. There are a great many cities of our country not situated upon the seaboard. They do not exhibit any of that infinite host of forms expressing wave work, beaches and bars, spits and lagoons, nor wave-cut cliffs; the physiographer cannot see a coastal plain at first hand, nor may he see the immediate effects of change of sea level, either those of uplift or those of drowning. Then consider all of our southern cities, which are denied the features of glaciation, either of the local type or of the continental type, such as are so perfectly expressed in our immediate vicinity.

And, moreover, we live in the heart of a great center of population which has at its command unrivaled means of transportation in the form of railroads, trolleys, river and ocean steamboats, and automobile roads of superb quality. There are cities, towns, and villages everywhere offering us their hospitality. We are assured of a comfortable resting place

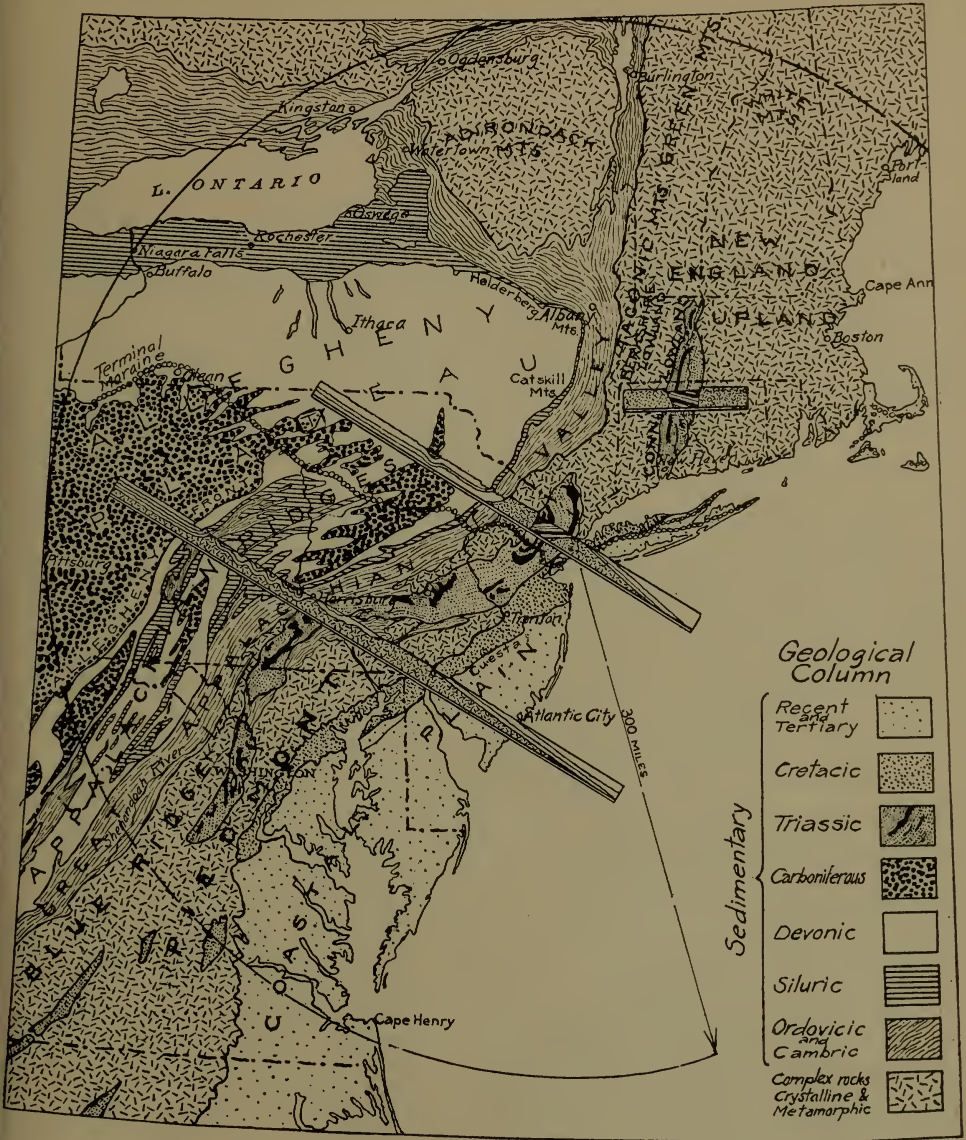


FIG. 1.—*Generalized geological map and typical cross-sections of the region within a radius of 300 miles of New York City*

The oldest rocks of the region are those comprised in the crystalline areas of the Adirondacks, New England, and the Blue Ridge and Piedmont portions of the Older Appalachians. These three areas may be roughly pictured as an oldland enclosing an inland sea or depression on the west where the Cambric, Ordovicic, Siluric, Devonic, and Carboniferous sedimentary deposits were laid down. The Cambric and Ordovicic formations are essentially limestones and shales, not resistant to erosion, which accounts for the persistence of the present Great Appalachian Valley along the western flank of the oldland.

After the deposition of the Siluric, Devonic, and Carboniferous beds there occurred the compression of the region which produced a general folding of the sedimentary beds next to the oldland where the Appalachian ridges and valleys appeared. Further west there was no disturbance, the horizontal bedding is preserved and the region is characterized as a plateau.

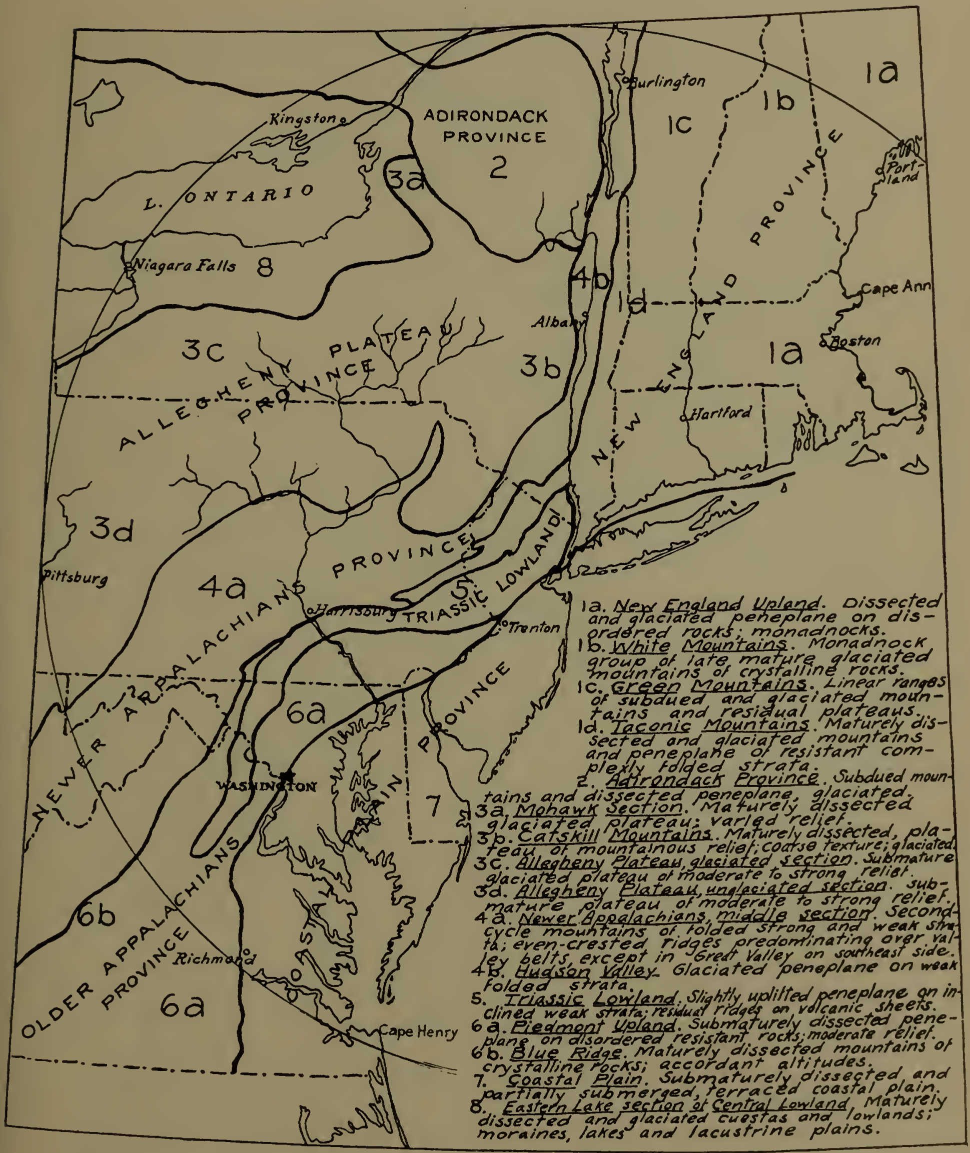
During a later period (the Triassic) certain regions in the original oldland became covered with red sand deposits interbedded with extensive lava flows, and portions of these areas were preserved from later denudation by being downfaulted into the crystallines. They now constitute the Connecticut Valley and the Triassic Lowland.

The latest geological formations are those comprising the present coastal plain on the eastern side of the oldland mass.

at the end of each day's journey, and this indeed is a very essential item in good physiographic work.

To facilitate our observations and to aid us in understanding the features of the region under consideration, we have at our command an almost inexhaustible amount of literature. Probably no other region of the world has been studied so intensively and in so truly a scientific way as the area that interests us. The work of many masters, fostered by the institutions of learning concentrated here in the east and developed out of the earlier fundamental studies in geology and physiography, is accessible to every one of us and there is no literature in any branch of knowledge so easy of reference and so well catalogued as the geological and physiographic literature of this country.

Then there is a practical and even more important reason why we should turn our attention toward these opportunities so near at hand. The war has brought before us a great problem to which we have to adjust ourselves. Travel must be kept at a minimum. The railroads are overburdened with traffic and traveling for pleasure cannot be encouraged. Moreover, we are all practicing economy in every direction. Since these things are true, would it not be better for us to stay at home altogether? Decidedly not! Our most important duty, if we are unable to take an active part in the furtherance of the war, is to carry along our tasks in the most efficient and excellent way possible, and it fortunately happens in the case of the physiographer that he can combine the means of taking recreation with the improvement of himself in a professional way. At the present time he must do these things without going so very far afield. When I tell you that I propose to keep him within a circle having a radius of 300 miles and centering in New York, I am prepared to defend it on several grounds. If it seems too generous I must argue that this circle just includes within its margin several points of particular interest: Niagara Falls, Norfolk and Cape Henry, the Blue Ridge and Shenandoah Valley, the Adirondacks, the Allegheny Front in western Pennsylvania, and the White Mountains. If it seems too small my argument then is that the traveler must go far beyond its limits to find a region offering any new types of physiography materially different from those thus circumscribed, for he has here a great concentration of physiographic provinces. The New England Upland, with its monadnock groups and its extension southward in the Manhattan and Reading prongs, the Adirondack portion of the great Archean massive, parts of the Great Lakes Province, the Allegheny Plateau, the Older Appalachians terminating northward in the Cumberland and Trenton prongs, the Newer Folded Appalachians so exquisitely developed in Pennsylvania, the



1a. New England Upland. Dissected and glaciated peneplane on disordered rocks; monadnocks.
1b. White Mountains. Monadnock group of late mature glaciated mountains of crystalline rocks.
1c. Green Mountains. Linear ranges of subdued and glaciated mountains and residual plateaus.
1d. Taconic Mountains. Maturely dissected and glaciated mountains and peneplane of resistant complexly folded strata.
2. Adirondack Province. Subdued mountains and dissected peneplane, glaciated.
3a. Mohawk Section. Maturely dissected glaciated plateau; varied relief.
3b. Catskill Mountains. Maturely dissected, plateau of mountainous relief; coarse texture; glaciated.
3c. Allegheny Plateau, glaciated section. Submature glaciated plateau of moderate to strong relief.
3d. Allegheny Plateau, unglaciated section. Submature plateau of moderate to strong relief.
4a. Newer Appalachians, middle section. Second-cycle mountains of folded strong and weak strata; even-crested ridges predominating over valley belts, except in Great Valley on southeast side.
4b. Hudson Valley. Glaciated peneplane on weak folded strata.
5. Triassic Lowland. Slightly uplifted peneplane on inclined weak strata; residual ridges on volcanic sheets.
6a. Piedmont Upland. Submaturely dissected peneplane on disordered resistant rocks; moderate relief.
6b. Blue Ridge. Maturely dissected mountains of crystalline rocks; accordant altitudes.
7. Coastal Plain. Submaturely dissected and partially submerged, terraced coastal plain.
8. Eastern Lake section of Central Lowland. Maturely dissected and glaciated cuestas and lowlands; moraines, lakes and lacustrine plains.

FIG. 2.—*Outline map of northeastern United States showing the limits of the main physiographic provinces*

Their subdivisions are briefly characterized above

Coastal Plain, and the Triassic Lowland are points all practically within this area and within a day's travel of New York.

The teacher of physiography in presenting the principles of the subject to a class usually takes it up in a systematic way, dwelling first upon the work of the various destructive forces which carve out the features of the earth as the rivers, glaciers, waves, and wind, and then taking up the great groups of land forms which are conveniently classified according to their underground structure, the plains being those of simple undisturbed and almost horizontal strata, and mountains those regions of more involved character, distinguished by doming, faulting, folding, complex metamorphic or crystalline rocks, and by volcanic action.

WORK OF DESTRUCTIONAL FORCES

Streams.—The work of streams is brought to the understanding of the student by developing in a deductive way the life history of a stream where drainage has been initiated by uplift of a land mass above sea level. The different stages of youth, maturity, and old age are recognized as depending upon the degree of adjustment which the stream has acquired. The peculiarities which characterize each stage are noted, the necessary new terms are introduced, and all of these constitute the data of fundamental information which makes up this part of the subject.

When the characteristics of a youthful stream are under consideration the instructor calls to witness the rapids, the waterfalls, the narrow rocky gorge of the Bronx River, its pot-holes, its swift current, and its pronounced gradient, or he can go further afield and cite the swift brooks of the Highlands, the Deerfield George in the New England Upland of Massachusetts, or the mountain torrents of the Adirondacks. He may cite the Niagara River system bearing the marks of youth in Niagara Falls, the wonderful gorge, the racing current, and the interruption of its course by the presence of lakes Erie and Ontario.

The features of maturity are illustrated by the upper portion of the Bronx River, where it pursues a meandering course upon a limestone lowland. An occasional abandoned meander may even be cited. Other splendid examples are offered by the Wallkill River and its broad valley in New Jersey and New York, and among other streams which have developed wide open courses upon the softer beds of the folded Appalachians are the Rondout and Esopus Creeks. The Mohawk River in part of its course is a mature stream. Some of the very finest references to mature valleys may be drawn from parts of the New England region, notably in eastern New Hampshire and western Maine, where broad

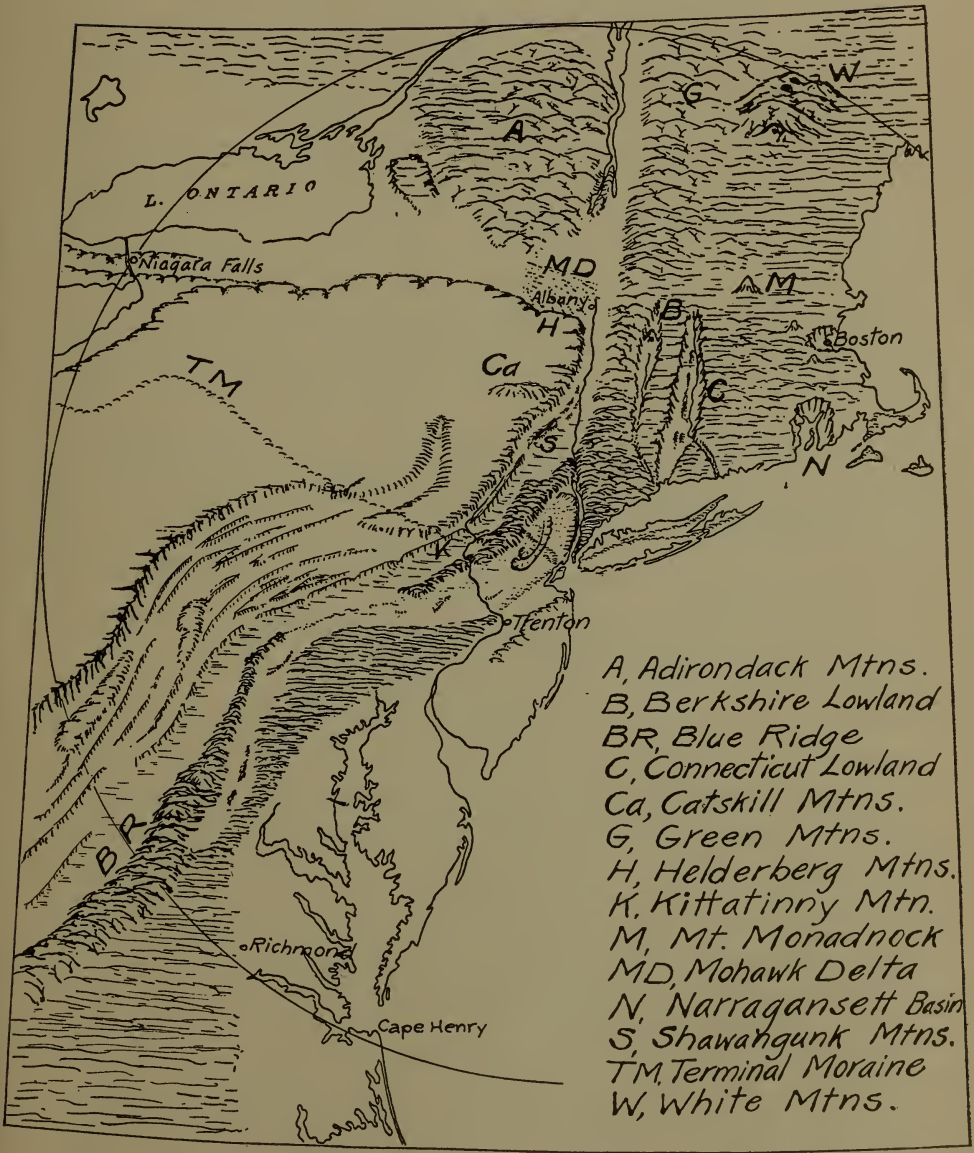


FIG. 3.—*Diagrammatic map of northeastern United States showing the salient relief features*

mature valleys have been opened out below the general upland by such streams as the Saco River and the Merrimac and its tributaries.

When consideration is given to the final stage of a stream's history, that of old age, after erosion has reduced the entire drainage basin to an almost flat surface, the instructor is able to place before his class an unparalleled example in the New England peneplane (Fig. 4). The even crest of the Palisades truncating the westward dipping formations, and impressive for this reason, serves as an illustrative example close at home. Throughout New England, the Hudson Highlands, Schooley Mountain, the rest of the Highlands of New Jersey, and Kittatinny Mountain, the even crest lines of the folded ridges of Pennsylvania, and the Blue Ridge of Virginia this same peneplane finds expression and is known variously as the New England, the Schooley, the Kittatinny, and the Cretaceous peneplane. It is true that this peneplane no longer stands at the level to which it had been reduced. The fact that it has been elevated only makes it the more valuable as an object for study. It provides an example when rejuvenation and the matter of several cycles are discussed. The gorge of the Deerfield River (Fig. 4) and many other New England streams cut below the upland level serve to illustrate the essential features of a topography first reduced to old age and then dissected as a result of later uplift, but even still finer examples are to be had in the case of the Monongahela River in Pennsylvania with its great swinging meanders incised below the Cretaceous peneplane of the Alleghany Plateau, and the really remarkable entrenched meanders of the Potomac River in its course through the folded mountains of Maryland whose crests still preserve that upland level. To carry out still further the idea of repeated uplift with renewed erosional activity in each cycle reference is made to the three cycles so well displayed throughout the folded Appalachian belt (Figs. 15, 16, 17, 19, 20). The old stage resulting in the Cretaceous peneplane on the summits marks the first cycle, a second and post-mature stage resulting in the Tertiary peneplane

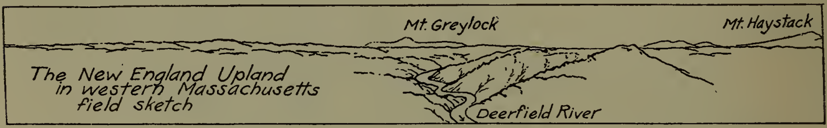


FIG. 4.—*Sketch of New England peneplane having an elevation of 1,400 feet in western Massachusetts*

As seen looking west from Mt. Massaemet, near Shelburne Falls. Two or three monadnocks rise above the peneplane, and the Deerfield River has incised itself several hundred feet below that level.

developed on the broad valley floors represents the second cycle, and finally the post-Tertiary trenching is the work of the present erosion cycle. No better location can be cited for the observation of these elements of the topography than near Hackettstown, New Jersey (Fig. 15), although they exist almost anywhere in the newer Appalachian belt. Even in the gorge of the Hudson River through the Highlands, the Tertiary cycle is preserved by a great bench or terrace especially well developed on the west side of the stream, a feature readily seen by the traveler from the cars of the New York Central, or even better from the boats on the river (Fig. 5). West Point is apparently built upon part of this bench.

With rejuvenation resulting from uplift there should be considered the alternative possibility, that of depression, which may or may not impose old age characteristics upon the streams involved. There are no more suitable examples of a drowned coast with embayed river systems to be had than the northeastern shores of the United States. The ragged and bold coast of Maine and eastern New England, Narragansett Bay with its dismembered headwaters, the great fiord of the Hudson River from New York to Albany, the drowned inner lowland of Long Island Sound and New York Bay, Delaware Bay, and, finest and largest of all, the depressed portion of the Susquehanna River system now comprised in Chesapeake Bay and its numerous arms; these and many other smaller examples may all be cited at this time.

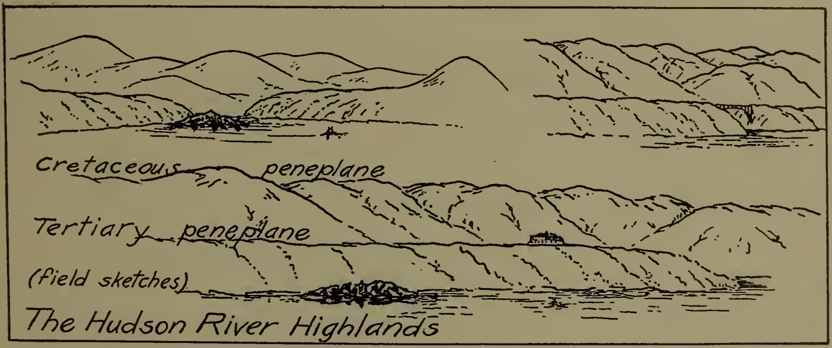


FIG. 5.—*Sketches in the Hudson Highlands*

Showing the characteristic expression of the topography as influenced by the Cretaceous peneplane on the tops of the mountains and the Tertiary peneplane preserved in an intermediate bench standing two to three hundred feet above the river.

Then, aside from elevation or depression, there may be certain accidents in the life of a stream which cause it to change its behavior in the matter of deposition or erosion. An overloaded condition and the development of a flood plain was brought about in many of the New England streams at the end of the glacial period when a greater amount of detritus was provided than the stream could handle. The remnants of these flood plains are now to be seen in the terraces of the Connecticut, the Westfield, Merrimac and other New England streams. The cutting away of alluvial plains to form terraces has been studied here in detail and hardly any topic in physiography is more fascinating than this one. The Hudson River and Delaware River show similar features.

In this connection there is the question of deltas built by streams. The teacher of physiography in this region can hardly cite any good deltas formed by streams entering the Atlantic Ocean at the present time, probably because the tides and currents are strong enough to prevent the accumulation of material, but he can cite several splendid examples built into the estuary of the Hudson River during glacial time, when its waters stood at a higher level than now. Croton Point is the remnant of a delta built by the Croton River; the clays that encourage the brick industry at Haverstraw come from a similar delta (Fig. 6), and finally there is the large delta built by the Mohawk River at the head of this estuary, whose flat surface is so well seen by one riding over it between Schenectady and Albany. Trenton, N. J., is built upon a similar delta and the very level coastal region at Norfolk, Virginia, is a part of the earlier delta of the Potomac River.

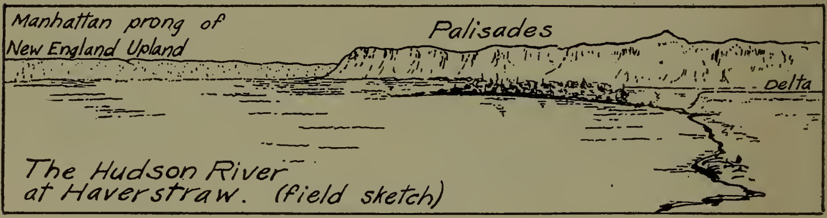


FIG. 6.—*View looking down the Hudson River at Haverstraw, New York*

The east side of the river is bordered by a portion of the New England upland; the west side by the Palisades, which here swing around in a big arc. At their base may be seen a portion of the delta built into the estuary of the Hudson in glacial time.

Among other topics usually mentioned when the work of streams is under discussion is the subject of stream capture, and citation is always made of the excellent case in the Catskill Mountains where the headwaters of Schoharie Creek have been diverted by the Kaaterskill, so that there may now be pointed out the sharp elbow of capture, the falls and the misfit upper course of the Schoharie, which are so significant.

If the teacher wishes to discuss the effect of Ferrel's Law upon the flowage of rivers he may cite the tendency of the short streams on the south side of Long Island to cut most strongly against their right hand or western banks. If he wishes to speculate upon the former extent of the coastal plain over southern New England and northern New Jersey he may use the Connecticut, the Housatonic, the Bronx, and even the Hud-

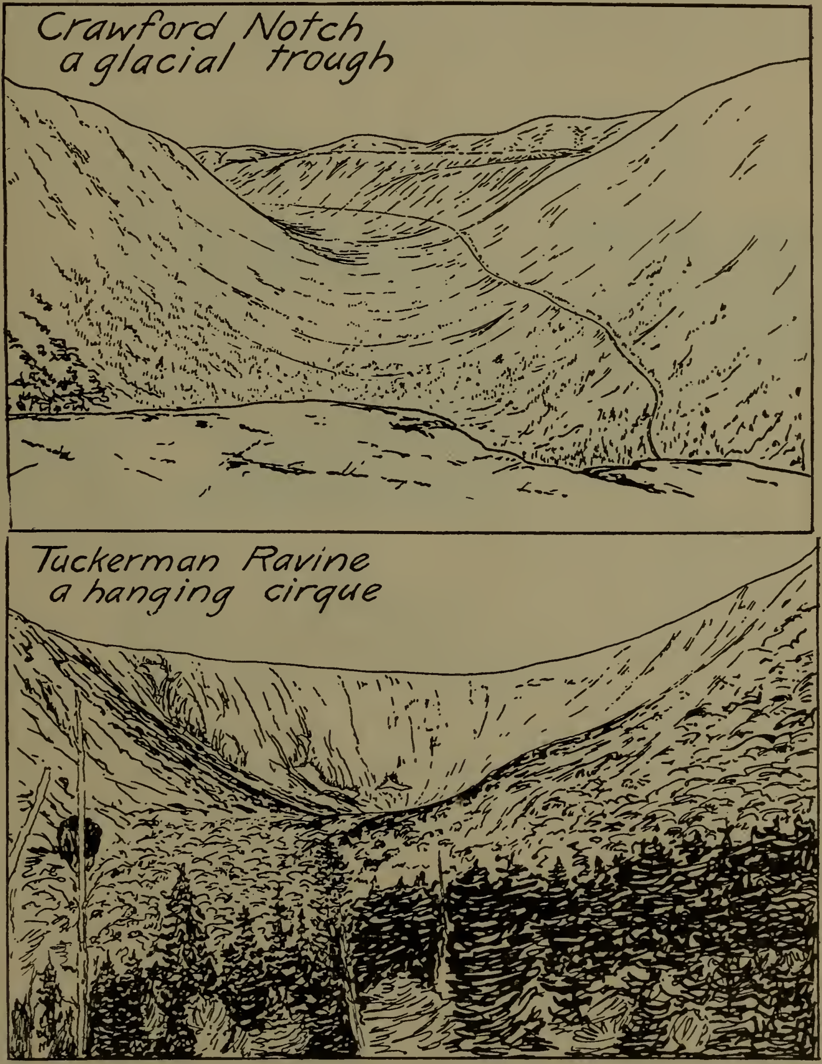


FIG. 7.—*Features of local glaciation in the White Mountains*

son River as examples of superposed streams now cutting gorges through the harder rocks discovered by them, although their upper courses are broad and open and significantly adjusted to the less resistant formations.

Glaciers.—The subject of glaciation naturally falls under two heads, that resulting from local valley glaciers and usually referred to as alpine, and that resulting from the passage of a continental glacier or ice sheet.

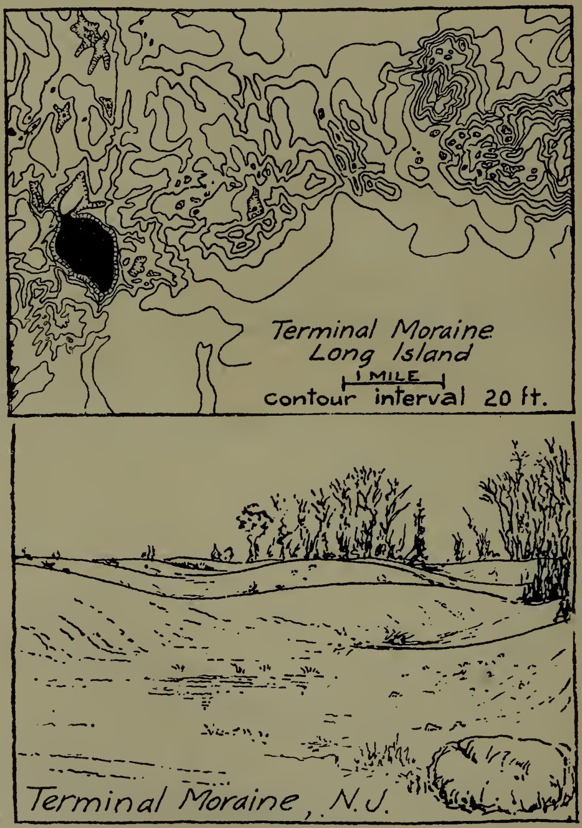


FIG. 8.—*Characteristic view and map of portions of the terminal moraine*

In the White Mountains as well as in the Adirondacks and possibly in the Catskills, too, very good evidences of alpine glaciation exist. The instructor may with confidence refer to the head of Tuckerman Ravine (Fig. 7), Great Gulf and King Ravine as well formed cirques on the slopes of Mount Washington and the Presidential Range (Fig. 25). Hermit Lake is apparently a little tarn. The mere names of some of the other ravines and features are suggestive, as Ravine of the Castles, Ravine of the Cascades, and Castellated Ridge. Note, too, how all of these features are concentrated on the north and east side of the range. Most of these ravines show the characteristic trough-form of glaciated valleys, but the example par excellence in the White Mountains is Crawford Notch (Fig. 7), which for true charm of outline can hardly be equaled even in the well known glaciated mountains. In the Adirondack Mountains Lake George lies on the floor of a glaciated trough of superb beauty (Fig. 23) and several of the finger lakes of western New York occupy similar valleys of rounded profile.

In developing the subject of continental glaciation the teacher refers to the terminal moraine (Fig. 8) with its characteristic knob and kettle topography so easy of access on Staten Island, its continuation across the "Narrows" into Prospect Park, Brooklyn, its bifurcation further east where two terminal moraines form the backbone of Long Island and its fish-like tail at its eastern end, and then on into Block Island, Nantucket, and Marthas Vineyard. Westward in New Jersey it may be seen in rather classic perfection at Plainfield and at Hackettstown.

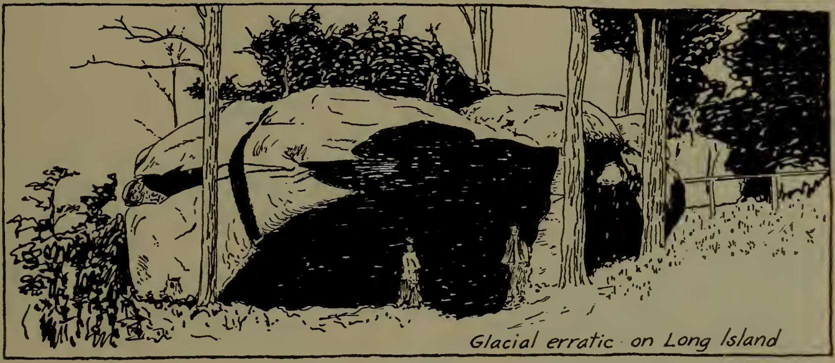


FIG. 9.—*The largest erratic on Long Island and one of the largest in the eastern United States*

It is a mass of crystalline rock carried in the ice sheet from New England over Long Island Sound

The lobate form of the ice front is shown by the festoon-like trend of the moraine in New Jersey (Fig. 29) and in Marthas Vineyard. Then there is the great outwash plain fringing the southern side of Long Island and the islands to the east. The city of Plainfield, New Jersey, stands upon such a plain, whence it derives its name. The contrast between glaciated and non-glaciated areas, the difference in soil, the disturbed drainage, the rapids and waterfalls and numerous lakes in one case, their absence in the other, the effect of these things upon the activities of the people—all of these topics are readily illustrated in our immediate area.

In Bronx Park glacial striæ, rôches moutonnées, and erratics are under our feet at every step. The "Rocking Stone Restaurant" takes its name from a near-by erratic (Fig. 9). The drumlins of the Boston Bay region and the great swarm of western New York (Fig. 10), the eskers of southern Maine and an occasional one in New Jersey, the sand plains of New England, the kame hills scattered over New York and New Jersey, are topics of interest. There is also the subject of marginal lakes illustrated by Lake Passaic in New Jersey, Lake Bascom in the Berkshire region, and Lake Iroquois in New York. Their outlet channels may still be pointed out, that of Lake Passaic at Moggy Hollow and of Lake Iroquois at Rome, New York, and a later marginal channel at Covey Gulf on the northern flank of the Adirondacks.

FIG. 10.—*Characteristic view and map of glacial drumlins*

In strong contrast with all of this there are the normal and undisturbed erosion features of the southern half of our district, where lakes are practically absent and where the soil is all of the residual type. Boulder-covered fields in southern Pennsylvania, Maryland, and Virginia are not known. The aspect of the country is different and this difference is reflected in the industries and economic development of the region.

Waves.—The subject of wave work is no less limited in the prolificacy of examples available. The development of the features upon an emerged shoreline is illustrated in the unrivaled offshore bars and lagoons of the Long Island and New Jersey coast, both typically in the youthful stage, though it may be held that in northern New Jersey where the bar has been pushed back against the mainland maturity is reached.

Abandoned shorelines and beach ridges exposed as a result of emergence are beautifully displayed in western New York in the old basin of Lake Ontario and it is upon these ridges that the so-called ridge roads have been built.

Shorelines of submergence in a region of strong relief are shown in the early stages of youth along the coast of New England where wave work has had but little effect, and the outline of the shore is extremely irregular. The New Jersey coast also comes under this class as well as under that of emergence, but the region is one of low relief and is made up of non-resistant formations more readily influenced by wave action, so that bars have been built across the estuaries and a smooth, sinuous outline has been attained, representing a further advance in the youthful stage over that of New England.

The activity of waves in cutting cliffs, destroying islands, tying islands to each other or to the mainland by throwing up sand bars, the building of cobblestone beaches and other features, finds splendid illustrations in the eroded drumlins of the Boston Bay region and the tombolos of Nantasket, Nahant, and other beaches. The shore of Lake Ontario likewise exhibits the work of waves in cutting away drumlins. The construction of spits by currents where waves are cutting against headlands may be studied in the greatest detail in the compound recurved spits of Cape Cod and Sandy Hook, or the simple recurved spit of Cape Henry, or the successive offsetting spits of Fire Island, Oak Island, Jones Beach, Long Beach, Rockaway, and Coney Island.

Fig. 11.—*Giant sand dunes on Cape Henry, Virginia, encroaching upon an evergreen forest which borders the coast*

Wind.—On all of our beaches the work of the wind in the building of dunes is to be seen. Most noteworthy are the giant dunes of Cape Cod and the great dunes of Cape Henry, now encroaching upon a forest (Fig. 11). The barrier beaches of Long Island and New Jersey are everywhere covered with dunes rising ten to twenty feet above sea level.

CONSTRUCTIONAL FORMS

Plains and Plateaus.—Study of the constructional group of land forms is introduced by consideration of plains and plateaus characterized by a simple and almost horizontal structure. The subject begins most naturally with coastal plains. The well defined elements of the recent coastal plain of the Atlantic coast, comprising its oldland in southern New England, New York, northern New Jersey, and the Piedmont further south; its inner lowland partly drowned in Long Island Sound, Lower New York and Sandy Hook Bays, then followed by the main transportation routes between New York and Philadelphia, occupied by the Delaware River from Trenton to the Bay, and thence southward; the features of the fall line seen in the rapids at Trenton, N. J., the falls of the Schuylkill at Philadelphia, the Great Falls of the Potomac at Washington, and those of the James River at Richmond; the main cuesta forming the foundation of Long Island, the Atlantic Highlands at Sandy Hook, its ragged front making up the hilly belt of southern New Jersey, its flat surface the pine barrens which incidentally provide a suitable location for Camp Dix, whose site is near the cuesta front, are all features which may be pointed out in much greater detail than here indicated (Fig. 12). The various genetic types of streams—consequent, subsequent, obsequent, resequent, and insequent—can be illustrated by examples almost too numerous to mention.

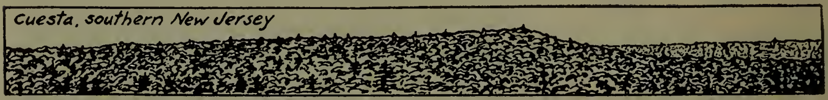


FIG. 12.—*Profile view of the coastal plain cuesta, near Clementon, New Jersey*

It is 15 miles east of Philadelphia and a few miles south of Camp Dix, which is built upon the flat back slope of the cuesta. The soil here is loose and unconsolidated, is very sandy and dry, and supports an open forest of pines and rhododendrons.

In central New York the ancient coastal plain provides even bolder features and somewhat greater variety. Its oldland in Canada and the Adirondacks, its inner lowland in Mohawk Valley and the basin of Lake Ontario, its cuestas in the Helderberg Mountains and the Allegheny and Niagara escarpments and many other details could be cited (Fig. 13).

Stages in the development of a plain or plateau are illustrated by the very youthful drainage systems of the coastal regions of Maryland and Virginia, by the deeper but still youthful dissection of the Allegheny Plateau, by the headwaters of the Susquehanna River in New York, and by the mature dissection of the Catskill Mountains and of the western Pennsylvania Plateau region where extreme ruggedness prevails.

The economic dependency of people upon the features of a dissected coastal plain, the contrast between the different belts, the routes of travel, the position of towns, the controlling influence of the fall line, the location of towns, railroads, and roads upon the surface of a youthful plain, but in the valleys of a maturely dissected one, the occurrence of the extensive bituminous coal beds in the Allegheny Plateau region, the advantageous methods of mining there compared with those in the folded anthracite region, these are only some of the topics that may be taken up here with profit.

FIG. 13.—*The cuestas and lowlands of western New York*

Block Mountains.—The subject of block mountains offers opportunity to mention some isolated examples like Snake Mountain in Vermont near Lake Champlain and others in that general region. A related topic is fault-line scarps illustrated by the really excellent example bounding the New Jersey Highlands on the east and extending northward into New York State, and again the abrupt margins of the Connecticut Lowland separating it from the upland on either side (Fig. 18). Downfaulted grabens or more truly basins resulting from the erosion of downdropped less resistant rocks are represented by the Boston and Narragansett Basins, the long Connecticut River lowland, and the Pomperaug or Southbury Valley in western Connecticut. Rectangular drainage systems along lines of faulting give strong character to a map of the Adirondacks. Tectonic valleys characterize the New York City region where the Manhattan Street depression, the Dyckman Street cross valley (Fig. 14), the Harlem River, and some of the notches of the Palisades owe their position to ancient lines of dislocation. At Saratoga the mineral springs are believed to follow similar lines of displacement. The offsetting and overlapping of ridges resulting from faulting, planation, and later dissection of a region of dipping alternating resistant and non-resistant beds is illustrated in the Hanging Hills of Meriden and other trap ridges of Connecticut (Fig. 18).

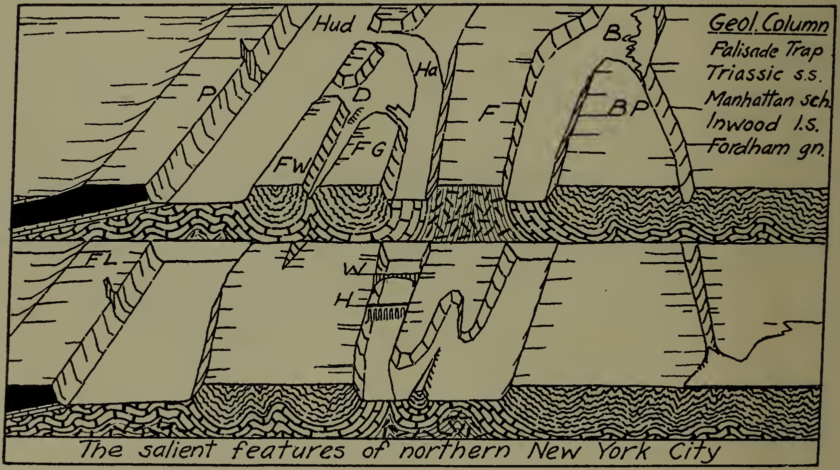


FIG. 14.—*Diagrammatic representation of the essential relief features of northern New York City, with cross-sections showing the underground structure*

The resistent character of the Fordham gneiss, the Manhattan schist, and the Palisade trap is noteworthy, as is also the development of the valleys upon the limestone belts. The letters on the diagram refer to the following features: B, Bronx River; B P, Bronx Park; D, Dyckman street cross valley; F, Fordham Heights; F G, Fort George Heights; F W, Fort Washington Heights; F L, Fort Lee; H, Highbridge; Ha, Harlem River; Hud, Hudson River; P, Palisades; W, Washington Bridge.

Folded Mountains.—When the presentation of folded mountains is introduced the teacher may be proud that he can cite examples from this region unexcelled in the entire world. Around Kingston and Catskill the study may be taken up in miniature, but with all the essentials of form. The Little Catskill Mountains make it possible for one in a half day's journey to see an anticlinal, synclinal, and monoclinal mountain and an anticlinal, synclinal, and monoclinal valley, all in close juxtaposition to each other. The Shawangunk Mountains and Rondout hills are within easy reach. In western New Jersey Kittatinny Mountain may be studied at Delaware Water Gap (Fig. 17). At Harrisburg, Pennsylvania (Fig. 19), the zig-zag ridges developed on pitching anticlines and synclines are of classic renown, and throughout central Pennsylvania the folded Appalachians provide examples of infinite variety and perfection. This whole belt in Pennsylvania, Maryland, and Virginia is so replete with material for the study of folded mountains that it hardly seems feasible to draw any further examples in particular from it. That portion forming the Wyoming syncline or the anthracite coal basin (Fig. 27) might receive especial mention as well as two or three other coal basins of the east when attention is given to the economic side of the question. This topic would touch also upon the extent of the Great Valley from Lake Champlain along the Hudson River, through Kittatinny Valley, Lebanon Valley, Cumberland Valley, and Shenandoah Valley southward. It would also take up the location of towns and railroads in the longitudinal valleys, the character of the soil and related matters.

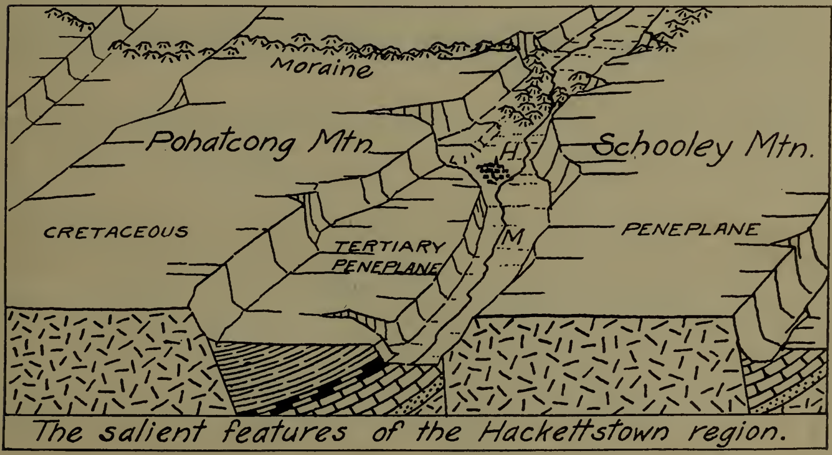


Fig. 15.—*Diagrammatic representation of the essential relief features of the Hackettstown, New Jersey, region*

The infolded, or down-dropped, belts of limestone and shale determine the position of such valleys as that of the Musconetcong River (M) and German Valley next to the east, while the resistent Archean crystallines still preserve the Cretaceous peneplane on the New Jersey Highlands. H indicates the position of Hackettstown, just outside of but within actual view of the terminal moraine. The geological column in descending order is as follows: Martinsburg shale, Jacksonburg limestone, Kittatinny limestone, Hardyston quartzite, Byram gneiss, all of which may be recognized in the cross-section by their symbols and relationship to each other.

Complex Mountains.—Complex mountains carved out of a foundation of crystalline, metamorphic or highly contorted strata find excellent examples in the Adirondack Mountains, the White Mountains, the Green

Mountains, and in fact all of New England, which is only the stump of a worn-down complex mountain mass extending southward in the New Jersey Highlands (Figs. 1, 2, 3). New York City (Fig. 14) is a part of this area. In Pennsylvania, Maryland, and Virginia we find this same type of crystalline rock appearing again in the Piedmont (Fig. 26) and the Blue Ridge portion of the older Appalachians.

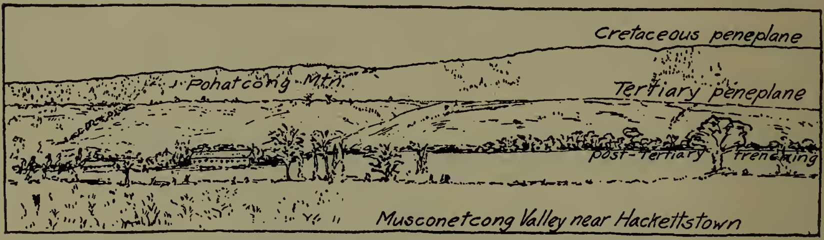


FIG. 16.—*The Cretaceous and Tertiary levels as seen looking west from the base of Schooley Mountain, south of Hackettstown, New Jersey*

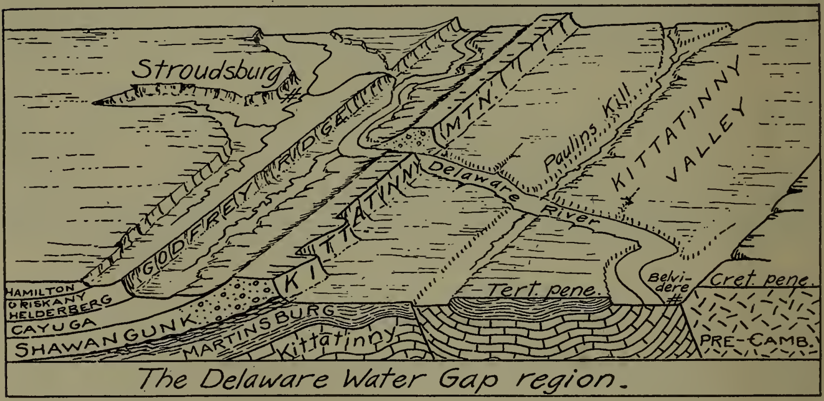


FIG. 17.—*Diagrammatic representation of the main relief features in the Delaware Water Gap region*

The Cretaceous peneplane is preserved on the hard resistant Shawangunk conglomerate, which forms Kittatinny Mountain, and on the pre-Cambric crystallines which form the New Jersey Highlands to the east. The Tertiary peneplane on the floors of the valleys and the post-Tertiary stream dissection are distinctly indicated.

Volcanic Mountains.—Topographic features resulting from volcanic activity in our neighborhood are limited mainly to the trap ridges of Connecticut (Fig. 18), and the Triassic belt of New Jersey (Fig. 29), Pennsylvania, and Virginia, where the Palisades, the Watchung Mountains, and Cemetery Ridge at Gettysburg provide examples worthy of mention. In New England the roots of old volcanoes like Ascutney

Mountain in Vermont may be cited, although their present form is due entirely to later erosion. In Lebanon County, Pennsylvania, Bunker Hill appears to be an old volcanic neck.

FIELD TRIPS

Thus far our efforts have been given to illustrating the principles of the subject of physiography. When the teacher conducts a class into the field or when he undertakes a little more strenuous work there on his own account he will find that all these examples which he has been citing are not grouped there in that nice and orderly way according to topics or following the arrangement of the text book. If he would profit to the greatest extent from what can be seen in the field the investigator must be prepared not only to observe and study whatever features present themselves, disregarding entirely the lack of order in which he finds them, but he must also understand the relation which the different steps in the history of the region bear to each other, so that he may grasp and keep in mind, in some sort of coherent and logical order, all of the features before him. In other words, he must knit together the different threads of knowledge which he has heretofore been spinning independently of each other into a fabric of complex pattern whose design will be manifest only when seen in its entirety.

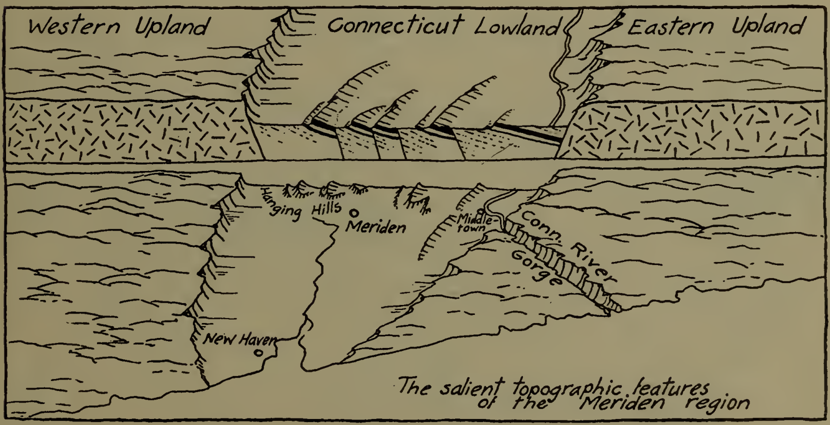


FIG. 18.—*Diagrammatic representation of the essential relief features of the southern Connecticut Valley*

The New England upland preserving the Cretaceous peneplane upon its resistant crystalline rocks and the down-dropped series of Triassic strata with their interbedded trap sheets forming parallel and more or less offsetting ridges as a result of faulting, and also the divergent course of the Connecticut River across a portion of the upland, are all clearly indicated.

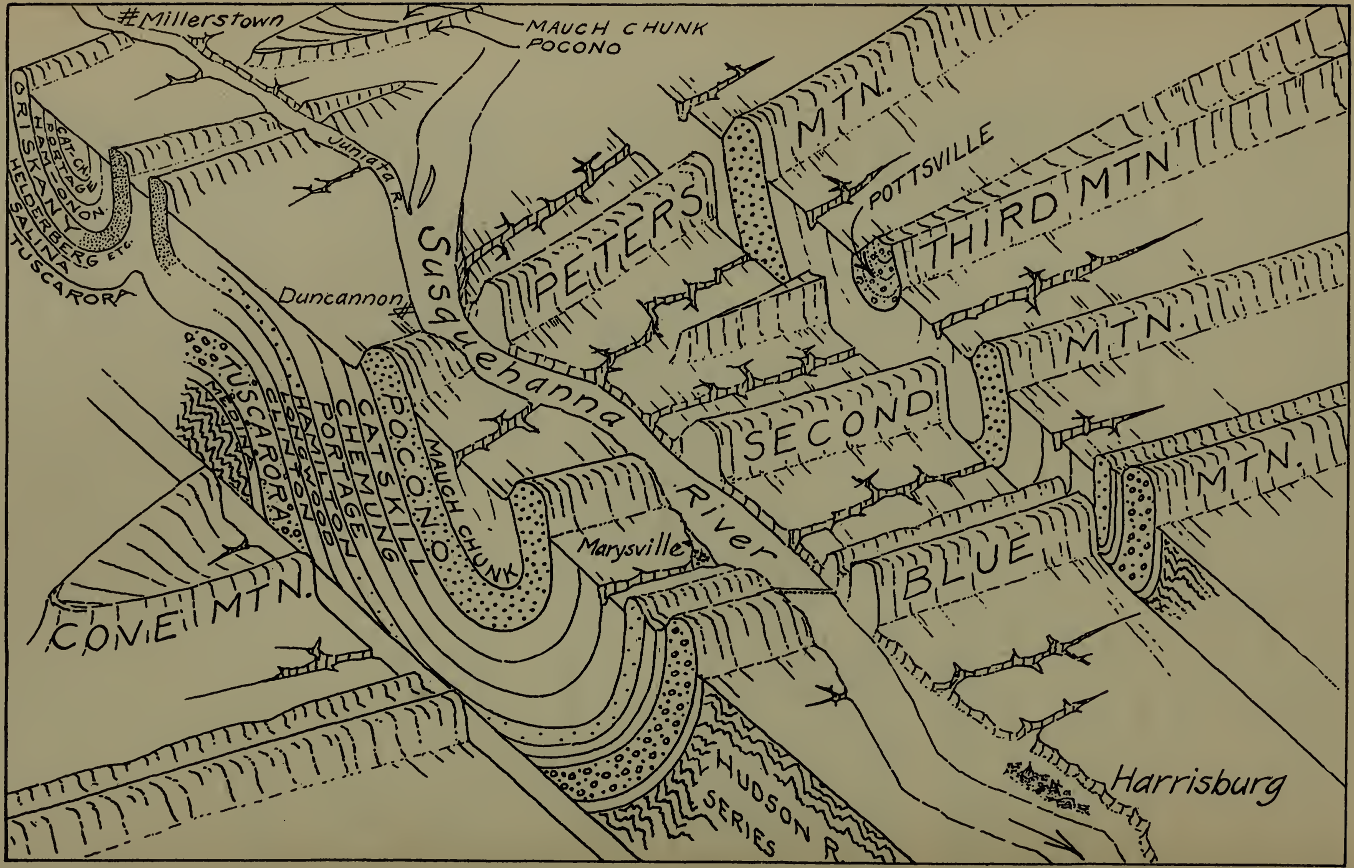


FIG. 19.—*Diagrammatic representation of the essential relief features of the Harrisburg region*

They are primarily due to a northeastward pitching and slightly overturned syncline, in which three or four ridge-forming members are involved. The transverse course of the Susquehanna River across the ridges, and the subsequent tributaries, are strongly brought out. The Cretaceous peneplane remnants on the ridge crests, the Tertiary peneplane as developed on the broad valley floor and the post-Tertiary dissection are the salient elements of the topography.

The teacher of physiography placed in New York with a knowledge of the principles of the subject but not having a speaking acquaintance with the regional physiography of this area would proceed to enlighten himself in this respect in some such manner as follows: He would arrange a series of excursions which might be classified, according to the length of time necessary, as half-day excursions, full-day excursions, week-end trips consuming one day and one night, two days and one night, two days and two nights, three days and two nights, and finally more extended trips of a week or so, and perhaps a vacation jaunt over the whole district.

Suppose we outline a few of these and suggest briefly the main points of interest in each case, as well as the literature which he would look over before going into the field, and the maps and notes which he would take with him.

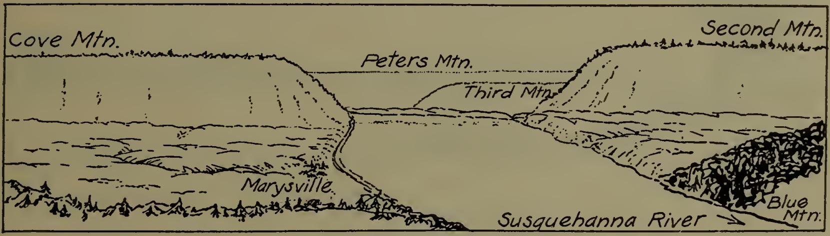


FIG. 20.—*View upstream from the summit of Blue Mountain at the Susquehanna Water Gap*

Showing the even-crested ridges and the broad valley floors with their intrenched streams

HALF-DAY TRIPS

Staten Island.—The first half-day of freedom would find our explorer on his way to Staten Island armed with a topographic and geologic map of the region and perhaps somes notes gleaned from a perusal of Folios 83 and 157 of the Geological Survey. He probably has looked over Hollick's (182) paper on Staten Island drift. The contrast between glaciated and non-glaciated areas, the difference in soil, pre-glacial erosion, the terminal moraine, its knob and kettle topography, the character of the drift and source of the material are some of the topics which would engage his attention.

Palisades.—A second opportunity for a half-day's trip will result in a study of the Palisades (Fig. 14), going by way of Fort Lee and returning by way of the Dyckman Street Ferry. As usual, topographic and geologic maps should be taken. Folio 83 and the New Jersey State Geological

Map both provide structural cross-sections of the region. Essays by Davis (136, 137, 138) on the geographical development of northern New Jersey and on the dates of origin of topographic forms on the Atlantic Coast, and reports by Kümmel (141, 142) of the New Jersey State Survey, as well as other New Jersey (254, 256) reports on the physical features of the State, should be looked over. Consideration on this trip would be given to the formation of vertical cliffs in resistant formations, the Cretaceous peneplane, the origin of the Hudson River, the alluvial terraces, notches produced by cross-faulting, and also to the matter of glaciation.

Inwood and Bronx Park.—A third half-day trip will include a study of the Dyckman lowlands (Fig. 14), the anticlinal limestone valley through which Broadway runs, between the Fort Washington and Fort George Heights, tranverse faulting in the New York City region, the youthful gorge of the Bronx River with its pot-holes, the mature upper portion, small subsequent valleys in the Manhattan schist, glacial striæ, and erratics of Palisade trap. Folio 83 should be studied and articles by Hobbs (45, 46, 47) on faulting and by Kemp (49) on the Bronx River should be kept in mind.

FIG. 21.—*The great stone arch bridge of the Pennsylvania Railroad at the Susquehanna Water Gap*

The piers of the bridge are built upon the same hard formation which makes up the Blue Mountain. Owing to its resistance, this rock occasionally outcrops in the river and forms a series of rifts or rapids, which is true also of most of the other ridge-forming strata.

ONE-DAY TRIPS

Watchung Ridges.—A profitable one-day's excursion will be a study of the Watchung Ridges at Plainfield, N. J. (Fig. 29). The necessary topographic maps, the Passaic Folio, and the New Jersey Geological Map should be on hand. Articles of reference will include essays by Davis (136, 137, 138) on northern New Jersey; also articles by Lewis (143), Kümmel (141, 142), Salisbury (144), and Darton (134). The day's study is devoted to a consideration of trap ridges, water and wind gaps, warping or faulting of the beds, the stream development of this area, the question of streams superposed from an extensive coastal plain and the Passaic Lake Basin. The terminal moraine is visited near by and note is made of the outwash plain upon which Plainfield stands.

Hackettstown. — Another day's trip takes the student to Hackettstown (Figs. 15, 29). From the car window he observes many of the features already seen—the trap ridges, the terminal moraine, and the Passaic Lake Basin; in the field he stands upon the Schooley peneplane at Schooley Mountain, he notes the Tertiary base level and post-Tertiary trenching in Musconetcong Valley (Fig. 16), he understands the origin of the valley structurally, he visits the terminal moraine, and sees evidence of earlier drift farther down the valley. Topographic maps, the New Jersey geological map and one or two State reports should be consulted as well as the essays already referred to.

Long Island. — A third day's trip takes one out to the Hempstead Bay region of Long Island where glaciation is the main topic. Two terminal moraines, outwash plains, erratics, and

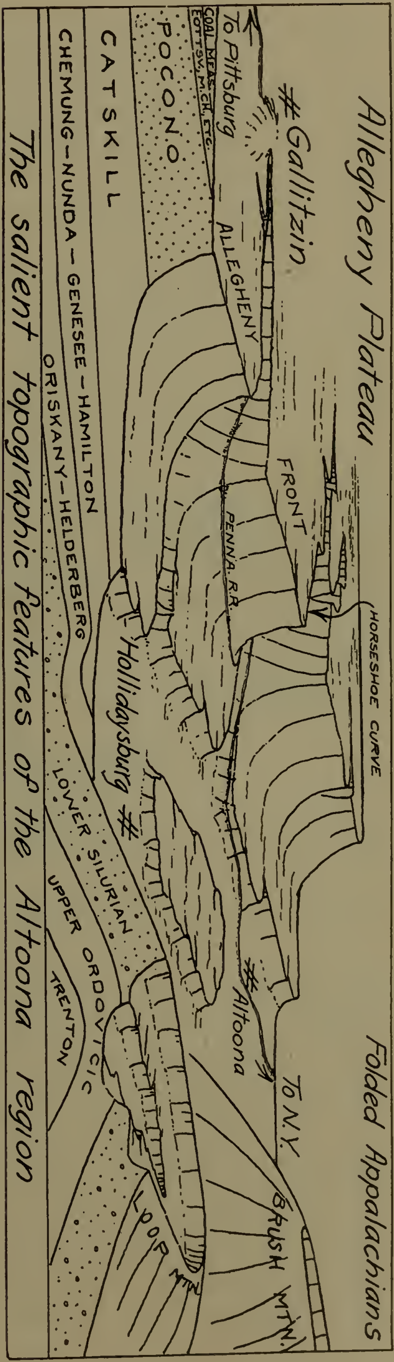


FIG. 22.—*Diagrammatic representation of the essential relief features of the Altoona region.* Incidentally showing the route of the Pennsylvania Railroad from the Appalachian valleys to the surface of the Allegheny Plateau. The bold front of the plateau gives it the aspect of mountains from the valley below, whence the expression Allegheny Mountains.

alternating beds of stratified drift and till are to be seen. Minor features, such as a mid-bay bar, provide a little variety. The chief papers of interest on this trip are Fuller's Professional Paper on Long Island (175), which contains a splendid map of the areal geology, and Veatch's Professional Paper (197) on the water resources of Long Island, which contains useful cross-sections.

Long Branch.—Another trip for a day is the one by boat to Long Branch, giving opportunity to see a part of the cuesta of the coastal plain in Atlantic Highlands, and the drowned inner lowland of New York Bay, the great Sandy Hook spit, and other coastal features, including the little wave-cut cliff on the mainland. Besides having the topographic and geologic map the student should have read Davis' (173) analysis of the development of Cape Cod and referred to Johnson (183) on shorelines.

Delaware Water Gap.—A day may be devoted to a study of the Delaware Water Gap (Fig. 17), and in this connection the recent topographic sheet of this region published by the Geological Survey, with a physiographic description, illustrations and diagrams printed on the back, is most useful. The two peneplanes and the post-Tertiary trenching—in short, the complete history of the Appalachian folds—should be taken up. The articles of Willis (124, 125), Davis (119), and Chamberlin (116) are invaluable in understanding the Appalachian folds. Finally, the vicinity of Paterson offers attractions for another day's trip.

One-Day and One-Night Trips

Shawangunk Mountains.—The question of week-end trips may now receive our attention. By leaving New York late Saturday afternoon the student is still able to reach the field of operations the same night, be ready for an early start the next day and return home late that evening.

For example, he may go to Newplatz, either via the West Shore to Highland or the New York Central to Poughkeepsie, then by ferry to Highland, continuing his journey by electric car. The next day's walk over the Shawangunk Mountains and down to Rosendale, where he takes the train for Kingston, gives him a chance to see the open Wallkill Valley, the rock terraces along its sides representing the Tertiary level, the folded Shawangunk Mountains, delightful in their picturesqueness; the great cliffs of conglomerate, erratics scattered over the plain, glacial striæ on the summits, and some of the smaller folded hills, where a splendid cross-section is provided by the gorge of the Rondout at Rosendale. At a distance he may look over the Hamilton plateau whose abrupt eastern edge is analogous to the Allegheny Front further south, and he may also obtain glimpses of the Catskill Mountains. He may conjecture regarding the position of the Cretaceous peneplane in this area. Besides the topographic map, and possibly the State geologic map which he carries with him, the literature to which he refers will include the New York State Bulletin on the geological history of New York (252), and in this he will be careful to note Darton's interesting stereogram drawing of the Shawangunk Mountains, and he will also take note of Tarr's Physical Geography of New York.

Catskill.—Another profitable trip of this size is the one to Catskill. By leaving New York on the night boat a party may find itself at Catskill next morning ready for the field. During the day they are able to study the folded hills of the Little Catskills, where every conceivable type of Appalachian mountain and valley is presented. Davis' (118) articles with sectional block diagrams unravel the whole secret for us.

FIG. 23.—*Vista down the open trough of Lake George*

The islands on the lake floor are frequently characterized by stoss and lee slopes, indicating a southward movement of the ice tongue

Meriden.—A third trip would set one down in the evening at Meriden, Connecticut, amidst a wealth of interesting features (Fig. 18). The Connecticut Lowland, the faulted trap ridges, forming the Hanging Hills of Meriden, the New England upland, the sharp departure of the Connecticut River from the lowland into its gorge at Middletown may be seen at first hand, and thought should be given to the physical history of this part of New England. Topographic and geologic maps are essential and reference should have been made to Davis' splendid survey

FIG. 24.—A typical portion of the well developed New England peneplane with isolated monadnocks in southern New Hampshire

reports (24, 28), his papers and to some of the articles by Hobbs (44) upon the rivers of the region. The Connecticut State bulletin by Rice (259) on the geology of the State and Barrell's (258) bulletin, entitled Central Connecticut in the Geological Past, are almost indispensable.

TWO-DAYS AND ONE-NIGHT TRIPS

If two entire days and the intervening night may be spent in the field, perhaps the most advantageous results of all may be obtained, especially in the matter of economy. Combinations of several of the one-day trips are thus possible.

Hackettstown.—For instance, the Hackettstown and Delaware Water Gap excursions may be made on successive days by spending the intervening night at Hackettstown or even at the Water Gap.

Beacon Mountain.—Another trip of the same length may be outlined as follows: Leave on the Hudson River day boat, arriving at Fishkill about noon. Go upon Beacon Mountain in the afternoon, continue to Poughkeepsie, cross over to Newplatz, where the night is spent. The next day walk over Shawangunk Mountains to Rosendale, and proceed to New York by train via Kingston. The first day makes possible the observation of the entire length of the Palisades, the Croton delta, the Haverstraw delta (Fig. 6), the gorge of the Hudson with the remnants of the Tertiary level (Fig. 5), the three erosion cycles represented in the region, and in general the salient topographic features of southern New York. The Shawangunk Mountain excursion has already been discussed. For this trip, in addition to the litertaure mentioned, the student should look over Berkey's (250) aqueduct report and the papers by Davis. Possibly the New York State Poughkeepsie Bulletin would be useful.

TWO-DAYS AND TWO-NIGHTS TRIPS

Catskills.—By spending two days and two nights on the journey the circle of operations is still further widened.

For instance, the party may leave by night boat for Catskill, spend the next day studying the Little Catskill folded mountains, stay over that night in Catskill village, and leave the next morning for the Catskill Mountains by way of the inclined railway, arriving in New York the same night. To the topics previously mentioned there is added the opportunity to study a splendid case of stream capture as well as to see the big features of the maturely dissected Catskill plateau, and to have an inspiring view over the adjacent lower country. The additional literature would include a paper by Darton (79) on stream capture and several articles by Rich (90, 91), who has devoted considerable attention to the Catskill region, as well as to papers by Heilprin (86) and Guyot (85).

Harrisburg and Altoona.—Again, by leaving New York late in the afternoon the student may reach Harrisburg that evening, and the next morning go by trolley toward Marysville (Fig. 19). He may then walk through the water gap of the Susquehanna River and see some of the great pitching folds of the Appalachians, continuing by train to Tyrone or Altoona for the night. The next morning he may go upon the Allegheny Front (Fig. 22) and possibly spend the day walking back along the railroad around Horseshoe Curve, returning to New York that evening. Such a trip gives a good cross-sectional view of the Appalachian folds whose historical development, comprising the three cycles of erosion, is worthy of careful study. Davis' (119) paper on the rivers of Pennsylvania should in spite of its close reading and strenuous logic have been carefully studied. The very valuable monograph and annual report by Willis (124, 125) upon the mechanism of Appalachian structure, papers by Chamberlin (116) and Campbell (78), and the very easily understood articles by Tower (98) on topography and travel in Pennsylvania, as well as one by Brigham (115), all contribute to an understanding of the region, and finally there is that little manual of Lesley (120) which, although published in 1856, is still highly suggestive.

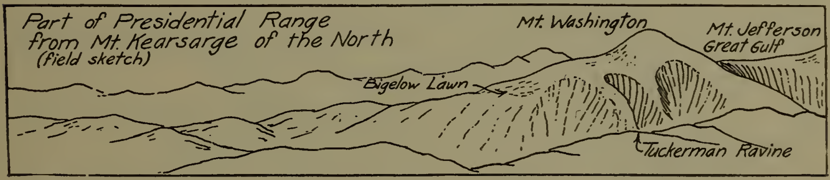


FIG. 25.—*The cirques on the east side of Mt. Washington in the White Mountains*

THREE-DAYS AND TWO-NIGHTS TRIPS

Lake George.—Other slightly longer week-end trips may be made to consume three days and two nights, three days and three nights, or even three days and four nights.

One of the popular three-days and two-nights trips is that taken each year in the Columbia University summer field work. The party leaves New York by day boat in the morning for Fishkill, visits Beacon Mountain that afternoon, proceeds by train to Saratoga, where the first night is spent. The next day it proceeds to Lake George and by boat as far as Silver Bay, returning to Albany for the night. An early train the next morning takes the party to Catskill for a study of the Little Mountains, and New York is reached that evening. This trip always averages less than $25 in cost, covering everything, and provides opportunity at least to see most of the physiographic provinces of the east. In addition to points of interest already noted for other trips, this one introduces the Mohawk delta, the terraces of the Hudson, and the beautiful glacial trough of Lake George (Fig. 23). Several papers by Kemp (70, 71), as well as by other authors, deserve note.

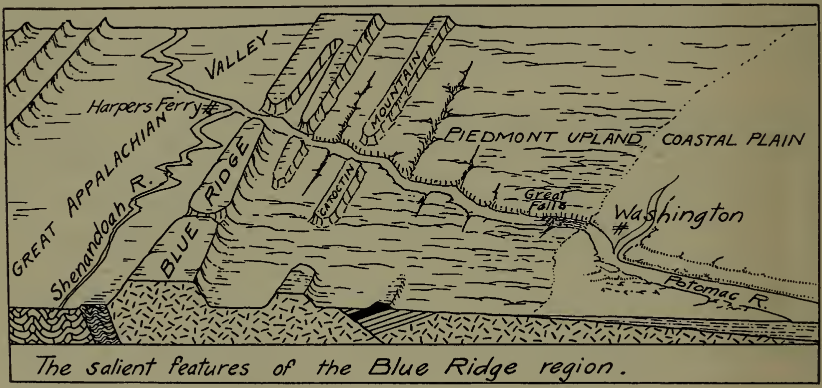


FIG. 26.—*Diagrammatic representation of the essential relief features of the Blue Ridge and Piedmont region*

Part of the folded Appalachian ridges are visible at the extreme left. The Great Falls of the Potomac River are worthy of notice because of their physiographic significance.

Boston Bay.—A splendid week-end adventure is a trip to Boston Bay and Cape Cod. The night boat puts one in Boston next morning ready for a day at Nahant or Nantasket Beach. The following two days may be devoted to a study of Cape Cod. In this connection Johnson (48) on Nantasket Beach and Davis (173) on Cape Cod may be cited. The student would do well also to be acquainted with the writings of Shaler (56), Emerson and Perry (34) on Narragansett Basin and Shaler's (195) survey report on Cape Cod. The New England peneplane, Blue Hill monadnock, the Boston Basin, drumlins, complex tombolos, beach ridges, wave work, a great compound recurved spit, and sand dunes provide much of interest.

One to Two Weeks Trip

New England.—A somewhat more extended trip may be taken which will give a good grasp of all of New England physiography. Leaving New York in the morning the traveler proceeds to North Adams, Massachusetts, in the Berkshire lowland. A day may be spent climbing Mount Greylock, and possibly another one walking over that portion of the New England upland pierced by the Hoosac tunnel (Fig. 4). Study of the gorge of the Deerfield River, its terraces and those of the Connecticut and other streams is then conveniently taken up, after which Mount Monadnock forms a good objective (Fig. 24). The climb up this peak is a very feasible one, although near-by accommodations for the traveler are almost lacking. From there procedure is made to the White Mountains by way of Lake Winnepesaukee. If this trip is undertaken before the last part of June it is likely that the railway to the top of Mount Washington will not be in operation, but the walk up by trail from Crawford House is very practicable. From the Tip-top House, which now has accommodations for overnight visitors, a carriage road leads down to the Glen House, which is a reasonable and convenient place to stop. The next day a really strenuous climb will take the hardy individual over the northern summits of the range down to Gorham, where he can catch a train for Portland that afternoon. The trip from Portland to New York may be interrupted at Boston for a study of the drumlin region and Cape Cod. If the arm of the cape is rounded by train the explorer will find himself within easy reach of Nantucket and Marthas Vineyard, after which a day's stop at Meriden, Connecticut, will round out a very comprehensive journey. This trip embraces almost every topic in New England physiography, the peneplane and its monadnocks, the longitudinal valleys forming the Berkshire and Connecticut lowlands, the fascinating topic of river terraces, the White Mountain monadnock group, with its glacial features, its cirques and troughs, the drumlins and the work of the waves upon them, the Cape Cod spit, the lobate terminal moraine of Marthas Vineyard and the mainland, and finally the faulted trap ridges of Connecticut. The available literature is rather extensive and would include the contributions of Davis, Shaler, Goldthwait, Johnson, Hobbs, Emerson, Jefferson, Dale, Gulliver, Woodworth, and others. This trip is one which would occupy between one and two weeks and would cost probably between $50 and $75.

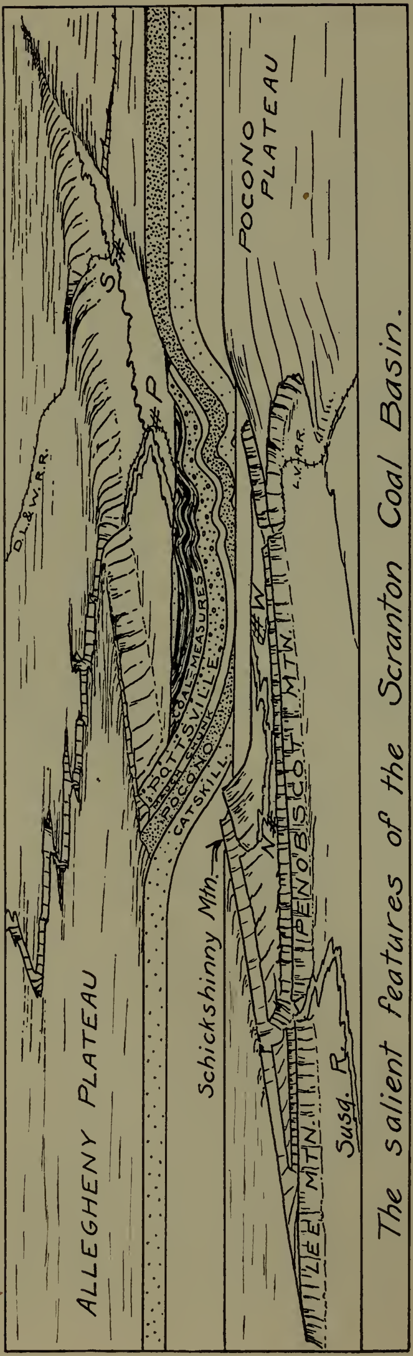


FIG. 27.—*Diagrammatic representation of the principal relief elements of the Wyoming, or northern, anthracite coal basin*

Owing to its synclinal structure the coal-bearing formations were here preserved from erosion. This is the largest of the anthracite coal areas of eastern Pennsylvania. All are more or less similar in structure. The letters refer to the following cities: S, Scranton; P, Pittston; W, Wilkes-Barre; N, Nanticoke.

Several other trips of similar length to different points of the compass might now be outlined, but it seems more advisable to combine them in one big swing around the circle, which will bring the traveler at occasional intervals within easy reach of New York.

ONE-MONTH TRIP

Entire Area. — The journey may start by boat and have as its first objective the city of Norfolk, Virginia. From this point electric trains make easy a visit to Virginia Beach and the giant dunes of Cape Henry (Fig. 11). The Norfolk Folio of the Geological Survey and minor articles, such as those by Hitchcock (180), should be studied in this connection. The old delta of the Potomac River, the shifting dunes, and the drowned coast offer the main topics of interest. If time and funds permit a short side trip may be made to the Dismal Swamp, which is described in Shaler's (187, 190, 193) survey reports. After Norfolk, the journey may be directed to

Washington, either by boat or train via Richmond. The drowned Chesapeake Bay is to be seen if the first alternative is adopted, and some of the folios of this region should have been glanced over. The investigations of Darton, Shaler, Willis, Fontaine, Clark, Miller, Hunter, and especially McGee (184, 185), throw light upon this region. In case the Richmond route is taken opportunity is given to see some of the isolated Triassic occurrences of the south and to note the location of the Fall Line. Darton's Richmond bulletin (172) may be useful as well as Surface's (160) account of the physiography of Virginia. At Washington a visit should be made by electric car to the Great Falls of the Potomac, and realization should be had of the high and low terraces of the Potomac River. The necessary data may be found in the Washington Folio. From Washington a splendid electric line runs sixty miles over the rolling Piedmont country to Bluemont at Snicker's Gap on the Blue Ridge (Fig. 26). During this ride other occurrences of the Triassic are to be seen. From this point the traveler should walk over the ridge into Shenandoah Valley to take the train for Luray. The important literature covering western Virginia physiography and related topics is in the form of a report by Keith (154) on the Catoctin belt, Bascom (150) on the Piedmont, Geiger and Keith (153, 163) on Harpers Ferry, and Surface's (160) article already mentioned. An account of the Luray Caverns appears in the National Geographic Magazine (127). The next lap of the journey is by train to Cumberland, Maryland. The entrenched meanders of the Potomac River below the even crest of the folded Appalachians are followed by the railroad. The structural relations of the various ridges may be learned from the Papaw-Hancock Folio of the U. S. Geological Survey. Additional valuable material may be found in Clark and Mathew's Maryland Survey report on the physical features of the State (265), and articles by Clark, Martin, and Campbell. Between Cumberland and Altoona the traveler rides in the broad longitudinal valley at the foot of the Allegheny Front (Fig. 22). After a visit to the crest of the plateau he may continue east to Philadelphia, stopping at Harrisburg on the way. Topics and literature pertaining to this important section have been mentioned. A day around Philadelphia gives occasion to see the falls of the Schuylkill, now artificially modified, and the terraces marking a former shoreline on the oldland in Fairmont Park. A trip out to Chester Valley is well worth while. The main elements of Philadelphia physiography are outlined in the Philadelphia Folio. If the traveler does not now feel obliged to come on to New York he may take train for Wilkes-Barre and Scranton and on the way enjoy a ride on the very crest of some of the Appalachian ridges in the Pottsville coal region. The environs of Scranton are not likely to be attractive to the visitor unless he is buoyed up with an enthusiasm for the study of the features (Fig. 27). It takes almost half a day to go by train and to walk the necessary distance from Archbald, a few miles north of the city, in order to visit the largest pot-hole in the country, which oddly enough is to be found almost at the top of one of the ridges and was presumably ground out by a subglacial torrent (262). The northward continuation of this journey is highly delightful. Stops may be made at Ithaca and at Watkins Glen. The finger lakes of western New York are studied and some attention is given to the preglacial pattern of the area. Grabau's studies on this phase of the subject are invaluable. Articles by Campbell (78), Hubbard (88), Tarr (93, 94, 95, 96, 97), Fairchild (82), and Dryer (81) regarding the finger lakes region are very readable. Several folios, especially the Watkins Glen-Catatonk one, should be noted. Niagara Falls is the next important stopping place, and because of its physiographic significance should be studied with great care (Fig. 28). The excellent Niagara Falls Folio ought, if possible, to be on hand. Important papers are those by Gilbert (217, 220), Upham (229, 230), Coleman (208, 209, 210), Taylor (228), Spencer (225, 227), Wilson (231), Leverett (222), and Grabau's (251) guide of the region. Of course there is a trip through the gorge to Lewiston. Not far east of Niagara Falls are the ridge roads, built on the old beach ridges of Lake Iroquois. Between Buffalo and Albany the drumlin area should be visited and the physiographer should see the old glacial channel at Rome, N. Y., as well as other similar features of interest. The significance of the Mohawk Valley lowland should be thoroughly appreciated. From Albany the traveler may easily return to New York or if he can devote eight or ten days more he can go on to Lake George, Lake Champlain, Ausable Chasm, the

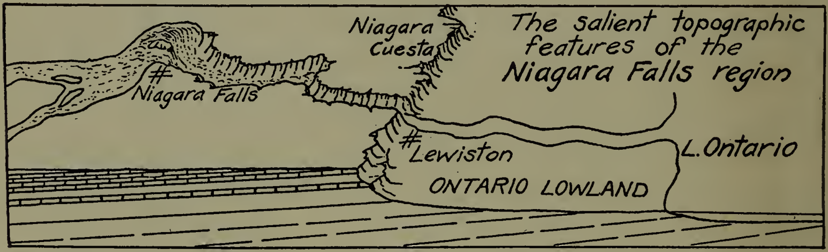


FIG. 28.—*Diagrammatic representation of the main relief features at Niagara Falls*

The seven-mile gorge cut during the retreat of the falls from their earlier position at Lewiston is the most striking element in the landscape. The two resistent limestones serving as cuesta formers are indicated in the section.

Green Mountains, the White Mountains, Portland, Boston and then home. Most of the topics of this last portion have already received attention. One of the most important papers to which the student should have reference on this long journey, as well as on many of the smaller ones, is the paper by Fenneman (6) on the physiographic provinces of the United States. It includes an excellent map and summary description.

The total length of time necessary for this swing around the circle, whose radius is within 300 miles of New York, need not be more than thirty days and ought easily to be accomplished for less than $150. In educational value it would outweigh the total of many college courses and would prove a continual source of inspiration to the teacher of physiography in the eastern United States.

FIELD PREPARATION

May I conclude now with a word regarding the preliminary preparation of the student before going into the field. To really be alert in appreciating what he sees and to make the most efficient expenditure of his time and money, the student should put himself to quite a little trouble if necessary to look over before each field trip all the literature that is available. Not only should he look it over and glean from it the essence which seems to pertain to the work in hand, but he should prepare in a compact and easily carried form a digest of the articles he reads. A small note book which will nicely go into the pocket may, by the use of fine though legible handwriting, be made to contain summaries of a great many bulky articles. In case diagrams and maps would be helpful in the field and copies are not available for this purpose, they may be traced off directly in ink upon tracing paper, more or less roughly, and these pasted with the notes they illustrate.

The form in which maps are taken into the field has a great deal to do with the use which is made of them. If they are taken along all rolled up the way they come from the publisher, they do not invite frequent reference and a listless attitude of mind is likely to result in the user. But if the maps are conveniently mounted on cloth so as to fold up in pocket size their utility is many times enhanced. This applies not only to topographic sheets but to State geologic maps which may be cut into several pieces and each piece mounted in sections so as to fold.

The particular style in which one travels depends upon the character of the individual, upon the length of the trip, upon the nature of the region visited, as well as upon the object of the work. As a general thing, when the undertaking smacks a little of exploration and adventure, as it does frequently when the exact route to be followed cannot be predetermined, or when train schedules are not known, or when the walking ability of the explorer cannot be reduced to mathematical exactitude, or when hotel accommodations of towns have not been ascertained, or when all the features to be seen have not been evaluated correctly, then it becomes necessary to travel practically without a detailed schedule, stopping at night wherever one happens to be. This precludes the carrying of much impedimenta. A knapsack, which will hold a few note books, maps, some extra underclothing, handkerchiefs, sweater, thin rain coat, and a pair of tennis shoes, can be readily carried all the time, and will not be actually intolerable for ten days or so at a stretch. In fact, this manner of traveling gives a certain delightful sense of freedom not to be had in any other way.

ACKNOWLEDGMENTS

The bulk of this paper was first given essentially as it now stands in an address before the Physiographers' Club of New York. It was intended primarily to embody in a compact form a mass of suggestions for teachers, and it now appears in a more permanent character through the courtesy of the New York Academy of Sciences. Owing to its condensed arrangement it has been impossible to treat the various field trips in the detail which might seem desirable and many points of interest are necessarily quite ignored. It can therefore hardly be classed as a handbook, though it may serve imperfectly as a guide.

The subject of physiography has proved to be of high intrinsic value in the present war, and it is no mere braggadocio to say that the man who has been trained in physiography and geology has developed certain qualifications essential to the officer in the field, the ability to use and read maps, the sense of direction, the habit of being out of doors and "on your own," the knack of making rough sketches and simple maps and especially that "sense of terrain," which comes only from work in the open, map in hand. The desire to encourage such studies has been the prime reason for preparing this paper.

The importance to the physiographer of using and being familiar with maps of all kinds can hardly be overexaggerated, and it is only because they are so essential and should be used in the original that more of them have not been introduced into this article.

For the use of maps and photographs, credit is due as follows: Fig. 1, Geological Map, generalized from U. S. G. S., geological map of North America accompanying Profes. Pap. 71; Fig. 2, Map of Physiographic

Provinces after Fenneman, slightly modified, descriptions of provinces after Fenneman and Johnson; Fig. 8, Map of terminal moraine from Islip, N. Y., sheet; Fig. 10, Map of drumlins from Clyde, N. Y., sheet, sketch after Tarr; Fig. 13, Cuestas and lowlands of western New York, after map in Niagara Folio; Fig. 21, Susquehanna Water Gap, from Nat. Geog. Mag.; Fig. 23, Lake George, after Detroit Photo. Co.

During the preparation of the diagrams the informal criticisms of Mr. F. K. Morris, of the Department of Geology, Columbia University, were distinctly helpful.

BIBLIOGRAPHY

The references below are grouped according to physiographic provinces. Those preceded by a star are deemed most important from the physiographic viewpoint. In the text the numbers following the names of authors refer to this list.

The chief journals and periodicals to which reference may be made are: American Journal of Science, American Museum Journal, Annals of the Association of American Geographers, Annals of the New York Academy of Sciences, Appalachia, Bulletin of the Geological Society of America, Geographical Review (formerly Bulletin of the American Geographical Society), Journal of Geography, Journal of Geology, National Geographic Magazine, and Science. The standard text-books on geology and physiography contain much information upon the features of the northeastern United States.

The most convenient bibliographies are those provided in the following bulletins of the U. S. Geological Survey, which are indexed by both subject and author: 44 (1886), 75 (1887-1889), 91 (1890), 99 (1891), 127 (1732-1891), 130 (1892-1893), 135 (1894), 146 (1895), 149 (1896), 156 (1897), 162 (1898), 172 (1899), 188 and 189 (1892-1900), 203 (1901), 221 (1902), 240 (1903), 271 (1904), 301 (1901-1905), 372 (1906-1907), 409 (1908), 444 (1909), 495 (1910), 524 (1911), 545 (1912), 584 (1913), 617 (1914), 645 (1915), 665 (1916).

I.—General

*1. Bowman, I. 1911. Forest physiography.
2. Brigham, A. P. 1903. Geographic influences in American history.
3. Davis, W. M. 1898. Physical geography.
4. Emerson, F. V. 1908. Geographic interpretation of New York city. Bull. Am. Geog. Soc., XL, p. 587.
5. Fenneman, N. M. 1914. Physiographic boundaries in the U. S. Ann. Assn. Am. Geog., IV, p. 84.

*6. Fenneman, N. M. 1916. Physiographic divisions of the U. S. Ann. Assn. Am. Geog., VI, p. 19 (with map).
7. Gratacap, L. P. Geology of the city of New York.
*8. Powell, J. W. 1895. Physiographic regions of the U. S. Nat. Geog. Soc. Monographs, p. 65.
9. Salisbury, R. D., and Atwood, W. W. 1908. Interpretation of topographic maps. Profes. Pap. U. S. G. S., No. 60.
10. Semple, E. C. 1903. American history and its geographic conditions.
11. Tarr, R. S. 1902. Physical geography of New York state.
12. Tarr, R. S., and Martin, L. 1917. College physiography.
13. Tower, W. S. 1905. Geography of American cities. Bull. Am. Geog. Soc., XXXVII, p. 577.
14. Van Hise, C. R., and Leith, C. K. 1909. Pre-cambrian geology of North America. Bull. U. S. G. S., No. 360.
15. Willis, B. 1912. Index to stratigraphy of North America. Profes. Pap. U. S. G. S., No. 71 (with geol. map).

II.—New England Province

*16. Barrell, J. Central Connecticut in geologic past. Bull. Conn. Geol. Surv., No. 23.
17. Barrell, J. 1913. Terraces of northern Appalachians. Bull. Geol. Soc. Am., XXIV, p. 688.
18. Clapp, F. G. 1908. Glacial period in New England. Bull. Geol. Soc. Am., XVIII, p. 505.
19. Dale, T. N. 1892. Rensselaer grit plateau in New York. 13th Ann. Rept. U. S. G. S., Part 2, p. 291.
20. Dale, T. N. 1898. Slate belt of New York and Vermont. 19th Ann. Rept. U. S. G. S., Part 3, p. 153.
21. Dale, T. N. 1905. Taconic physiography. Bull. U. S. G. S., No. 272.
22. Daly, R. A. 1903. Ascutney mountain, Vermont. Bull. U. S. G. S., No. 209.
23. Darton, N. H. 1894. Geologic relations from Green Pond, N. J., to Skunnemunk Mtn., N. Y. Bull. Geol. Soc. Am., V, p. 367.
24. Davis, W. M. 1888. Triassic of Connecticut valley. 7th Ann. Rept. U. S. G. S., p. 455.
25. Davis, W. M. 1890. Glacial sand plains. Bull. Geol. Soc. Am., I, p. 195.
*26. Davis, W. M. 1891. Dates of origin of topographic forms on Atlantic slope. Bull. Geol. Soc. Am., II, p. 545.
*27. Davis, W. M. 1895. Physical geography of southern New England. Nat. Geog. Soc. Monographs, p. 269.
*28. Davis, W. M. 1897. Triassic of Connecticut. 18th Ann. Rept. U. S. G. S., Part 2, p. 1.
*29. Davis, W. M. 1902. River terraces in New England. Bull. Mus. Comp. Zool., XXXVIII, p. 281 (also in essays).
*30. Davis, W. M. 1909. Geographical essays.
31. Emerson, B. K. 1891. Triassic of Massachusetts. Bull. Geol. Soc. Am., II, p. 451.
32. Emerson, B. K. 1898. Old Hampshire county, Mass. Monog. U. S. G. S., No. 29.

33. Emerson, B. K. 1899. Geol. of eastern Berkshire county, Mass. Bull. U. S. G. S., No. 159.
34. Emerson, B. K., and Perry, J. H. 1907. Crystalline rocks of Rhode Island. Bull. U. S. G. S., No. 311.
35. Fairchild, H. L. 1914. Pleistocene marine submergence of Connecticut and Hudson valleys. Bull. Geol. Soc. Am., XXV, p. 219.
36. Fettke, C. R. 1914. Manhattan schist of southeastern New York state. Ann. N. Y. Acad. Sci., XXIII, p. 193.
37. Fuller, M. L. 1899. Elements in sand-plain formation. Jour. Geol., VII, p. 452.
38. Fuller, M. L. 1901. Pre-Wisconsin till in southeastern Mass. Jour. Geol., IX, p. 311.
*39. Goldthwait, J. W. 1914. Remnants of an old graded upland on the Presidential Range of White mountains. Am. Jour. Sci., XXXVII, p. 451.
40. Gulliver, F. P. 1893. Newtonville sand plain. Jour. Geol., I, p. 803.
41. Hitchcock, C. H. 1896. Geol. of New Hampshire. Jour. Geol., IV, p. 44.
42. Hobbs, W. H. 1893. Housatonic valley. Jour. Geol., I, p. 780.
43. Hobbs, W. H. 1900. Pomperaug valley. 21st Ann. Rept. U. S. G. S., Part 3, p. 7.
*44. Hobbs, W. H. 1901. River system of Connecticut. Jour. Geol., IX, p. 469.
*45. Hobbs, W. H. 1904. Lineaments of Atlantic border region. Bull. Geol. Soc. Am., XV, p. 483.
46. Hobbs, W. H. 1905. Rock floor of greater New York. Bull. U. S. G. S., No. 270.
*47. Hobbs, W. H. 1905. Origin of channels surrounding Manhattan island. Bull. Geol. Soc. Am., XVI, p. 151.
*48. Johnson, D. W., and Reed, W. G. 1910. Form of Nantasket beach. Jour. Geol., XVIII, p. 162.
49. Kemp, J. F. 1896. Glacial or post-glacial diversion of the Bronx river. Trans. N. Y. Acad. Sci., Dec. 15, 1896, p. 18.
*50. Kemp, J. F. 1913. Buried river channels of the northeastern states. Proc. Wyom. Hist. and Geol. Soc., XIV.
51. Kümmel, H. B. 1893. Rivers of Connecticut. Jour. Geol., I. p. 371.
*52. Lobeck, A. K. 1917. New England peneplane in White mountains. Geog. Rev., III, p. 53.
53. Perry, J. H. 1904. Geol. of Monadnock mountain. Jour. Geol., XII, p. 1.
54. Pumpelly, R., Wolff, J. E., and Dale, T. N. 1894. Green mountains in Massachusetts. Monog. U. S. G. S., No. 23.
*55. Rice, W. N., and Gregory, H. E. Manual of geology of Connecticut. Bull. Conn. Geol. Surv., No. 6.
56. Shaler, N. S., Woodworth, J. B., and Foerste, A. F. 1899. Narragansett basin. Monog. U. S. G. S., No. 33.
57. Stone, G. H. 1893. Osar gravels in Maine. Jour. Geol., I, p. 246.
58. Stone, G. H. 1899. Glacial gravels of Maine. Monog. U. S. G. S., No. 34.
59. Wolff, J. E., and Brooks, A. H. 1897. Age of Franklin white limestone of Sussex, N. J. 18th Ann. Rept. U. S. G. S., Part 2, p. 425.
60. Woodworth, J. B. 1894. Typical eskers of New England. Proc. Boston Soc. Nat. Hist., XXVI, p. 197.

61. Woodworth, J. B., and Marbut, C. F. 1896. Queen's river moraine in Rhode Island. Jour. Geol., IV, p. 691.
*62. Holyoke Folio, U. S. G. S., No. 50.
*63. New York Folio, U. S. G. S., No. 83.
*64. Passaic Folio, U. S. G. S., No. 157.
65. Franklin Furnace Folio, U. S. G. S., No. 161.
*66. Raritan Folio, U. S. G. S., No. 191.

III.—Adirondack Province

*67. Alling, H. L. 1917. Glacial lakes of central Adirondacks. Bull. Geol. Soc. Am., XXVII, p. 645.
*68. Brigham, A. P. 1898. Note on trellised drainage in Adirondacks. Am. Geol., XXI, p. 219.
69. Cushing, H. P. 1907. Asymmetric differentiation in bathylith of Adirondack syenite. Bull. Geol. Soc. Am., XVIII, p. 477.
*70. Kemp, J. F. 1897. Physiography of eastern Adirondacks. Bull. Geol. Soc. Am., VIII, p. 408.
*71. Kemp, J. F. 1906. Physiography of Adirondacks. Pop. Sci. Mo., March, 1906.
72. Miller, W. J. 1910. Trough faulting in southern Adirondacks. Science, XXXII, p. 95.
73. Miller, W. J. 1911. Preglacial course of upper Hudson river. Bull. Geol. Soc. Am., XXII, p. 177.
(See also several New York state bulletins.)

IV.—Allegheny Plateau Province

*74. Brigham, A. P. 1893. Finger lakes of New York. Bull. Am. Geog. Soc., XXIV, p. 23.
75. Brigham, A. P. 1897. Glacial flood deposits in Chanango valley. Bull. Geol. Soc. Am., VIII, p. 17.
*76. Brigham, A. P. 1898. Topography of Mohawk valley. Bull. Geol. Soc. Am., IX, p. 183.
77. Butts, C. 1906. Devonian section near Altoona. Jour. Geol., XIV, p. 618.
*78. Campbell, M. R. 1903. Geog. development of northern Penn. and southern N. Y. Bull. Geol. Soc. Am., XIV, p. 277.
*79. Darton, N. H. 1896. Stream-robbing in the Catskills. Bull. Geol. Soc. Am., VII, p. 505.
*80. Davis, W. M. 1891. Dates of origin of topographic forms on Atlantic slope. Bull. Geol. Soc. Am., II, p. 545.
*81. Dryer, C. R. 1904. Finger lake region of western New York. Bull. Geol. Soc. Am., XV, p. 449.
*82. Fairchild, H. L. 1895. Glacial lakes of western New York. Bull. Geol. Soc. Am., VI, p. 353.
83. Fairchild, H. L. 1905. Ice erosion a fallacy. Bull. Geol. Soc. Am., XVI, p. 13.
84. Foshay, P. M., and Hice, R. R. 1891. Glacial grooves at southern margin of drift. Bull. Geol. Soc. Am., II, p. 457.
85. Guyot, A. 1880. Physical structure and hypsometry of the Catskill mountain region. Am. Jour. Sci., 3rd ser., XIX, p. 429.

*86. Heilprin, A. 1907. The Catskill mountains. Bull. Am. Geog. Soc., XXXIX, p. 193.
87. Hice, R. R. 1903. Northward flow of ancient Beaver river. Bull. Geol. Soc. Am., XIV, p. 297.
88. Hubbard, G. D. 1906. Drumlinoids of the Catatonk region. Bull. Am. Geog. Soc., XXXVIII, p. 355.
89. Quereau, E. C. 1898. Jamesville lake, N. Y. Bull. Geol. Soc. Am., IX, p. 173.
*90. Rich, J. L. 1914. Catskill mountains. Bull. Geol. Soc. Am., XXV, p. 68.
*91. Rich, J. L. 1915. Notes on physiography and glacial geology of the northern Catskills. Am. Jour. Sci., 4th ser., XXXIX, p. 137.
92. Shaw, E. W. 1911. High terraces and abandoned valleys in western Pennsylvania. Jour. Geol., XIX, p. 140.
93. Tarr, R. S. 1894. Lake Cayuga a rock basin. Bull. Geol. Soc. Am., V, p. 339.
*94. Tarr, R. S. 1905. Drainage features of central New York. Bull. Geol. Soc. Am., XVI, p. 229.
95. Tarr, R. S. 1905. Moraine of Seneca and Cayuga lake valleys. Bull. Geol. Soc. Am., XVI, p. 215.
96. Tarr, R. S. 1905. Gorges and waterfalls of central New York. Bull. Am. Geog. Soc., XXXVII, p. 193.
*97. Tarr, R. S. 1910. Towns and cities of central New York. Bull. Am. Geog. Soc., XLII, p. 738.
*98. Tower, W. S. 1906. Regional and economic geography of Pennsylvania. Bull. Geog. Soc. Phila., IV, pp. 9, 113, 193, 271; V, p. 21.
99. Piedmont Folio, U. S. G. S., No. 28.
100. Monterey Folio, U. S. G. S., No. 61.
101. Gaines Folio, U. S. G. S., No. 92.
102. Elkland-Tioga Folio, U. S. G. S., No. 93.
103. Brownsville-Connellsville Folio, U. S. G. S., No. 94.
104. Waynesburg Folio, U. S. G. S., No. 121.
105. Elders Ridge Folio, U. S. G. S., No. 123.
106. Rural Valley Folio, U. S. G. S., No. 125.
107. Ebensburg Folio, U. S. G. S., No. 133.
108. Beaver Folio, U. S. G. S., No. 134.
109. Rogersville Folio, U. S. G. S., No. 146.
110. Accident-Grantsville Folio, U. S. G. S., No. 160.
111. Watkins Glen-Catatonk Folio, U. S. G. S., No. 169.
112. Sewickley Folio, U. S. G. S., No. 176.
113. Barnesboro-Patton Folio, U. S. G. S., No. 189.

V.—NEWER APPALACHIANS PROVINCE

114. Baldwin, S. P. 1894. Pleistocene of Champlain valley. Am. Geol., XIII, p. 170.
*115. Brigham, A. P. 1905. The great roads across the Appalachians. Bull. Am. Geog. Soc., XXXVII, p. 321.
116. Chamberlin, R. T. 1910. Appalachian folds of Pennsylvania. Jour. Geol., XVIII, p. 228.

*117. Clark, W. B., and Mathews, E. B. 1906. Physical features of Maryland. Md. Geol. Surv., Spec. Pub., VI (with geol. map).

*118. Davis, W. M. 1884. The little mountains east of the Catskills. Appalachia, III, p. 20; also Bull. Mus. Comp. Zool., VII, p. 310.

*119. Davis, W. M. 1889. Rivers and valleys of Pennsylvania. Nat. Geog. Mag., I, p. 183 (also in essays).

*120. Lesley, J. P. 1856. Manual of coal and its topography.

121. Stoek, H. H. 1901. Pennsylvania anthracite coal field. 22nd Ann. Rept. U. S. G. S., Part 3, p. 55.

*122. Tower, W. S. 1905. Topography and travel in Pennsylvania. Bull. Am. Geog. Soc., XXXVII, p. 145.

123. Williams, E. H. 1894. Extramorainic drift between the Delaware and Schuylkill. Bull. Geol. Soc. Am., V, p. 281.

*124. Willis, B. 1895. Northern Appalachians. Nat. Geog. Soc., Monographs, p. 169.

*125. Willis, B. 1892. Mechanics of Appalachian structure. 13th Ann. Rept. U. S. G. S., Part 2, p. 211.

126. Willis, B. 1907. Potomac river basin. Wat. Sup. Pap. U. S. G. S., No. 192.

127. ———. 1906. Luray caverns. Nat. Geog. Mag., XVII, p. 358.

128. Harpers Ferry Folio, U. S. G. S., No. 10.

129. Staunton Folio, U. S. G. S., No. 14.

130. Piedmont Folio, U. S. G. S., No. 28.

131. Franklin Furnace Folio, U. S. G. S., No. 161.

132. Waynesburg-Chambersburg Folio, U. S. G. S., No. 170.

133. Papaw-Hancock Folio, U. S. G. S., No. 179.

VI.—Triassic Lowland

134. Darton, N. H. 1890. Traps of Newark system in New Jersey. Bull. U. S. G. S., No. 67.

135. Davis, W. M. 1880. Triassic sandstones. Bull. Mus. Comp. Zool., VII, p. 249.

*136. Davis, W. M. 1890. Geographic development of northern New Jersey. Proc. Boston Soc. Nat. Hist., XXIV, p. 365.

*137. Davis, W. M. 1890. Rivers of northern New Jersey. Nat. Geog. Mag., II, p. 81 (also in essays).

*138. Davis, W. M. 1891. Dates of origin of topographic forms on Atlantic slope. Bull. Geol. Soc. Am., II, p. 545.

139. Hobbs, W. H. 1902. Former extent of Newark system. Bull. Geol. Soc. Am., XIII, p. 139.

140. Keith, A. 1893. Catoctin belt. 14th Ann. Rept. U. S. G. S., p. 285.

141. Kümmel, H. B. 1897. Newark system of New Jersey. Jour. Geol., V, p. 541.

142. Kümmel, H. B. 1899. Newark system of New Jersey and New York. Jour. Geol., VII, p. 23.

143. Lewis, J. V. 1907. Newark trap. Bull. Geol. Soc. Am., XVIII, p. 195.

*144. Salisbury, R. D., and Kümmel, H. B. 1895. Lake Passaic. Jour. Geol., III, p. 353.

*145. New York Folio, U. S. G. S., No. 83.

*146. Passaic Folio, U. S. G. S., No. 157.

VII.—Older Appalachians Province

147. Barrell, J. 1913. Terraces of northern Appalachians. Bull. Geol. Soc. Am., XXIV, p. 688.
148. Bascom, F. 1893. South mountain structure. Jour. Geol., I, p. 813.
149. Bascom, F. 1896. Volcanic rocks of South mountain, Pa. Bull. U. S. G. S., No. 136.
150. Bascom, F. 1905. Piedmont of Pennsylvania. Bull. Geol. Soc. Am., XVI, p. 289.
151. Darton, N. H. Economic geology of Richmond. Bull. U. S. G. S., No. 483.
152. Eaton, H. N. 1912. Geology of South mountain, Pa. Jour. Geol., XX, p. 331.
153. Geiger, H. R., and Keith, A. 1891. Structure of Blue Ridge near Harpers Ferry. Bull. Geol. Soc. Am., II, p. 155.
*154. Keith, A. 1893. Catoctin belt. 14th Ann. Rept. U. S. G. S., Part 2, p. 285.
155. Mathews, E. B. 1905. Maryland and Pennsylvania Piedmont. Bull. Geol. Soc. Am., XVI, p. 329.
*156. McGee, W J. 1896. Geographic history of Piedmont plateau. Nat. Geog. Mag., VII, pp. 96, 261.
157. McGee, W J. 1898. Geographic development of District of Columbia. Nat. Geog. Mag., IX, p. 317.
*158. Shaler, N. S., and Woodworth, J. B. 1898. The Richmond (triassic) basin. 19th Ann. Rept. U. S. G. S., Part 2, p. 385.
159. Shaler, N. S. 1899. Spacing of rivers with reference to hypothesis of baseleveling. Bull. Geol. Soc. Am., X, p. 263.
*160. Surface, G. T. 1906. Physiography of Virginia. Bull. Am. Geog. Soc., XXXVIII, p. 741.
*161. Tower, W. S. 1906. Regional and economic geography of Pennsylvania. Bull. Geog. Soc. Phila., IV, pp. 9, 113, 193, 271; V, p. 21.
162. Williams, G. H., and Keyes, C. R. 1891. Piedmont of Maryland. Bull. Geol. Soc. Am., II, p. 301.
*163. Harpers Ferry Folio, U. S. G. S., No. 10.
164. Fredericksburg Folio, U. S. G. S., No. 13.
*165. Washington Folio, U. S. G. S., No. 70.
*166. Philadelphia Folio, U. S. G. S., 162.
*167. Trenton Folio, U. S. G. S., No. 167.

VIII.—Coastal Plain Province

*168. Abbe, C., Jr. 1899. Physiography of Maryland. Md. Weather Service, I, p. 41.
169. Clark, W. B. 1897. Upper cretaceous of New Jersey, Delaware, and Maryland. Bull. Geol. Soc. Am., VIII, p. 315.
*170. Clark and Mathews. 1906. Physical features of Maryland. Md. Geol. Surv., Spec. Pub., Vol. VI (with geol. map).
171. Darton, N. H. 1896. Artesian well prospects in Atlantic coastal plain. Bull. U. S. G. S., No. 138.
172. Darton, N. H. 1911. Economic geology of Richmond. Bull. U. S. G. S., No. 483.

*173. Davis, W. M. 1896. Outline of Cape Cod. Proc. Am. Acad. Arts and Sci., XXXI, p. 331 (also in essays).

174. Fuller, M. L. 1905. Geology of Fisher's Island, N. Y. Bull. Geol. Soc. Am., XVI, p. 367.

*175. Fuller, M. L. 1914. Long Island. Profes. Pap. U. S. G. S., No. 62.

*176. Gilbert, G. K. 1884. The sufficiency of terrestrial rotation for the deflection of streams. Am. Jour. Sci., 3rd ser., XXVII, p. 427.

177. Gulliver, F. P. 1896. Cuspate forelands. Bull. Geol. Soc. Am., VII, p. 399.

*178. Gulliver, F. P. 1904. Nantucket shorelines. Bull. Geol. Soc. Am., XV, p. 507.

179. Harper, R. M. 1911. The Hempstead plains. Bull. Am. Geog. Soc., XLIII, p. 351.

180. Hitchcock, A. S. 1904. Controlling sand dunes. Nat. Geog. Mag., XV, p. 43.

*181. Hobbs, W. H. Lineaments of Atlantic border region. Bull. Geol. Soc. Am., XV, p. 483.

182. Hollick, A. 1899. Staten Island drift. Bull. Geol. Soc. Am., X, p. 2.

*183. Johnson, D. W. 1918. Shorelines and shore topography.

*184. McGee, W J. 1888. Head of Chesapeake bay. 7th Ann. Rept. U. S. G. S., p. 537.

185. McGee, W J. 1890. The Lafayette formation. 12th Ann. Rept. U. S. G. S., p. 353.

186. Newsom, J. F. 1899. Effect of sea barriers upon drainage. Jour. Geol., VII, p. 445.

*187. Shaler, N. S. 1885. Seacoast swamps. 6th Ann. Rept. U. S. G. S., p. 353.

*188. Shaler, N. S. 1888. Martha's Vineyard. 7th Ann. Rept. U. S. G. S., p. 297.

*189. Shaler, N. S. 1889. Nantucket. Bull. U. S. G. S., No. 53.

*190. Shaler, N. S. 1890. Morasses of U. S. and Dismal Swamp. 10th Ann. Rept. U. S. G. S., Part I, p. 255.

*191. Shaler, N. S. 1892. Geological history of harbors. 13th Ann. Rept. U. S. G. S., Part 2, p. 93.

192. Shaler, N. S. 1894. Pleistocene distortions of Atlantic coast. Bull. Geol. Soc. Am., V, p. 199.

*193. Shaler, N. S. 1895. Beaches and tidal marshes. Nat. Geog. Soc. Monographs, p. 137.

194. Shaler, N. S. 1895. Change of sea level. Bull. Geol. Soc. Am., VI, p. 141.

195. Shaler, N. S. 1897. Cape Cod district. 18th Ann. Rept. U. S. G. S., Part 2, p. 497.

196. Spencer, J. W. W. 1903. Submarine valleys of Atlantic coast. Bull. Geol. Soc. Am., XIV, p. 207.

*197. Veatch, A. C. 1906. Water resources of Long Island. Profes. Pap. U. S. G. S., No. 44.

*198. Woodworth, J. B., and Curtis, G. C. 1899. Nantucket, a morainal island. Jour. Geol., VII, p. 226.

199. Fredericksburg Folio, U. S. G. S., No. 13.

200. Nomini Folio, U. S. G. S., No. 23.

*201. Washington Folio, U. S. G. S., No. 70.
*202. Norfolk Folio, U. S. G. S., No. 80.
203. St. Marys Folio, U. S. G. S., No. 136.
204. Dover Folio, U. S. G. S., No. 137.
205. Patuxent Folio, U. S. G. S., No. 152.
*206. Trenton Folio, U. S. G. S., No. 167.
207. Choptank Folio, U. S. G. S., No. 182.

IX.—Central Lowland, Eastern Lakes Section

208. Coleman, A. P. 1899. Lake Iroquois. Bull. Geol. Soc. Am., X, p. 165.
209. Coleman, A. P. 1904. Beaches of Ontario. Bull. Geol. Soc. Am., XII, p. 129.
210. Coleman, A. P. 1904. Iroquois beach in Ontario. Bull. Geol. Soc. Am., XV, p. 347.
211. Cushing, H. P. 1908. Paleozoic in northwestern New York. Bull. Geol. Soc. Am., XIX, p. 155.
212. Fairchild, H. L. 1896. Kames of western New York. Jour. Geol., IV, p. 129.
*213. Fairchild, H. L. 1896. Glacial Genesee lakes. Bull. Geol. Soc. Am., VII, p. 423.
214. Fairchild, H. L. 1897. Lake Warren shorelines in western New York. Bull. Geol. Soc. Am., VIII, p. 269.
215. Fairchild, H. L. 1898. Glacial waters in Finger lake region. Bull. Geol. Soc. Am., X, p. 27.
216. Gilbert, G. K. 1885. Topographic features of lake shores. 5th Ann. Rept. U. S. G. S., p. 69.
*217. Gilbert, G. K. 1895. Niagara Falls. Nat. Geog. Soc. Monographs, p. 203.
218. Gilbert, G. K. 1897. Recent earth movements in Great Lakes region. 18th Ann. Rept. U. S. G. S., Part 2, p. 595.
219. Gilbert, G. K. 1899. Glacial sculpture in western New York. Bull. Geol. Soc. Am., X, p. 121.
*220. Gilbert, G. K. 1907. Recession of Niagara falls. Bull. U. S. G. S., No. 306.
221. Goldthwait, J. W. 1910. Isobases of Algonquin and Iroquois beaches. Bull. Geol. Soc. Am., XXI, p. 227.
*222. Leverett, F. 1910. Outline of history of Great Lakes. 12th Rept. Mich. Acad. Sci., p. 19.
223. Spencer, J. W. W. 1890. Ancient shore phenomena of Great Lakes. Bull. Geol. Soc. Am., I, p. 71.
224. Spencer, J. W. W. 1891. Post-Pleistocene subsidence *vs.* glacial dams. Bull. Geol. Soc. Am., II, p. 465.
225. Spencer, J. W. W. 1910. Niagara river and glacial period. Bull. Geol. Soc. Am., XXI, p. 433.
226. Spencer, J. W. W. 1913. Earth movements about Lake Ontario. Bull. Geol. Soc. Am., XXIV, p. 217.
*227. Spencer, J. W. W. 1913. Relation of Great Lakes to Niagara limestone. Bull. Geol. Soc. Am., XXIV, p. 229.
*228. Taylor, F. B. 1898. Whirlpool rapids and gorge. Bull. Geol. Soc. Am., IX, p. 59.

*229. Upham, W. 1896. Origin of Great Lakes. Am. Geol., XVIII, p. 169.

*230. Upham, W. 1898. Niagara gorge and St. Davids channel. Bull. Geol. Soc. Am., IX, p. 101.

*231. Wilson, A. W. G. 1908. Shorelines of lakes Ontario and Erie. Bull. Geol. Soc. Am., XIX, p. 471.

*232. Niagara Folio, U. S. G. S., No. 190.

X.—GLACIAL FEATURES

233. Branner, J. C. 1888. Glaciation in relation to Lackawanna-Wyoming region. Proc. Lack. Inst. Hist. and Science, I, p. 3.

*234. Chamberlin, T. C. 1883. Terminal moraine of the second glacial epoch. 3rd Ann. Rept. U. S. G. S., p. 291.

235. Chamberlin, T. C. 1888. Rock scorings of great ice invasions. 7th Ann. Rept. U. S. G. S., p. 147.

236. Chamberlin, T. C. 1899. Cause of glacial periods. Jour. Geol., VII, p. 545.

237. Clapp, F. G. 1908. Glacial period in New England. Bull. Geol. Soc. Am., XVIII, p. 505.

*238. Davis, W. M. 1890. Glacial sand plains. Bull. Geol. Soc. Am., I, p. 195.

*239. Davis, W. M. 1892. Catskill delta in Hudson estuary. Proc. Bos. Soc. Nat. Hist., XXV, p. 318.

*240. Fairchild, H. L. 1913. Pleistocene geology of New York. Bull. Geol. Soc. Am., XXIV, p. 133.

*241. Goldthwait, J. W. 1913. Glacial cirques near Mt. Washington. Am. Jour. Sci., 4th ser., XXXV, p. 1.

242. Goldthwait, J. W. 1913. Following the trail of the ice-sheet and valley glacier on the Presidential Range. Appalachia, XIII, p. 1.

*243. Johnson, D. W. 1917. Date of local glaciation in the White, Adirondack, and Catskill mountains. Bull. Geol. Soc. Am., XXVIII, p. 543.

*244. Lewis, H. C. 1882. Great terminal moraine across Pennsylvania. Proc. Am. Assn. Adv. Sci., XXXI, p. 389.

*245. Ogilvie, I. H. 1902. Glacial phenomena in the Adirondacks and Champlain valley. Jour. Geol., X, p. 397.

*246. Rich, J. L. 1906. Local glaciation in the Catskill mountains. Jour. Geol., XIV, p. 113.

247. Salisbury, R. D. 1909. Physiography of the Pleistocene. Jour. Geol., XVII, p. 589.

*248. Upham, W. 1894. Englacial drift. Bull. Geol. Soc. Am., V, p. 71.

249. Upham, W. 1899. Epeirogenic movements causing the ice age. Bull. Geol. Soc. Am., X, p. 5.

XI.—STATE REPORTS

New York

The present publications of the State Geologist are distributed as bulletins of the New York State Museum and cover the geology of various quadrangles and regions and special topics. A complete list may be found in almost any one of the recent bulletins. The most important ones are the following: Nassau County and Queens, No. 48; Canandaigua and Naple quads., No. 63; Little

Falls region, No. 77; Watkins and Elmira quads., No. 81; Tully quad., No. 82; Mooers quad., No. 83; Schoharie region, No. 92; Northern Adirondacks region, No. 95; Paradox Lake quad., No. 96; Buffalo quad., No. 99; Penn Yan and Hammondsport quads., No. 101; Rochester and Ontario Beach quads., No. 114; Long Lake quad., No. 115; Portage and Nunda quads., No. 118; Remsen quad., No. 126; Geneva and Ovid quads., No. 128; Port Leyden quad., No. 135; Auburn and Genoa quads., No. 137; Thousand Islands region, No. 145; Poughkeepsie quad., No. 148; Honeoye and Wayland quads., No. 152; Broadalbin quad., No. 153; Schenectady quad., No. 154; North Creek quad., No. 170; Syracuse quad., No. 171; Attica and Depew quads., No. 172; Lake Pleasant quad., No. 182; and especially:

*250. Berkey, C. P. 1907. Geology of the Catskill aqueduct. Bull. N. Y. State Mus., No. 146.

*251. Grabau, A. W. 1901. Geology of Niagara Falls. Bull. N. Y. State Mus., No. 42.

*252. Miller, W. J. 1913. Geological history of New York State. Bull. N. Y. State Mus., No. 168.

New Jersey

The publications of the geological survey of New Jersey are comprised in a series of bulletins, the first one appearing as Bulletin 1 in 1910, and in a series of final reports, thus far eight in number, the first one being that issued in 1888. The most important of these are:

253. Report of State Geologist, 1888. I. (Topography, with shaded relief map.)

*254. Report of State Geologist, 1895. IV. (Physical geography.)

*255. Report of State Geologist, 1902. V. (Glacial geology.)

*256. Lewis, J. V., and Kümmel, H. B. 1915. Geology of New Jersey. Bull. N. J. State Geol. Surv., No. 14. (Summary and description of the geological map, 1910-1912, scale 1:250,000.)

New Hampshire

257. Hitchcock, C. H. 1874. Geology of New Hampshire.

Vermont

The available reports to date of the Vermont State Geologist run from Vol. I to Vol. X, each covering two years from 1897 to 1916. They are well illustrated and occasionally contain geological maps of local areas. Several sections treat of glacial features, local and continental.

Connecticut

The present publications of the Connecticut State Geological and Natural History Survey are issued as bulletins, No. 1 appearing in 1903. The most important physiographically are:

*258. Barrell, J. 1915. Central Connecticut in the geological past. Bull. Conn. Geol. Surv., No. 23.

*259. Rice, W. N. 1906. Manual of geology of Connecticut. Bull. Conn. Geol. Surv., No. 6.

Pennsylvania

The most important reports of Pennsylvania are those of the Second State Geological Survey, comprising a long series of volumes covering the geology of the various counties, together with annual and special reports, of which the following deserve special note:

*260. Lewis, H. C. 1884. The terminal moraine in Pennsylvania and western New York. Second State Geol. Surv. Rept. Z. (This report includes a simple hachure map showing the topography of the State.)

261. Final summary report in three volumes, 1895. (With general index printed separately, and atlas in folder containing geological map of Pennsylvania.)

262. Ashburner, C. A. 1885. Archbald pot-holes. Ann. Rept. Second State Geol. Surv., 1885, p. 615.

The present publications are the reports of the Topographical and Geological Survey Commission. Report I appeared in 1910. These are usually local and economic in character.

Maryland

The present publications of the Maryland Geological Survey appear as reports running from Vol. I, 1897, and in addition a series of volumes in the same uniform style, dealing with the systematic geology of the State, but not definitely numbered. They are arranged according to counties and geological horizons.

The reports of the Maryland Weather Service run from Vol. I, 1899, and comprise to date three or four volumes containing helpful physiographic material.

The following deserve special note:

*263. Abbe, C. 1899. Physiography of Maryland. Rept. Md. Weather Service, I.

264. Rept. Md. Geol. Surv., 1897, I, p. 143. (Physiography.)

*265. Rept. Md. Geol. Surv., 1906, VI, p. 55. (Physiography.)

Virginia

The publications of the State Geologist are embodied in a series of bulletins. These are usually economic in character, but the following may be particularly noted:

*266. Clark, W. B., and Miller, B. L. 1912. Physiography and geology of the coastal plain province of Virginia. Bull. Vir. Geol. Surv., No. 4.

XII.—Geological Maps

267. Geological Map of North America. 1911. Scale 1:5,000,000 (with Profes. Pap. U. S. G. S., No. 71).

268. N. Y. Geol. Map. 1901. Scale 1 in. = 5 mi.

269. N. J. Geol. Map. 1912. Scale 1:250,000.

270. Mass. and R. I. Geol. Map. 1916. Scale 1 : 250,000.
271. Conn. Geol. Map. 1907. Scale 1 : 250,000 (with Bull. Conn. Geol. Surv., No. 7).
272. Penn. Geol. Map. 1893. Scale 1 in. = 6 mi. (with final report of Second Penn. Geol. Surv.).
273. Md. Geol. Map. 1907. Scale 1 : 500,000.
274. Virginia Geol. Map. 1916. Scale 1 : 500,000.

XIII.—Selected List

Fifty topographic maps covering practically all of the regions outlined for field work may be obtained from the Director of the U. S. Geological Survey, Washington, and will cost, when ordered in lots of 50 or more, 6 cents each.

New York:
- Niagara Falls
- Luzerne
- Bolton
- Glens Falls
- Catskill
- Kaaterskill
- Rosendale
- Poughkeepsie
- Harlem
- Paterson
- Staten Island
- Brooklyn
- Oyster Bay
- Clyde
- Plattsburg

New Jersey:
- Plainfield
- Hackettstown
- Sandy Hook
- Delaware Water Gap
- Atlantic City
- Long Beach
- Barnegat

Pennsylvania:
- Harrisburg
- New Bloomfield
- Hollidaysburg

Maryland:
- Harpers Ferry
- Washington

Maryland (continued)
- Papaw
- Hancock
- Frostburg

Virginia:
- Norfolk
- Luray

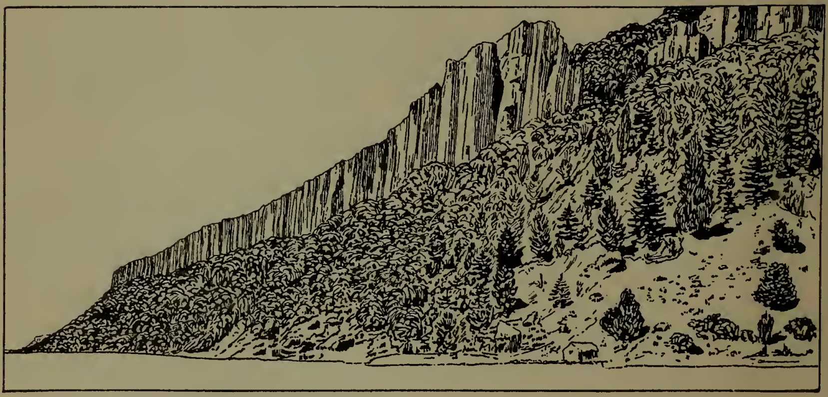
Maine:
- Portland
- Casco Bay

Massachusetts:
- Provincetown
- Wellfleet
- Boston
- Boston Bay
- Housatonic
- Taconic
- Marthas Vineyard
- Nantucket

Connecticut:
- Meriden
- Middletown

New Hampshire:
- Mt. Washington
- Gorham
- Crawford Notch
- North Conway
- Monadnock
- Peterboro

The following folios are still in stock at prices named: Niagara, No. 190, 50 cents; Raritan, No. 191, 25 cents; Papaw-Hancock, No. 179, 5 cents; Watkins Glen-Catatonk, No. 169, 5 cents; Choptank, No. 182, 5 cents.



ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Vol. XXVIII, pp. 51–166, pll. I–XIII

Editor, Ralph W. Tower

A MEMOIR ON THE PHYLOGENY OF THE JAW MUSCLES IN RECENT AND FOSSIL VERTEBRATES

BY

Leverett Allen Adams

NEW YORK
PUBLISHED BY THE ACADEMY
15 January, 1919

THE NEW YORK ACADEMY OF SCIENCES

(Lyceum of Natural History, 1817–1876)

Officers, 1919

President—Ernest Ellsworth Smith, 50 East 41st Street
Vice-Presidents—George B. Pegram, Frank H. Pike,
Edmund O. Hovey, Pliny E. Goddard
Corresponding Secretary—Henry E. Crampton, American Museum
Recording Secretary—Ralph W. Tower, American Museum
Treasurer—John Tatlock, 37 Wall Street
Librarian—Ralph W. Tower, American Museum
Editor—Ralph W. Tower, American Museum

SECTION OF ASTRONOMY, PHYSICS AND CHEMISTRY

Chairman—George B. Pegram, Columbia University
Secretary—K. George Falk, Harriman Research Laboratory, the Roosevelt Hospital

SECTION OF BIOLOGY

Chairman—Frank H. Pike, College of Physicians and Surgeons
Secretary—William K. Gregory, American Museum

SECTION OF GEOLOGY AND MINERALOGY

Chairman—Edmund O. Hovey, American Museum
Secretary—Charles C. Mook, American Museum

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

Chairman—Pliny E. Goddard, American Museum
Secretary—Robert H. Lowie, American Museum

The sessions of the Academy are held on Monday evenings at 8:1 o'clock from October to May, inclusive, at The American Museum o Natural History, 77th Street and Central Park, West.

Description.

Five physiographic provinces are represented on this diagram, all of them forming belts trending in a northeast-southwest direction.

1. A small portion of the Allegheny Plateau Province appears at the top, along the right bank of the Delaware River. To the west of Delaware Water Gap it is known as the Pocono Plateau and further north in New York it forms the Catskill Mtns

2. The belt of Newer or Folded Appalachians is narrower here than at any other point. Kittatinny Mountain is the most prominent ridge, and is of the monoclinal type, dipping westward. The broad valley to the eastward, known here as the Kittatinny or Wallkill Valley, is a part of the Great Appalachian Valley.

3. The belt of crystalline rocks forming the New Jersey Highlands may be seen extending from the gorge of the Hudson diagonally across the state and into Pennsylvania. Because it ends at Reading and because it is really an extension of the New England Province it is known as the Reading Prong of the New England Upland.

4. The next belt, the Triassic Lowland, is developed upon a series of sandstones infaulted or downwarped into the older crystallines. The interbedded and resistant trap sheets determine such pronounced features as the Palisades and Watchung Ridges.

5. The rest of the area is embraced in the Coastal Plain Province whose cuesta may be seen extending from the Navesink or Atlantic Highlands southward where it forms the hilly belt of southern New Jersey.

Fig. 29

BLOCK DIAGRAM
SHOWING
THE RELIEF FEATURES
OF
NORTHERN NEW JERSEY

Armin K Lobeck Columbia University

[ANNALS N. Y. ACAD. SCI., Vol. XXVIII, pp. 51–166, Pls. I–XIII.
15 January. 1919]

A MEMOIR ON THE PHYLOGENY OF THE JAW MUSCLES IN RECENT AND FOSSIL VERTEBRATES[1]

BY LEVERETT ALLEN ADAMS

(Presented before the Academy, 8 March, 1915)

CONTENTS

---

[1] Studies in Comparative Osteology and Myology, No. 2, issued under the direction of Dr. William K. Gregory, Assistant Professor of Vertebrate Palæontology, Columbia University, and Research Associate, American Museum of Natural History.

INTRODUCTION

This paper attempts first to trace the muscles of mastication from their origin in the primitive gnathostomes to their perfected development in the higher vertebrates and secondly to discover the co-adaptations of musculature and skull structure.

There has been a great neglect of the correlation between osteology and myology. Hundreds of monographs are at hand on both subjects, yet synthetic studies that deal with both and with their interrelationships are extremely rare. As muscle was no doubt in existence before bone, and as there is the closest relation between the two, we should naturally consider myology and osteology together instead of under separate heads.

Many monographs have been written on the myology of special forms, but usually with little consideration of the conditions to be found in related groups. Apart from the great work by Ruge on the seventh nerve, there have been few general surveys attempted. Ruge traced the facialis nerve and its musculature from the elasmobranchs to mammals, giving us one of the best types of comparative work at present available. Toldt, Bijvoet, Chaîne, Rouvière, Parsons, Dobson and others have traced the digastric muscle in the mammals, giving homologies and tracing the muscle to its origin in the lower forms. The many writers on the muscles of special groups have used synonymous names and the nomenclature is far from clear at the present time. Many names for muscles are used in special cases that might well be changed to give a more uniform system.

The influence of the musclature upon the evolution of the skeleton in vertebrates has also been neglected in most of the general works on comparative anatomy. Much has been written on the changes that have taken place in the skulls of the vertebrates, but with too little reference to the muscles. The palæontologists and anatomists have traced the shiftings and changes of each bone in the skull so that the migrations of the hyomandibular and of the quadrate, for example, are known from the time when they appear as cartilages in the selachians to their final resting place in the mammalian ear. Thus during the last decade or two osteology has made great progress as an interpretative science. From the work done on the fossil forms the evolutionary history of the skeleton is not nearly so obscure as it was a few decades ago. The structure of many of the fossil forms is being gradually worked out and some of the great vertebrate phylogenies are being cleared up by the recent developments in palæontology and comparative anatomy. For example, the relatively close relationship between the reptiles and the amphibians is becoming very clear, for the discovery of new Carboniferous forms has added much to our knowledge, so that more and more structures common to the two classes have been observed. The same applies to the relationship of reptiles and mammals. The recent discoveries in South Africa of a number of new cynodont reptiles have given much new light on the evolution of the mammals from the reptilian stock, so that great advances have been made in the early history of these relatively modern groups. Many morphological problems, such as the problem of the mammalian pterygoid and its origin, of the ossicles of the ear, of the development of a new joint on the dentary, and its new articulation with the squamosal, have received illumination from the synthesis of palæontology and comparative anatomy. In all such studies the great working tool of the palæontologist is comparative anatomy, as without it he is helpless to determine the relationships of the fossil forms, just as the student of modern forms is helpless if he attempts to work out the relationships of the modern fauna without considering the maze of ancestral types that preceded them in the past. Thus the importance of the modern forms is demonstrated every day in the great museums of palæontology and comparative anatomy where many of the new discoveries are due to the synthesis of the study of present forms with those of the past, so that a department of palæontology should combine in its collections a complete series of the modern with the fossil forms, if correct interpretations are to be made of the fossil material.

The factor that has been most neglected has been the study of the myology along with the bony structure of the fossil forms. The bones of the skeleton should be studied not as independent elements, but as supports for the muscles that covered or were attached to them. The skull of an ophidian studied merely as an osteological specimen shows much in the way of specialization and peculiar development, but without the study of the motive power for which it furnishes the support the results are rather barren, as too much has been left out of consideration. It is like making a study of a complex series of levers without taking into consideration the forces that move them. A few papers and books do indeed consider the correlation of the bones and muscles in modern forms, especially man, such as Bardeleben (1903), Fick (1904-1910-1911), Strasser (1908). These studies on modern forms give the key for similar work on the fossils, as the principles of mechanics concerned hold throughout. Prof. W. K. Gregory (1912) has endeavored to correlate palæontology, osteology and myology in his studies on the evolution of the limbs of recent and fossil ungulates. His discussion of the angle of insertion of the muscles upon the limb bones, in relation to power and speed, bears upon the study of jaws and jaw muscles. Realizing the need of further studies of this kind, Dr. Gregory suggested that I should take up the problem of the evolution of the jaw muscles of vertebrates in relation to skull structure.

In this paper I have accordingly had before me the following aims: first, to follow the jaw muscles through a selected series of vertebrates ranging from shark to man and to express the essential facts in clear and semidiagrammatic drawings of uniform character and treatment, to facilitate comparison; second, to discover and summarize the homologous relations of the several jaw muscles throughout the series and thus attempt to clear up and harmonize the confusing synonymy due to varying systems of nomenclature founded on special types; third, to discover the adaptational relations between skull structure and musculature; fourth, to apply these principles to a reconstruction of the musculature in certain extinct vertebrates, especially those of great general phylogenetic importance in the different classes.

STATEMENT OF THE PROBLEM

The problems of the musculature of the jaws and of the homology of these muscles throughout the vertebrates are of great potential importance in the future development of comparative anatomy. As the jaw muscles are concerned in all the movements of the skull and have developed with it, their influence in modifying the skull in the early history of the vertebrates is well worthy of detailed study. The jaw muscles also offer much of interest in their relation to the origin and evolution of the dentition and in the evolution of the mammalian skull from the reptilian type. Such great themes as the origin of the mammalian auditory ossicles, the origin of the peculiar mammalian articulation of the mandible with the squamosal, the transformation of the reptilian jaw into the mammalian type, and the homology of certain skull bones in different groups are also involved. The mechanical problems connected with the specialized jaw movements of some of the higher vertebrates are also interesting, especially in cases where the close relation of the jaw muscles and the specialized skull structures are readily discovered. The jaw muscles are also sometimes of value in testing relationships of closely related groups, especially where specialization has not gone so far as to obliterate all the primitive conditions, since with a few exceptions the arrangements of the jaw muscles are remarkably constant in fundamental characters in each of the vertebrate classes.

CRITERIA OF HOMOLOGY

The problem of homology in the muscular system is a most difficult one, as the muscles are very unstable elements, given to shifting their positions, splitting up into fragments, and combining with other elements like themselves.

There are four tests that may be applied to a muscle to determine its possible homology with a similar muscle in another animal: (1) embryology, (2) nerve supply, (3) origin and insertion, (4) function. If all of these agree there is great probability that the homology assumed is correct.

EMBRYOLOGY

Embryology is helpful in determining origins and in giving a clew, at least, to the relations of the muscle. Keibel and Mall (1910) in their Human Embryology show that primitive relationships are evident in certain early stages of development. They describe the origin of the human jaw muscles that are innervated by the fifth nerve as follows:

> In the 7 mm. embryo the mandibular arch is filled with a closely packed mesenchyme, with only slight traces of condensation about the peripheral end of the mandibular nerve. In the 9 mm. embryo, however, this condensation is clearly to be recognized. This peripheral mass, in which the N. mandibularis ends, lies at about the middle of the arch. In a 11 mm. embryo, this egg-shaped pre-muscle mass has increased in size but still shows no indications of splitting into the various muscles. The pre-muscle is, from the beginning, closely associated with the condensed mesenchyme of the mandible, and with the differentiation of the proximal end of the mandible, the pre-muscle mass is partially split into a Y-shaped mass, the handle representing the M. temporalis, the outer limb corresponding to the M. masseter, and the inner, deeper limb, separated from the outer by the proximal end of the mandible, representing the mass for the Mm. pterygoidei externus and internus.

Thus it is seen that all these jaw muscles arise from the same group.

The relations of the jaw muscles to the body muscles as a whole are as follows: In the early stages of the vertebrate embryo the myotome is a hollow body with a splanchnic inner layer and an outer or somatic layer. This myotome grows down until it almost meets its fellow on the opposite side, the two remaining separated from each other by a connective tissue septum, the linea alba of the fishes. The myotome is also divided by a longitudinal line of connective tissue that follows along the lateral line of the fishes and the urodeles and divides the myotome into a dorsal or epaxial epimere and a ventral or hypaxial hypomerē. The muscles of the body are accordingly divided into three groups—appendicular, axial and visceral. The appendicular muscles take their origin from the axial, and both in turn are derived from the dorsal or epaxial (epimere) part of the myotome. The visceral muscles, including those of the head region, are derived from the ventral or hypaxial portion of the myotome (hypomeres). (Wilder, 1909, p. 190.) The visceral or hypaxial muscles of the head region are further divided into a dorsal and a ventral series according to their position as depressors or levators of the gill arches.

NERVE SUPPLY

The primitive innervation of the myotomes in *Amphioxus* is shown by Goodrich (1909, p. 2). The myotomes are supplied by the ventral roots of the serial nerves, the dorsal roots passing between the myotomes to supply the skin and the sensory nerves. The dorsal and ventral roots of the serial nerves remain separate. Regarding the innervation of typical vertebrates Goodrich (1909, p. 3) says:

It is important to notice that while the myotomes and the muscles derived from them (such as the limb muscles) receive their motor nerves exclusively from the ventral roots of the spinal nerves, the splanchnic muscles, the skin, the mucous membrane and their sense organs are supplied by the dorsal, ganglionated roots.

The embryology of *Petromyzon, Amphioxus* and the fishes give some very illuminating evidence of the evolution of the muscular and the nervous system in the early vertebrates, and from them we may get a better understanding of the muscles and serial nerves of the higher vertebrates. Thus a study of the embryology gives much aid in tracing the homology of the capitimandibularis muscle in the reptiles, where it is an undifferentiated mass, as in the embryo of man. Again the problem of the musculature of the middle ear is very much clarified by the embryological investigations of Gaupp, Versluys, Fuchs and other students of the ear, where the development gives an explanation of the origin of these elements.

As the nerves and muscles start out together very early in the life of the embryo, the nerve supply has always been taken as one of the best tests of homology. It is almost an axiom in comparative anatomy that a muscle is always followed by its nerve, and while in most cases this is true, it is occasionally not true. The stapedius muscle of the middle ear illustrates the constancy of the nerve supply. This muscle is followed from its position as a levator of the hyoid arch through many changes to its final resting place in the middle ear, with the innervation by the facialis remaining constant. The tensor tympani muscle also represents a slip of the reptilian pterygo-mandibularis that has shifted to the middle ear. The facialis in its migration from the hyoid arch over the face gives another fine example of the constancy of the nerve supply to the muscle. In man the platysma, sphincter colli and facial muscles of the eye, nose and mouth have migrated from their original position on the side of the neck to the most anterior portion of the face. In this case the seventh nerve has overlapped the territory of the trigeminus and the serial nerves anterior to it, while the muscles of the fifth nerve have remained in their original position. The pectoralis and latissimus dorsi muscles of man give another example of shifting muscles that carry their nerves with them. They shift from their original position to cover large areas of the trunk that were formerly innervated by the several serial nerves of the myotomes. In the external oblique of man and the rectus abdominis there is a fusion of the elements, their originally separate condition being shown by their nerve supply.

The digastric is also a muscle with a double nerve supply, and is very probably a muscle with a double origin, since it originally has two bellies, the anterior innervated by the fifth nerve and the posterior belly by the seventh.

In spite of some seeming contradictions, the nerves offer the best means of determining homologies in the muscles. Wilder (1909, p. 196) says:

> Were it possible to follow each motor nerve fiber from its origin to its connection with its muscle, it would probably serve as an absolute criterion for muscular homology, but there is a chance for error in the fact that an anatomical nerve is not a single fiber, but a bundle of them, and while each fiber is presumably constant in its supply, there is some variation in the way in which they are put into bundles, so that no one can be sure that a given nerve is quite homologous with one in a like location in another animal.

Most anatomists agree with Wilder's statement of the case. We may suppose that these changes of the contents of the bundle are responsible for some of the examples of apparent non-homology that often occur in animals that are closely related. We may assume that in the original condition of the vertebrates the myotomes were placed in regular order and each myotome was supplied with a serial nerve. With the gradual changes that took place in development the higher vertebrates disguised the metameric arrangement until only slight remnants of them remain in a few muscles like the obliquus externus of man. The myotomes are evident through the fishes and tailed amphibians, but are not so evident in the reptiles and mammals. The elements of certain of the myotomes usurped the position of the others and developed into the larger muscles of the trunk, carrying with them their original nerves, thereby destroying the primitive arrangement.

In a paper by D. J. Cunningham (1891) the problem of nerve and muscle is very carefully considered. He considers the nerve supply a good guide but not an infallible one. He says that a solution of the problem can only be obtained by approaching the question from two points of view: first, by studying the early connections which exist between the nervous and the muscular system in the embryo; second, by examining one or more groups of muscles, the homologies of which are undoubted, in a large series of animals or in a large number of individuals of the same species, and observing whether in every case the nerves of supply are the same.

In many cases the nerves are found fusing into a plexus. Cunningham's paper favors the view that the same ganglion cells are invariably connected with the same muscle fibers, but that the fibers may adopt a different path and thus reach their connection through another route. This seems incapable of proof, but it is a good working hypothesis. He mentions two cases worked out by Sir William Turner where the long buccal nerve proceeded from the superior instead of the inferior maxillary of the fifth nerve. He also gives some observations of his own on *Elephas, Hyrax,* and *Castor,* where the internal plantar nerve invades the territory of the external plantar and seizes upon muscles which usually do not belong to it. In the fox-bat the opposite occurs and the external plantar lays hold upon a muscle which under typical conditions is controlled by the internal plantar. This piracy of the nerve terminals finds its analogue in the capture of branches of the carotid, as described by Tandler. This may well be considered a changing of the paths of the fibers and not a change of the ganglionated cells and of the muscle fibers. In the case of certain muscles of doubtful homology in *Ornithorhynchus* Ruge has shown a substitution of the nerve supply from a different plexus from that which supplies the supposedly homologous muscles in other mammals. He solves the problem by deciding that the muscles concerned are not homologous.

Gadow gives some cases of truly homologous muscles being supplied in different types by a different plexus. He shows that, in *Iguana,* the ischio-femoral muscle is supplied by the ischiadic plexus; that in the Crocodile it is supplied by another nerve, the obturator; while in *Varanus* it is supplied by both. In placental mammals the adductor magnus is innervated by two nerves, one from the obturator nerve and one from the sacral plexus. In marsupials the adductor magnus is supplied solely by the sacral plexus.

Cunningham offers the following possible explanations of these anomalies:

> (1) Complete obliteration, and then complete reconstruction of both nerves and muscles, the muscle assuming its old origin and insertion.
>
> (2) Retention of both nerve and muscle elements but the adoption of new and more convenient paths.
>
> (3) A retention of the muscular elements but a substitution of new nerve elements.

He rejects the first, does not give much consideration to the third and seems to agree with Fürbringer "that the nerve supply is the most important and indispensable guide but is not infallible."

Goodrich (1909, p. 82) concludes that, "in a series of metameric myotomes and nerves each motor nerve remains, on the whole, faithful to its myotome throughout the vicissitudes of phylogenetic and ontogenetic modifications."

In the case of the jaw muscles experience shows the great importance of the nerve supply in determining the homologies of muscles.

ORIGIN AND INSERTION

The origin and insertion of the muscles must be taken into consideration in the determination of their homologies, but as some of the skeletal elements shift and drop out in the different classes, this criterion must be used with care in cases where the animals compared are not closely related.

The known changes and disappearance of the bones of the skull as we pass from Palæozoic to modern vertebrates suggest that, if the supposed homology of a muscle is based on the origin and insertion, the history of the bone to which it is attached must be known and completely traced; for example, in tracing the changes that have taken place in the remodeling of the cynodont skull, in its evolution into the mammalian type, there is difficulty in following the origin and the insertion of certain muscles, as the shifting of bones is so marked in the jaw region that some muscles have changed their origin and insertion and some have dropped out and been replaced by slips from neighboring muscles. Although it seems reasonable to infer that muscles became readapted, yet if there was a mechanical or other reason for the dropping out of a muscle we may assume that a new slip was separated from another muscle that filled the requirements of the new function. Great changes from the primitive reptilian type must have taken place in the line leading to *Cynognathus, Gomphognathus* and *Sesamodon.* The posterior end of the dentary increased in importance and the coronoid process of the dentary gradually overshadowed the posterior end of the mandible as an attachment for muscles, so that muscles formerly attached to the surangular and to other posterior bones of the jaw moved forward and acquired an attachment on the upgrowing coronoid process. Finally the reduced muscles of the movable pterygoid of the reptiles must have shifted, disappeared or possibly be left as remnants such as the pterygo-spinosus of the edentates or the pterygo-tympanic that is sometimes found in man.

FUNCTION

The jaw muscles are on the whole remarkably stable throughout the vertebrates with minor adaptive changes. The larger muscle masses can be traced through the different classes, but some of the minor slips must be followed closely in their development through a number of forms if the homology is to be certain. The history of the changes of function can be traced from their innervation and their relation to their supports. The fact that they are derived from the visceral muscle system indicates that they arose as muscles for contracting and dilating the gill openings, drawing in water containing food and oxygen, and finally that they were used in snapping at prey (Gregory, 1915). The predatory habits of the primitive fishes were responsible, it is believed, for the change of the gill muscles into true jaw muscles. Even in mammals the muscles are still intimately related with the branchial arches, with the tongue and even with the ear. The point of attachment and the function of a muscle must then be considered as one of the available criteria of homology. This should always be considered when the history of the bone to which the muscle is attached has been thoroughly studied through a number of classes and when also its developmental history is certain.

Neomorphs have often arisen as slips from some of the muscles; muscles frequently have split up into slips that eventually have become separate and taken a part of the parent nerve with them as in the pterygoids of the mammals. We have numerous examples of this splitting: for example, the derivation of the anterior belly of the digastric of mammals from the mylohyoid, or the subdivision of the "adductor mass" into numerous slips in *Amia.* If this splitting is carried further and the slips separate, it becomes correspondingly more difficult to trace their homology.

Acknowledgments

This work has been carried on in the Department of Vertebrate Palæontology at the American Museum of Natural History, under the general direction of Professor W. K. Gregory, from whom the author has constantly received critical suggestions and helpful advice. I am also grateful to Professor R. C. Osburn for the loan of private material used in a part of the work on the teleosts; and to Mr. J. T. Nichols for other specimens of fish needed in the teleost series. To Dr. L. Hussakof my thanks are due for his placing at my disposal numerous specimens from the collection of Arthrodira in the Department of Ichthyology. Finally, in common with many other investigators, I am mindful of a larger debt to the American Museum of Natural History for liberty to use its extensive resources.

A series of 26 existing types of vertebrates has been dissected as follows: Elasmobranchii 1, Chondrostei 2, Holostei 1, Teleosti 3, Crossopterygii 1, Dipnoi 1, Urodela 3, Anura 1, Chelonia 1, Rhyncocephalia 1, Lacertilia 2, Crocodilia 1, Aves 1, Mammalia 7. In each case special attention has been paid to the innervation of the muscles as a guide to homologies. By means of these data, and of the principles that became apparent as the work proceeded, reconstructions of the jaw musculature were attempted in the following series of extinct forms: *Dinichthys* (Arthrodira), *Eryops* (Temnospondyli), *Labidosaurus* (Cotylosauria), *Tyrannosaurus* (Theropoda), *Cynognathus* (Cynodontia).

THE JAW MUSCLES IN RECENT VERTEBRATES

Pisces

ACANTHIAS

Plate I, Figs. 1, 2

The elasmobranchs as primitive gnathostomes are far superior in rank to the pregnathostome stage represented by the ostracoderms, for the first two visceral arches have already taken their places as the future supports of the jaws and hyoid arch. For many geological ages the teeming multitudes of pregnathostomes no doubt tried to develop a perfected form of jaws, but up to the appearance of the elasmobranchs the attempts to develop something besides a suctorial mouth were hardly satisfactory.

Somewhere in early Palæozoic times the vertebrates acquired the cartilaginous jaws, for the acanthodians as far back as the upper Silurian had already developed the type of jaw that is to continue through the rest of the vertebrate series. The cartilages of the skull and body in the elasmobranch give a fairly firm and stable attachment for the muscles. The great advance has been in the change of function of the two anterior visceral arches. The first two arches of the visceral series have lost their function as supports for the gills, and form the cartilaginous structure that is to become the jaw and hyoid apparatus of the gnathostomes. The first arch has grown forward under the brain case and has attached itself to the ethmoid region at the anterior end and to the hyomandibular region posteriorly. The palato-quadrate bar is continuous, forming a long bar extending from the anterior end to the posterior part of the side of the skull.

The teeth have already developed in the sharks. The denticle-covered skin has been drawn into the mouth and by growing together or enlarging the denticles have developed into fairly efficient teeth.

The jaw system in the shark is just the opposite of that in *Dinichthys.* The maxillary region is securely fastened to the skull, although it may be movable, while the mandible is the movable agent with the articulation in the quadrate region of the palato-quadrate bar. This mandible in the shark is capable of movement only in one direction. There is no side movement in these forms as there is no muscular system to operate it.

The adducting movement of the mandibles is accomplished by the great adductor muscles, while the opening of the jaw is left to the long muscles of the ventral region. The muscles of the elasmobranch head are very simple, showing traces of the segmental condition in many particulars and indicating the homology of the jaw muscles with the branchial muscles. They are attached to the cartilages and to the fascia of the skin, but the skin has not assumed the importance that it does in the higher forms where it has become ossified to form plates as in *Amia.* In the sharks the skin gives some support to the muscles but it is not of great importance.

One of the first to work on the jaw musculature of the elasmobranchs[2] was Benjamin Vetter (1874). On page 406 he gives a system for the naming of the muscles of the head and branchial region that is still used, with some modifications, in the literature of the subject. He regards the adductor mandibulæ as part of the series of "adductores arcuum visceralium (Mittlere Beuger der Bogen)"; these are small muscles on the inner sides of the branchial arches stretched between the lower end of the upper middle segment and the upper end of the lower middle segment (p. 445). He divided the musculature as follows:

> Die muskulatur der Visceralbogen zerfällt nach Lage und Innerverirung in vier Gruppen oder Systemen: (1) Oberflächliche Ringmuskulatur, (2) Obere Zwischenbogenmuskeln, (3) Mittlere Beuger der Bogen, (4) Ventrale Längsmuskulatur.

Vetter subdivides the muscles of the "Oberflächliche Ringmuskulatur" (Constrictor arcuum visceralium) as follows:

> Bei den Selachiern treten folgende Muskeln als gesonderte Differencirung dieses Systems auf: (1) M. constrictor superficialis, oberflächlicher Constrictor; (2) Mm. interbranchiales, Kiemenscheidewand Muskeln; (3) M. levator maxillæ sup., Heber des Oberkiefers; (4) M. trapezius, Heber und Vorwärtszieher des Schultergürtels.

In the description of the jaw muscles of *Acanthias* the following muscles of the adductor or temporal group (innervated by V_3) are considered:

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ (Adm.).
Levator labialis superioris (L. l. s.).
Levator maxillæ superioris (L. m. s.).
Constrictor superficialis dorsalis (C_1 s. d.).

---

[2] The authors followed and compared in the study of the elasmobranchs were: Vetter (1874), Tiesing (1895), Marion (1905) and Drüner (1903).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Constrictor 2 superficialis dorsalis (C_2md, Ruge; Csd_2, Marion).
Coracomandibularis (Co. m.).
Coracohyoideus (Co. hy.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ (Adm.).—This is the large adductor muscle of the shark which closes the mandible against the maxillary or palatoquadrate bar. It lies on the skull, anterior to the hyomandibular, and fills the lower part of the space between this and the eye. It arises along the dorsal margin of the quadrate. A superficial layer arises on the postorbital process and some of the fibers come from the tendinous mass back of the eye. At the postero-ventral region a few of the fibers from C_1sv join with the adductor. The insertion is on the cartilage of the mandible along the whole length of the exterior surface and slightly on the upper edge of the inner surface. A tendon extends to the levator labii superioris (L. l. s.) somewhat as it does in the teleosts, where a tendon connects with the adductor from the premaxillary region of the skull. Marion (1905, p. 23) gives a similar muscle in *Raia* which he calls levator rostri.

In *Acanthias* the adductor muscle is a large mass made up of fibers from several sources, as in the teleosts and ganoids. It is more divided and specialized in *Raia* than in the typical sharks. The typical condition of this muscle in the lowest forms shows fibers from several sources, and this is suggestive of the subdivisions of the mucle in the higher forms, where the same mass in the amphibians and reptiles is divided to a greater or less extent, according to the form of the animal and the type of jaws. Tiesing (1895, pp. 87-90) discusses the adductors of the various elasmobranchs, showing this splitting of the muscle in some of them, especially *Rhinobatus*.

Levator labii superioris (L. l. s.) is a small muscle arising on the ventral portion of the skull, under the eyes and anterior to them, extending around the labial cartilages to meet and join with the adductor mandibulæ.

Vetter (1874, p. 406) calls it Add. β in *Acanthias* and places it with the "Oberflächliche Ringmuskulatur" (Constrictor arcuum visceralium). Marion (1905, p. 21) follows Vetter and places it with the similar constrictor, as a serial homologue of the M. levator maxillæ superioris. Tiesing (1895, p. 84) gives the origin in *Mustelus* "von vorderer Wand der Augenhöhle unterhalb des Processus præorbitalis." Tiesing (Idem., p. 86) classes this muscle with the dorsal constrictors: "Mit der Erkenntnis dass es sich um die Versorgung durch den Ramus III trigemni handelt, verliert auch der M. Levator labii superioris die ihm von früheren Autoren zuerkannte selbständigkeit und reiht sich dem system der levators resp. dorsalen Constrictors im Trigeminusgebiet an."

Levator maxillæ superioris (L. m. s.).—This is one of the dorsal constrictors which arises on the skull, just anterior to the constrictor superficialis dorsalis 1 (C_1sd). It is inserted on the dorsal surface of the palato-quadrate bar. This muscle is so closely associated with C_1sd in both origin and insertion that most writers have placed them together. Vetter (1874) places it with the dorsal constrictors and Marion (1905) follows his determination. Vetter (1874, p. 408) gives the function of the two muscles as follows: "Der Levator maxillæ superioris und C_1sd heben den Oberkiefer, der erstere dreht ihn dabei um sein Gelenk mit dem Schädel nach vorn, der letzere nach hinten."

Constrictor (1) superficialis dorsalis (C_1sd).—This small muscle is just posterior to the levator maxillæ superioris and is closely associated with it. Both muscles represent a division of one of the dorsal series as mentioned in the discussion of the other muscles. Its origin is on the wall of the skull above the spiracle, from where it curves around the anterior border of the spiracle to the insertion on the palato-quadrate bar, just posterior to the insertion of the levator maxillæ superioris. This constrictor represents the dorsal part of the original dorsal constrictor (C_1sd) and in some pre-elasmobranch stage was probably much larger.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(*INNERVATED BY VII*)

There is no true depressor attached to the mandible in the elasmobranchs that has any connection with the dorsal part of the skull. The depressing is performed by the long muscles of the hyoid region, assisted by the coraco-mandibularis and coraco-hyoideus. These are hyoid arch muscles and both are innervated by nerve VII as would be expected, as they belong to the region of the second superficial constrictor.

Constrictor (2) superficialis dorsalis (C_2sd).—This is the large, undifferentiated constrictor that in the higher forms is to become the depressor mandibulæ of the Amphibia, birds and reptiles; but in the Pisces it is a wide muscle arising from the posterior part of the skull and from the fascia of the back muscles. It is inserted in the quadrate region of the upper jaw onto the cerato-hyal cartilage and onto the tendinous bridge of the dorsal and ventral constrictors.

Coraco-mandibularis (Co. m.).—This lies along the ventral medial line of the under part of the throat. It is an azygos muscle belonging to the long muscles of the ventral system. It arises on the fascia of the long muscles (coraco-arcuales), extends forward as the most superficial of the ventral muscles, and is inserted on the mandibular cartilage, near the symphysis. It is the true depressor muscle of the elasmobranchs and acts in depressing the jaw. Tiesing calls it a depressor, but it adds confusion to the nomenclature, and it should be regarded as a ventral muscle, used below the amphibians for this purpose.

Coraco-hyoideus (Co. hy.).—This also assists in the depression of the mandible. While it is not attached to the mandible, it is close to the coraco-mandibularis and assists in drawing down the mandible by pulling on the arch. It is a paired muscle, attached by fascia in its origin to the coraco-branchialis and coraco-arcualis communes. It is inserted on the underside of the hyoid arch near the median line.

POLYODON

Plate I, Fig. 4

The skull on the whole approaches the shark type. It consists largely of cartilage, the derm-bones being much reduced. The rostrum is enormously prolonged and flattened. The skull is extremely hyostylic, the long slender jaws being connected with the skull chiefly through the small symplectic and the long backwardly inclined hyomandibular. The muscles of the hyomandibular are large and well developed. As the fish feeds on small food particles, the jaws and their muscles are weak. The adductor muscle arises on the palato-quadrate bar, and passes over a pulley-like groove at its posterior end and is inserted into the mandibular fossa.

The jaw muscles of *Polyodon,* as described by Danforth (1913), resemble those of the sturgeon but are less reduced. They are also fundamentally similar to those of the elasmobranchs.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ 1 (Ad. m.[1], adm. of Danforth).
Adductor mandibulæ 2 (Ad. m.[2], adm.[1] of Danforth).
Protractor hyomandibularis (P. hy.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Retractor hyomandibularis et operculi (R. hy. et o.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

The adductor mandibulæ is divided into two parts: a large anterior portion, and a smaller deep part. The large portion extends anteriorly along the palato-quadrate bar, while the posterior, deep, portion is a short muscle from the quadrate region.

Adductor mandibulæ 1 (M. adm. of Danforth).—This is the larger section of the adductor which lies over the palato-quadrate bar, curves around the quadrate and is inserted in the suprameckelian fossa. Its origin starts on the dorsal, anterior end of the palato-quadrate and extends backward, overlapped slightly along its ventral side by the maxilla; it curves downward under the maxilla at a sharp angle and is inserted into the suprameckelian fossa and also on the dentary. Its curve is very abrupt, so that its insertion is at right angles to the main mass of the muscle.

Adductor mandibulæ 2 (M. adm.[1] of Danforth).—Just posterior to the abrupt curve of the adductor mandibulæ 1 arises the adductor mandibulæ 2 on the posterior end of the palato-quadrate bar. It extends ventrally to be inserted on the dentary and in the suprameckelian fossa.

Danforth (1913, p. 116) mentions some speculations in regard to the adductor mandibulæ 1 of *Polyodon* that are rather interesting and perfectly justified from the conditions. He says:

> In *Acipenser* there is, in addition to the adductor mandibulæ, a strong constrictor (Cs of Vetter) which overlies it. The latter arises from the antorbital process and extends around the lower jaw. The anterior part of the adductor in *Polydon* has a superficial resemblance to this muscle, but none of its fibers arise from any part of the cranium proper and I have been unable to find any indication that they ever pass over into the ventral constrictor, below the jaw. Consequently from the adult material alone, it cannot be stated with any certainty that the anterior adductor of *Polydon* finds its homologue in the constrictor of *Acipenser*, although there is a possibility that such is the case.

From its position, it could be a part of the constrictor superficialis 1 of Vetter, as Danforth suggests. It is tempting to imagine that the old origin on the skull has been lost and that it slipped down to its present position. Several other forms have a muscle of this type and the embryology should show the truth or falsity of the assumption. This muscle protracts and closes the mouth.

Protractor hyomandibularis (P. hy.).—This muscle strongly suggests the similar muscle in *Acipenser*. It is a double-headed muscle that arises from the base of the skull at the posterior end of the roof of the mouth and from the post-orbital process, anterior to the spiracle. It extends to the hyomandibular and is inserted along its anterior margin, with a long insertion extending almost to the distal end of the bone. It protracts the hyomandibular, pulling the distal end outwards and forward. The homology of this muscle is interesting. Danforth (1913) says: "The partial division of this muscle is of some interest, since the homologies of the levator arcuus palatini and the dilator operculi in the teleosts are rather uncertain."

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Retractor hyomandibularis et operculi (levator and add. operculi?) (R. hy. et o.).—This is a large sheet of muscle that arises along the groove in the cranium, under the long pterotic. It may represent the levator operculi and the adductor operculi of *Amia*. The fibers spread out and are divided into small bundles and are attached to the posterior edge of the hyomandibular. Posteriorly they attach themselves to the whole dorsal border of the degenerate operculum. A few superficial fibers extend over this sheet from the anterior part of the origin to the operculum. These muscles raise the hyomandibular and operculum.

ACIPENSER

Plate I, Fig. 3

The dermal plates of the skull are superficial ossifications. The cartilaginous skull of this form is more degenerate than in *Polyodon,* as the mouth is reduced to a small sucking disc, while *Polyodon* has duck-like jaws. The adductor is shrunken to a small, short muscle, as there is very little demand for a strong muscular action. The opercular and hyomandibular region have large muscles, as there is much movement in these parts during the ingestion of food.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

(1) Adductor mandibulæ (Ad. m.).
(2) Protractor hyomandibulæ (P. h.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

(1) Retractor hyomandibularis (R. hy.).
(2) Levator operculi (L. o.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Adductor mandibulæ (Ad. m.).—This is a small muscle that arises on the upper side of the palato-quadrate region. It curves around and is inserted on the small Meckelian cartilage. It raises the mandible and presses it against the marginal cartilages of the maxillary region.

Protractor hyomandibularis (P. h.).—This is a large muscle in the sturgeon. It arises in the post-orbital region, extends ventro-posteriorly and is inserted on the hyomandibular. It is concerned in the action of the gill apparatus and in the sucking action.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

(INNERVATED BY VII)

Retractor hyomandibularis (R. h.).—It arises on the skull wall back of the spiracle and is inserted on the dorsal edge of the hyomandibular. It raises the gill apparatus.

Levator operculi (L. o.) (Vetter, 1874).—This arises along the side of the skull, just posterior to the origin of the retractor hyomandibularis. It is inserted on the operculum on the inner side. It pulls up the operculum.

AMIA

Plate II, Figs. 1, 2

In the very primitive skull of *Amia,* the chondrocranium is but little ossified and the dermal plates are still on the surface and very much of the primitive ganoid pattern. The hyomandibular and preopercular are sunken deeper into the skin, so that the adductor is of the teleost type, with its origin on the anterior face of the preopercular. The cartilaginous palato-quadrate and the Meckelian cartilage are incased in their dermal bones, and good teeth have developed, so there is need of good muscular development for the jaws. The quadrate, preoperculum and the cartilaginous skull make a good insertion for the splendid muscular system found in this group. The insinking of the preoperculum gives the adductor plenty of room for development and full advantage has been taken of this opportunity.[3]

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Levator maxillæ superioris (L. m. s.).

---

[3] This study on *Amia* follows the work of Allis (1897) and McMurrich (1885).

Levator arcus palatini (L. a. p.).
Adductor mandibulæ (Ad. m.).
Protractor hyomandibularis (P. h.).
Dilator operculi (D. o.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Adductor hyomandibularis (Ad. h.).
Adductor operculi (Ad. o.).
Levator operculi (L. o.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Levator maxillæ superioris (L. m. s.).—This is derived from the muscle of the same name in the selachians. It arises on the hyomandibular and along the side of the cartilaginous part of the skull; part of it is anterior to the eyes. It is attached to the adductor muscle and to the dermis, between the maxilla and the palatine arch.

Levator arcus palatini (L. a. p.).—Arises on the post-orbital process and is inserted on the metapterygoid and the hyomandibular.

Adductor mandibulæ (Ad. m.).—There is a great change here from the condition of the selachians. The adductor mass is now attached to the bony elements of the mandible and is differentiated into three parts, the second of which is again divided into two.

(*a*) Pars superficialis (Ad. $m.^1$).
(*b*) Pars temporalis lateralis (Ad. $m.^2$).
(*c*) Pars temporalis medialis (Ad. $m.^3$).
(*d*) Pars intramandibularis (Ad. $m.^4$).

(*a*) Pars superficialis (Ad. $m.^1$, A^2 Allis) arises from the post-orbital process and the under surface and outer edge of the pterotic, and from the outer face of the preoperculum, hyomandibular, quadrate, and symplectic. It is inserted on the coronoid and extends into the supra-meckelian fossa. A tendon from this part extends to the inner side of the maxilla as in the selachians. This tendon represents a muscle of the selachians (levator labii superioris) that is lost in *Amia,* the tendon only remaining.

(*b*) Pars temporalis lateralis (Ad. $m.^2$, A^3). The deep portion arises from the hyomandibular, quadrate, and the outer part of the metapterygoid. It joins Ad. $m.^1$ near its insertion on the jaw. It is partly subdivided into the two parts Ad. $m.^2$ and Ad. $m.^3$

(*c*) Pars temporalis medialis (Ad. m.^{3}) is the inner slip of the medial layer pars temporalis lateralis.

(*d*) Pars intramandibularis (Ad. m.^{4}, A ω Vetter) is the part of the adductor mass that extends forward into the hollow ramus of the jaw as in the teleosts. It arises from the fascia on the other two parts of the adductor and fills the hollow ramus, being attached to the splenial and the dentary.

Protractor hyomandibularis.—This muscle is not present in *Amia* as a separate muscle, but its function is taken by the posterior part of the levator arcus palatini, this has a small insertion on the underside of the hyomandibular, thus acting as a protractor of that element.

Dilator operculi (D. o.).—This arises on the pterotic, extends through the usual fossa in the hyomandibular and is inserted on the anterior, inner face of the operculum by a tendon. The path of this muscle over the hyomandibular, just above the preoperculum is well marked, as it is in all fishes. This muscle raises and pulls the opercular region outwards.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

These muscles of the facialis group represent the C$_2$sd of Vetter, that is the dorsal part of the "second constrictor" pertaining to the hyoid arch (C$_2$sd).

Adductor hyomandibularis (Ad. h.).—This arises from the otic region and is inserted on the inner face of the hyomandibular, along the posterior edge to the articulation for the operculum. It pulls the hyomandibular dorsally.

Adductor operculi (Ad. o.).

Levator operculi (L. o.).—These two muscles of the operculum both arise on the pterotic and parietal, the adductor operculi being the anterior slip. They extend down to the operculum and spread out on its inner face. They raise the operculum.

LEPIDOSTEUS

Plate II, Fig. 3

Lepidosteus has a well developed skull with a great elongation of the mandible and maxillæ. The great forward prolongation of the quadrate and mandible gives what is demanded for a catcher of fish, namely, a quick snap. The enormous adductor with its temporal and masseter slips must serve to close the jaw with a very quick snap, so that the numerous sharp pointed teeth get a hold on the slippery prey. These muscles are inserted at a very oblique angle and the leverage is such as to give a very rapid movement with comparatively slight power.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ (Ad. m.). (Divided into three parts.)
Protractor hyomandibularis (P. h.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Adductor operculi (A. o.).
Levator operculi (L. o.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ (Ad. m.).—This muscle is divided into three parts: Adductor 1 (to preoperculum), adductor 2 (along the roof of the skull), adductor 3 (to quadrate). Adductor 1 takes its origin in a fan-shaped mass along the outer face of the operculum. It extends anteriorily, becoming tendinous at the posterior border of the eyes, and is inserted in the space above the Meckelian cartilage. Adductor 2 is a long muscle arising along the entire face of the cartilaginous region of the skull, from the preorbital region to the hyomandibular. It extends along the roof, dorsal to the eyes and to the anterior edge of the mandible. The two pair almost meet in the median line, as only a thin cartilaginous plate separates them. It is inserted in the Meckelian fossa with the other parts of the adductor mass. Adductor 3 is a short portion of the adductor that arises on the tiny quadrate, spreads out in a thin sheet and is inserted on the coronoid process of the mandible. It is a very small muscle, lying under adductor 1.

Protractor hyomandibularis.—This muscle is between the dorsal and the ventral parts of the adductor mandibulæ. It arises on the orbitosphenoid with a small tendon at its anterior end and a fleshy attachment to the side of the skull as it extends posteriorly to its insertion on the hyomandibular. It resembles a homologous muscle found in *Acipenser,* and Vetter calls it by the same name.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Adductor operculi (A. o.).—This is a small muscle that arises on the hyomandibular and curves around to be inserted on the inner face of the operculum, near its anterior edge. It pulls the operculum forward and is homologous with the muscle of the same name in *Amia.*

Levator operculi (L. o.).—This arises on the occipital region of the skull, spreads out in a fan-like insertion on the upper, inner face of the operculum. It raises the operculum. Both of these muscles are probably the homologues of Csd_2 of Vetter and the C_2md of Ruge.

ESOX

Plate III, Figs. 1, 2

In *Esox,* as in other teleosts, the dermal bones have sunk into the skin so that the adductor region is free on the outside. The preoperculum, metapterygoid, quadrate, and post-frontal regions give the adductors a good surface for insertion. The teleost mandible becomes enlarged and the articulation with the quadrate is greatly improved in its mechanics. As the maxillæ are reduced and have lost the power to meet the mandibles, their teeth have disappeared and the mandibles are inclined inwards to meet the teeth of the palatines.

The following description is based partly on that by Vetter (1878):

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Adductor mandibulæ 4 (Add. ω of Vetter).
Adductor mandibulæ 1 (Superficial).
Adductor mandibulæ 2 + 3 (To symplectic, etc. Deep.).
Levator arcus palatini (Vetter).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Adductor hyomandibularis (Vetter).
Dilator operculi (Vetter).
Levator operculi (Vetter).
Adductor operculi (Vetter).
For homologies see Table I, p. 156.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

The muscles of *Esox* have been worked out by Vetter (1878, p. 494). His names are used for the most part in the present description, although the nomenclature of the adductor mandibulæ is changed, as explained in the notes. The adductor has three distinct parts.

Adductor mandibulæ 4 (Add. ω of Vetter, 1878, p. 494).—This large muscle mass fills the suprameckelian fossa and is attached to the side of the fossa and to the cartilage. It is homologous with that found in *Amia* (Ad. m.^{4}) and in several other forms where the Meckelian fossa is large.

Adductor mandibulæ 1 (Vetter, 1878, p. 494).—This is the outer sheet of the adductor, which completely covers the rest of the muscle. It takes its origin from the edge of the frontals, from the postorbitals to the articulation of the hyomandibular, along the face of the hyomandibular and the anterior face of the preoperculum; the lower part arises from the symplectic and the postero-ventral portion of the quadrate. It ends at the mandible with a short, wide tendon and joins with the rest of the adductor mass, to be inserted in the mandible, in the coronoid region and in the suprameckelian fossa.

Adductor mandibulæ 2.—This is underneath the superficial adductor (Add. m.^{1}). It arises on the metapterygoid, preoperculum, quadrate, and has a slight origin on the hyomandibular and operculum. This complex muscle becomes tendinous at the anterior end and extends to the jaw medial to the superficial adductor. It extends into the suprameckelian fossa to join the rest of the adductor.

Adductor mandibulæ 3.—The deepest portion of the adductor mass. Its tendon joins that of Ad. m.^{2}.

Levator arcus palatini (L. a. p.) (Vetter).—This is found along the upper part of the post-frontal region, after the adductor mandibulæ 1 is removed. It arises on the pterotic and alisphenoid and is inserted on the metapterygoid and hyomandibular. It pulls up on the palatine region and closes the gills.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Adductor hyomandibularis (Ad. hy.) (Vetter, 1878, p. 502).—A small muscle between the hyomandibular and the skull that arises on the skull wall in the otic region and is inserted on the inner side of the hyomandibular. It adducts the hyomandibular, as its name indicates.

Dilator operculi (D. o.).—This muscle is not to be seen until the adductor mandibulæ 1 is lifted off. It extends from the pterotic to the operculum. It arises on the pterotic and hyomandibular and extends over the hyomandibular and under the tip of the preoperculum to be inserted on the upper, inner face of the operculum. It opens the opercular cavity.

Levator operculi (L. o.).—This muscle is just posterior to the dilator operculi. It arises on the posterior end of the pterotic with a slight attachment to the hyomandibular. It is inserted on the upper edge of the operculum where it spreads out in a fan-shaped mass. It raises the operculum.

Adductor operculi (A. o.).—This is a short muscle that arises on the posterior limb of the pterotic and in the epiotic groove. It is inserted under the levator operculi on its anterior edge and is also attached to the opercular process of the hyomandibular and to the origin of the adductor mandibulæ 2 (Vetter). It closes the operculum and pulls it dorsally.

ANGUILLA

Plate II, Figs. 4, 5

The peculiar reduction of the maxillæ and premaxillæ in the Apodes has made the mandibles incline inwards to meet the teeth on the palatines. The extreme is reached in the Murænidæ, where the maxillæ and premaxillæ are lost and the palatines and pterygoids assume their function. The eels have a reduced pterygoid region and the maxilla and premaxilla are small or lost, the vomers and palatines being supplied with teeth, and functioning as the maxillary elements. The mandible is changed in position so that it is inside of the palatines when it is closed.

The muscular development of *Anguilla* is remarkably like that of certain reptiles. The dipnoans and Apodes are about the only examples among the fishes that show the adductor muscles extending up to the median line of the skull and meeting there, separated only by fascia. The condition in Apodes is unique in this respect, for the muscles are free to extend to the median line and have their movements entirely unhampered by any covering of bone. Thus the adductor muscle resembles the capiti-mandibularis of the reptiles and compares favorably with the temporalis muscle of some mammals in shape and development. Although the adductors meet on the median line their fibers do not mix, as they are separated by fascia.

The hyomandibular is large and well muscled.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ.
Dilator operculi.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Levator operculi.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ.—This muscle completely covers the skull posteriorly, covering the dorsal, median line to a depth of three or four millimeters. It is in two layers, a superficial (Add. 1) and a deep (Add. 3). The superficial layer arises on the frontal, parietal, pterotic, and hyomandibular, and is inserted on the coronoid region of the mandible. The origin of this muscle is far different from that of the usual teleost muscle, which takes origin from the preoperculum. It has spread over the skull and arises much as in the reptiles. The great development of the hyomandibular and the reduction of the opercular bones is the probable cause of the change of origin.

The deep layer (Add. 3) arises on the parasphenoid, sphenotic, hyomandibular, and quadrate. It joins the outer layer and is inserted on the mandible.

Dilator operculi (D. o.).—This muscle is covered by the adductor. It arises on the sphenotic and hyomandibular and is inserted on the upper portion of the anterior border of the operculum. It raises the operculum and pulls it forward.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Levator operculi (L. o.).—This arises on the posterior part of the pterotic and spreads out in a fan-shaped sheet on the outside of the operculum. It raises the operculum. This muscle is on the inside of the operculum in most teleosts but in the Apodes it creeps to the outside. The reduction of the opercular bones probably has something to do with this change.

PALINURICHTHYS

Plate III, Figs. 3, 4, 5

The skull is fundamentally similar to that of the perch but is short antero-posteriorly and with large orbits.

The principal muscles of the jaws are as follows:

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Adductor mandibulæ (1 and 2).
Levator arcus palatini (L. a. p.).

Protractor hyomandibularis (P. h.).
Dilator operculi (D. o.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Levator operculi (L. o.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

The adductor is divided into two layers and a third is present as the intramandibular slip. There is a connection by a rudimentary tendon with one of the anterior levator maxillæ muscles that arises at the anterior of the premaxilla and joins the adductor near its tendon. The main adductor arises along the anterior face of the preoperculum, following down along this bone to its tendon near the mandible. The deeper layer arises on the quadrate and metapterygoid region, joining the rest of the adductor and ending in a crescent-shaped tendon near the coronoid region of the mandible. This connects with the muscle in the mandible (Adm^4) which is the Add. ω of Vetter. This consists of a mass of fibers attached to the dentary, with all of the fibers converging to a central tendon, which is connected with the tendon of the main adductor.

Levator arcus palatini (L. a. p.).—When the eye is removed this muscle is seen with its fibers extending ventrally to be attached to the palatines and pterygoids. It arises on the parasphenoid and most of the short fibers are inserted with a fleshy attachment to the palatine and a few to the pterygoids. It raises the palatine region.

Protractor hyomandibularis (P. h.).—This muscle arises on the sphenotic and extends under the dorsal end of the adductor, to be inserted on the outer face of the hyomandibular. It draws the hyomandibular and opercular apparatus forward.

Dilator operculi (D. o.).—It arises on the sphenotic under the protractor hyomandibularis and extends posteriorly to be inserted on the anterior, dorsal portion of the operculum. It pulls the operculum forward and raises it slightly.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Levator operculi (L. o.).—It arises on the posterior end of the pterotic and extends downward to its insertion on the inside of the upper, inner face of the operculum. It raises the operculum and pulls it slightly forward.

POLYPTERUS

Plate IV, Figs. 1, 2

The condition of the skull in *Polypterus* is extremely primitive, as all the dermal elements are on the surface. The skull is broken up into small elements so that the comparison with the Devonian Rhipidistii, such as *Osteolepis,* is easily made. The elements may not be exactly the same, but they represent the breaking up of the hard dermal shell to allow the necessary movement occasioned by the muscular development. It might be possible to account for all of the breaks by making a phylogenetic study of the muscles in the fossil forms. In this connection Gregory (1915, p. 327) offers the following very interesting and suggestive hypothesis:

> It may be stated as a general hypothesis that in the dermocranium of the primitive fishes the position and arrangement of the sutures and the subsequent pattern of the osseus elements are the evolutionary resultants of the various symmetrically balanced stresses induced by the action of the underlying muscles of the eyes, jaws, branchial arches and pectoral limbs, in composition with the position and size of the olfactory, optic and auditory capsules. It is at least a fact that sutures and articulations define loci of greatest mobility, centers of ossification define loci of least mobility. Differential growth of one region of the skull, as in the rapid elongation of the snout, also results in more or less rearrangement of the sutures and osseus elements.

An examination of the skull of *Polypterus* shows that Dr. Gregory's hypothesis works out well, as most of the breaks in the skull might be explained by the stress of the muscles actually present. The adductor mandibulæ would tend to make the break over the frontal and parietal region, as this is at right angles to the pull. The pull of the masseter would cause the break in front of the preoperculum by its pull against the squamosal and quadrate elements. The spiracle and its muscle might account for the broken condition in that region with its many small plates. The breaks in the region in front of the orbits are more difficult to account for, but in the sharks and some of the other fishes there is a levator maxillæ which might have caused the breaking up in this region.

The jaw muscles of *Polypterus* have been figured and described by Pollard (1892).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Adductor mandibulæ (Ad. m.).
Protractor hyomandibularis (P. h.).
Levator maxillæ superioris (L. m. s.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Adductor hyomandibularis (Ad. h.).

Adductor branchialis (Pollard).

The differences in the musculature of the shark and of *Polypterus* are due to the fact that the latter has a bony skull roof and requires a different form of musculature.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Adductor mandibulæ.—This muscle is somewhat more complex than the adductor of the selachians, where the mass is rather compact. It may be divided into a temporal (Adm^2), masseter (Adm^1) and pterygoid portions (Adm^3).

(*a*) The masseter (Adm^1) is the largest part of the adductor and stretches across the face of the mass, so that the pull is almost along the line of the skull base. It is covered by the preopercular plate, so that it, as well as the rest of the adductor, is not seen from the outside. The muscle slip arises along the back part of the skull where the preoperculum joins the hyomandibular and quadrate. These bones bound a triangular region at the posterior part of the skull where the masseter slip arises. It is attached to the preoperculum along the inner face, where it overlaps the hyomandibular and extends to the quadrate. The insertion is on the coronoid process of the mandible.

(*b*) The temporal portion (Adm^2) of the adductor, as well as the pterygoid slip, are at right angles to the masseter portion, so that the combined pull of the three parts is at an angle of about 45° to the top of the skull as a base line. This slip arises on several bones of the dorsal part of the skull, on the postorbital and frontal. The attachment to the frontal (after Pollard, 1892, p. 391) is "to its under surface between its projecting edge and its articulation with the orbito-sphenoid, extending even above the eye." The insertion of the temporal portion is in the suprameckelian fossa. This part is anterior to the pterygoid slip and overlies it somewhat. It is at right angles to the masseter.

(*c*) The pterygoid slip (Adm^3) arises behind the temporal and beneath it, on the orbitosphenoid and parasphenoid, and its insertion is on the mandible along with the temporal. This mass of muscle represents a part of the capiti-mandibularis of reptiles and the adductor of the selachians.

Protractor hyomandibularis (P. h.).—Two muscles connected with the adductor group assist in the movement of the operculum, the protractor hyomandibularis and the levator maxillæ superioris. They are closely associated with each other and by their retraction pull the operculum outward and help in moving the water in the gill chamber. The protractor arises on the postfrontal and is inserted on the operculum and hyomandibular where the two bones meet. A small slip of this muscle, according to Pollard, is attached to the bones around the spiracle and assist in regulating its closing and opening.

Levator maxillæ superioris (L. m. s.) Add. β Vetter.—This muscle is closely connected with the protractor. It arises on the postfrontal and is attached to the metapterygoid and quadrate and to the lower edge of the hyomandibular.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(*INNERVATED BY VII*)

Adductor hyomandibularis (Ad. h.).—This is the retractor hyomandibularis of Pollard. It arises in the otic region on the proötic and along the ridge of the postero-external process. The anterior part of the muscle is called the retractor. The insertion is on the hyomandibular, above the posterior articulation of this bone with the operculum. It is attached to the anterior part of this articulation and on the inner side of the bone.

Adductor branchialis (Ad. br.) (Pollard).—There is a small muscle at the angle of the jaw that, according to Pollard (1892, p. 389), may represent the adductor arcus branchialis of the selachians. It is in the ligaments that connect the hyomandibular, quadrate and stylohyal.

NEOCERATODUS

Plate IV, Figs. 3, 4

The wide massive skull of *Ceratodus* (*Neoceratodus*) is correlated with the peculiar development of the splenial, vomerine and palatine teeth. The cartilaginous skull is covered by the superficial derm bones and with a great space reserved at the posterior region for the accommodation of the large adductor mandibulæ. The opercular region is reduced and the hyomandibular is vestigial or absent. Günther (1871, p. 524) saw this little vestige of both the hyomandibular and the symplectic but did not recognize them as such. Huxley (1876, pp. 3-4) says:

> It is obvious that this little cartilage is the homologue of the hyomandibular element of the hyoidean arch of other fishes, the small conical process being the rudimentary symplectic, and, therefore, that it is itself the dorsal element of the hyoïdean arch, attached in its normal position, as its relations to the seventh nerve show. (Huxley's observation on Günther's work. Günther, 1871, p. 524.)

This small cartilage, then, represents the hyomandibular and the symplectic of the teleosts. It is in the correct position for these bones and there is little doubt of the homology. With its reduction there has been quite a change in the opercular region, as the opercular bones are reduced and changed together with the preopercular. Günther thought that a small bit of cartilage on the anterior edge of the opercular was the vestige of the preoperculum. Goodrich (1909, pp. 237-238) says:

> It is in the connection of the skull with the visceral arches that the dipnoi have diverged most conspicuously from the other fishes. The modern genera are completely autostylic. The pterygo-quadrate bar is firmly fused to the cranium in front and behind. The spiracle disappears and the hyoid arch is well developed, with a medial basihyal, paired hypohyals and large ossified ceratohyals. But the hyomandibular takes no share in the support of the jaws. It disappears, indeed, entirely in the Dipneumones where the ceratohyals alone remain, and, as Huxley showed, is represented in *Ceratodus* by a minute vestigial cartilage, overlying the hyomandibular branch of the seventh nerve.

The skull of *Ceratodus* has a continuous dermal temporal roof as in the stegocephalians. Parts of the skull resemble the cartilaginous structure in the urodele embryo, especially in the region of the arches, but here the resemblance stops.

FIGURE 1

Mandible of *Neoceratodus forsteri* with the tendinous fascia of the adductor mandibulæ muscle

In the arrangement of the jaw muscles this dipnoan is very simple. The skull consists of a massive cartilaginous part with a covering of dermal bones which gives the head its large size. The space between the cartilage surrounding the brain and the dermal bone is filled with the enormous temporal muscle which supplies the motive power for the great crushing apparatus. The general aspect of the head is amphibian-like to an extent found in no other fish but the eels. There is a space along the mid-dorsal region of the cartilaginous skull that is covered with the temporal muscle and with the muscles of the neck region. In *Polypterus* and *Amia* the muscles of the skull top make no approach to this extension in the dorsal region, but in the eels the temporal muscles extend up and the muscles of the two sides meet in a reptilian way. The musculature of *Neoceratodus,* in fact, represents a highly specialized dipnoan type, retaining very little of the primitive fish type. The loss of the hyomandibular causes the loss of several muscles common to the elasmobranchs and the teleosts.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Adductor mandibulæ (Ad. m.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Levator operculi (L. o.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Adductor mandibulæ.—The adductor muscles of *Neoceratodus* are the largest found in fishes. The adductor is divided into two slips—a masseter (Adm^1) and a temporal (Adm^2)—which give the cutting and crushing power to the powerful dental plates.

(*a*) The masseter slip ($\mathrm{Adm.}^1$) is quite small and much shorter than the temporal portion of the adductor. It arises in the quadrate region and extends forward to be inserted behind and below the insertion of the rest of the adductor. It also has a small tendinous sheet, but it is small in comparison with the sheet of the main adductor.

(*b*) The temporal slip (Adm^2) is the larger of the two muscles. It arises along the cartilaginous brain case, extending from a point anterior to the eyes to the posterior part of the brain capsule and extending well down on the sides. It is also attached to the bones of the roof of the skull, where they cover it. In dissection the muscle is seen to be broken up into small bundles that are attached to the side walls of the skull. In the median line the cartilaginous skull does not extend to the roof of the skull in the region of the adductor muscles, so that the muscles fill this gap. They nearly meet in the midline, being separated only by some tendons of the long neck muscles and by fascia. This part of the adductor is divided by a great tendinous sheet to which the fibers from both sides join. It is very heavy and thick, thus giving great power. It is inserted on the coronoid region in the Meckelian cartilage region.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Levator operculi.—The levator is the only other muscle in the upper part of the skull. It arises on the posterior face of the lower part of the cartilaginous capsule and is inserted on the inner side of the opercular region.

The mandibles are depressed by the long ventral muscles that are attached to the mandibles close to the symphysis and by the hyoid muscles.

The loss of the hyomandibular and the degeneration of the opercular bones has caused the loss of the usual muscles of this region of teleosts.

AMPHIBIA

RANA

Plate V, Figs. 1, 2

The fundamental resemblance in the skull of Anura to some of the fossil Amphibia, for example, such as *Cacops* and *Eryops,* is quite striking. These are indeed so much like the Anura that in studying them for restoration of the muscles it was found that the musculature demanded was invariably of the anuran type. *Cacops* in side view shows a type of covered skull that has opened out to a certain extent in the temporal region, while remaining solid in the dorsal region. Some of the modern Anura, *i. e., Pipa americana,* show something of the covered condition found in the stegocephalians, giving some likenesses to these fossil forms, although this resemblance may well be secondary. *Eryops,* also, is very much like the Anura in the palatal region, although the dorsal part of the skull appears to be quite different, because of the complete covering of dermal bones which it has retained from its early fish ancestors.

The frog skull represents a fenestrated condition of the roofed skull, with the palatal, postorbital and temporal region cleared of their bony covering. There is a light musculature in the jaw region to meet the conditions of the weak mandibles. It has been suggested (Gregory, 1917) that this similarity of the Anura and the stegocephalians is more genetic than convergent and that our Anura may indeed represent certain remnants of stegocephalians in which the roof of the skull became fenestrated.

The jaw muscles in the frog, on account of the great open palatal region, are all on the posterior part of the skull, as there is no place for the muscles at the front part of the skull. The jaw muscles of the Anura are given the mammalian names by Ecker and Wiedersheim (1896-1904, pp. 133-136).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Capiti-mandibularis superficialis.
    (*a*) Pars major (Masseter major of E. and W.).
    (*b*) Pars minor (Masseter minor of E. and W.).
Capiti-mandibularis profundus (Pterygoideus of E. and W.).
Pterygoideus anterior (Temporalis of E. and W.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ (E. and W.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Capiti-mandibularis superficialis.—This muscle is divided into two parts by Ecker and Wiedersheim and called by them masseter major and masseter minor. It seems to be a muscle representing the superficial part of the capiti-mandibularis mass and may represent the two portions, as it is divided in the reptiles in this paper.

(*a*) Pars major.—This arises by two heads, one from the zygomatic process of the squamosal and the other from the lower quadrant of the tympanic annulus. It is inserted on the upper edge and outer side of the mandible and serves to tighten the ear-drum, thus acting as a tensor tympani.

(*b*) Pars minor.—This is smaller than the major and posterior to it. It is double-headed also, arising from the anterior border of the posterior arm of the squamosal and from the lateral knob of the quadratojugal. It is inserted on the mandible, posterior to the major. It is much shorter than the major.

Capiti-mandibularis profundus (Pterygoideus of E. and W.).—This is posterior to the eye and is covered by the pterygoideus anterior (temporalis of E. and W.). It originates on the fronto-parietal and proötic and is inserted on the coronoid process, just posterior to the insertion of the pterygoideus anterior (Temporalis).

Pterygoideus anterior (Temporal of E. and W.).—This is a large muscle that fills most of the space between the proötic and the eyes. It curves around the annulus of the ear, covering the capiti-mandibularis profundus and going under the pars major of the capiti-mandibularis superficialis. It is a double-headed muscle, one head arising on the ridge between the proötic and the fronto-parietal, while the second head, arising on the anterior edge of the posterior limb of the squamosal, joins the first and is inserted on the coronoid process of the mandible. I call it pterygoideus anterior because it appears to be homologous with a muscle of the same name in the Reptilia.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ (Ecker and Wiedersheim).—The depressor of the jaw is a large muscle that covers the posterior part of the skull, overlapping the other muscles of that region. It is double-headed, arising on the posterior upper limb of the squamosal and from the lower part of the annulus tympanicus and from the dorsal fascia. The anterior head arises on the posterior limb of the squamosal and from the lower part of the tympanic annulus. It joins with the posterior portion and is inserted on the angular. The head that arises on the dorsal fascia springs from the region of the upper part of the scapula and extends down to join the anterior or cephalic portion of the muscle. The anterior head tightens the ear-drum and lowers the jaw.

CRYPTOBRANCHUS

Plate V, Figs. 3, 4

The skull of *Cryptobranchus* (using this name in a broad sense to include the American and Japanese forms) is much depressed and widened. The squamosal is far up on the skull, making a shoulder and groove around which the temporal muscles ride, so that their path is well fixed. The pterygoids are flattened out to fill the region posterior to the palate and to supply good origins for the muscles.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).
 = Masseter (Osawa).
 = Petro-tympanicus (Hoffmann).
Capiti-mandibularis profundus (C. m. p.).
 = "Temporalis" (Osawa).
Pterygoideus posterior.
 = Pterygoideus (Hoffmann and Osawa).
Pterygoideus anterior.
 = Temporalis of Osawa.
 = Fronto-parieto-maxillaris of Hoffmann.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

(INNERVATED BY VII)

Depressor mandibulæ (D. m.^{1}, D. m.^{2}).
 = Digastric of Humphrey.
 = Cephalo-dorso-maxillaris of Hoffmann.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).—This muscle covers the lower part of the temporal muscles. Its fibers extend posteriorly as they do in most urodeles. It arises on the whole outer face of the squamosal and extends over the pterygoid bone to be inserted on the posterior half of the exterior face of the mandible.

Capiti-mandibularis profundus (C. m. p.).—This is the posterior slip of the muscle called "temporal" by Osawa. It is a thin muscle that arises on the third neck vertebra, extends forward to join the pterygoideus anterior and is inserted on the inner side of the mandible.

Pterygoideus posterior.—Very small in this form.

Pterygoideus anterior (Pt. a.).—This is the anterior part of the temporal muscle of Osawa. It arises on the pre-frontal and fronto-parietal, extends under the eye and converges rapidly to a narrow tendon, and is inserted on the coronoid process and in the fossa. This muscle is a part of the muscle usually called a temporal muscle, but it is considered as the homologue of the muscle found in the reptiles called pterygoideus anterior in this paper.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ (D. m.[1], D. m.[2]).—This is a double-headed muscle, as it is in all of the amphibians. It arises on the dorsal and posterior part of the squamosal, with a second part arising from the dorsal fascia. The anterior part arises from the otic region and from the posterior, upper face of the squamosal. Both parts are inserted on the upper and outer face of the angular bone of the mandible.

AMPHIUMA

Plate V, Fig. 5

The skull is elongated and there is a prominent sagittal crest so that a deep fossa is formed for the muscles of the upper part of the skull. The skull roof is open so that the muscles have free play, as in most urodeles. The pulley arrangement of the dorsal muscles gives a very definite action to the jaws and is probably correlated with the backward extension of the capiti-mandibularis profundus, which is attached to the vertebræ of the neck.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis superficialis.
  = Masseter.
  = Petro-tympano-maxillaris of Hoffmann.
Capiti-mandibularis profundus.
  = Posterior head of the temporal of others.
  = Fronto-parietal maxillaris (Post part) of Hoffmann.
Pterygoideus posterior.
  = Pterygoideus.
  = Pterygo-maxillaris of Hoffmann.
Pterygoideus anterior.
  = Anterior slip of the temporal of others.
  = Anterior part Fronto-parieto-maxillaris of Hoffmann.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).—This is the outer or masseteric slip of the temporal mass, which covers over the other temporal muscles. It has a double head; the anterior arising on the large, outer face of the squamosal, while the posterior head arises on the ventral part of the same face. It is inserted on the outer face of the mandible on the posterior half.

Capiti-mandibularis profundus (C. m. p.).—This posterior part of the temporal mass arises from the fourth cervical vertebra, extends around over the groove on the skull, and, becoming tendinous, joins with the anterior part of the muscle called pterygoideus anterior in this paper. It is inserted on the coronoid region and in the fossa.

Pterygoideus posterior (Pt. p.).—This is a large muscle in *Amphiuma,* arising on the pterygoid under the capiti-mandibularis superficialis. It is inserted on the coronoid process, posterior to the insertion of the other temporal muscles.

Pterygoideus anterior (Pt. a.).—This is the anterior part of the muscle usually called the temporal. It arises along the groove on the fronto-parietal and from the orbito-sphenoid. It extends downward, rapidly converging, joins with the capiti-mandibularis profundus, and is inserted in the coronoid region of the mandible.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ (D. m.).—This is a double-headed muscle, as in most urodeles. The anterior portion arises on the posterior face of the squamosal, the posterior from the dorsal fascia. They are inserted on the outer, dorsal face of the posterior end of the mandible.

AMBLYSTOMA

Plate V, Figs. 6, 7

The remaining urodeles are very similar in musculature, at least in the three forms studied in this paper. About the only difference is the separation of the lower, inner part of the temporal mass to form a separate pterygoideus posterior.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).
  = Masseter.
Capiti-mandibularis profundus (C. m. p.).
  = Posterior slip of the temporal.
Pterygoideus posterior (Pt. p.).
  = Pterygoideus.
Pterygoideus anterior (Pt. a.).
  = Anterior head of the temporal.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibularis (D. m.).

REPTILIA

CHELYDRA

Plate VI, Figs. 1, 2

The primitive chelonian *Proganochelys* is the earliest known representative of the Chelonia. Unfortunately it is known only by the cast of the interior of the shell. Although the skull is unknown it was probably of the heavily roofed type, something like that of the existing *Chelone.* Watson (1914, pp. 1011-1020) describes the Permian genus *Eunotosaurus* as a probable ancestor of the Chelonia. It is quite probable that the ancestral chelonians were like the cotylosaurs with the temporal region of the skull covered and that there never has been a representative of this group with any fenestration of the lizard type. They have adopted a different scheme for the opening of the temporal muscle region by the posterior excision of the temporal roof, leaving the muscles of the head more or less bare. Except posteriorly, the roof is complete in *Chelone* and there is a progressive reduction of the roof in the modern forms through *Chelydra* and *Trionyx,* until finally the opening is complete in *Cistudo,* where even the jugal has lost its hold on the quadrate. These forms thus give a morphological series. The reduction of the temporal roof is analogous to the fenestration of the skull in other orders of reptiles, where the temporal roof is perforated dorsally and laterally.

The great occipital crest indicates a corresponding temporal muscle in Chelonia, where the muscle extends behind the condyle and back over the vertebræ of the neck. The quick snap of the jaws of *Chelydra* and *Trionyx* is due to the extension of the occipital crest which gives the temporal muscle a long origin and an oblique angle of insertion. The great separation of the squamosal from the parietal causes the depressor mandibulæ to slip down from its usual origin on the parietal to the outwardly projecting squamosal.

The turtle with its monimostylic skull has very simple jaw muscles, only three muscles being differentiated.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Capiti-mandibularis (C. m.).
  = M. Occipito-squamoso-maxillaris, Hoffmann (1890).
  = Schläfenmuskeln, Wiedemann.
  = Temporalis, Bojanus, Stannius, Cuvier, Owen.
Pterygoideus anterior (Pt. a.).
  = Pterygo-maxillaris, Hoffmann.
  = M. Pterygoideus, Bojanus, Owen.
  = Flügelmuskel, Wiedemann.
  = Pterygoideus internus, Stannius.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

(INNERVATED BY VII)

Depressor mandibulæ (D. m.).
  = Digastricus maxillæ, Bojanus.
  = Squamoso-maxillaris, Hoffmann.
  = Masseter (apertor oris), Wiedemann.
  = Apertor oris, Owen.
  = Senker des unterkiefers, Stannius.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Capiti-mandibularis (C. m.).—This represents the large capiti-mandibularis of the other reptiles and the adductor mandibularis of fishes, or at least a part of it. It is peculiar in the turtles in that they have developed a great occipital spine that supports this muscle. It arises on the following bones: proötic, quadrate, parietal, squamosal, occipital spine, opisthotic. It is inserted on the posterior part of the mandible.

Pterygoideus anterior (Pt. a.).—This is the large pterygoid muscle of reptiles with a monimostylic skull. It covers the floor of the pterygoid and palatine region and has a firm hold on the edge of the palatal vacuities. It arises on the pterygoids and palatines, extending almost under the eyes, from the parietal, pterygoid, proötic and quadrate. It is inserted on the inner face of the prearticular. It does not wrap around the mandible on the outside as it does in most reptiles.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

(INNERVATED BY VII)

Depressor mandibulæ (D. m.).—The backward growth of the squamosal has captured this muscle so that it now is attached to it, instead of to the parietal, as in most reptiles. In *Chelydra* the whole origin is on the large and prominent squamosal, which may be explained by the assumption that the growth of the squamosal pushed back on the depressor mandibulæ (parieto-mandibularis), and that, gradually, the attachment on the squamosal became more important, and finally the origin on the parietal was lost, as a result of the shifting of the bones of the skull. The depressor mandibulæ is attached along the upper, posterior face of the squamosal and is inserted on the under surface of the articular.

There is much in the condition of the skull in turtles to suggest the cotylosaurs, and I assume that the muscular system must have been similar.

SPHENODON

Plate VI, Figs. 3, 4

The supratemporal fenestra of *Sphenodon* gives exit to the temporal portion of the capiti-mandibularis on top of the skull, while the lateral temporal fenestra permits the masseter portion to expand freely in mastication. Owing to the fixed or monimostylic condition of the quadrate, there is very little movement either of the fore part of the skull upon the back part or of the pterygoid region. In correlation with this immobility the specialized pterygoid muscles are absent.

The jaw muscles of *Sphenodon* are slightly more subdivided than those of *Chelydra,* in correlation with the more open construction of the skull.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.
- (*a*) Capiti-mandibularis superficialis (C. m. s.).
  - = Outer fibers of Osawa's temporal.
- (*b*) Capiti-mandibularis medius (C. m. m.).
  - = Temporalis, Osawa (superficialis).
- (*c*) Capiti-mandibularis profundus (C. m. p.).
  - = Pterygoideus externus, Osawa.

Pterygoideus anterior (Pt. a.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ (D. m.).
= Parieto-mandibularis, Osawa.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.—This muscle is the large muscle mass of the reptiles and it is taken to represent the mother mass of several muscles, as is mentioned elsewhere in this paper. It seems to be the conjoined masseter and temporal fibers, so that the divisions of the muscle are given the names used below.

(*a*) *Capiti-mandibularis superficialis* (C. m. s.).—This part of the temporal mass consists of the fibers that always extend over the deeper fibers in the reptiles.

(*b*) *Capiti-mandibularis medius* (C. m. m.).—This is the inner part of the main mass, or the temporal of Osawa. The capiti-mandibularis mass arises in the temporal fossa on the parietal, squamosal, quadrate, the inner side of the jugal and from the temporal fascia. It is inserted on the point of the coronoid and on the inside and outside of the posterior third of the mandible.

(*c*) *Capiti-mandibularis profundus* (C. m. p.).—This deeper section of the temporal mass is separated in this form from the rest of the temporal mass. It arises on the parietal, postfrontal, proötic, epipterygoid, the membrane between epipterygoid and the proötic and from the outer face of the pterygoid.

Pterygoideus anterior (Pt. a.).—This short, strong muscle arises on the ventral border and inner side of the quadrate, from the inter-orbital floor, pterygoid and transverse. It has the typical reptilian insertion of this muscle, wrapping around the posterior end of the articular. It is inserted on the medial face and ventral border of the posterior fifth of the mandible.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ (D. m.).—This muscle, the homologue of the depressor of other animals, is called parieto-mandibularis by Osawa. It is a large muscle which arises from the posterior border of the parietal, from the ligamentum nuchæ, and to a slight extent from the squamosal. It is inserted on the posterior face of the articular or on its retroarticular process.

ALLIGATOR

Plate VI, Figs. 5, 6

In the alligator skull there is a great reduction of the posterior region and a corresponding elongation of the antorbital region. The palate is closed by the approximation of the secondary shelves of the maxillæ, palatines and pterygoids, so that the condition partly resembles that of the mammals. The pterygoids are also very closely appressed, so that the posterior internal nares are forced far to the rear and are almost ventral to the articulation of the mandible with the quadrate. There has been a progressive reduction of the temporal fenestræ, so that the heavily roofed skull of the alligator represents the specialized modern form of an ancient order that had a much more open skull with large fenestræ and very different proportions of the skull. The supratemporal fossa has been reduced until it is almost rudimentary, while the rest of the posterior region has also been encroached upon until the muscle space is quite small. The quadrate has shifted its position by inclining posteriorly, giving the animals a much larger gape; the quadrate is fixed or monimostylic. The auditory region is much changed by the secondary closing of the otic notch, so that the meatus appears to be in a different position; but this condition is merely the result of the closing in of the notch, so that its original position is masked. The small size of the posterior region of the skull and the corresponding reduction of the capiti-mandibularis is in a way compensated for by the great development of the pterygoideus anterior muscle which has extended over the floor of the palate and into the maxillæ. This muscle has an important part in the closing of the long mandibles.

The jaw muscles of the alligator are of the type found in monimostylic reptiles. The fixed pterygoids and palatines demand no muscles for their movement and consequently the muscles that function in *Varanus* and other streptostylic forms are not differentiated. The muscles of the capiti-mandibularis are pinched up, especially in the temporal section, as the temporal fossa is much reduced in most modern Crocodilia. This reduction is secondary, for the early fossil forms show no such reduction, but rather the opposite condition, with large supratemporal and laterotemporal fenestræ and small orbits. Most of the Mesosuchia show a large supratemporal fenestra as in *Teleosaurus,* where the fenestræ are of large size. There is a progressive closing of this fenestra from *Teleosaurus* of the Jura through *Geosaurus, Goniopholis* and *Tomistoma.* This closing and the pinching in of the temporal region means that the outer, or masseter, slip of the capiti-mandibularis (capiti-mandibularis superficialis) is enlarging and is taking over the principal work of closing the jaws, while the temporal slip is being progressively reduced. The pterygoid muscle is peculiar in that its anterior portion (pterygoideus anterior) has dug its way under the eye and into the maxilla, extending to a point far anterior to the eye, since it lies on the palatine and penetrates far into the maxilla. The depressing of the jaw is done by the usual muscle, the depressor mandibulæ. The Crocodilia spend much of their time lying on the mud, and the action of the depressor in this position is to raise the head if the mandible is resting on something fairly firm. The Crocodilia have some peculiar external ear muscles, necessary in the crocodile from the advanced condition of the ear with its external flap. The nerves divide the muscles into two groups.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.
  (*a*) Capiti-mandibularis superficialis.
    = Masseter portion.
  (*b*) Capiti-mandibularis medius.
    = Temporal slip.
  (*c*) Capiti-mandibularis profundus.
    = Deep part of temporal mass.
Pterygoideus anterior.
    = Pterygo-mandibularis, Bradley.
Pterygoideus posterior, Lubosch.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Capiti-mandibularis.

(*a*) *Capiti-mandibularis superficialis* (C. m. s.).—This is the outer slip of the temporal mass, which does most of the work in the closing of the jaw. It arises on the parietal, squamosal, quadrate and quadratojugal and is inserted in the suprameckelian fossa, extending forward into the dentary. It fills the region of the skull behind the pterygoids. The large external fenestra of the mandible gives the muscle room for expansion. The superficial layer (masseter) is subdivided into several layers, one being attached to the surangular.

(*b*) *Capiti-mandibularis medius* (C. m. m.).—This is the smaller of the slips of the mass. It extends down on the inner side of the capiti-mandibularis mass, arising on the bones surrounding the supratemporal fossa, into which it extends. It arises on the parietal, squamosal and postfrontal. Its insertion is on the coronoid, where it curves around the anterior edge of the capiti-mandibularis superficialis and extends under this slip to the mandible. The mandibular nerve separates it from the superficial slip. A small capiti-mandibularis profundus (pterygoideus post. Lubosch) attaches to the tendon of this muscle. Lubosch (1914, p. 699) says:

> Sehen wir vom Masseter und Pterygoideus anterior ab, so inseriert der sehr schwache, zweischichtige Temporalis mit einer kräftigen kurzen Sehne am Complementare. Ein Teil der Fasern endet an einer knorpelharten Zwischensehne. Von dieser Zwischensehne entspringen fraglichen Muskelportionen, welche ihrerseits zum Pterygoideus posterior gehören.

(*c*) *Capiti-mandibularis profundus* (C. m. p.).—This small muscle which joins the temporal mass is given this name, as it is assumed to belong to the inner layer of the temporal mass.

Pterygoideus anterior.—This anterior slip arises on the palatine, maxilla, pterygoid and transverse (ectopterygoid), extending over the floor formed by these bones and digging into the maxillæ. It extends inward to the limits of the narial passage. This muscle is the same as the great pterygoid muscle in *Chelydra* and is typical of the monimostylic reptiles. In the crocodile, however, it has a much greater forward extension.

Pterygoideus posterior.—This muscle (called pterygoideus posterior by Lubosch, who also includes a small slip that joins the capiti-mandibularis), arises on the quadratojugal and quadrate and joins with the anterior slip to be inserted on the mandible. A small slip from this joins the temporal mass and is designated as the profundus in this paper. These pterygoid muscles wrap around the posterior end of the mandible, where they swell out, making a large mass on the postero-ventral side of the jaw. This enlargement of the muscle at its insertion is paralleled in *Cryptobranchus,* as observed by Lubosch (1914, p. 698), who says: "Der Pterygoideus, zerfällt seiner Innervation nach wiederum in zwei Komplexe, der Pterygoideus anterior und der Pterygoideus posterior, worin Übereinstimmung mit Verhältnissen der Urodelen besteht."

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ.—This is the typical depressor of the reptiles, arising on the parietal, squamosal and exoccipital. It is firmly inserted on the posterior prolongation of the articular.

IGUANA

Plate VII, Figs. 1, 2

The skull of *Iguana* is of the streptostylic type, although it is quite solidly constructed and much less specialized than that of *Varanus.* There is very little movement in the quadrate and pterygoid region, so that the muscles that move these parts in *Varanus* are not differentiated. The rest of the jaw musculature is very similar to that of *Varanus,* which is more fully described under its section in this paper. The fenestration in the temporal region of the skull of *Iguana* is similar to that of *Varanus,* with a large supratemporal fenestra and with a large sinus below the postorbital and squamosal, this giving the muscles plenty of room to expand. The skull has accommodated itself to the muscles in several ways. The supratemporal fenestra is large and the parietal has expanded dorsally and posteriorly to make a large origin for the capiti-mandibularis.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.
- (*a*) Capiti-mandibularis superficialis.
  - = Masseter slip.

(*b*) Capiti-mandibularis medius.
= Temporalis.
(*c*) Capiti-mandibularis profundus.
= External pterygoid of Mivart.
= Pterygoideus externus, Hoffmann.
= Pterygo-mandibularis, Hoffmann.
= Internal pterygoid, Sanders.
= Entopterygoid, Sanders.
= Pterygoidien externe, Cuvier, Duméril.

Pterygoideus anterior.
= Pterygoidien interne, Cuvier, Stannius.
= Pterygoideus internus, Hoffmann.
= Internal pterygoid, Mivart, Edgeworth.
= External pterygoid, Sanders.
= Ectopterygoid, Sanders.
= Pterygo-mandibularis, Bradley, Watkinson.
= Pterygoideus, Versluys.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.—This is the large temporal muscle which is divided into three slips in this paper.

(*a*) *Capiti-mandibularis superficialis* (C. m. s.).—This masseter slip is lower down on the outside of the mass. It arises on the quadrate, squamosal and quadratojugal. Its fibers extend over the fibers of the temporal slip and blend with them to be inserted on the coronoid and the dorsal edge of the mandible. They extend down on the outer face to quite an extent, which is not common in the reptiles, as usually the insertion is entirely on the inner side of the mandible. They also extend down on the inner side. This crossing of the temporal and the masseter slips gives two pulls to the mandible, a straight dorsal and a posterior one.

(*b*) *Capiti-mandibularis medius* (C. m. m.).—The temporal or median slip fills the temporal fossa; it arises on the parietal, postfrontal and squamosal. The supratemporal fossa is large and the parietal is extended out, so as to furnish a large insertion for this part of the muscle. It extends down between the masseter and the inner slip to be inserted on the mandible.

(*c*) *Capiti-mandibularis profundus* (C. m. p.).—This muscle is the homologue of the muscle of the same name in *Varanus* and is strongly developed in reptiles with a columella cranii (epipterygoid). It arises on the outer face of the epipterygoid and on the outer face of the pterygoid, extends ventrally, and is inserted on the mandible on the lower part of the posterior inner face of the mandible.

Pterygoideus anterior (Pt. a.).—This arises on the pterygoid and wraps around the end of the mandible. The origin is on the under side of the pterygoid; from there it extends around the end of the mandible, making a large belly at the posterior ventral end. It is inserted along the ventral face of the angular and wraps around the articular, so that it is on the inside of the mandible at the posterior end.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ (D. m.).—This muscle arises on the posterior face of the parietal, extends ventrally, and is inserted on the retroarticular process of the mandible.

VARANUS

Plate VII, Figs. 3, 4, 5

The almost snake-like skull of *Varanus* is a typical example of the streptostylic skull, with the bones of the skull more or less movable, especially in the quadrate region. There is a joint between the frontals and the parietals which has possibilities of movement, while the quadrate with its loose articulation on the squamosal and pterygoid forms another movable element. In fact the jaws, pterygo-palatine, and the quadrate region are all movable, with the posterior part of the skull as a base. The fenestræ are large so that the muscles have room for development. The large supratemporal fenestra serves as the origin of the temporal slip of the capiti-mandibularis, while the lateral fenestra gives it room for development. This fenestration approaches the ophidian type where the opening out has been complete.

The musculature of the pterygoid region is very musch specialized in the streptostylic forms and is a cænotelic character. These special muscles could not have been present in the cotylosaurs or stegocephalians, where there is no need of them, as the skull is rigid. The special muscles for moving the upper jaw and the facial part of the skull arise on the parietals, epipterygoid and basisphenoid and are attached along the whole upper surface of the pterygoid from the articulation with the transverse to the quadrate. This type of musculature is carried to the extreme in the Ophidia, where the streptostylism is complete and practically all of the bones are movable. There is a sharp contrast between the streptostylic and the monimostylic types of musculature; the streptostylic represents high specialization, with great mobility of the skull parts and the demand for many muscles, while the solid monimostylic skull is rigid with the bones solidly fixed and attached by strong sutures, while the muscles present are of a simpler kind, namely, those needed to raise and lower the mandible.

There is much confusion in the nomenclature of the muscles owing to the fact that the mammal names are applied to them by most workers. The nomenclature would be cleared if the entire list of names were dropped and a new set adopted that had no direct reference to the names of the mammalian muscles.[4]

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.
  (*a*) Capiti-mandibularis superficialis (C. m. s.).
    = Outer fibers of the capiti-mandibularis.
  (*b*) Capiti-mandibularis medius (C. m. m.).
    = Temporal of Bradley (whole mass).
  (*c*) Capiti-mandibularis profundus (C. m. p.).
    = Upper slip of the pterygoid of Bradley.
    = Pterygoideus externus of Mivart.
Pterygoideus anterior (Pt. a.).
    = Pterygo-mandibularis of Bradley.
    = Pterygoideus internus of others.
Pterygoideus posterior (Pt. p.).
    = Lower slip of the Pterygoideus of Bradley.
Pterygo-parietalis (Pt. par.) (Bradley).
Pterygo-sphenoidalis posterior (Pt. sph. po.) (Bradley).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ (D. m.).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.—This is the large temporal muscle mass, divided into three parts in this paper.

---

[4] The papers used in the study of *Varanus* were: Bradley (1903) and Watkinson (1906).

(*a*) *Capiti-mandibularis superficialis* (C. m. s.) = Masseter portion. Arises on the quadratojugal, squamosal and quadrate.

(*b*) *Capiti-mandibularis medius* (C. m. m.)—This is the inner part of the temporal sheet arising on postfrontal, proötic, squamosal and quadrate under the fibers of the outer or masseteric portion. These two slips are not separate.

(*c*) *Capiti-mandibularis profundus* (C. m. p.).—The deeper portion of the mass. It arises on the parietal and is inserted on the coronoid along with the rest of the capiti-mandibularis. (A lower part of this muscle arises from the columella cranii and is considered as pterygoideus posterior.)

Pterygoideus anterior (Pt. a.).—This muscle arises on the whole outer surface of the pterygoid (except the branch to the palatine) and is inserted on the posterior part of the jaw.

Pterygoideus posterior (Pt. p.).—This with the exception of the lowest part arises on the columella cranii and is inserted on the mandible, posterior to the insertion of the capiti-mandibularis profundus.

Pterygo-parietalis (Pt. par.).—This muscle is peculiar to reptiles with a rodlike columella cranii. It arises on the downward projection of the parietal and is inserted on the whole upper surface of the pterygoid, immediately in front of the articulation with the columella. It seems to represent a part of the inner layer of capiti-mandibularis profundus that separated off for the service of the pterygoid. The same might be said of the muscle following.

Pterygo-sphenoidalis posterior.—This muscle arises on the basisphenoid below the gasserian notch and is inserted on the upper and lower surface of the pterygoid for its whole length to a level of the articulation of the basipterygoid process of the sphenoid and the pterygoid. It pulls the pterygoid upward and backward. This may represent a lower slip from the capiti-mandibularis profundus.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ (D. m.).—It arises on the parietal and nuchal fascia and is inserted in the end of the mandible.

Aves

GALLUS

Plate VIII, Figs. 1, 2, 3

The musculature of the bird, *Gallus,* follows in most particulars that of reptiles. It offers one of the most convincing items of evidence that the birds and the reptiles are very close in their origin. The most important characters of the bird skull are:

(1) Great expansion of the brain case with corresponding changes in the base of the cranium.

(2) Loss of the upper temporal arcade, the lower temporal arcade (quadratojugal and jugal) being left intact.

(3) Radical changes in the pterygoid and palatine region where great changes occur even within the class.

(4) Loss of teeth and assumption of a beak.

(5) Loss of sutures and lightening of all the elements. The bird skull is fundamentally similar to that of the primitive pseudosuchian *Euparkeria capensis* of Broom (1913). The maxillæ, jugal and quadratojugal articulate with the quadrate in true reptilian fashion, while the quadrate is movable as in many reptiles.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3*)*

Capiti-mandibularis.
  (*a*) Capiti-mandibularis superficialis (C. m. s.).
      = Masseter of Shufeldt and Gadow.
  (*b*) Capiti-mandibularis medius (C. m. m.).
      = Temporalis of Shufeldt, Gadow.
  (*c*) Capiti-mandibularis profundus (C. m. p.).
      Not present in *Gallus.*
Pterygoideus anterior (Pt. a.).
Pterygoideus posterior (Pt. p.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3*)*

The capiti-mandibularis mass of the bird is divided into separate muscles, and we assume that they are represented in the reptiles as unseparated parts of the capiti-mandibularis, and for that reason they are given the names used in the reptiles.

(*a*) *Capiti-mandibularis superficialis* (C. m. s.).—This muscle may be divided into two parts; one rises as a tendon from the bony ridge of the squamosal, above the auditory entrance; the other head which is fleshy arises from the quadrate. The insertion on the mandible is by tendon and by a fleshy slip; the tendon is inserted on the coronoid process and the fleshy slip extends along the outside of the mandible. This muscle is the most important of the mandible, as it extends along the side and has a very wide attachment.

(*b*) *Capiti-mandibularis medius* (et *profundus*) (C. m. et p.).—This muscle, usually called the temporal, is assumed to represent the middle and deep part of the reptilian capiti-mandibularis. The region for its origin is much reduced and there is no room for much differentiation of this part of the muscle. It fills the temporal fossa in the bird. It arises from the bones surrounding the fossa, extends downward, posterior to the postorbital process, and is inserted on the coronoid process of the mandible.

Pterygoideus anterior (Pt. a.).—This is a large muscle that covers the floor of the skull at the posterior part of the palatines. It arises along this posterior part of the palatines, spreading out over this to a part of the pterygoids and the orbito-sphenoid. The insertion is on the under side of the articular process and along the inner side of the mandible. This muscle pulls inward and forward on the mandible, thus pulling the quadrate forward—a movement that is very important in the Psittaci, where the maxillæ are raised with the anterior part of the skull.

Pterygoideus posterior (Pt. p.).—This is a smaller muscle that crosses the pterygoideus anterior, going under it. It arises on the orbital process of the quadrate and is inserted on the inner side of the mandible near the posterior end. It draws the mandible backward and pulls down on the quadrate, thus aiding in the closing of the jaw.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ (D. m.).—The depressor of birds is the same as that of reptiles and amphibians, being a part of the C_2md of Ruge and innervated by the seventh nerve. In the birds it is short and thick, more like the same muscle in the Chelonia than like that of *Sphenodon* or *Varanus*. It arises on the squamosal as in the Chelonia, as this region has grown out laterally, so that the origin on the parietal is no longer available. It arises along the ridge of the squamosal and is inserted on the retroarticular process as in reptiles. It opens the mandibles with the aid of some of the long, ventral hyoid muscles of the throat region.

Mammalia

The jaw muscles of the mammals are remarkably constant in character throughout the group, except in the monotremes and some edentates where extraordinary conditions occur. Throughout the group the muscles are closely correlated with the dentition and with function. The chewing muscles are limited to the digastric, masseter, temporal, pterygoideus externus and pterygoideus internus. There is much individual variation in these muscles, but they are always present, except the digastric, which is absent in some monotremes and edentates, and the internal pterygoid, which is sometimes not differentiated from the temporal.

The temporal fossæ of the mammals are opened out, so that there is free play for the muscles, except where there is a secondary covering of plates.

The ramus mandibularis of the trigeminus nerve innervates all the muscles of mastication except the posterior belly of the digastric and its allies. The muscles innervated by V_3 represent what remains of the capiti-mandibularis of the reptiles. The temporal is the largest muscle of this group in most of the mammals. It is closely associated with the masseter, which is a slip that has separated completely in the mammals, but still remains a part of the temporal mass in the reptiles. The temporal is variable in its size, as the masseter is often larger, usurping its functions in the rodents and in some other groups. It is partially divided in the mammals, as we find it with a single head in *Homo* and with three in the monotremes, but although the condition may vary the origin and insertion remain quite constant.

The masseter is much more variable than the temporal muscle. It is double-headed in man, and also is divided into two muscles in the monotremes, each with two slips, and we may have as many as five slips in the rodents. Its size and condition depend on the special conditions and the importance of the muscle. In the rodents, where it takes the place of the temporal to a certain extent, it is large and very much specialized. Its origin varies, as it may partly cover the temporal as in *Didelphys,* or may extend forward, anterior to the eyes in the rodents, or divide into two separate muscles as in the monotremes. This muscle in the mammals is always associated with the development of the zygomatic arch and represents the outer portion of the temporal mass that may be traced from the Pisces to reptiles, where the outer fibers of the capiti-mandibularis mass are always slightly differentiated from the deep fibers by having a different direction, although there is no separation in the reptiles to the extent found in mammals. The pull of the masseter is usually slightly forward, against the pull of the temporal, which, together with the pull of the pterygoid muscles, gives the steadiness that is necessary in the mandibles. In many cases there is a connection of the masseter with the auditory region. In *Tamandua* (Lubosch, 1908, p. 541) this small muscle is seen, as it were, in the process of splitting off from the masseter and attaching itself to the tympanic. *Bradypus villosus* (Lubosch) shows this same condition, where a small muscle extends from the angle of the jaw to the tympanic. This small muscle is innervated, according to Lubosch, by the auriculo-temporalis nerve. The tendency of the masseter to extend to the auditory region probably may go back to the reptilian condition, where this muscle was attached to the quadrate or to one of the bones in this region.

The pterygoid muscles arise on the basicranial or pterygoid region and, although usually small, they are of importance in the working of the jaws. They vary in form in different groups and the relation between the pterygoids and the dentition is very close. They are largely developed in herbivorous but small in carnivorous mammals. They function in giving the jaw steadiness in opening and closing; they prevent the heavy temporal muscles from tearing the mandibles apart in forms with a loose symphysis and they make possible the grinding motion of the teeth in herbivorous forms. The edentates and monotremes offer exceptional conditions, for here the reduced or modified condition of the mandible makes the pterygoid muscle of little importance.

The internal pterygoid is the more important of the two, as it aids in the closing of the jaw and pulls inward against the pull of the temporal, masseter, etc. The external pterygoid pulls the jaw forward, out of the glenoid cavity, and assists in this way in opening the jaw and in the forward movement of the jaw in herbivorous forms.

The origins of these muscles are plainly seen in mammalian skulls and the condition of the pterygoid region has probably been very much modified by their action, as a comparison with the reptilian condition shows that the pterygoid region is pinched in and pulled to the rear. We assume that this condition has been brought about largely by the action of pterygoid muscles. In cynodonts the opposite pterygoid bones meet in the mid line, but in mammals the pterygoids have become much reduced and separated so as to leave the primary floor of the brain case exposed (basisphenoid, presphenoid) (Gregory and Adams, 1915).

The capiti-mandibularis profundus (external pterygoid) of the reptiles seems to be in a favorable position to give rise to the whole pterygoid mass of the mammals, since it is inserted on the coronoid region of the mandible, and might easily shift its insertion down on the inner side of the upgrowing dentary without interfering with the other muscles. No doubt its importance increased when the new joint was formed between the dentary and the squamosal and when the old anterior pterygoid muscle became reduced. Its subdivision into two slips followed, which are the external and internal pterygoid of mammals.

The digastric muscle of mammals (Fig. 4) represents a part of the second constrictor of the Pisces, joined with one of the ventral muscles of the throat region (A, V_3). It is a muscle with two bellies, a tendon usually separating them, but this varies in different forms; so we may say that the muscle varies from the so-called monogastric to the typical double-bellied condition. As stated below, the muscle is constant in mammals with the exception of monotremes and some edentates. It is the only compound muscle in the muscles of the jaw and represents two muscles, one innervated by the facialis, the other by the ramus mandibularis trigemini, joined end to end, but still retaining the old innervation. The older anatomists all homologized the posterior belly of the digastric with the depressor mandibulæ of reptiles and amphibians, but the work done on the innervation by Schulman, Lubosch, Ruge and others has shown that there is a common origin for them, but that they represent different slips from the same constrictor.

The variation of the digastric has been discussed by Chaîne, Toldt, Bijvoet, Parsons, Rouvière, Fürbringer, Dobson, Futamura and others, so that there is not much left to work out in this line, although the interpretations of the authors are very variable.

Chaîne (1914) classifies the digastric of mammals as follows:

(*a*) Those with two bellies:
    Macropus
    Delphinus (Toldt)
    Rodentia
    Chiroptera
    Insectivora[5]
    Prosimiæ
    Bradypus
    Artiodactyla
    Carnivora
    Pteropus
    Simiæ

(*b*) Those with a single belly:
    Hydrochœrus
    Dolichotes
    Cavia
    Lepus

(*c*) Digastric absent:
    Monotremes
    Tatusia
    Delphinus
    Tursiops

---

[5] In *Talpa europœus* there is a small tendon from the posterior belly to the mandible.

Parsons' views (1898, pp. 436-437) are expressed in the following quotations:

> The most important point to bear in mind, in considering this muscle, is that it is not always really a digastric, but that even when it appears monogastric it has a double nerve supply. Our knowledge of the anatomy of fishes tells us that the muscles developed from the first, or mandibular arch, are supplied by the fifth nerve, while those formed in the second, or hyoid arch, derive their nerves from the seventh. In three Ornithorhynchi I found a muscle running from the sub-hyoid septum, outward and a little forward to the mandible, not far from the angle; it was supplied by the fifth nerve and lay superficial to the mylohyoid muscle, of which it appeared to be a delamination, and with which the fibers had the same general direction. In the same animal a single muscle runs from the long, tubular external auditory meatus to the subhyoidean septum; it is supplied by the facial nerve, and probably corresponds to the combined stylohyoid and posterior belly of the digastric. From this I am inclined to think that the anterior belly is an older muscle than the posterior, or, in other words, that the anterior belly is differentiated from the mylohyoid layer before the posterior belly is split off from the stylohyoid. This possibility may be the reason why the absence of the anterior belly of the digastric is rare in man, but the absence of the stylohyoid is fairly common.

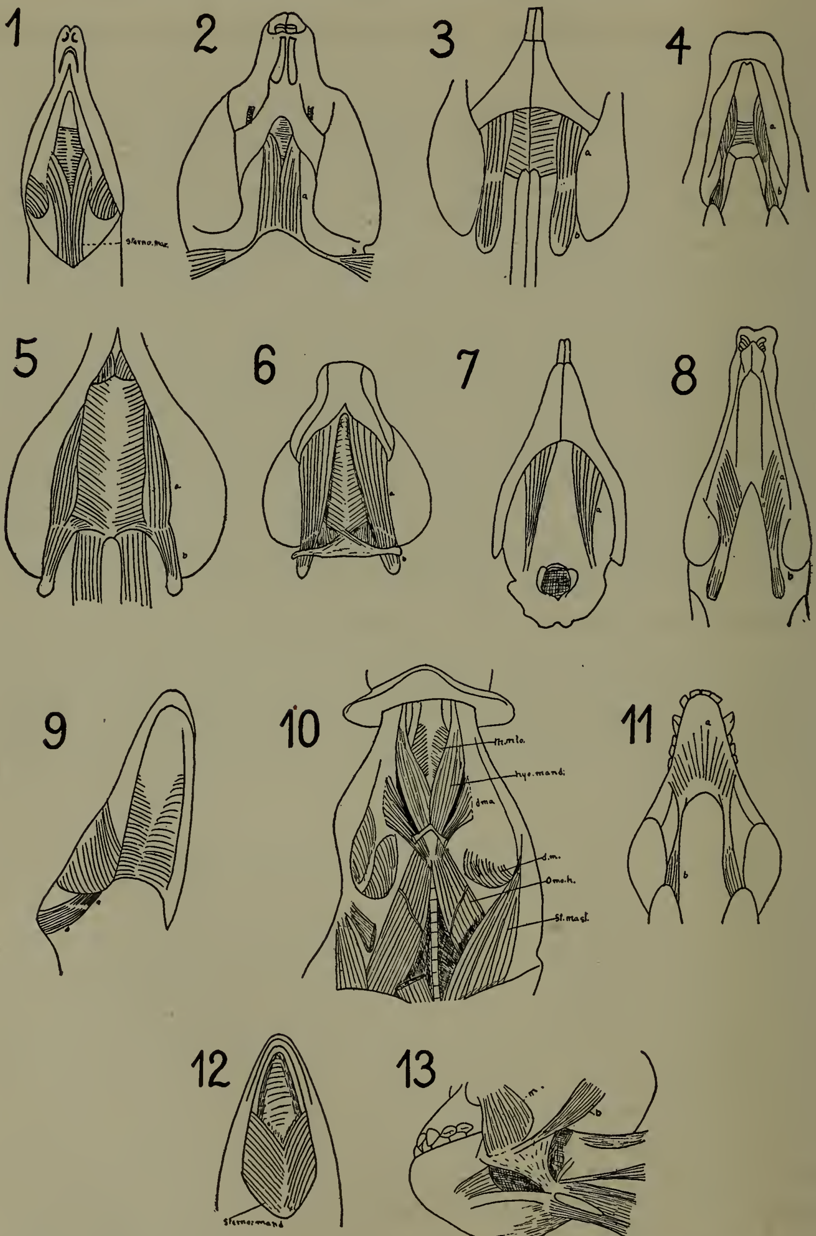
Describing the digastric with two bellies, Parsons says:

> In the first [type] the anterior and the posterior bellies are separated by a considerable length of tendon. The posterior belly runs forward until it is over the hyoid and then runs inward and meets its fellow from the opposite side, forming an arch. The anterior bellies of the digastric spring from this arch and go forward. The muscle is not attached to the hyoid but is connected by connective tissue.

This type is found in many rodents (sciuromorphs, *Pteromys*), in most cynomorph monkeys and in certain anthropoid apes (orangs, chimpanzee).

Parsons places under his second division those with a pseudo-monogastric muscle. Here the muscle seems to have one belly, but there is always a small rudiment of the median tendon. This type attaches to the mandible, midway between the symphysis and the angle, and instead of forming flat planes meeting along the median line of the neck they are rounded, as some expanse of mylohyoid separates them.

Parsons' third type is that found in man, where the bellies are distinct with a tendon separating them, the anterior bellies not meeting in the median line of the neck but forward near the symphysis. This type is found in most lemurs, many monkeys, especially the platyrhini, gibbons (*Hylobates*) and in many specimens of gorilla. The stages are all united by transitional stages.



1. *Tatusia*
2. *Pteromys*
3. *Cavia*
4. *Bos*
5. *Macropus*
6. *Felis leo*
7. *Lepus*
8. *Gazella*
9. *Galeopithecus*
10. *Ornithorhynchus*
11. *Cynocephalus*
12. *Tursiops*
13. *Simia*

FIGURE 2

Parsons also mentions a fourth type, where there is a true monogastric muscle in which the anterior or the posterior belly is suppressed. It is found in lagomorph, or hare-like rodents. The posterior belly is represented by a small tendon in these. In many orangs the anterior belly is wanting and the posterior belly is attached close to the angle.

Parsons' division differs from Chaîne's in that he takes into consideration the condition of the anterior belly, whether joined with its fellow of the opposite side or free from it. Humphrey considered that the anterior belly was from the same myotome as the pterygoids, and the posterior belly was from the hyoid arch muscles, or hyoid myotome. He considered the tendon as a remnant of the myocommata connecting the two myotomes. These divisions of the digastric as given by Chaîne and Parsons show some of the variations that are met with in this muscle. The posterior part of the muscle is not troublesome, but the anterior part, or the part innervated by nerve V_3, has caused the anatomists much trouble.

Some of the ideas as to the homology of the anterior belly are interesting, and show the diversity of opinion on this topic. Bijvoet (1908) gives an interesting summary of the ideas of different authors as to its origin. He considers that *Ornithorhynchus* shows the primitive stage of the

DESCRIPTION OF FIGURE 2

Variations of the digastric in mammals. (Mainly after Chaine and Parsons.)

The digastric muscle is found only in typical mammals and is not clearly recognizable in the monotremes. It is a compound muscle typically consisting of anterior and posterior bellies united by ligament. The anterior belly is probably a derivative of the primitive throat muscles of reptiles and is innervated by the mylohyoid branch of nerve V_3. The posterior belly probably represents a separate slip from the stylohyoid muscle, and both muscles are innervated by closely associated branches of the seventh nerve. Probably both bellies of the digastric formerly converged toward the lower surface of the basi-hyal cartilages, along with the mylohoid and other muscles, and the tendinous portion between the anterior and posterior bellies may represent part of the fascia into which they were formerly inserted.

Probably the most primitive type is seen in the monotreme *Ornithorhynchus* (10). Here the "detrahens mandibulæ anterior" (*D. m. a.*) (which may be a slip of the mylohyoid) may represent the anterior belly of the digastric, while the posterior belly is not yet separate from the stylohyoid (Parsons).

The marsupial *Macropus* (5) shows well the association of the anterior belly (*a*) with the mylohyoid and the connection of both bellies with the basi-hyal. In most types the anterior and posterior bellies are both present and separated by tendon (as in Figs. 2, 4, 5, 6, 8, 9, 11). Either one of the bellies may be vestigial or wanting. In No. 7 the posterior belly is reduced to a small tendon. In No. 13 the anterior belly is tendinous. The so-called monogastric types (3, 6, 9) generally show at least a vestige of the tendinous septum between the two bellies. In Nos. 1, 12 the digastric is entirely absent, being functionally replaced by other muscles. The posterior belly usually arises from the paroccipital process of the exoccipital. The insertion of the anterior belly varies greatly as well as its relations both to its fellow of the opposite side and to the mylohyoid (cf. Nos. 2, 3, 7, 9, 11). It is primitively inserted on the inferior border of the mandible beneath the masseter, but may shift either to the region of the symphysis (2) or to the posterior part.

formation of the digastric and that the anterior belly is the detrahens mandibulæ, a muscle related to the stylohyoideus.

Chaîne (1914) thought that the digastric came from a muscle that originally stretched from the jaw to the sternum, that it lost its hold on the sternum and moved first to the vertebræ and then to its hold on the mastoid. He accounted for the tendon between the bellies of the digastric by assuming that it was a remnant of the segmental areas found in primitive muscles.

Dobson does not consider the digastric.

Futamura (1906, 1907) had some interesting ideas on the origin of the digastric of man. In the first paper on the digastric of man he says: "The digastric is at first entirely supplied by the nervus facialis; later, as the anterior belly becomes constricted off from the posterior, the former obtains its motor nerve secondarily from the nervus mylohyoideus" (translation). He recants this in a later paper (1907) as follows:

> Der proximal Teil des Digastricus teilt sich in zwei Teile deren vorderer am Reichertschen Knorpel inseriert, deren hinteren um die hintere Seite des Knorpels herum ventralwärts verläuft und am ventralen Ende des Meckelschen Knorpels inseriert. Der Muskel wird von zwei Nerven bereits innerviert; N. facialis und N. mylohyoideus. Beim Menchen glaubte ich aussprechen zu dürfen dass die zwischensehne an der doppelten Innervierung des Muskels schuld sei. Das kann aber doch nicht der Fall sein, weil beim Schwein, bei dem der Biventer keine zwischensehne besitzt, doch die zweifache Innervierung nachzuweisen ist.

Gegenbaur (1898, p. 632) held that the anterior belly of the digastric came from the mylohyoid by splitting. He took the anterior belly from the mylohyoid and the posterior belly from the depressor mandibulæ of the reptiles. He cited the horse with its peculiar condition, where there is a secondary insertion of the posterior belly on the angle of the mandible, as an indication of this.

His (1885, p. 92) derived the digastric from the sterno-cleido-mastoid, which he separates into two parts: the mylohyoideus and the outer tongue muscles. He derives the anterior belly of the digastric from the superficial layer and the posterior belly from the deep layer of the sterno-cleido-mastoid.

Leche (1889) had the same idea as Futamura and thought that the digastric was a muscle with a single nerve and that it acquired, secondarily, a second supply from the trigeminus.

Rouvière (1906) derived the anterior belly from the same origin as the geniohyoid and says that in the fishes, amphibians, reptiles and birds, only the anterior belly is present. He derives the posterior belly from the m. jugularis transversus, the same mass from which the stylohyoid is separated. He considers the digastric to be the result of the joining of these two muscles.

Toldt (1908) gives the following points on the anterior belly of the digastric:

(1) The digastric as such is found only in the mammals. The attempts to derive it from the muscles of the non-mammalia have not been successful. The hinder belly is not the depressor mandibulæ of the Sauropsida nor is it derived from the depressor of the monotremes. (Schulman shows that it is not derived from the depressor of monotremes.)

(2) The depressor of the monotremes is a special primitive condition and is a slip from the masseter innervated by V_3. The writer thinks this is not a primitive condition but a very specialized condition in a primitive form.

(3) The anterior belly of the digastric has its origin with the m. mylohyoideus muscle and belongs with the visceral muscles that extend along the floor of the mouth. They are innervated by V_3.

(4) The posterior belly is a part of the stylohyoideus in the lower vertebrates and is originally a visceral muscle intercalated between the musculature of the mouth floor and throat and directly or indirectly connected with the tongue bones.

(5) The joining of this originally separate muscle to the digastric, as well as the identity of the hinder belly and the stylohyoideus, is shown well in the monotremes. The line of separation is shown by the inscriptio tendinea.

Toldt correlates the condition of the digastric with the type of food that the animal eats and with the question whether the food is held in the mouth or swallowed immediately. This, he thinks, gives an explanation of the joining of the forward bellies in some forms and separation of them in some of the carnivorous forms. But a comparison of the varying forms of digastric seems to show that there is no correlation with food habits, as there seems to be no definite functional criteria by which the different conditions may be classified.

From a review of the literature on the digastric the variations are plainly evident both in the muscle and in the ideas concerning it. There seems to be no very stable insertion for the anterior belly. Its insertion varies from the inside of the chin, as in *Homo,* to the posterior part of the mandible, on the angle in some other forms. Only the anterior part is of uncertain origin, as most of the writers agree on the derivation of the posterior belly. The anterior part lends itself to hypotheses, as nothing definite seems to have been brought forward at the present time and all may be more or less right. The double innervation and the tendon seem to make certain the fact that the muscle has a double origin. Some of the older writers speak of a single-bellied digastric, but most of them agree that some evidence of the double origin always exists, and that in the monogastric muscles remains of the tendon are in evidence in the middle of the muscle, or, as in *Lepus,* the anterior muscle may be almost gone while the tendon remains to represent the junction of the two parts. In a few forms undoubtedly one of the muscles is missing—that is, one belly is missing and it is not really a monogastric muscle but a single belly in the sense that either the anterior or the posterior belly has disappeared, and not that the one represents both bellies.

So far I have spent very little time on the mylohyoid and the other ventral muscles, reserving them for future work on the comparative musculature throughout the vertebrates. The discussion of this phase of the jaw muscles is made very brief and merely points out some of the comprehensive work of Toldt, Chaîne, Rouvière, Bijvoet and others on the digastric musculature in the mammals.

The relation of the jaw muscles to the special types of dentition is very close throughout the mammalian groups. In fact a highly differentiated muscle system in which each muscle does a certain type of work alone makes possible the highly specialized dentitions of rodents and ungulates. The teeth of mammals are, roughly, of three kinds—herbivorous, carnivorous and degenerate. The herbivorous dentition is correlated with the peculiar type of condyle and glenoid joint that makes its specialized work possible. The condyle of the typical herbivorous animal is much rounded and the articulation in the glenoid cavity is flat, so that there is much freedom of movement. In chewing the jaw is rotated in a lateral, antero-posterior and vertical movement, so that to accommodate this movement the articulation must be very loose. Accordingly, there is always a well developed pterygoid region in the basicranial region, with well developed pterygoid muscles. This strong development of the pterygoid muscles is characteristic of *Macropus, Halmaturus, Castor, Sciurus, Equus* and *Bos.* In these animals the molar teeth bear cross-ridges and the transverse motion needed for trituration is given by the strong pterygoid muscles. Many herbivorous mammals chew on one side at a time. The pterygoid muscle, acting in connection with the large temporal and masseter muscles of one side, make this movement possible.

In the rodents where the symphysis is weak the pterygoid muscles also counterbalance the pull of the huge masseters, as in some of the forms with a weak symphysis the pull of the masseters alone would tear the jaws apart. The carnivorous mammals have an entirely different arrangement, as their jaw action is primarily a straight opening and closing movement, either a hard, steady pull, or with a snap. The opposite halves of the mandible are usually strongly fastened together at the symphysis. The condyle is lengthened out laterally toward the median line and the glenoid cavity has a large protecting shelf to give a firm hold on the condyle. In fact in some of the carnivorous types with strong jaws the articulation is locked, so that the borders of the glenoid cavity must be broken in order to separate the mandible from the skull (*Gulo luscus*). With the shearing teeth and the locked type of articulation for the condyles of the jaw the pterygoid muscles are of little value and in carnivorous forms are always weak, as in *Canis, Gulo, Lutra, Didelphys.* In these animals the basicranial region of the skull shows the reduction of the pterygoid muscles.

MONOTREMES

Plate IX, Figs. 1-7

Skull.—The skull and jaws in both *Ornithorhynchus* and *Echidna* are of very aberrant and more or less degenerate types. In both genera, also, the pterygoid region is highly modified, and thus the homology of the so-called pterygoid elements is open to question. *Ornithorynchus* requires fairly strong jaws for the crushing of small mollusc shells, while *Echidna* has practically vestigial jaws and depends mostly on the tongue muscles.

The condition of the jaw musculature in the monotremes is quite suggestive of the reptiles. The massed condition of the temporal-masseter group suggest the condition of the capiti-mandibularis of the reptiles. The head muscles as a whole seem to be homologous with those of other mammals, especially as regards the temporalis-masseter, pterygoideus externus and muscles of the ventral hyoid group, with the exception of the anterior belly of the missing digastric, which may be represented by the muscle called depressor mandibulæ anterior. However, this hyoid region in the monotremes is very specialized, so that the derivation of the anterior belly from this region is rather obscure, although some anatomists hold this opinion. It is probably a slip from the mylohyoid. The ducklike bill of the *Ornithorhynchus* requires a special musculature which is developed from the V_3 muscles.

The monotremes are so different from other animals in many important details of their myology that it is probably correct to assume that they split off from the mammalian stem at a very early period. This assumption is strengthened by the fact that the osteology and soft anatomy are also very aberrant, so that it is not strange to find different conditions in the musculature. The jaw muscles of monotremes include the following:

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Masseter
Temporalis
Pterygo-spinosus
Pterygo-tympanicus
Depressor mandibulæ anterior
Detrahens mandibulæ

MUSCLES OF THE DIGASTRIC GROUP
(INNERVATED BY VII)

These are not present.

Monotremes have the following peculiar conditions of the jaw muscles: They have no true digastric. The masseter and temporal muscles are massed together. They have no pterygoideus internus. Presence of the pterygo-spinosus and pterygo-tympanicus. Presence of the detrahens mandibulæ instead of the digastric. Extensive development of the mylohyoid group of muscles.

Absence of the digastric.—The digastric is fairly constant in the mammals except monotremes, edentates and some Cetacea. Perhaps it is absent in the monotremes because they separated from the mammal stem at a very early period and thus have missed this arrangement. *Ornithorhynchus* with its fairly large jaws needs a depressor, and this function is filled by the detrahens muscle and by the depressor mandibulæ anterior of the hyoid group. *Echidna* is so degenerate in the mandibular region that there is very little need for a specialized depressor. Other mammals in which this muscle is missing have degenerate jaws. Chaîne mentions *Tatusia* of the edentates and *Delphinus* of the Cetacea, where the true digastric has been lost.

Imperfect separation of the masseter and temporal.—The condition of the masseter-temporal mass in the monotremes is very suggestive of the capiti-mandibularis in the reptiles, as it is not differentiated as much as in other mammals. The mass has several heads, but the separation is not so complete. The peculiar shape of the skulls in the monotreme may be responsible for this condition. There is very little room for muscles in *Echidna,* as the mass is completely covered by bone. Schulman (1906) gives a division of the muscles showing their complexity and tendency to break up into small slips.

Absence of the internal pterygoid.—The absence of the pterygoideus internus is striking, as it is one of the constant muscles of the mammalian skull. Some writers gave the monotremes an internal pterygoid, but from the recent work of Schulman (1906) it seems that this is a mistake. Evidently its separation from the temporal mass is not complete. Schulman says that the pterygoideus internus of Meckel is innervated by a nerve that supplies the temporalis and assumes that this muscle is a part of the temporalis, which he calls "caput anterius." He offers the suggestion that it might have appeared in the mammals after the monotremes had been cut off from the mammalian line. He says:

> Der M. pterygoideus internus wird, aller Wahrscheinlichkeit nach, bei Ornithorhynchus vermisst. Nicht einmal das Mikroskop zeigte in der ventral und medial von dem R. III trigemini befindlichen Gegend Muskelreste zwischen dem Schädel und dem Unterkiefer, d. h. an dem Platz, wo dieser muskel bei den Säugethiere vorzukommen pflegt.
>
> Ob die Wesenheit des M. pterygoideus internus bei den Monotremen ein Rückbildungserscheinung ist, oder ob dieser Muskel erst mit dem Typus der über den Monotremen stehenden echten Säugethiere enstanden ist, bleibt vorläufig eine offene Frage.

The homology of the "pterygoid" in monotremes is in question, and if the conclusions of some of the authors are true, the small muscle called the pterygo-spinosus might be called a pterygoid muscle but for the fact that it appears in man as a rudiment or an anomaly and appears as a regular element in *Cholœpus, Tamandua, Manis, Tatusia* and *Dasypus.*

Presence of the pterygo-spinosus and pterygo-tympanicus.—The presence of the pterygo-spinosus and the pterygo-tympanic suggests the unsettled state of the pterygoids in mammals, for in the animals in which it is found the attachment greatly varies. Its positions are as follows:

(*a*) It is attached to the sphenoid in man and to the lamina lateralis of the pterygoid process (Thane, McAllister, Poland, Kreutzer).

(*b*) It is attached to the ligament assessorium mediale (Kreutzer).

(*c*) It is attached to the mandible (Gruber, Kreutzer).

(*d*) It is attached to the pterygoid internus (Poland, Gruber, Kreutzer).

From these variations Lubosch believes that the insertion is lost. Schulman (1906) says:

> Es kann daran gedacht werden, die bei den höheren Säugethieren vorkommen zwei Muskeln auf das Velum palatinum sich ausbreitenden M. tensor veli tympani und den an einem unbeweglichem Pterygoidknochen sich anheften rudimentären M. pterygo-spinosus, vor einen, bei den Promammalia mit einem beweglichen Pterygoideum verbunden, undifferenzirten Muskel abzuleiten, der danach as Muttermuskel für die M. tensor veli palatini und pterygo-spinosus anzusprechen wäre. Doch bedarf es zur Sicherung dieser Vermutung viel ausgebreiteterer Untersuchungen als die hier angestellten. Auch wäre heirbei die Frage zu erörtern, ob die Beweglichkeit des Pterygoids von *Ornithorynchus* eine primäre oder sekundäre ist.

The most typical attachment of this muscle is to the annulus of the ear and to the pterygoid bone from the mandible. In spite of all the work done on the pterygoids of mammals, one may say that they are of rather unsatisfactory status as yet. Gaupp assumes that they are derived from the parabasals and that they are not homologous with those of other mammals. It is hoped that the problem will be solved as a result of Watson's recent studies on the development of the skull in the monotremes.

Presence of the detrahens mandibulæ.—This pair of muscles serves as the depressor of the mandible in monotremes where the digastric is entirely absent. It originates on the mastoid and squamosal region of the skull, wraps around the lower part of the head, and is inserted on the lower edge of the mandible with a good attachment on the sides, so that it has a firm hold. It is peculiar to the monotremes and is not homologous with the parieto-mandibularis (depressor mandibulæ) of reptiles which has a similar position and function. The reptilian analogue is innervated by the seventh nerve, while the detrahens mandibulæ in monotremes is innervated by the trigeminus. Schulman, Toldt, Bijvot and Gaupp believe that it belongs to the dorsal muscles of the head. Gaupp and Schulman both believe that it is a slip of the capiti-mandibularis (masseter portion) of the reptiles that has slipped back to act as the depressor. The earlier investigators thought that it was a part of the mammalian digastric, as they did not know of the nerve supply. All of these investigators have changed their opinion with the working out of the innervation by Schulman, who showed that it is innervated by the trigeminus nerve. Schulman says:

> Es unterliegt somit meiner meinung nach keinen zweifel, dass der M. detrahens mandibulæ zu den dorsalen Kaumuskeln gehört, und keinen Bauche des M. digastricus mandibulæ der höheren Mammalia homolog ist.

The meaning of this musculature in the monotremes seems to be that the reptilian articulation of the mandible to the jaw was lost, as the Reichert Theory would assume, and that in the shifting of the muscles in monotremes the new depressor was developed from the capiti-mandibularis instead of from the depressor mandibulæ or its mother mass. This would place the monotremes in a different line, and their anatomy justly places them at some distance from the rest of the mammals, so perhaps this conclusion is not far wrong.

DIDELPHYS

Plate X, Figs. 1, 2

The skull of *Didelphys* is remarkably similar to that of lower Eocene Carnivora in so far as it has a very narrow brain case, high sagittal crest, long heavy muzzle, stout zygomata and stout curved mandibles. The pterygoid bones are reduced, as is frequently the case in carnivorous mammals.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Masseter
Temporalis
Pterygoideus externus
Pterygoideus internus
Digastricus (pars anterior)

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

(INNERVATED BY VII)

Digastricus (pars posterior)

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Masseter.—This is a very large and strong muscle, arising on the under side of the zygomatic arch and from the fascia extending up over the temporal muscle. The insertion is on the posterior, ventral part of the angle of the mandible.

Temporalis.—This is a large muscle filling the temporal fossa and extending to the high sagittal crest. The insertion is on the coronoid process of the mandible.

Pterygoideus externus.—Arises behind the pterygoideus internus on the alisphenoid and is inserted on the inner side of the mandible.

Pterygoideus internus.—Arises on the pterygoid wing of the alisphenoid and is inserted on the inner side of the angle of the mandible.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

(INNERVATED BY VII)

Digastricus posterior.—This is quite a large muscle, arising on the mastoid and inserted on the inner side of the mandible, well forward.

SOLENODON

Plate X, Figs. 3, 4

The skull of *Solenodon* is remarkable for its degenerate zygomata, for the great elongation of the muzzle, verticality of the enlarged anterior incisor, small brain case with low sagittal crest, and sharply tritubercular molars.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Masseter
Temporalis
Pterygoideus externus
Pterygoideus internus
Digastricus (pars anterior)

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Digastricus (pars posterior)

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Masseter.—A thick, heavy muscle arising on the zygomatic process of the maxillary and from the fascia over the temporalis. It wraps around the posterior angle of the jaw.

Temporalis.—A large muscle arising in the temporal fossa and on the squamosal. The insertion is on both the inner and outer surfaces of the coronoid process.

Pterygoideus externus.—A small muscle with a small origin on the alisphenoid. Inserted on the inner side of the head of the condyle. The muscle is slight, as the animal has a carnivorous dentition.

Pterygoideus internus.—Arises in the pterygoid fossa and is inserted on the inner side of the posterior angle of the mandible.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Digastricus (pars posterior).—This is a large heavy muscle which arises on the mastoid process and is inserted on a bony process on the lower side of the mandible under the coronoid process.

MUS

Plate X, Figs. 5, 6

The relations of the jaw muscles to the dentition and form of jaw and skull are nowhere more apparent than in the rodents.

The rodents have a great development and differentiation of the masseters which overshadows the temporals. This is characteristic of the group and the jaw action is very complex.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Masseter
Temporalis
Pterygoideus externus
Pterygoideus internus
Digastricus (pars anterior)

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Digastricus (pars posterior)

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Masseter.—This muscle is very large and much subdivided. It arises along the zygomatic arch, extending some distance in front of the eyes where the zygomatic process of the mandible is much expanded to give it a foundation.

The posterior part of the expanded mandible forms the base of the insertion. This insertion is very large in comparison with that of most mammals.

Temporalis.—This muscle arises in the temporal fossa and is inserted on the inner side of the mandible. It is of medium size in *Mus,* although in some of the rodents it is much reduced.

Pterygoideus externus.—This muscle arises on the pterygoid fossa and is inserted on the mandible, where it has a good hold on the expanded angle. It holds against the pull of the masseters and pulls the mandible forward.

Pterygoideus internus.—This muscle is much larger than the external pterygoid, arising in the pterygoid fossa and inserted with a large insertion on the large expanded angle of the mandible. It holds against the pull of the other temporal muscles and prevents the tearing apart of the jaws where the symphysis is weak, as it is in many rodents.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Digastricus (pars posterior).—The digastric as a whole is a large muscle arising on the mastoid and inserted on the lower edge of the mandible, posterior to the symphysis.

FELIS

The cat furnishes a good example of a specialized carnivorous jaw with chiefly orthal or vertical movement.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Masseter
Temporalis
Pterygoideus externus
Pterygoideus internus
Digastricus (pars anterior)

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Digastricus (pars posterior)

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Masseter.—This has three layers in the cat, but it has about the same insertion and origin as in man.

Temporalis.—This is more extended than in man, reaching to the parietal crest. Its insertion is on the outer side of the coronoid process.

Pterygoideus externus.—Arises in the external pterygoid fossa between the foramen rotundum and the spheno-palatine foramen. Its insertion is on the inner side of the coronoid process. The coronoid process is very high and the condyle very low, so that the muscle has changed its insertion.

Pterygoideus internus.—Arises in the pterygoid fossa in about the same position as in man. The insertion is on the inner border of the mandible and extends back to the angle. Its fibers on the inner side go to the masseter, and it is partly united with the pterygoideus externus and the stylo-hyoid ligament.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Digastricus (pars posterior).—The digastric as a whole arises on the mastoid and occipital bones. Inserted on the lower edge of the mandible, just anterior to the first premolar. It is entirely inside of the jaw.

HOMO

Plate X, Figs. 7, 8

Riegner (1906) gives the results of some interesting experiments that he had made upon chloroformed apes. He stimulated the jaw muscles of the unconscious apes and watched the jaw actions, which may be summarized as follows:

> The masseter lifts the jaw and pulls it laterally.
>
> The temporalis lifts the opened jaw.
>
> The pterygoideus externus opens the closed jaw to some extent, pulling it slightly medianward and toward the opposite side.
>
> The pterygoideus internus closes or lifts the open jaw and pulls in opposition to the masseter, *i. e.,* toward the opposite side.
>
> The digastric (anterior belly) opens the jaw. Without it a nominal movement to the opposite side takes place. The hinder belly has little to do with the jaw movements in the ape.
>
> The geniohyoid gives the jaw a straight pull in opening it.

This work on the apes gives about the action that takes place in man, but it is not an entirely accurate account of what happens in some of the mammals with a different type of skull (see also Strasser, 1908).

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Masseter
Temporalis
Pterygoideus externus
Pterygoideus internus
Digastricus (pars anterior)

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Digastricus (pars posterior)

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Masseter.—Arises from the lower border and inner surface of the zygomatic arch and is inserted on the outer face of the posterior end of the mandible and on the coronoid process.

Temporalis.—Arises from the whole surface of the temporal fossa, extends down under the zygomatic arch and attaches itself to a point of the coronoid process, the insertion extending slightly down on both sides.

Pterygoideus externus.—Arises by two heads, from the under surface of the great wing of the sphenoid and from the outer surface of the external pterygoid plate. It is inserted in a depression in front of the neck of the mandibular condyle and in the inter-articular fibro-cartilage and capsule of the temporo-maxillary articulation.

Pterygoideus internus.—Arises by two heads: one from the deep surface of the external pterygoid plate and another by a stout tendon from the tuberosity of the mandible. Both heads are inserted in a triangular area on the inner, posterior surface of the mandible.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

Digastricus (pars posterior).—The digastric as a whole arises in the digastric groove of the mastoid process of the temporal and is inserted in the lower, inner border of the anterior portion of the mandible. It is a two-bellied muscle, the two bellies being separated by a stout tendon. A slight tendon also attaches to the middle of the muscle to the hyoid bone.

RECONSTRUCTIONS OF THE JAW MUSCLES IN CERTAIN EXTINCT VERTEBRATES

Placodermi

The great class of the Placodermi, including many specialized forms, apparently never attained true gnathostome jaws. Gregory says:

> All the known ostracoderms appear to be aberrantly specialized in certain directions, but long consideration of their many peculiar characters has convinced me that they stand far below the true fishes and that the group as a whole may represent an important stage in the genealogy of the vertebrates.

In the upper Silurian we have many forms, like *Birkenia* and *Lasanius* of the order Anaspida, *Lanarkia* and *Thelodus* of the order Heterostraci, without true gnathostome jaws, so far as has been discovered. The mouth in these forms was probably a sucking type with a sphincter around it. Dr. Gregory (1915) has the same idea:

> Of the many beautifully preserved specimens of *Birkenia*, *Lanarkia*, *Drepanispis*, *Pteraspis*, *Tremataspis*, *Cephalispis* and allied genera, none show the least indications of an internal skeleton, nor is there ever any trace of the branchial arches and internal jaws. . . . The ostracoderms represent a stage in chordate phylogeny immediately preceding the acquisition of a cartilaginous skeleton impregnated with mineral salts; their first visceral arches, if present, had not been transformed into primary or cartilaginous jaws; the process of cephalogenesis was in a low stage and the elements of their shelly exoskeleton were potentially homologous with cosmine, vasodentine and isopodine of the primitive ganoids. To that extent they stand in a "pre-gnatho-

> stome" stage of evolution and probably represent the forerunners of the ganoids and Tetrapoda, while possibly having remote relationships also in another direction with ancestral elasmobranchs. . . . The Antiarchi have advanced beyond the typical Ostracoderms in having the head sharply differentiated from the thorax and the mouth armed with functional jaws, which are fashioned from the dermal skeleton. But not even the exquisitely preserved specimens of *Bothriolepis* described by Patten (1912) show any traces of the cartilaginous jaws, branchial arches or cartilaginous axial skeleton.

In another passage this author writes:

> The upper Silurian *Birkenia* of Traquair apparently had no biting jaws and may have sucked in small particles of food like the larval lamprey. Well preserved material showed that none of the Ostracoderms had cartilaginous jaws or teeth, but the dermal plaques around the oral hood sometimes functioned as jaws. Typically carnivorous habits, involving true cartilage jaws, true teeth, and both paired and median fins, are first shown in the Acanthodian sharks of the upper Silurian and Devonian.

We may therefore assume that cartilaginous jaws first appeared as such in the true fishes (elasmobranchs). In the Silurian and Devonian ostracoderms there is a progressive series that shows some of the many attempts to produce workable jaws. The Anaspida, though fish-like in form, have progressed but slightly toward the true fishes. *Lasanius* had some structures back of the poorly formed head that suggest dermal gill supports. In certain Heterostaci (*Thelodus* and *Lanarkia*) the skin was covered with denticles that resemble those of elasmobranchs. These denticles would strengthen the skin and give the muscles of the skin fascia much better support. The Drepanaspidæ show marked progress in the strengthening of the skin by the formation of plates of different sizes. *Drepanaspis* and *Pteraspis* show a differentation in the head region, but it is more to be compared to the hard covering of some insects, as the cartilaginous supports of the interior were feeble or lacking. The mouth was unlike that of either elasmobranchs or teleosts, but seems to have been a wide slit stiffened by dermal scutes. The Ostrastraci show more specialization along this same line, but with no better results. The clumsy plates of *Cephalaspis, Tremataspis,* etc., give little promise of anything that would be much better than the arthropod jaw. The placoderm fishes of the order Antiarchi made a more clearly defined attempt to have movable jaws formed from dermal plates. A study of the fossils shows that they had a mouth that was functionally analogous to the mouth of fishes—that is, their dermal jaws correspond in position, but are not homologous with dermal premaxillæ, maxillæ and mandibles. The head is slightly movable on the shoulder, as in Arthrodira, and the jaws could apparently move laterally as well as vertically. Patten (1912) holds that they were bottom-

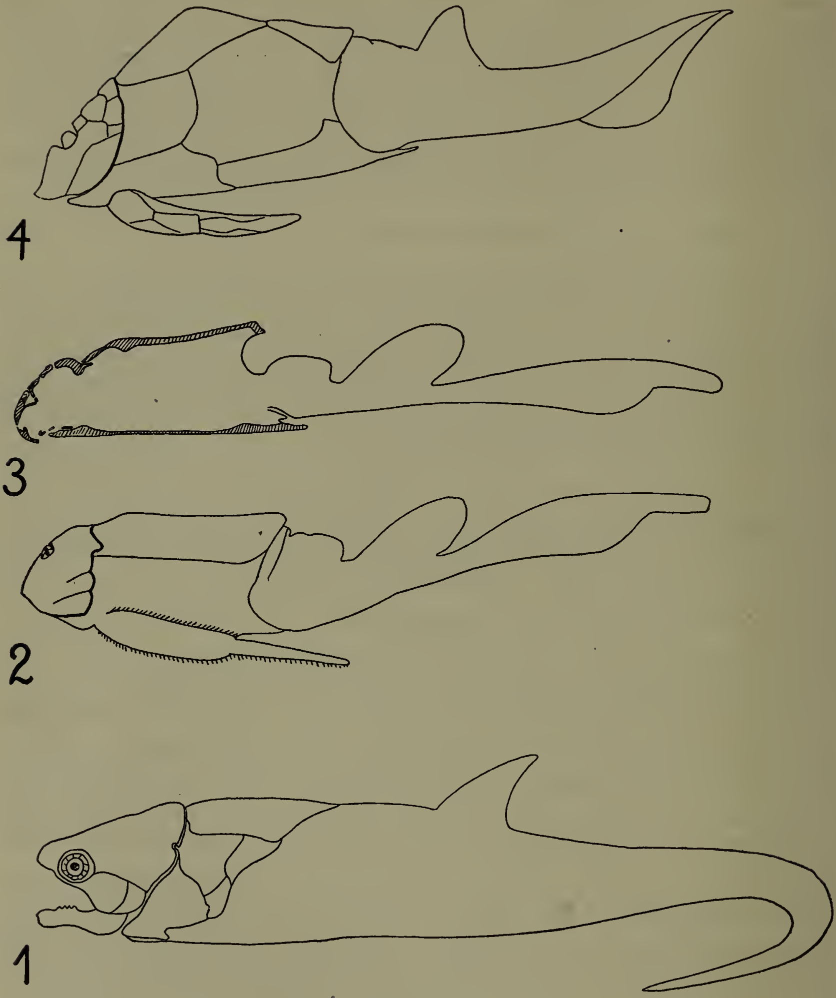


FIGURE 3

1. Outline restoration of *Coccosteus,* a primitive arthrodire. After Patten.

The well-armored head and thorax are sharply differentiated from each other. They are connected by a peg-and-socket joint in the neck region.

2. Outline restoration of an antiarch, *Bothriolepis.* After Patten.

Head and thorax are well defined, but the head is less movable than in *Coccosteus.* Very probably the oral and the branchial pouches with their respective muscles were becoming differentiated from each other.

3. Longitudinal section of *Bothriolepis,* showing the lack of endoskeletal structures, such as calcified visceral arches and the dermal character of the functional jaws. After Patten.

4. Outline of *Pterichthys.* After Patten.

feeders and either took slow-moving animals that they could engulf or fed on vegetation. Patten says that they were herbivorous, for he found carbonaceous residue in their bodies.

The right combination of cartilage jaws covered with bony dermal plates was first worked out by the ganoid fishes, ancestors of the modern fishes on the one hand and of the land-living vertebrates on the other.

DINICHTHYS

Plate XI, Figs. 1, 2

The great arthrodires of the Devonian made the best pregnathostome attempt to form a mouth with skeletal supports, but they made the fatal error of trying to form those supports solely from the bony plates of the skin rather than from the branchial cartilages. *Coccosteus* and *Dinichthys* both show in the skull a fine apparatus that serves for seizing their prey. The arthrodiran jaw must have been a formidable weapon, as it was armed with great sharp bony projections analogous to teeth. That these great jaws were much used for biting and shearing is shown by their worn shearing surfaces. Hussakof (1906) says: "The deep scars found on the outer side of certain *Dinichthys* plates also bear testimony to the savage attacks of their fellows."

The jaws seem to have worked on the principle of the joints of the insect leg, with most of the muscles attached chiefly to the plates of the body and head. The Arthrodira made another fatal mistake in that they moved the head perhaps more than the mandible. There is a joint between the head and the shoulder plates (Fig. 2), with a good peg-and-socket articulation, so that while the mandibles remained more or less stationary the great head with its dermal plates moved up and down against them; thus we have the anomaly in the vertebrates of a relatively stationary jaw and a movable head, just as though the mandible of the gnathostomes was attached immovably to the sternum, while the maxillæ and skull moved against it.

It seems surprising that in the discussions as to the relationships of the Arthrodira so little importance should have been given to the peculiar motion of the head upon the thoracic shield, which is unknown among true Pisces. The movement of the mandible of *Dinichthys* has been very carefully studied by Dr. Hussakof (1906), to whose kindness I owe the opportunity of studying the great collection of arthodiran fossils in the American Museum of Natural History. The movement of the head upon the mandible appeared, however, to have received too little attention, and this I have accordingly studied with great care.

The mandibles in the arthrodires were not stationary, but they have no sign of the ordinary piscine articulation even in the best preserved fossils (Fig. 4). They appear to have been attached to the skull plates somewhat as the scapula in mammals is attached to the body, namely, by ligaments, muscles and connective tissue. From the mechanical point of view, there seems to be three possibilities for movement in these arthrodiran jaws: first, they might have had the muscles so arranged that there would have been a synchronous movement of the head and jaws, and from a study of *Dinichthys* this seems to be the best arrangement, as it is the one that lends itself best to the arrangement of the muscular system; secondly, the jaws might have been arranged so as to work against the skull, but the movable joint at the back of the head seems to make this rather disadvantageous, as the head is not a stationary structure, and part of the force of the movement would be lost, as the joint in the neck would give and the head would be pushed back until it touched the dorsal shield. The usual joint or condyle in the neck region is not prominent and must have been an uncalcified cartilaginous articulation, if anything, for the dorso-ventral movement of the head would tend to dislocate any ordinary articulation between the head and the neck.

In brief, these agnathous forms developed their dermal plates just as the gnathostomes did, but while the gnathostomes put the emphasis on the cartilaginous substratum and developed from it the principal structures of the head and jaws, thus making the membrane bones subservient to the cartilage and finally drawing them in as a covering for the cartilage, the ostracoderms and arthrodires put all the stress on the outer dermal plates and developed the movable parts from these elements, while apparently neglecting the development of the cartilaginous viseral arches.

The peculiar head structure of the Arthrodira seems to imply an equally peculiar musculature as follows: (1) The joint between the dermal plates of the head and dorsal shield implies the existence of muscles to raise and lower the head. (2) As stated above, there appears to be no surface on the mandible that could articulate with a quadrate in the ordinary piscine fashion, so that from the present knowledge of arthrodiran anatomy the adductor mandibulæ of the Pisces could not be applied to these forms. Thus it seems probable that any system of musculature that would be effective in its mechanical action would be entirely unfishlike. Accordingly, in Plate XI the musculature of *Dinichthys* is figured according to the mechanical requirements and follows no fish type. The movements of the head would require two large muscles in order to move the head up and down on the ginglymoid joint. One pair would be in the posterior region of the skull where the marks are plain

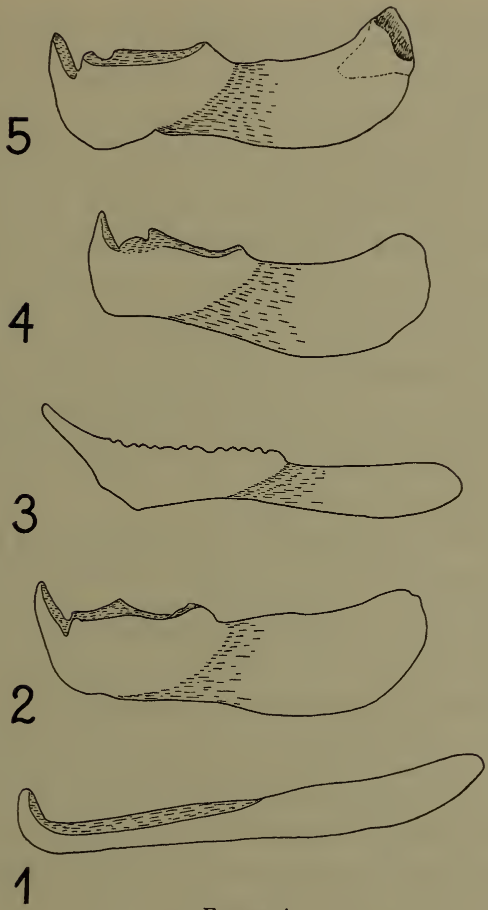


FIGURE 4

Dermal jaw bones of various arthrodires, lateral surfaces; from specimens in the American Museum of Natural History.

The dermal lower jaws of arthrodires were probably not connected with the upper jaw by means of quadrate and articular cartilages as in true fishes, but may have been fastened in the thick dermis surrounding the oral cavity.

1. *Stenognathus gracilis.*—This represents a long-jawed specialization from a *Dinichthys*-like type.
2. *Dinichthys intermedius.*—The shearing portion of the jaw is raised above the plane of the horizontal ramus which was probably embedded in the thick dermis.
3. *Diplognathus mirabilis.*—A very peculiar offshoot of the coccosteid type. The symphyseal border of the lower jaw bears tooth-like projections which apparently indicate that each jaw plate could be twisted on the long axis in a manner impossible in true fishes (Dean).
4. *Dinichthys curtus.*
5. *Dinichthys intermedius.*—To the upper end of this specimen on the outer side is attached a triangular bone which may have served for the insertion of muscles and fascia movably connecting the mandible with the inner side of the skull, somewhat as the scapula of mammals is connected with the body.

in the specimens, showing that there were large muscles there. These muscles might be called the *levator capitis* muscles, as they raise the head. From the insertion areas this appears to have been a double muscle, one on each side of the median line. The attachment would be under the dorsal shield, where there is a strong keel that would serve as a good insertion for so important a muscle. The *depressor capitis* must have arisen on the heavy, inner part of the skull, and the specimens show areas that might well have served for this purpose. There is a large depression at the posterior end of the inner side and a strong ridge along the side of the large paired elements that might have covered the cartilage protecting the brain and might have given a base for the muscles. The insertion of this muscle is problematical. It could hardly be inserted on the plastron, for there it would be in the way of the digestive tract. The only other likely place for the insertion of the *depressor capitis* muscle would be on the so-called "clavicular element," as the muscle could not have been attached to any part of the skull itself.

The problem of the musculature of the mandibles is even more of a puzzle than the musculature of the skull. This mandible has been interpreted in various ways: as a splenial by Eastman and as some other elements by various writers. Whatever its history has been, it is apparently similar to nothing in the Pisces. If it is a splenial it is utterly unlike the splenial of the dipnoans, for they all show a distinct concavity on the outer side of the splenial for the reception of the Meckelian cartilage; and examination of the specimens in the American Museum of Natural History shows no arthrodiran that has any concavity for the Meckel's cartilage. The splenial of *Ceratodus* is quite concave on the outer side and is shaped in a peculiar manner at the posterior end where the articulation with the quadrate takes place. There is none of this in any of the Arthrodira. If this mandible represents one of the outside bones of the gnathostome mandible, the same difficulty remains, for the dipnoan shows that the outer elements are concave on the inside to make a place for the Meckelian cartilage. Thus the arthrodiran mandible seems to be something quite different. From the texture of the outside of the mandible, it would appear that at least the anterior half has been on the surface, while the depressed, posterior half might have been imbedded in tissue. The shape of the posterior end of the mandible makes it very evident that it is more or less free, as is seen in the free end of the teleost maxilla or operculum, where the free end is always thin and blade-like. From analogy, we might well conclude that the same is true in the Arthrodira.

In the American Museum of Natural History a new mandible of *Dinichthys,* which will be fully described by Dr. Hussakof, shows a peculiar triangular plate on the outer face, and at the posterior end this triangular plate is roughened for the insertion of a supporting cartilage or ligament. Very probably it articulated with the inside of the cheek plate or with some other external plate and not with a quadrate. In the mandible of *Mylostoma* Dr. Eastman (1906) found an irregular mass on the inner side which he interpreted as the Meckelian cartilage. But if these mandibles were articulated with a quadrate they should show some indication of it at their posterior end. If the mandible, with the strong action that must have been present, as evidenced from the great marks of the shear, were pulled against the quadrate by the usual adductor muscles of the Pisces, it is reasonable to suppose that instead of being blade-like the arthrodiran mandible would show the characteristic rounding and blunting that comes with this kind of strain, as is shown in every mandible of Pisces where there is strong pressure in the back part of the mandible.

The reconstruction of the musculature of *Dinichthys* mandibles, as shown in Plate XI, is worked out from a mechanical point of view, as it appeared to be impossible to adapt the ordinary piscine musculature to the arthrodiran jaws. In this reconstruction it is considered that there must have been a synchronous movement of the skull and mandibles, and the musculature is figured out on this basis. From the peculiar construction of the head, it is inferred that *Dinichthys* and its allies are the end members of a group that moved the head and had the jaws more or less fixed. The most efficient mechanical construction seemed to require that the inner face of the mandible should be connected by ligament or muscle with the "clavicular element," which extends forward on the inside of the mandible. If the attachment at this place were by ligament and fascia and the posterior end were appressed to the inner side of the cheek plate or to some other plate in this region and worked as the scapula works on the body of a mammal, we would have the movement desired, as the raising of the head would aid in raising the back part and lowering the front part of the mandible, while lowering the head would close it. The mechanism of this part must have been very perfect, for the shear is always in one plane, with no rounding of the edges. On the inner side of the mandible at the anterior end are depressions that show where the mandibles were fastened by strong ligaments.

In conclusion, the evidence gained from a study of the jaw mechanism of *Dinichthys* seems to favor the conclusion which has been advocated by many writers, especially Dean and Hussakof, that the Arthrodira are related by common origin with the Antiarchi.

ERYOPS

Plate XII, Fig. 1

The massive, frog-like skull of *Eryops,* a Permian stegoceph, is restored with the anuran type of musculature, though some modifications have been made because of the changes that have taken place in the anuran skull. The skulls of the stegocephalians and of the Anura are strikingly similar in general pattern; that of *Eryops* with the dermal roofing bones covering the whole skull; that of the Anura with these bones modified, partly eliminated, and all more or less sunken beneath the skin. The large palatine vacuity is similar in both. Gregory has suggested that the ancestor of the Anura was an animal much like *Eryops,* but that through the changes of the geologic ages the anuran skull became simplified, specialized, and the dermal temporal covering became fenestrated, partly as a result of the action of the muscles. The pterygoid region has changed slightly and has lost the flange that in *Eryops* projects down in a very reptilian-like manner. The mandibles are quite similar, although *Eryops* did not have the backward extension of the articular for the insertion of the depressor mandibulæ as in the frog, and the frog has lost the prominent suprameckelian fossa in the mandible that is so prominent in *Eryops.* In the Anura the muscles are all very far back on the skull, and we may assume from the *Eryops* skull that its muscles had a similar position, except that to make the jaw stable it should have had an anterior pterygoid muscle on the floor of the downwardly projecting pterygoid process. The loss of the anterior pterygoid muscle in the Anura is a peculiar specialization which, very probably, had not been attained by *Eryops.*

The restoration of *Eryops* gives the following muscles:

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).
Capiti-mandibularis medius (C. m. m.).
Capiti-mandibularis profundus (C. m. p.).
Pterygoideus anterior.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).—The masseter element would occupy the posterior part of the skull in the space under the squamosal. It would probably have its origin on the inner side of the squamosal and quadratojugal, with a few fibers running to the quadrate and extending ventrally; it would be inserted on the borders of the supra-meckelian fossa of the mandible. It is on the outside of the mandible in the Anura; but from the shape of the skull and the mandible there is no chance for it to be inserted there in *Eryops.* The muscle is split in the Anura and so the masseter of *Eryops* might have had two parts, the smaller one posterior, in the region of the small quadrate.

Capiti-mandibularis medius (C. m. m.).—This temporal slip of the adductor mass would be under the superficial portion and over the pterygoid muscle. It would have its origin on the inner side of the parietal, with perhaps a slight attachment on the postfrontal. It would be inserted in the suprameckelian fossa. The muscle could extend quite far in the parietal region, taking hold under the skull roof. Possibly the deep part of this mass may have had a separate slip, corresponding to the capiti-mandibularis profundus or "pterygoideus externus" of reptiles.

Pterygoideus anterior (Pt. a.).—The pterygoid muscle of *Eryops* was probably not homologous with the so-called "pterygoid" of the frog, but was more probably homologous with the anterior pterygoid muscle of primitive reptiles. The pterygoid bone is quite different from that of Anura, in that it has a descending flange, much like that of the Crocodilia, that fits snugly along the inside of the mandible and serves as a guide for it. As this flange in the reptiles is functionally connected with the anterior pterygoid, it seems probable that *Eryops* had an anterior pterygoid muscle that extended along the pterygoid bone as far as the orbit. A pterygoid muscle is needed here for mechanical reasons, as from the teeth one would judge that the jaw was used differently from that of Anura, and there is need of a muscle here to oppose the pull of the temporal muscles, which would tend to pull the symphysis apart. Thus a pterygoid in this region would steady the jaw and pull the jaw forward against the other muscles. It would have to be inserted in the suprameckelian fossa, possibly extending to the back part.

Capiti-mandibularis profundus (C. m. p.).—There is a strong possibility that there was a deep slip of the adductor mass, deep under the muscles, that would correspond to pterygoideus posterior of the reptiles.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ.—The articular of *Eryops* does not have the posterior process and the muscle must have been inserted on the under side of the articular. In some American Museum specimens the mandible seems to show a place where the depressor could have been attached. The origin of the depressor would have been on the squamosal, alongside the otic notch, since in the Anura the origin is on the posterior limb of the squamosal and on the tympanic annulus. The Anura have a second part of the depressor arising from the dorsal fascia, and *Eryops* also could well have had this second part of the depressor.

From the inferred arrangement of the muscles in *Eryops,* perhaps some explanation may be given of the changes and losses that have taken place in the anuran skull. First, the capiti-mandibularis medius was no doubt attached to the parietal region and the capiti-mandibularis superficialis to the squamosal. To account for the open condition of the temporal roof in the Anura and for the loss of the tabulare, supratemporal, squamosal, postfrontal and postorbital, we may adopt the hypothesis that these muscles were pulling against one another; that the region between them gave way and made breaks and openings which did not exist in the primitive form with its unbroken temporal covering. The region between the parietal and the squamosal would lie between the pulls of these muscles and the first break would appear here. The disappearance of the dermosupraoccipitals, tabulars and supratemporals was probably correlated with the opening out of the temporal region and with the extension of the temporal muscles up on to the top of the skull.

LABIDOSAURUS

Plate XII, Figs. 2, 3, 4

This primitive cotylosaur shows the covered or roofed temporal region, which it has inherited from the Stegocephalia and from such fishes as *Osteolepis, Polypterus* and *Amia,* in which the dermal bones are still in their primitive position in the skin and not sunken below it. The quadrate is fixed, so that in that region there is no movement. The stout teeth demand strong jaw muscles and there is ample room for a large capiti-mandibularis beneath the temporal roof. The massive lower jaw with its large suprameckelian fossa also requires large muscles. The pterygoid region and the base of the brain case are essentially similar to those of *Sphenodon* and imply a corresponding similarity in the pterygoid muscles.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP

(INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).
Capiti-mandibularis medius (C. m. m.).

Capiti-mandibularis profundus (C. m. p.).
Pterygoideus anterior (Pt. a.).

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Capiti-mandibularis superficialis (C. m. s.).—This slip of the capiti-mandibularis would cover the deeper fibers and arise from the quadrate, squamosal and jugal and be inserted with the medius in the suprameckelian fossa.

Capiti-mandibularis medius (C. m. m.).—This slip would arise on the upper part of the skull and be attached to the parietal, squamosal, and perahps to some of the bones of the otic region. It would join the rest of the capiti-mandibularis in its insertion.

Capiti-mandibularis profundus (C. m. p.).—This deep slip would arise on the alisphenoid and outer face of the pterygoid and be inserted with the rest of the mass on the mandible. The whole capiti-mandibularis mass would probably be inserted in the suprameckelian fossa. It would be attached to the bones surrounding the fossa and extend down into it, after the manner of other reptiles, where the whole insertion of the capiti-mandibularis is on the inside of the mandible.

Pterygoideus anterior (Pt. a.).—This muscle was no doubt strongly developed as in all typical reptiles. It arose on the under side of the pterygoid and might have extended over the upper face of the pterygoid region as in *Chelydra.* The form of the articular shows plainly that the muscle must have been inserted on the ventral side of the articular, for there is no evidence that it extended more than slightly into the outer face of the bone.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ (D. m.).—This muscle was no doubt arranged as in other reptiles. It arose on the parietal and extended around the squamosal to be inserted on the upper face of the retroarticular process of the articular, which plainly shows the marks of the insertion.

TYRANNOSAURUS

Plate XIII, Fig. 1

The reconstruction of this form was attempted after some comparative study of types like *Alligator, Chelydra,* Aves and *Euparkeria* (Fig. 5). The skull in *Tyrannosaurus* is secondarily monimostylic, as the quadrates and the upper jaws were less movable than in the more primitive *Allosaurus.* The monimostylic type is quite stable in its musculature and the reason for this is evident, as the complicated musculature needed for the movable quadrate and pterygoid is lost when the bones become fixed.

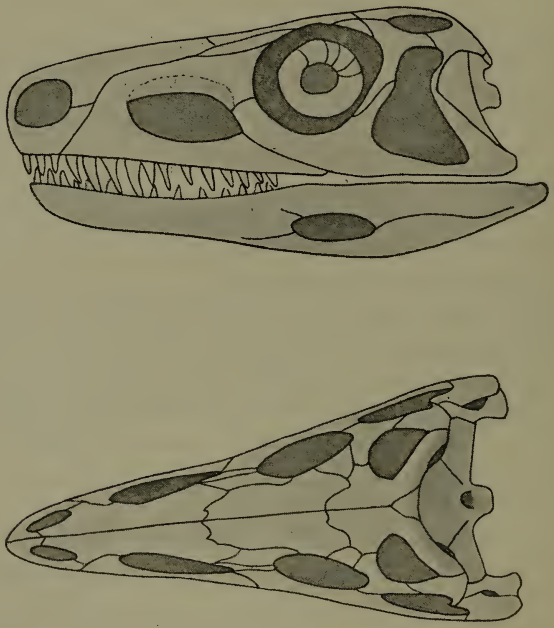


FIGURE 5

Skull of a pseudosuchian, *Euparkeria capensis.* After Broom

The borders of the large preorbital fenestra may serve for the attachment of the anterior part of the pterygoideus anterior muscle. Around the bony margin of the supratemporal fenestra arose the capiti-mandibularis. Both the supra- and the lateral temporal fenestræ gave room for the expansion of the capiti-mandibularis, while the lateral fenestra of the mandible served a like function for the lower end of the same muscle.

Tyrannosaurus was a huge carnivorous type with massive skull and jaws; thus the musculature must have been very heavy.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Capiti-mandibularis (with three unseparated slips).
    (*a*) Capiti-mandibularis superficialis.
    (*b*) Capiti-mandibularis medius.
    (*c*) Capiti-mandibularis profundus.
Pterygoideus anterior.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Capiti-mandibularis.—This muscle is considered to have three slips, designated as superficialis, medius and profundus. They are not competely separated in the Reptilia. The temporal fenestræ show that this muscle had retained its freedom of movement, which it had inherited from some remote aëtosaur-like ancestor. There is a long fenestra under the eye, a lateral temporal and a supratemporal fenestra. The capiti-mandibularis would probably conform to the *Alligator* or *Chelydra* type. The presence of the supratemporal fenestra means that the temporal or medius slip extended through and was attached to the parietal crest. Thus the *medius* slip probably arose on the parietal, extended through the supratemporal fenestra and under the superficial slip to be inserted on the coronoid or in the suprameckelian fossa which is large. The *superficialis* slip would have fibers extending posteriorly over the rest of the mass. This slip would arise on the squamosal, quadratojugal and be inserted along the upper edge of the mandible and in the suprameckelian fossa. In a few forms this muscle is partly inserted on the outside of the mandible, but the outside insertion is small in typical reptiles. A deep slip might have been present, representing the capiti-mandibularis profundus.

Pterygoideus anterior.—The insertion of this muscle is plainly indicated in the mandible of specimen No. 5027, American Museum, which shows the place where the anterior pterygoid was wrapped around the posterior end of the jaw as in typical reptiles. The muscle probably arose in the space below and in front of the orbits and above the palatines and pterygoid, as in *Alligator*. The existence of antorbital fenestræ was held by Dollo and by Gregory and Adams (1915) to be correlated with the anterior extension of the anterior pterygoid muscle—a view adopted here.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

This muscle is constant in the Reptilia and its insertion is evident on the specimen No. 5027, American Museum. In many reptiles where the back part of the skull is not greatly modified its origin is on the parietal, but here it seems to have been on the paroccipital. The muscle arose on the ventral end of the paroccipitals, the ventral ends of which are roughened for a muscle insertion. Its insertion on the mandible was on the articular, posterior to the articulating surface, where there is a depression similar to that seen in most reptiles.

CYNOGNATHUS

Plate XIII, Figs. 2–5

The skull is reptilian as a whole, but parts of it very plainly show the mammalian characters, especially the squamosal, the jugal, the dentition and the basicranial region. The quadrate is reduced. The jaw, although reptilian, is of a type that foreshadows that of mammals. The dentary had enlarged from the primitively slender dentary of the early reptiles until it was the most important part of the mandible and must have carried the greater part of the musculature. The coronoid process of the dentary is large and ascends far into the temporal fossa. The angle of the dentary is developing and shows plainly. The posterior part of the jaw, consisting of the articular and other elements, is becoming small and is so loosely attached to the dentary that in fossil specimens it is usually missing or found separate from the skull. The old reptilian articulation with the skull had become reduced, but was still functional. Although the new articulation with the jaw had not yet been formed, I infer, from the shape of the temporal fossa and from the direction of the muscles, that the jaw was pulled not directly against the quadrate but toward a point above it on the squamosal.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP
(INNERVATED BY V_3)

Capiti-mandibularis.
    (*a*) Capiti-mandibularis superficialis.
    (*b*) Capiti-mandibularis medius.
    (*c*) Capiti-mandibularis profundus.
Pterygoideus anterior.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP (INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE ADDUCTOR OR TEMPORAL GROUP (INNERVATED BY V_3)

Capiti-mandibularis.—In *Cynognathus* this mass of muscle, which is the reptilian muscle of the same name, must have been well subdivided; thus there was probably a large temporalis or medius slip filling the large temporal fossa and a superficial or masseter slip arising along the zygomatic arch, both outside and inside, both muscles being attached on the large dentary. The large carnivorous jaws of this form indicate a correspondingly powerful muscle which not only filled the temporal fossa but also must have been attached to the outside of the zygomatic arch. The attachment must have been on the ascending process of the dentary, for the posterior bones of the jaw are too small. Watson (1912, p. 581) says:

> It is a remarkable fact that in Cynodonts increasing size of the dentary and of the masticatory muscles, which in *Cynognathus* must be inserted on it, is correlated with a reduction and weakening of the back part of the jaw, which alone articulates with the skull; not only are the actual bones small, but their attachment to the dentary is weak; they merely rest in the groove in that bone and are often displaced in the fossil skulls.

As the ascending process of the dentary affords ample space, the capiti-mandibularis must have been attached chiefly to this bone, as in mammals.

(*a*) *Capiti-mandibularis superficialis.*—On the outside of the dentary there is a large fossa for the masseter, which must also have been large to match the large temporal mass. It probably had a hold on the inner and outer side of the zygomatic arch, extending forward to the large anterior tubercle on the lower border of the zygoma. The attachment is probably in the depression on the outside of the dentary. From the condition in other reptiles, this superficial slip could extend partly over the rest of the mass and be connected with the fascia of that region. As mentioned before, the pull of these muscles would tend to pull the jaw upwards against the squamosal and not so much against the quadrate. This gave the posterior part of the jaw the opportunity to complete its separation from the dentary in some more advanced form of theriodont and to enter on its new mammalian function in connection with the middle ear.

(*b*) *Capiti-mandibularis medius.*—This part of the temporal mass would fill the temporal fossa and be inserted on the inner and outer sides of the dentary.

(*c*) *Capiti-mandibularis profundus.*—This deep slip must have taken its origin on the inner side of the temporal mass and have been inserted on the ascending process of the dentary.

Pterygoideus anterior.—To counterbalance the pull of the capiti-mandibularis mass the anterior pterygoids must have played an important part. The ascending process of the pterygoid is quite large, thus giving an attachment for large pterygoids. There is no need for the complex musculature of the type found in streptostylic reptiles, so it was probably more of the chelonian or rhynchocephalian type. The pterygoid bones of *Cynognathus* are bowed inward to the mid line, covering the primary skull base and forming on each side an extended longitudinal fossa for the origin of the anterior pterygoid muscle. Although the articular, prearticular and angular bones are small, they seem sufficiently large for the insertion of the anterior pterygoid in the normal place at the back part of the jaw. The insertion of this muscle in all recent reptiles is at or near the rear end of the jaw, and in view of the general fact that insertion areas are less variable than origin areas, there seems no reason for regarding *Cynognathus* as having an exceptional insertion of the anterior pterygoid. The pull of the anterior pterygoid muscle would counterbalance that of the capiti-mandibularis mass and take some of the strain off the weak quadrate articulation. The dentary, imbedded in the temporal mass, would thus act as a cushion and the action of the jaw would be the same as though a strong articulation were present. That this action of the jaw was effective is shown by the robust character of the teeth and jaw. If *Cynognathus* had relied only upon the old articulation by way of the quadrate and articular, a bite on a piece of bone might have dislocated the jaw. As the dentition is carnivorous, the jaws did not have much lateral motion. The reason *Cynognathus* had a large ascending ramus of the dentary is that it was derived from therocephalians and ultimately from primitive Theromorpha, in which the coronoid bone was functionally replaced by an obliquely ascending process of the dentary.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP
(INNERVATED BY VII)

Depressor mandibulæ.—This muscle was in its usual position, as the posterior end of the mandible shows the insertion. In all reptiles there is a remnant of the C_2md of Ruge, and from this the mammalian digastric was probably derived. With the loss of the posterior end of the reptilian jaw the depressor mandibulæ of these forms would disappear and a new digastric would be formed from this sheet of muscle that has persisted from the fish stage. The long ventral muscles of the throat could give much aid in lowering the mandible. Watson (1912, pp. 581-582) says:

> As it is impossible that a muscle should increase while its point of attachment is degenerating, it appears probable that the pterygoid muscles were mainly inserted onto the postero-inferior angle of the dentary, which is thickened. Thus inserted, these muscles, while tending to close the mouth, would produce stresses in the hinder part of the jaw, in the opposite direction to those induced by the masseter and temporal muscles, in this way permitting the reduction of the hinder part of the jaw which we actually see. The fact that in higher Cynodonts all the masticatory muscles have their attachments on the dentary renders the freeing of the articular and quadrate demanded by the quadrate-incus theory of the mammalian ossicula auditus much more understandable.

It would seem that Watson's hypothesis that all of the muscles were on the dentary might be questioned, for the cast of the skull of *Cynognathus* shows plainly the insertion of the depressor mandibulæ on the posterior end of the articular, while the insertion of the anterior pterygoid seems to have been in the usual position, wrapping around the end of the mandible as in other reptiles. This last muscle may have been reduced, but its insertion areas on the articular and prearticular seem evident.

HOMOLOGIES OF THE JAW MUSCLES IN VERTEBRATES

(Tables I–V)

Introduction

The first attempts to homologize the jaw muscles in the different groups of vertebrates were based purely upon similarities of function and position; and while the work was useful and gave a start in the right direction, it was not altogether reliable. The older writers quickly took up the innervation, as its importance in comparative anatomy became known, and applied it to the determination of the muscles. Thus a much more certain classification arose. Most of the work has been on restricted groups. Vetter in his works on the elasmobranchs and other fishes gave for the muscles of these groups the names that are still used. He divided the muscles up into groups according to their innervation and position and gave the best basis for the classification of the piscine musculature.

One of the few papers dealing with the entire vertebrate group is a dissertation by Dr. Ernst Teutleben, published in 1874 under the title, Ueber Kaumuskeln und Kaumechanismus bei den Wirbelthiere. He examined a series of vertebrates and gave a very good description, for the time, of the jaw muscles in some of the common vertebrates; he also made some observations on the mechanics of the jaw action. He studied the following forms: Dog, horse, sheep, porpoise, bird, *Crotalus durissus,* alligator, frog, pike and whiting. He failed to differentiate many of the muscles and made no mention of innervation, which is one of the chief criteria used at the present time. The names applied were based upon the origin and insertion of the muscles. He applied this principle to the different classes and gave the muscles names. He did not attempt homologies, except as based upon similar function. He misinterpreted the detrahens mandibulæ of *Ornithorhynchus,* as all the others had done until the neurology was worked out by later workers.

The greatest stimulation to the work was given by the researches of Ruge on the facialis nerve. He studied this throughout the vertebrates from the elasmobranchs to mammals and gave a reliable basis for the determination of the muscles of this group. Schulman, in his work on the trigeminus musculature of the monotremes, cleared up some of the puzzles that this aberrant group present. Lubosch, Fürbringer and others have added much to this work, so that the comparative anatomist now has extensive material for comparison. Gaupp in his work on Reichert's theory of the origin of the auditory ossicles and Versluys in his studies on the auditory organs in reptiles have worked in this rich field and have given the material a definite meaning, especially in some of the troublesome problems relating to the changes that took place in the shifting of the bones and muscles, when reptiles of some sort were changed into mammals.

Many other investigations have given much information on the musculature of special forms of vertebrates. Chaîne, Rouvière, Bijvoet, Toldt, Parsons and others have collected the necessary data on the digastric muscle and have given very full accounts of the condition of this muscle in the mammals. Toldt, in his paper on the jaw articulation and its problems, gives us a basis for the classification of the types of vertebrate jaws, of their articulations and of the correlated types of musculature. Apparently the present work is the first to give a general illustrated review of the jaw muscles of vertebrates and to apply this knowledge to an interpretation of the skull structure of recent and fossil types.

The study of 26 different forms, representing the classes Pisces, Amphibia, Reptilia, Aves and Mammalia, has demonstrated that the muscle masses in general are severally homologous from the Pisces to Mammalia, and that they may be grouped into two great systems: First, the muscles innervated by the ramus mandibularis trigemini V_3, and, second, the muscles innervated by the facial nerve (VII). There is a sharp line between these muscular systems and their general position has been the same throughout. The trigeminus innervates the muscles of mastication that lie in front of the quadrate, while the facialis innervates the muscles behind the quadrate and those of the hyoid region. These regions in the mammals overlap on the surface, for the reptilian sphincter colli has crept forward over the deeper muscles of the trigeminus and has formed the mimetic muscles of the face, so that while the deep muscles, anterior to the hyoid arch, are innervated by the trigeminus the superficial muscles are innervated by the facialis. This is an example of the faithfulness with which the nerves follow the muscles in their migration (Ruge, 1897).

Starting with the elasmobranchs, we find the adductor mandibulæ muscles, which are undifferentiated masses, derived from the pro-branchial muscles before the anterior branchial arches were transformed into jaws. The adductors are not separated into special muscles, but represent the "mother mass" of the chief jaw-muscles of the V_3 group in all the higher classes of vertebrates. A depressor mandibulæ is not differentiated in the elasmobranchs or in the other classes of Pisces, but is represented by the second dorsal superficial constrictor throughout this group, a true depressor first appearing in the Amphibia.

In the development of the Amphibia from some of the Pisces the jaw musculature was carried over in its general plan, but the muscle masses took on the peculiar modifications needed in each group. We may conceive that these "mother masses" C_1 and C_2 became differentiated in many ways throughout the different classes of vertebrates, and that various slips were given off from these masses which served their purpose and the needs of the animal, only to be dropped in the future development, while new slips arose in the higher forms. We may further conceive that these mother masses were innervated by the nerves V_3 and VII, and that in the first stages of the origin of a new muscle slip there was a mere branching of the nerve into small twigs; in this stage there was no differentiation into special nerves and no division of the muscles into separate slips, but merely partially separated portions with the nerve twigs following and gradually becoming more differentiated, as conditions demanded further separation. Finally, when these slips were separated off from the main mass, the nerve twig became a branch, and the muscle, having lost all connection with the fibers of the parent mass, might be called a separate muscle. This is my conception of the origin of the special muscles in the different classes, and with this view the precise homology, except within the class, is sometimes doubtful, unless very primitive or annectent forms between widely separate groups are available for study.

This separation of the muscle slips from the mother mass may be shown in embryology; for the muscle groups start as undifferentiated masses and then become divided into the different slips. Lubosch (1913) describes the separation from the "temporal mass" of a slip which becomes the "pterygoid" of the urodele. This splitting of the muscle is quite definitely known, and in this paper I have made frequent use of this fact in endeavoring to determine the homologies of the different groups and in reconstructing the muscular systems in extinct forms. (See chapter on reconstructions.)

Some individual muscles may, however, be followed through all the classes of vertebrates. If the history of a bone has been traced from the Pisces to the Mammalia, there is no reason for assuming that the muscles associated with it have changed, provided that they are present in all of the classes and have retained their origin, insertion and to a certain extent their function. Perhaps the hyomandibular (= stapes), the preopercular (= squamosal), and other bones whose history is pretty well known, might be considered as having taken their muscles with them throughout the evolutionary changes from the fishes to mammals, if there is no mechanical or other reason for the dropping of the old and development of new muscle slips. Muscles are pliable tissues having the power of changing, either by shifting their origin or, if there is no demand for their service, by dropping out. Vestigial muscles found in each of the classes have been carried over from an earlier class and have lost their usefulness and atrophied. A long list of such muscles might be compiled from the Mammalia or from any class. The vestigial muscles of the ears in *Homo,* carried over from the simian stage, vestigial muscles in birds, carried over from the Reptilia, the vestiges of the levator arcus palatini in *Cryptobranchus* and *Amphiuma,* carried over from the Pisces (Lubosch, 1913, p. 71), the "adductor maxillæ" in *Cryptobranchus* from the Pisces, are all vestigial and more or less functionless muscles carried over from one class to another.

Homology of the Jaw Muscles in the Pisces

(Table I)

The primary division of the musculature may be made with the innervation as a guide, as there is a natural grouping of the muscles of the head into two systems—the muscles innervated by the fifth or trigeminus and those innervated by the seventh or facialis nerve. The muscles also divide into the same two divisions if we group them first as muscles anterior to the quadrate region and secondly as those posterior to it. The exceptions to this grouping are the mimetic muscles of the face in mammals, which represent the muscles from the second constrictor, innervated by the facialis, that have extended over the face and taken their nerves with them.

If we assume that the jaw and hyoid elements represent the first two visceral arches that have changed their function in some pregnathostome stage, it is also fair to assume that the muscles went with them, and that the jaw muscles represent the much divided and specialized constrictors and adductors of primitive branchial arches. Vetter's analysis of the muscles of the visceral arches appears to hold good at the present day. He held that the adductor mass of the jaws of fishes was homologous with the "adductores arcuum visceralium," which were small muscles on the inner side of the branchial arches, "mittlere Beuger der Bogen," lying between the dorsal constrictors above and the ventral constrictors below. As these branchial arches changed into jaws and the development of the hyomandibular, quadrate and opercular elements proceeded, the constrictor and adductor muscles, which were already in position, would require but little change to take on new functions as jaw and opercular muscles. Accordingly, the constrictors of the pre-gnathostomes may be regarded as the primitive head muscles. In the elasmobranchs the constrictor became divided into different sections, so that there were dorsal, median and ventral sections, which were either further differentiated to be used as needed or held in reserve for future changes, as in the case of the digastric muscle. This is represented in the elasmobranchs (Ruge, 1897) by the undifferentiated second constrictor, which retains its constrictor-like form until it becomes specialized in the amphibians into a definite muscle.

Throughout the gnathostomes we find muscle masses that may be homologized, but the homology of the separate slips is often questionable. In this paper the attempt is made to work out the homology of the main muscle masses ("Mother" masses) first and then, if possible, to point out the homologies of the separate slips of each mass, especially in the members of the same class and where possible between classes. To homologize the separate slips through the different classes means that one must know the ancestry and be able to demonstrate the movements and changes in the osteology, so that in default of such knowledge the result is often questionable.

The muscles of the piscine head may be divided as follows (the related muscles are placed together):

MUSCLES INNERVATED BY THE TRIGEMINUS NERVE

Levator maxillæ superioris.
Levator arcus palatini.
Protractor hyomandibularis.
Dilator operculi.
Adductor mandibulæ (often divided in the Pisces).

MUSCLES INNERVATED BY THE FACIALIS NERVE

Adductor hyomandibularis.
Levator operculi.
Adductor operculi.

MUSCLES INNERVATED BY THE TRIGEMINUS NERVE

Levator maxillæ superioris (Adductor β Vetter).

Levator arcus palatini 1–5 McMurrich.—These are a series of muscles that extend from the under side of the skull to the maxillæ. They vary in number in the Pisces from one to four or five. In *Acanthias* they arise in a mass anterior to the spiracle and the remains of the first constrictor dorsalis superficialis and extend to the maxillæ; here they form a single muscle. In *Amia* they are partly anterior to the eyes. They probably represent the dorsal part of the first constrictor superficialis and function in the movement of the maxillæ. In the teleosts they lose their importance and disappear, except for a few tendinous remains, while the levator arcus palatini becomes more important and usurps the place of the levators of the maxillæ.

Levator arcus palatini.—This muscle raises the bones of the palatine region and is of great importance in the fishes where this region is developed. In the elasmobranchs it is not needed, but is perhaps represented by the remains of the first constrictor, just anterior to the spiracle. It is prominent in most teleosts and Holostei, but drops out where this region becomes fixed. This muscle is closely related to the protractor hyomandibularis and the dilator operculi. McMurrich (1885) calls the protractor hyomandibularis "levator arcus palatini" in *Amia.* They are often close together and sometimes not entirely separated as in *Amia.*

Protractor hyomandibularis.—This draws the hyomandibular forward. It probably represents a part of the first constrictor. It is always closely connected with the levator arcus palatini. It varies in size, being very large in *Acipenser* and *Polyodon,* of good size in the teleosts, and absent in the dipnoans, where the hyomandibular is rudimentary or absent.

Dilator operculi.—This is the posterior slip of the first constrictor. It pulls the operculum forward and slightly raises it. It is closely connected with the protractor operculi, always lying just behind it, extending over the groove for it in the hyomandibular just above the preopercular. Often the preopercular also shows where the muscle extends over the upper end of it. Practically every skull studied showed this muscle area, so that it is easily demonstrated on any skull in the teleosts or other fish group. It is inserted on the under side of the opercular in most forms.

Adductor mandibulæ.—This is considered as the mother mass of the chief jaw muscles throughout the vertebrates. In the elasmobranchs it is almost a single mass, partially subdivided in the rest of the fishes and reptiles and completely divided in the Amphibia and Mammalia. It is innervated by the third branch of the trigeminus and represents a part of the first constrictor with its nerve. The condition in the elasmobranchs is usually as a single mass, although the fibers cross each other and do not always extend in the same direction, but there is no definite separation in those studied and none described in the literature on other forms. There is a tendency throughout the remaining Pisces for this mass to be partially divided. In general this muscle may be divided into two parts—a superficial part that extends across the other fibers and is attached in the quadrate and squamosal region and a deeper set of fibers which extend up to the postfrontal and parietal region. No attempt is made in this paper to homologize these portions, although they are constant and seen to be starting a condition that eventually may have resulted in the separation of these slips from the mother mass. The simplest adductor mandibulæ is found in *Acanthias* and the most complex in *Amia* and *Esox,* although the division is never complete. *Amia, Palinurichthys* and many other forms show a peculiar specialization, where a part of the adductor (Adm^4) extends into the suprameckelian fossa and excavates the dentary, so that the bone is completely filled with this part of the muscle.

MUSCLES INNERVATED BY THE FACIALIS NERVE

This series of three muscles is concerned with the movement of the opercular and hyomandibular bones. They represent a part of the second dorsal constrictor and show the characteristic innervation of this mass.

Adductor hyomandibularis.—This is a deep muscle which arises on the posterior part of the skull in the otic region, anterior to the other two. It is usually small and short and is not easily seen unless the opercular bones are removed. It opposes the protractor hyomandibularis and raises the hyomandibular bone. It is attached to the inner side or to the posterior border. It is shown in *Acipenser, Polyodon* and *Polypterus.*

Adductor operculi and levator operculi.—These are closely associated. Both arise on the posterior part of the skull in the otic region and are inserted on the inner side of the opercular bone. Often one of them is absent or perhaps they are not differentiated. They are present in almost all the Pisces with the exception of elasmobranchs. They are small in the dipnoans.

HOMOLOGY OF THE JAW MUSCLES IN THE AMPHIBIA

(Table II)

There is quite a difference between the muscles of the Pisces and those of the Amphibia, for in the latter muscles masses have become more specialized by a splitting off of the different slips, so that they may be called separate muscles. Some of these divisions were suggested in the Pisces by the direction of the fibers and by differences in the origin and insertion, but they remained a part of the parent mass, as they do, for the most part, also in the Reptilia. In the Amphibia the muscles of the anterior part of the piscine head have disappeared, being represented by vestiges only. Lubosch (1913, p. 71) says:

> Bisher unbekannte Muskelrudimente wurden gefunden bei *Amphiuma* und *Cryptobranchus*.
>
> (1) Ein M. levator arcus palatini bei *Amphiuma* und *Cryptobranchus*, von der knorpligen Nasseskapsel und (*Amphiuma*) der vertikalen Lamelle des Frontale (Wiedersheim) entsprigend und zur Membrana pterygomaxillaris zeihend.
>
> (2) Ein M. adductor maxillæ bei *Cryptobranchus* vom vorderen Rand des knöchernen Pterygoids und dem knorpligen Proc. pterygoideus quadrati entspringend und in der Nähe des Maxillare in der Membrana pterygo-maxillaris endend. Beide Muskeln werden mit feinen Aestchen aus demselben Nerven versehen, whelcher auch die Mm. pterygoidei versorgt.

The great changes in the skull of the Amphibia account for the reduction and dropping out of several of these typical piscine muscles. There is no need for the levator maxillæ superioris and the levator arcus palatini, as the parts controlled by these muscles are fixed. The new form of the bones demand a different musculature and the loss of others. The preopercular, symplectic, hyomandibular, opercular, inter- and sub-opercular and several of the bones of the skull and maxillary region have either been lost or changed their functions, so that new muscles are needed. If the hyomandibular is considered to be the stapes of the higher forms, it seems to have discarded its original musculature in the transformation, for there are no muscles in the forms with a stapes that could have been retained from the muscles of the hyomandibular. The two hyomandibular muscles—the protractor (V_3) and the levator (VII)—

could not have been carried through to the Mammalia, or at least there is nothing to show that such was the case, as the new stapedial muscle is regarded as a slip from the C_2md or from the reptilian depressor mandibulæ. The preoperculum, which is considered to be the squamosal of the forms above the Pisces, retains its old connection with the temporal muscle mass, so that the masseter (or superficial) slip of the urodeles and anurans is still associated with the transformed preoperculum. In the Amphibia the piscine operculum is absent, so that the three muscles attached to it in the Pisces would be lost.

The simplest condition of the musculature is found in the urodeles, where the muscles are well separated, but are not so specialized as in the Anura and retain more of their piscine condition. They are divided into slips, three or four in number. These are separate slips that compare with those indicated in the muscles of the reptiles, but are not regarded as fully homologous with them. The superficial slip is the typical masseter-like muscle with the same general direction of the fibers and the same relation to the main mass. The deeper muscles of the peculiar "Temporal mass" have a peculiar specialization, in that one slip extends back over the skull and arises no longer on the parietal, but on the neck vertebræ, sometimes as far back as the fourth cervical vertebra. (See urodeles.) The anterior temporal, which arises from the side of the skull, behind the eyes, and runs outward and backward to the inner side of the mandible, is apparently comparable to the pterygoideus anterior of reptiles. This pterygoideus anterior has separated from the under side of the capiti-mandibularis mass, but does not arise from the pterygoid.

The Anura show the highest specialization found in the amphibians, as the muscles are not only divided into slips, but the slips are well separated, both in their origins and in their insertions on the mandible. The striking thing in connection with the anuran jaw muscles is their connection with the auditory region, for the muscles of mastication and some of the neck muscles serve to keep the tympanum stretched taut. The division of the capiti-mandibularis superficialis (masseter) is suggested in the urodeles, where the fibers of the single muscle show an intermediate condition. The depressor mandibulæ is the same throughout the group. It has two slips, one from the skull and one from the dorsal fascia. They represent again the C_2md of Ruge, which is the mother mass of this group innervated by the VII nerve. It seems from the innervation, origin and insertion that the individual slips may be homologized throughout the Amphibia, and the homologies as they appear are shown in Table II.

Homologies of the Jaw Muscles in the Reptilia

(Table III)

The jaw muscles of the Reptilia and Aves show the same division into masses as do those of the Pisces and Amphibia. There is the same grouping of the masses into muscles innervated by V_3 and by VII and they have the same relative position as in the lower forms. The muscles show more specialization, as there is a higher specialization of the skull in Reptilia and Aves and consequently a more complex musculature. In the reptiles the capiti-mandibularis mass is more homogeneous than in the Amphibia, and while the pterygoid muscles have separated off, the capiti-mandibularis superficialis remains attached. In the birds there is a complete separation of the muscles.

The great specialization in the higher or streptostylic reptilian skulls is correlated with the great complexity of the musculature. The Reptilia are divided arbitrarily into two groups according to the fixity or movability of the quadrate; but this is a relative division, for all stages are found between the streptostylic and the monimostylic conditions. The jaw muscles of the Reptilia may be grouped according to the innervation, as follows:

MUSCLES OF THE CAPITI-MANDIBULARIS OR TEMPORAL GROUP

(INNERVATED BY V_3)

Capiti-mandibularis.
    (*a*) Superficial slip (not separate). Masseter.
    (*b*) Medius slip (not separate). Temporal.
    (*c*) Profundus slip (not separate). Deep layer.
    (*d*) Cranio-pterygoid.
Pterygoideus anterior.
Pterygoideus posterior.

MUSCLES OF THE DEPRESSOR OR DIGASTRIC GROUP

(INNERVATED BY VII)

Depressor mandibulæ.

MUSCLES OF THE CAPITI-MANDIBULARIS GROUP

(INNERVATED BY V_3)

Capiti-mandibularis.—This muscle is not divided into separate muscles, but the conditions suggest the divisions to appear later in the mammal-like reptiles. (*a*) The outer or superficial slip may apparently be traced from the fish to the mammal. It always arises from the squamosal region and is inserted on the coronoid region of the jaw along with the rest of the mass. (*b*) The medius slip also is not separate, the fibers being under the superficial slip and extending to the parietal region. (*c*) The profundus is represented by the deep part of the mass. (*d*) The cranio-pterygoid muscles are the special muscles developed in the pterygoid region of the streptostylic reptiles and are new developments.

Pterygoideus anterior and pterygoideus posterior.—The so-called pterygoid muscles of reptiles include two quite different groups; the posterior group represents the deepest part of the capiti-mandibularis mass. It is usually named the pterygoideus externus or external pterygoid, but it is probably only partly homologous with the mammalian external pterygoid. I have named it the capiti-mandibularis profundus. It is often subdivided into two heads, which may be named caput 1 and caput 2. The anterior pterygoid called by Mivart "Internal pterygoid" and in this paper "Pterygoideus anterior" represents the anterior part of the adductor mass or C_1smd of fishes and is foreshadowed in *Polypterus*. It may be the homolog also of the so-called "temporalis" of urodeles. It is far in front of the "Pterygoideus externus" and runs in the opposite direction, crossing it at a wide angle on its way from the orbital region to the back of the mandible. It is always present in the reptiles and acts in concert with the capiti-mandibularis mass in closing the jaw. More in detail the action is described in the section on reptiles.

MUSCLES OF THE DEPRESSOR GROUP
(INNERVATED BY VII)

The depressor mandibulæ acts as the depressor of the mandible. It is constant throughout the Sauropsida. It was retained throughout the series until the mammal was evolved, when probably a new slip was separated from the mother mass and the new depressor of the mammal was formed.

Futamura (1907, p. 570) on comparative and embryological evidence stated that the stapedial muscle of the mammals and man comes from the proximal or upper part of the muscles of the hyoid arch (innervated by VII)—that is, the mother mass of the depressor mandibulæ—and that the reptiles also derive their stapedial muscles from the same source. Futamura says:

> Der M. stapedius stammt von den Muskelfasern die sich vom proximalen Teil der Hyoidmuskulatur nach Gehörknöchelchen begeben: Bei den Reptilien (Krokodil, Lacerta) ist er mehrfach und in seine Funktion auch verschieden von der der Vögel und Säugethiere. Nach Killian finden sich beim Krokodile Ohrmuskeln, die Heber, Herabzieher der Ohrklappe und Spanner des Trommel-

felles sind. Bei der Eidechse konnte ich nur zwei Muskel finden, die sich dem Levator der Ohrklappe und dem Depressor der Ohrklappe und Spanner des Trommelfelles der Krokodile verglichen habe. Bei den Vögeln, Säugethiere und dem Menschen ist der Stapedius einfach, geht beim Vogel an der Columella und bei den Säugethiere an den Steigbügel. Hier verliert er damit die direkte Beziehung zum Trommelfell und macht auch einen Funktionswechsel durch, auf den ich hier aber nicht näher eingehen will.

SUMMARY

The relations of the jaw muscles of reptiles and Amphibia are well summarized by Lubosch (1913, pp. 72-73) as follows:

> Die Vergleichung mit den Reptilien (verg. die Beschreibungen von Fischer, d'Alton, Sanders, Mivart, Versluys, Watkinson, Bradley) Der Organizationstypus der Urodelen ist auch heir unverkennbar vorhanden. Die Muskulatur ist zwar mässiger, aber zweifellos weiniger eingreifend gegliedert als dort. (Bei Krokodilen ist sogar Masseter und Temporalis sehr réduziert.) Der Ramus mandibularis liegt auch hier zwischen Masseter und Temporalis aussen, Pterygoideus innen. Der Pterygoideuskomplex tritt auf als Pterygo-mandibularis (Bradley) (homolog dem Pterygoideus posterior der Urodelen) und als ein als, Pterygoideus (Bradley) auch "Pterygoideus internus" bezeichneter Muskel (Homolog dem Pterygoideus anterior der Urodelen) Bei Cheloniern (und Krokodilien . . .) sind alle Hauptteile der Muskulature scharf gesondert, bei Lacertiliern und Ophidiern scheinen sie nach den Angaben der Literature mehr zusammen-zuhängen. Besondere Eigentümlichkeiten bietet eine tiefe Masseter-portion dar, in betreff welcher auf die genauere Darstellung verweisen wird. Wichtig is nun vor allem die Differenzierung der motorischen Trigeminusäste.

HOMOLOGY OF THE JAW MUSCLES IN AVES

(Table III)

The musculature of the jaws in birds has been derived from the reptilian position with little change. As the bird skull is streptostylic, the reptile most easily compared with it is *Varanus* and some of the fossil forms as mentioned in the section on Aves. There is a separation of the muscles, so that the capiti-mandibularis is divided into a superficial, a median and deep portion. The deep portion fills its usual place and the superficial has its origin on the squamosal and quadrate. These muscles are opposed by two pterygoid muscles that are homologous with those of the reptiles.

The pterygoideus anterior (pterygoid internus) is the homolog of the muscle of the same name in the Reptilia; it does not wrap around the end of the mandible but is inserted on the inner, posterior face of the mandible as it does in some reptiles—*e. g.*, Chelonia. Pterygoideus posterior is the posterior slip from the capiti-mandibularis, which is separate in birds. It crosses the anterior pterygoid and is the homolog of the muscle of the same name in Reptilia.

The depressor mandibulæ is large and is the homolog of the depressor of the Reptilia.

The presence of the stapedial muscle in the Aves shows that in some of the reptiles and Aves the stapes was connected with a part of the depressor mandibulæ. Futamura (1907) has shown that this was true in the embryology of the sparrow and of the duck:

> Der Stapedius entspringt von der Gehörkapsel und geht zum Columella und zu der medialen Seite der Gehörgrube. Ein Teil der Muskelfasern scheint mit dem proximalen Abschnitt des Quadratum Beziehung zu haben. . . . In der Sperling der M. stapedius, der aus dem vorher erwähnten proximalen Teil der Facialismuskulatur entsteht, ist sogar schon ziemlich deutlich differenziert. Er liegt an der dorsalen Seite der übrigen Facialismuskulatur und zieht grösstenteils an der medialen Seite des Facialisstammes nach hinten, medial, und endet dicht an der Carotiswand der Nervus facialis ist bedeutend verlängert. In der Ente M. stapedius, digastricus und stylohyoideus differenzieren sich aus dem Blasten der post-auricularen Gegend.

Homologies of the Jaw Muscles in Mammals

(Table IV)

The great transformation of the reptilian skull into the mammalian skull has been correlated with equal changes in the jaw muscles. The temporal fossæ of mammals have opened out, so that the temporal and masseter muscles extend to the surface of the head and thus gain room and free action for diverse adaptation and for expansion. By the development of the sagittal and occipital crests the areas for the origin of the temporal and neck muscles are greatly increased. The masseter becomes enlarged and its origin spreads over the zygomatic arch. This specialization of the superficial part of the temporal mass is typically mammalian, as nothing like it is seen in the reptiles.

The great changes in the mandible, the reduction of the posterior jaw elements, and the development from them of the malleus and incus have been correlated with an equal transformation of the muscles. The insertion of the whole temporal mass has shifted from the coronoid region of the mandible to the dentary, while the external muscle gave rise to both the internal and external muscles of the mammals. The formation of accessory auditory ossicles from the reduced posterior jaw elements gave opportunity to certain of the reptilian muscles to assume new functions. The stapedial muscle, for example, would be homologized with the upper part of the reptilian depressor mandibulæ, as it has been shown in the sections on birds and reptiles that the depressor is in the position to gain the relations of the stapedial muscle of the mammals. It hardly seems possible, from the conditions seen in *Cynognathus*, that the depressor mandibulæ has been carried over from the reptiles as the posterior belly of the mammalian digastric. The most satisfactory conclusion appears to be that a part of the depressor became the stapedial muscle and that the mammalian digastric is a new slip from the second constrictor mass, which was still retained in the reptiles (Ruge). Wilder (1909), in discussing the origin of the stapedius, says: "A portion of the posterior belly, that is, of the second levator, becomes separated from it in the reptiles, and follows the stapes into the middle ear, whence it becomes the stapedius muscle, innervated by a special branch of the facialis." That the stapedius muscle is an ancient muscle appears to be shown by the great separation of the digastric and stapedial nerves, both of which are branches of nerve VII. In other groups of related muscles the nerves, although branching and becoming more than mere nerve twigs, still indicate their relationship by their proximity to each other, as in the case of the subdivisions of the nerve V_3, where the muscles that are closely related have their nerves coming off close together. The stapedial nerve comes off at the upper part of the facialis, while the digastric nerve comes off far below it. This seems to help the hypothesis of the derivation of the stapedial and the wide separation in time from the appearance of the mammalian digastric.

Two muscles, the tensor tympani and tensor palati, appear in the mammals for the first time. They are innervated by the ramus mandibularis of the trigeminus and, according to Gaupp, their homology may be looked for in one of the pterygoid muscles of the reptiles, namely, the "pterygomandibularis" of Bradley, which is the "anterior pterygoid" of the present work. This muscle is in the position that would permit it to be drawn into the middle ear as the tensor tympani, and it is also in a position to give rise to the tensor palati.

The anterior pterygoid of reptiles is attached to the posterior end of the mandible, and during the change from the reptilian to the mammalian condition it could be drawn into the middle ear without much change, as has been shown above. A review of Gaupp's discussion, however, leaves me in doubt whether these muscles have both come from the reptilian pterygoideus anterior or from the reptilian external pterygoid or from both. Their connection with the pterygoideus internus of man would indicate their derivation from the deep portion of the capiti-mandibularis of reptiles. The insertion of the tensor tympani on the handle of the malleus would, on the other hand, indicate relationship with the anterior pterygoid, which in reptiles is inserted on the back part of the mandible. The topographic relations of the tensor palati suggest one of the cranio-pterygoid muscles of reptiles. The tensor veli palatini (tensor palati) is called by Gaupp the homolog of the reptilian "pterygo-mandibularis" (anterior pterygoid). He points out that Kostanecki (1891) in *Didelphys* showed the close relation of tensor tympani and tensor veli palati. Killian (1890) also found that the two muscles were joined in the early stages of apes, man, Cheiroptera, etc. In man the two muscles appear at about the fourth month to become separate from the pterygoideus internus. These facts in the embryology would appear to show that tensor tympani and tensor veli palati are phylogenetically related; that they come from the pterygoid musculature of the reptiles, probably from the anterior pterygoid. Their close relations with the mammalian pterygoideus internus also indicates that they arose from the same region of the temporal mass. This derivation of the tensor tympani from one of the pterygoid muscles seems very plain, for it extends down along the side of the eustachian tube in the mammals and is attached to the handle of the malleus, so that the essential relations are not changed in the transformation of a jaw muscle into an auditory muscle.

The mammalian pterygoid muscles may possibly both be derived from the deep part of the capiti-mandibularis mass of reptiles—that is, from the capiti-mandibularis profundus or pterygoideus externus. The changes in the posterior part of the jaw and in the skull would make it almost impossible to derive these from the anterior pterygoid muscles. The difficulty in deriving the pterygoid muscles of mammals from the anterior pterygoid muscles of reptiles is that the latter are inserted on the posterior part of the mandible, an element which became vestigial, while the former are inserted wholly on the dentary. A study of the jaws and skull of *Cynognathus* and the other cynodonts indicates that it would be difficult to conceive clearly the transference of the insertion point of the anterior pterygoid from the angular and prearticular region to the back part of the dentary. On the other hand, the pterygoideus or capiti-mandibularis profundus, which is inserted in the region of the coronoid, is in such a position that the upgrowing, ascending ramus of the dentary might well invade its insertion area. In this way a muscular connection between the wall of the cranium and the inner side of the dentary might easily be established. As the reptilian palate and lower jaw became completely transformed, it is to be expected that the characteristically reptilian pterygoideus anterior would degenerate along with the elements on which it was inserted. From the innervation of the mammalian pterygoid muscles, which is from different parts of the ramus mandibularis, we may assume perhaps that the pterygoideus internus has long been separated from the temporal mass, and that the pterygoideus externus is the newer muscle that still bears a close relation to the temporal muscle in the mammals; and so far as I have discovered, the pterygoideus externus is present throughout the Mammalia, while the pterygoideus internus, which has been separated from the mass for a longer time, has in some cases (monotremes) disappeared or never developed.

Of the pterygoid externus Lubosch (1913, p. 75) writes:

> Der Pterygoideus externus hat keinfalls seinen Mutterboden in einem der Pterygoideusteile der Urodelen. Die Darstellung von Schulman, dass er einem tiefen Teile des Temporalis nähestehe, lässt sich aus den Verhältnissen der Urodelen verständlich machen, wo der Temporalis geradezu überraschende Differenzierungen in einzelne Portionen zeigt, so dass sich die Ansicht rechtfertigen lässt, das der Pterygoideus externus in bestimmten Teilen der Temporalis-muskulatur der Urodelen enthalten sei.

But unless the amphibian ancestry of the Mammalia were accepted, one would question the homology of the mammalian muscles with anything found in that group.

Of the pterygoideus internus Lubosch (1913, p. 75) writes as follows:

> Der Pterygoideus internus scheint hingegen alter Besitz der Ahnen der Säugethiere der sogar seinen Ursprung bewahrt hat. Hinsichtlich seiner Insertion ist zu errinnern, das schon bei Fischer Ausbreitungen am Dentale bis nach vorn vorkommen (Vetter) Auch er fehlt den Monotremen, so dass hier die gesamte bei Urodelen angelegte tiefe Temporalisschict nicht vorhanden ist, der 3. Ast des Trigeminus also unmittlebar unter der Wangenshleimhaut liegt. Da sich bei Urodelen der Pterygoideus internus aber auf allen Stufen der Emanzipation vom Temporalis zeigt, so lassen sich ausgangszustände auch für die Muskulatur der Monotremen mit Wahrscheinlichkeit feststellen, ohne dass die Frage hier erötert werden kann.

I certainly agree that there is no relation between the muscle of the urodele and the mammal, except in the general scheme of homology of the temporal mass, but the rest is special development in both groups, especially in the pterygoid musculature.

Regarding the digastric, it is now generally agreed that it is not the depressor mandibulæ of the Reptilia, Aves, or Amphibia, but an offshoot of the same parent mass, namely, the second constrictor, that has been retained throughout the vertebrates and has always supplied the depressor for the mandible, except in the monotremes.

General Summary of Homologies and Evolution of the Jaw Muscles in the Vertebrates

The following conclusions may be regarded as well established:

(1) The two chief muscle masses of the jaw, (*a*) the adductor mass innervated by the ramus mandibularis (V_3) and (*b*) the depressor or digastric mass innervated by the facialis (VII), are homologous throughout the Vertebrata.

(2) The adductor of the Pisces is the mother mass from which the muscles of mastication in front of the quadrate are derived throughout the vertebrates, by the separation of slips of this muscle and by their gradual complete separation in nerve supply through the growth of the originally small twigs into separate nerve branches. In the evolution from fishes this adductor has changed profoundly and much of it has been lost, but the original topographic relations of the muscle remain the same throughout the vertebrates, whether all parts are completely separated or not.

(3) Some of the so-called pterygoid muscles have been developed independently in the amphibians, reptiles and mammals. The new developments have been slips needed in the movements of the pterygoid region in streptostylic reptiles, and probably a new series of pterygoid muscles for the mammals.

(4) The amphibians retain rudiments of the levator arcus palatini of the fishes, but these muscles are lost beyond this group.

(5) In the streptostylic reptiles the complex pterygoid musculature was developed to meet the needs of the movable quadrate.

(6) The complicated musculature of the pterygoid in the streptostylic forms which was developed by the subdivision of the capiti-mandibularis mass into numerous slips.

(7) The birds inherit much from the reptiles, and parts of their pterygoid musculature are undoubtedly homologous with those of reptiles, as follows:

Pterygoideus profundus of the birds = capiti-mandibularis profundus in the reptiles.

Pterygoideus anterior of the birds = muscle of the same name in the reptiles.

The capiti-mandibularis superficialis and capiti-mandibularis medius = subdivided capiti-mandibularis of the reptiles.

(8) The tensor tympani and the levator veli palati of mammals appear to represent vestiges of the pterygoideus anterior of reptiles. The tensor tympani took on its modern functions when the back part of the

reptilian jaw gave up its primary function and was taken over into the service of the auditory organs. It retains its old relations with its insertion on the handle of the malleus (in reptiles it was inserted on the retroarticular process of the mandible and on the prearticular). The levator veli palatini seems to represent a part of the same pterygoideus anterior that has changed its relation slightly to serve in the region of the mammalian palate.

(9) The region innervated by the facialis has changed somewhat in the mammals. The depressor mandibulæ of the reptiles has given rise to the m. stapedius of the mammals and the rest of the muscle has disappeared.

(10) The posterior belly of the digastric of mammals appears to be a new development that has come from the remnants of the posterior part of the second constrictor (C_2sd) of reptiles. It is thus believed to be a new muscle which has nothing to do with the "Digastric" of the reptiles, although it has the same functions and the same innervation. To this posterior belly has been added or grafted on at the anterior end one of the long ventral V_3 muscles to make the anterior belly of the mammalian digrastic.

(11) The slip that functions as the m. stapedius in mammals appears to have started in the reptiles and has been retained from the depressor mandibulæ. This muscle, which is connected with the distal end of the stapes in mammals, started in the reptiles and reached its perfected condition when it was drawn into the middle ear in the course of the transformation of the mammal-like reptiles into the true mammals. As mentioned above in the sections on birds and reptiles, the future stapedial muscle was in the right position in the reptiles, where the depressor touches the distal end of the stapes, so it is not difficult to imagine how the depressor gave off a slip that became the future stapedius muscle.

Relations of the Jaw-Muscles to the Temporal Fenestræ of Reptiles

The following from Gregory and Adams (1915) summarizes their observations on the relations of the jaw-muscles to the temporal fenestræ:

(1) That in primitive vertebrates the chief temporal muscle-mass (adductor mandibulæ of sharks) was originally covered by the dermal, temporal skull-roof.

(2) That in modernized Amphibia and Reptilia, as well as in Aves and Mammalia, one or more slips of the primitive adductor mass had secured additional room for expansion by perforating the temporal roof

either at the top or at the sides or in both regions at once; much as in histricomorph rodents, a slip of the masseter has invaded the region of the infraorbital foramen, so that it now extends through a widely open arcade and finds room for expansion on the side of the face.

(3) A comparative study of the skull of *Tyrannosaurus* led to the suspicion that the pre-orbital fenestræ of the dinosaurs, phytosaurs, pterosaurs, etc., were also functionally connected with the muscles of mastication; but it was realized that proof of this view required a wider study of the jaw-muscles of living reptiles. It was afterwards found that Dollo (1884) had suggested that the pre-orbital fenestræ of extinct reptiles were filled by the pterygoid muscles.

(4) The inferred conditions of the jaw musculature of *Cynognathus* are in harmony with the view that in the mammal the back part of the reptilian jaw became transformed into the accessory auditory ossicles.

(5) As a working hypothesis, it is assumed that the transformation of certain elements in the temporal and occipital regions of early Tetrapoda was partly conditioned by the stresses induced upon the skull-roof by the jaw and neck muscles. Comparison with lizards, *Sphenodon,* etc., clearly indicates that the prolongation of the parietal into the postero-external process, joining the true squamosal, was correlated with the squeezing effect of the capiti-mandibularis and depressor mandibulæ muscles. This may also be responsible for the suppression of the supratemporal and survival of the squamosal in early reptiles. The shifting of the post-parietals (dermo-supraoccipitals) and tabularia from the dorsal to the posterior aspect of the occiput was no doubt influenced also by the forward growth of the neck muscles upon the occiput.

TABLE 1.—HOMOLOGY OF THE JAW MUSCLES IN THE FISHES

	MUSCLES INNERVATED BY V_3 (ADDUCTOR MASS)								MUSCLES INNERVATED BY VII		
	Levator maxillæ superioris	Levator arcus palatini	Adductor mandibulæ				Protractor hyomandibularis	Dilator operculi	Adductor hyomandibularis	Adductor operculi	Levator operculi
			1	2	3	4					
ELASMOBRANCHII											
Acanthias	present	Csd_1 Marion	Parts are not differentiated, although fibers are crossed				present in form of C_1sd	C_1sd	not differentiated from C_2sd		
CHONDROSTEI											
Polyodon	absent	absent	1	2			present		present (part of retractor hyomand.)	present (?)	present
Acipenser	"	"	Not divided, degenerate				"		present		"
HOLOSTEI											
Amia	present	present	1	2	3	4	not separate from lev. arcus pal.	present	"	present	"
Lepidosteus		present (?)	1	2	3		present	"	present (?)	"	"
TELEOSTEI											
Esox		present	1	2	3	4	not separate from lev. arc. pal.	"	present	"	"
Anguilla			1	2	3 (?)		present		"	not differentiated	"
Palinurichthys		"	1	2		4	"	"	present (?)	present (?)	"
CROSSOPTERYGII											
Polypterus	"		1	2	3		"		present		"
DIPNOI											
Ceratodus			1	2							"

1, Superficial or masseter slip of adductor mass.
2, Anterior or medius slip.
3, Deep slip.
4, Slip in the mandible (A ω of Vetter).

TABLE II—HOMOLOGY OF THE JAW MUSCLES IN THE AMPHIBIA

	MUSCLES INNERVATED BY V_3 (ADDUCTOR MASS)					MUSCLES INNERVATED BY VII
	Capiti-mandibularis superficialis	Capiti-mandibularis medius	Capiti-mandibularis profundus	Pterygoideus ant.	Pterygoideus post.	Depressor mandibulæ
ANURA						
Rana	is split into two parts	present	present	present	absent	two slips
URODELA						
Cryptobranchus	single	"	"	"	present	" "
Amphiuma	division into two parts is not complete	"	"	"	"	" "
Amblystoma	division not complete	"	"	"	"	" "

TABLE III—HOMOLOGY OF THE JAW MUSCLES IN THE REPTILES AND BIRDS

	MUSCLES INNERVATED BY V_3 (ADDUCTOR MASS)						MUSCLES INNERVATED BY VII
	Capiti-mandibularis (mass)			Pterygoideus posterior	Pterygoideus anterior	Pterygo-parietalis and Pterygo-sphenoidalis	Depressor mandibulæ
	Superficialis	Medius	Profundus				
Chelydra	capiti-mand. not divided				present		present
Sphenodon	present	present	present		"		"
Alligator	"	not divided	not divided	present	"		"
Iguana	"	present	present		"		"
Varanus	"	"	"	"	"	present	"
Gallus	"	"	not separate	"	"		"

TABLE IV—HOMOLOGY OF THE JAW MUSCLES IN THE MAMMALS

	MUSCLES INNERVATED BY V_3 (ADDUCTOR MASS)							MUSCLES INNERVATED BY VII		
									Digastric—posterior belly	
	Masseter	Temporal	Pterygoid int.	Pterygoid ext.	Tensor v. pal.	Tensor tympani	Detrahens mandibulæ	Stapedius	Ant. belly V_3	Posterior belly VII
Ornithorhynchus	present	present	not separate from temporal	present	present	present	present	present	depressor mand. ant. (?)	absent
Echidna	“	“	“	“	“	“	“	“	“	“
Didelphys	“	“	present	“	“	“	absent	“	present	present
Solenodon	“	“	“	“	“	“	“	“	“	“
Mus	“	“	“	“	“	“	“	“	“	“
Sciurus	“	“	“	“	“	“	“	“	“	“
Felis	“	“	“	“	“	“	“	“	“	“
Homo	“	“	“	“	“	“	“	“	“	“

TABLE V—HOMOLOGY OF THE JAW MUSCLES IN THE VERTEBRATE CLASSES

	MUSCLES INNERVATED BY V_3 (TEMPORAL OR ADDUCTOR MASS)							MUSCLES INNERVATED BY VII	
	Superficial Masseter	Medius Temporal	Profundus deep Pterygoideus internus	Pterygoideus internus	Levator veli pal.	Tensor tympani	Anterior belly of the Digastric	Posterior belly of the Digastric	Stapedius
MAMMALIA	present	present	present	present in mammals except in the Monotremes	present	present	present	new slip of C_2md. Not the homolog of the depressor of reptiles or Amphibia	present
REPTILIA and AVES	capiti-mandibularis mass present, but usually not divided		probably represented in the profundus of reptiles	capiti-mandibularis profundus	from the pterygoideus anterior		the long ventral muscles of throat	posterior part of C_2md	depressor mandibulæ
AMPHIBIA	superficialis medius not separate in the Urodeles			deep or profundus portion of the capiti-mand.	anterior portion of the temporal mass or pterygoideus anterior		"	"	"
PISCES	not differentiated in the Pisces							C_2md is not differentiated in the Pisces	

BIBLIOGRAPHY

D'Alton, E.
1834. Beschreibung des Muskelsystems eines Python bivitatus. Arch. f. Anat. u. Physiol., pp. 346, 432, 528.

Allen, H.
1880. On the temporal and masseter muscles of mammals. Proc. Acad. Nat. Sci. Phila., XXXII, pp. 385–396.

Allis, E. Phelps.
1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. Jour. Morph. (3), XII, pp. 487–808.

Bardeleben, Karl von.
1903. Muskelsystem und Mechanik. Ergebnisse d. Anat. u. Ent. Merkel u. Bonnet., XIII, pp. 114–164.

Bijvoet, W. F.
1908. Zur vergleichenden Morphologie des Musculus digastricus mandibulæ bei den Säugethieren. Zeitschr. f. Morph. u. Anthr., XI, pp. 249–316.

Bradley, Charnock O.
1903. The muscles of mastication and movement of the skull in Lacertilia. Zoöl. Jahrb. Abth. f. Anat. u. Ont., XVIII, Heft 4, pp. 475–486.

Broom, R.
1910. A comparison of the Permian reptiles of North America with those of South Africa. Bull. Amer. Mus. Nat. Hist., XXVIII, pp. 197–234.
1911. On the structure of the skull in cynodont reptiles. Proc. Zoöl. Soc. London, pp. 893–923.
1913. Notice of some new south african fossil amphibians and reptiles. Ann. So. Afr. Mus., VII, pp. 270–278.
1913*a*. On the Gorgonopsia, a suborder of the mammal-like reptiles. Proc. Zoöl. Soc. London, pp. 225–230.
1913*b*. On the South African pseudosuchian *Euparkeria* and allied genera. Proc. Zoöl. Soc. London, pp. 619–633.

Chaîne, J.
1914. Le Digastrique. Jour. de l'Anat. et Physiol., L, pp. 248–319, 393–417.

Cords, E.
1904. Beiträge zur Lehre vom Kopfnervensystem der Vogel. Anat. Hefte, XXVI, pp. 49–100.
1910. Zur Morphologie des Gaumensegels. Anat. Anz., XXXVII, pp. 305–318.

Cunningham, D. J.
1891. The value of nerve-supply in the determination of muscular homologies and anomalies. Jour. Anat. and Physiol., XXV, pp. 31–40.
1902. Text-book of anatomy. New York.

Danforth, C. H.
1913. The myology of *Polyodon*. Jour. Morph., XXIV, pp. 107–146.

DEAN, BASHFORD.

1909. Studies on fossil fishes (sharks, chimæroids and arthrodires). Mem. Amer. Mus. Nat. Hist., IX, Part 5, pp. 211–287.

DOBSON, G. E.

1882. On the digastric muscle, its modifications and functions. Trans. Linn. Soc. London, (2), II, pp. 259–264.

DOLLO, L.

1884. Cinquième note sur les Dinosauriens de Bernissart. Bull. Mus. Roy. de Belgique, III, pp. 129–146.

DRÜNER, L.

1903. Über die Muskulatur des Visceralskelettes der Urodelen. Anat. Anz., XXIII, pp. 545–571.

1904. Studien zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskeln der Urodelen. Zoöl. Jahrb. Abth. f. Anat. u. Ont., XIX, Heft 3, pp. 435–622.

EASTMAN, C. R.

1906. Structure and relations of *Mylostoma*. Bull. Comp. Zoöl. Harvard College. No. 1, pp. 1–29.

1906*a*. Dipnoan affinities of arthhrodires. Amer. Jour. Sci., XXI, pp. 131–143.

ECKER, A., and WIEDERSHEIM, R.

1896. Anatomie des Frosches. 3 Auflage. Braunschweig.

EDGEWORTH, F. H.

1903. The development of the head-muscles in *Scyllium canicula*. Jour. Anat. and Physiol., XXXVII, pp. 73–88.

1907. The development of the head-muscles of *Gallus domesticus*, and the morphology of the head-muscles in the Sauropsida. Quart. Jour. Mic. Sci., LI, pp. 511–556.

1911. On the morphology of the cranial muscles in some vertebrates. Quart. Jour. Mic. Sci., LVI, pp. 167–316.

FICK, R.

1904. Handbuch der Anatomie und Mechanik der Gelenke Thiel I-III. 1904–1911. Jena.

FÜRBRINGER, MAX.

1897. Über die spino-occipital Nerven der Selachier und Holocephalen und ihre vergleichende Morphologie. Festschr. f. Carl Gegenbaur, pp. 351–788.

FUTAMURA, R.

1906. Über die Entwickelung der Facialismuskulatur des Menchen. Anat. Hefte, XXX, Heft 2, pp. 435–514.

1907. Beiträge zur vergleichenden Entwickelungsgeschicte der Facialismuskulatur. Anat. Heft, XXXII, Heft 3, pp. 479–575.

GAUPP, E.

1905. Neue Deutung auf dem Gebeite der Lehre von Säugethierschädel. Anat. Anz., XXVII, pp. 273–310.

1905*a*. Die Nicht-homologie des Unterkiefers in der Wirbeltierreihe. Ver handl. der Anat. Gesell., Versammlung 19, pp. 125–140.

1911. Beiträge zur Kenntnis des Unterkiefers der Wirbeltiere. I–III. Anat. Anz., XXXIX, pp. 97–135, 433–473, 609, 666.

1913. Die Reichertsche Theorie. (Hammer-, Amboss- und Kieferfrage.) Archiv fur Anat. u. Phys. Jahrgang 1912. Anat. Abth. (Sup. Band).

GEGENBAUR, C.

1898. Vergleichende Anatomie der Wirbelthiere. I. Leipzig.

GOODRICH, E. S.

1909. A treatise on zoölogy. Lankester, E. Ray (editor), Pt. IX, pp. 7–9. London.

GREGORY, W. K.

1910. The orders of mammals. Bull. Amer. Mus. Nat. Hist., XXVII, pp. 1–524.

1912. Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. Ann. N. Y. Acad. Sci., XXII, pp. 267–294.

1915. Present status of the problem of the origin of the Tetrapoda. With special reference to the skull and paired limbs. Ann. N. Y. Acad. Sci., XXVI, pp. 317–383, pl. iv.

1917. The coal measures Amphibia of North America. Amer. Nat., LI, pp. 311–320.

GREGORY, W. K., and ADAMS, L. A.

1915. The temporal fossæ of vertebrates in relation to the jaw muscles. Science, N. S., XLI, No. 1064, pp. 763–765.

GÜNTHER, A.

1871. Description of *Ceratodus*, a genus of ganoid fishes, recently discovered in rivers of Queensland, Australia. Phil. Trans. London, CLXI, Part 2, pp. 511–571.

HAUGHTON, S.

1865. On the muscular anatomy of the leg of the crocodile. Ann. Mag. Nat. Hist., (3), XVI, pp. 326–331.

HIS, WILHELM.

1885. Anatomie menschlicher Embryonen. III, Zur Geschichte der Organe. Leipzig.

HUMPHREY, G. M.

1872. The muscles and nerves of *Cryptobranchus japonicus*. Jour. Anat. and Physiol., VI, pp. 1–61.

HUNTINGTON, GEO. S.

1903. Present problems of myological research and the significance and classification of muscular variations. Amer. Jour. Anat., II, pp. 157–175.

HUSSAKOF, L.

1906. Studies on the Arthrodira. Mem. Amer. Mus. Nat. Hist., IX, Pt. III, pp. 106–154.

HUXLEY, T. H.

1876. Contributions to morphology. Ichthyopsida. No. 1. On *Ceratodus forsteri*. Proc. Zoöl. Soc. London, pp. 24–59.

KEIBEL, F., and MALL, F. P.

1910. Manual of human embryology. I, pp. 505–509. Phila.

KILLIAN, G.

1890. Zur vergleichenden Anatomie und vergleichenden Entwicklungs geschicte der Ohrmuskeln. Anat. Anz., V. pp. 226–229.

1890. Die Ohrmuskeln des Crocodiles, Homologie des M. stapedius. Jen. Zeitschr. f. Naturw., XXIV, pp. 632–656.

KOSTANECKI, K. VON.

1891. Zur Morphologie der Tubengaumenmuskulatur. Arch. f. Anat. u. Physiol., Anat. Abth., pp. 145–181.

LECHE, W.

1889. Bronn's Klassen und Ordnungen des Thierreichs. VI, Abth. 5, Bd. 1, pp. 692, 708, 1874–1900.

LUBOSCH, W.

1908. Das Kiefergelenk der Edentaten und Marsupialier. Semon's Zoöl. Forschungsreisen in Australien, IV, Lief 4, pp. 519-556.

1913. Die Kaumuskulatur der Amphibien vergleichen mit der Sauropsiden und Säugethieren. Verhandl. d. Anat. Gesell., Versammlung 27, pp. 67–76.

1914. Zwei vorläufige Mitteilungen über die Anatomie der Kaumuskeln der Krokodile. Jen. Zeitschr. f. Naturw., LI, pp. 697–707.

MARION, G. E.

1905. Mandibular and pharyngeal muscles of *Acanthias* and *Raia.*. Tufts College Studies, II, No. 1, pp. 1–34.

MCMURRICH, J. P.

1885. The cranial muscles of *Amia calva* (L.), with a consideration of the relations of the post-occipital and hypoglossal nerves in the various vertebrate groups. Studies from the Biol. Lab. Johns Hopkins Univ., III, pp. 121–153.

MIVART, ST. G.

1867. Notes on the myology of *Iguana tuberculata.* Proc. Zoöl. Soc. London, XXXV, pp. 766–797.

1870. On the myology of *Chamæleon parsonii.* Proc. Zoöl. Soc. London, pp. 850–890.

OGUSHI, K.

1913. Anatomische Studien an der japanischen dreikralligen Lippenschildkrote (*Trionyx japonicus*). Morph. Jahrb., XLVI, pp. 299–562.

OSAWA, G.

1898. Beitrage zur Anatomie der *Hatteria punctata.* Arch. f. Mikros. Anat., LI, pp. 481–675.

OWEN, R.

1866. The anatomy of the vertebrates. II, pp. 93–94.

PALMER, R. W.

1913. Note on the lower jaw and ear ossicles of a fœtal *Perameles.* Anat. Anz., XLIII, pp. 510–515.

PARSONS, F. G.
1894. On the myology of the sciuromorphine and histricomorphine rodents. Proc. Zoöl. Soc. London, pp. 251–296.
1896. *Idem.*, pp. 159–192.
1898. The muscles of mammals with special relation to human myology. Jour. Anat. and Physiol., XXXII, pp. 428–450, 721–752.
1899. The joints of mammals compared with those of man. Jour. Anat. and Physiol., XXXIV, pp. 41–68.

PATTEN, W.
1904. New facts concerning *Bothriolepis*. Biol. Bull., VII, pp. 113–124.
1912. The evolution of the vertebrates and their kin. Philadelphia.

POLLARD, H. B.
1892. On the anatomy and phylogenetic position of *Polypterus*. Zoöl. Jahrb. Abth. f. Anat. u. Ont., V, pp. 387–428.

RABL, K.
1887. Ueber das Gebiet des Nervus facialis. Anat. Anz., II, pp. 219–227.

REIGHARD, J., and JENNINGS, H. S.
1902. Anatomy of the cat. New York.

RIEGNER [HANS].
1906. Beiträge zur Physiologie der Kieferbewegungen. Theil 2.—Die Kiefermuskeln und ihre Wirkungsweise beim Affen (*Macacus rhesus*). Arch. f. Anat. u. Physiol., Anat. Abdth., pp. 109–116.

RUGE, GEO.
1895. Die Hautmusculatur der Monotremen und ihre Beziehungen zu dem Marsupial- und Mammarapparate. Semon's Zoöl. Forschungsreisen in Australien, II, Lief. 2.
1897. Ueber das peripherische Gebiet des Nervus facialis bei Wirbelthieren. Festschr. f. Carl Gegenbaur, pp. 195–348.

ROUVIÈRE, H.
1906. Étude sur le Dévelopment phylogênique de certain Muscles Sus hyoidiens. Jour. de l'Anat. et Physiol., XLII, pp. 487–540.

SANDERS, A.
1870. Notes on the myology of *Platydactylus japonicus*. Proc. Zoöl. Soc. London, pp. 413–426.

SCHULMAN, H.
1906. Vergleichende Untersuchungen uber die Trigeminus-Muskulatur der Monotremen. Semon's Zoöl. Forschungsreisen in Australien, III. Theil 2, Lief. 3, pp. 297–400.

STANNIUS, H.
1846. Lehrbuch der Vergleichende Anatomie. Zweiter Theil.—Wirbelthiere, pp. 161–180.

STANNIUS, H., and SIEBOLD, C. T. E. VON.
1854. Lehrbuch der Vergleichende Anatomie. Zweiter Theil.—Wirbelthiere, pp. 1–128.

STRASSER, H.
1908. Lehrbuch der Muskel– und Gelenkmechanik, pp. 475–502. Berlin.

TEUTLEBEN, E. VON.
1874. Ueber Kaumuskeln und Kaumechanismus bei den Wirbelthieren. Arch. f. Naturw., pp. 78–111.

TIESING, B.
1895. Ein Beitrag zur Kenntnis der Augen-, Kiefer- und Kiemen muskulatur der Haie und Rochen. Theil 2. Jen. Zeitschr. f. Naturw., N. F., XXX, pp. 75–126.

TOLDT, C.
1905. Der Winkelfortsatz des Unterkiefers beim Menchen und bei den Säugetieren und die Beziehungen der Kaumuskeln zu demselben Theil 2. Sitz. d. Kais. Akad. d. Wiss. Wien. Math.-Naturw. Kl., CXIV, Abth. 3, pp. 315–476.
1908. Der Vordere Bauch des M. digastricus mandibulæ und seine Varietaten beim Menchen. Theil II. Sitz. d. Kais. Akad. d. Wiss. Wien. Math.-Naturw. Kl., CXVII, Abth. 3, pp. 229–321.

TULLBERG, T.
1900. über das System der Nagethiere. Nova Acta Reg. Soc. Scient. Upsaliensis. (3), XVIII, Fasc. 2, pp. 329–514.

VETTER, B.
1874. Untersuchungen zur vergleichenden Anatomie der Kiemen- und Kiefermuskulatur der Fische. Theil I. Jen. Zeitschr. f. Naturw., VIII, pp. 405–458.
1878. Theil II. Ebenda, XII, pp. 431–550.

VERSLUYS, JR., J.
1904. über Kaumuskeln bei Lacertilia. Anat. Anz., XXIV, pp. 641–644.

WATKINSON, GRACE B.
1906. The cranial nerves of *Varanus bivitatus.* Morph. Jahrb., XXXV, pp. 450–472.

WATSON, D. M. S.
1911. The skull of *Diademodon,* with notes on those of other cynodonts. Ann. Mag. Nat. Hist. (8), VIII, pp. 293–330.
1912. On some reptilian lower jaws. Ann. Mag. Nat. Hist. (8), X, pp. 573–587.
1913. On some features of the structure of the therocephalian skull. Ann. Mag. Nat. Hist. (8), XI, pp. 65–79.
1914. The Deinocephalia, an order of mammal-like reptiles. Proc. Zoöl. Soc. London, pp. 749–786.
1914*a*. *Eunotosaurus africanus* Seeley, and the ancestry of the Chelonia. Proc. Zoöl. Soc. London, pp. 1011–1020.

WILDER, H. H.
1909. History of the human body. New York. Pp. 245–248.

ABBREVIATIONS

Adductor branchialis	Ad. br.
Adductor hyomandibularis	Ad. hy.
Adductor mandibulæ	Adm.
Adductor operculi	A. o.
Capiti-mandibularis	C. m.
Capiti-mandibularis superficialis	C. m. s.
Capiti-mandibularis medius	C. m. m.
Capiti-mandibularis profundus	C. m. p.
Constrictor superficialis dorsalis 1	C. $_1$sd.
Constrictor superficialis dorsalis 2	C. $_2$sd.
Coraco-hyoideus	Co. hy.
Coraco-mandibularis	Co. m.
Depressor capitis	D. c.
Depressor palpebræ inferior	D. p. i.
Depressor mandibulæ	D. m.
Depressor mandibulæ anterior	D. m. a.
Detrahens mandibulæ	Det. m.
Digastricus	Dig.
Digastricus mandibulæ anterior	Dig. a.
Digastricus mandibulæ posterior	Dig. p.
Dilator operculi	D. o.
Ento-tympanicus	Ent. t.
Hyomandibular	Hyo. m.
Levator arcus palatini	L. a. p.
Levator capitis	L. c.
Levator labii superioris	L. l. s.
Levator maxillæ superioris	L. m. s.
Levator operculi	L. o.
Masseter	Mas.
Mylohyoid	My. hy.
Parieto-mandibularis	Pa. m.
Protractor-hyomandibularis	P. hy.
Pterygoideus anterior	Pt. ant.
Pterygoideus externus	Pt. ext.
Pterygoideus internus	Pt. int.
Pterygoideus posterior	Pt. post.
Pterygoideus parietalis	Pt. pa.
Pterygo-sphenoidalis	Pt. sph.
Pterygo-spinosus	Pt. s.
Pterygo-tympanic	Pt. ty.
Retractor hyomandibularis	R. hy.
Spiracular muscle	Spir.
Styloideus	St.
Temporalis	Tem.
Zygomatico-mandibularis	Zy. m.

EXPLANATION OF PLATE I

Jaw muscles of *Scyllium* and *Acanthias*, representing the Elasmobranchii, and of *Acipenser* and *Polyodon*, representing the Chondrostei

FIG. 1.—*Scyllium* (*Mustelus*). (Muscles mainly after Marion.)

The adductor mandibulæ (*Adm.*) is seen wrapped around the posterior ends of the palatoquadrate and Meckelian cartilages. It is not differentiated into separate parts, although the fibers are crossed in certain regions. The levator maxillæ superioris (*L. m. s.*) and the first dorsal superficial constrictor (*C.* $_1$*sd.*) lie in front of the spiracle and together with the adductor are innervated by the third branch of the fifth cranial nerve (V_3). All the pre-spiracular (pretrematic) jaw muscles of higher vertebrates are derived from this group.

FIG. 2.—*Acanthias*. (Muscles mainly after Marion.)

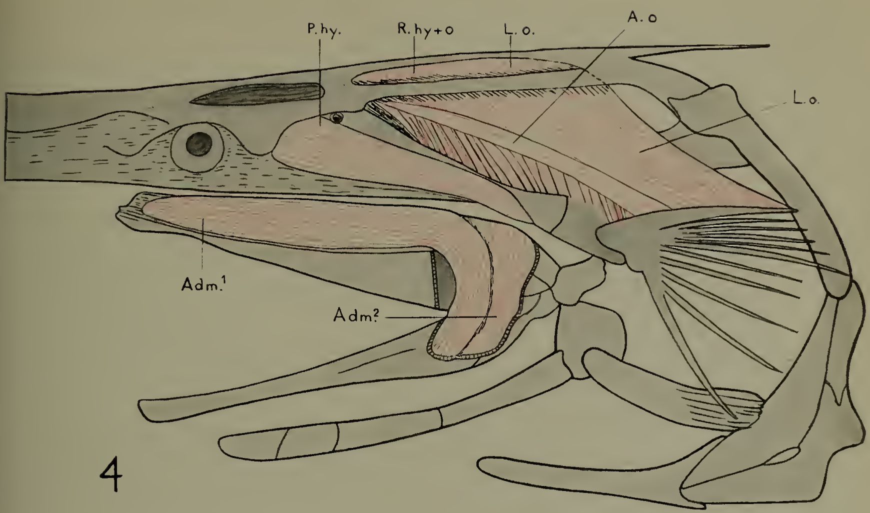
The muscles of the visceral arches may be divided into two sets according as they are derived from muscles which originally ran in a transverse (circular) or in a longitudinal direction (Kingsley). The jaw muscles belong to the circular group, which comprise dorsal and ventral series of constrictors and the adductors of the visceral arches. The levator labii superioris (*L. l. s.*), levator maxillæ superioris (*L. m. s.*) belong to the series of superficial dorsal constrictors (C. $_1$sd., C. $_2$sd., etc.). The adductor mandibulæ (*Adm.*) belongs to the adductor series.

FIG. 3.—*Acipenser*. (Muscles partly after Vetter.)

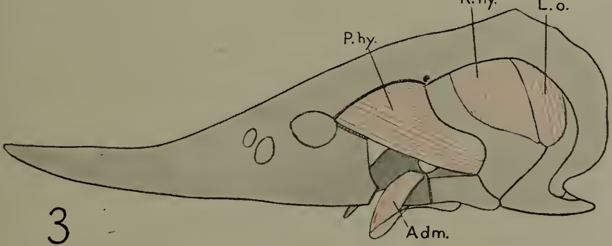
The adductor mandibulæ is small. The levator maxillæ superioris is either absent or not differentiated from the large protractor hyomandibularis (*P. hy.*). This represents C. $_1$sd. of the elasmobranchs. It lies in front of both the spiracle and the hyomandibular and is innervated by V_3. The retractor hyomandibularis (*R. hy.*) and the levator operculi (*L. o.*) represent C. $_2$sd. and are innervated by VII.

FIG. 4.—*Polyodon*. (Muscles partly after Danforth.)

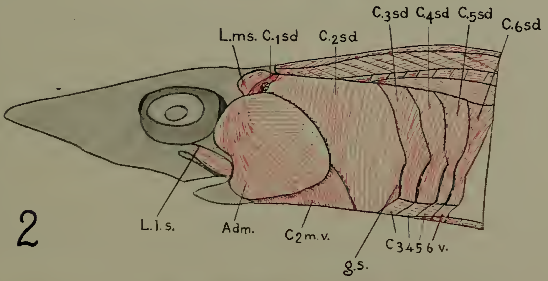
The adductor mandibulæ is divided into two muscles (Adm^1, Adm^2). The post-spiracular constrictor (innervated by VII) is more or less subdivided into retractor hyomandibularis plus operculi (*R. hy.* + *o.*), levator operculi (*L. o.*) and adductor operculi (*A. o.*).


P.hy.
R.hy+o
L.o.
A.o
L.o.
Adm.1
Adm.2

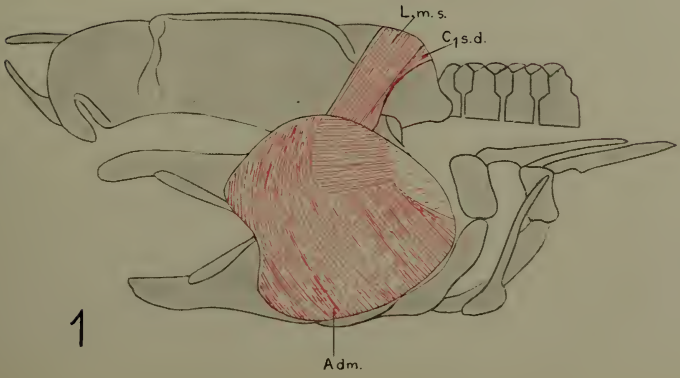
4


R.hy.
L.o.
P.hy.
Adm.

3


C.3sd
C.4sd
C.5sd
C.6sd
L.ms.
C.1sd
C.2sd
L.l.s.
Adm.
C2m.v.
C3456v.
g.s.

2


L.m.s.
C1s.d.
Adm.

1

Explanation of Plate II

Jaw muscles of *Amia* and *Lepidosteus*, representing the Ganoidei Holostei, and of *Anguilla*, representing the Teleostei Apodes

Figs. 1 and 2.—*Amia.* (Muscles mainly after Allis.)

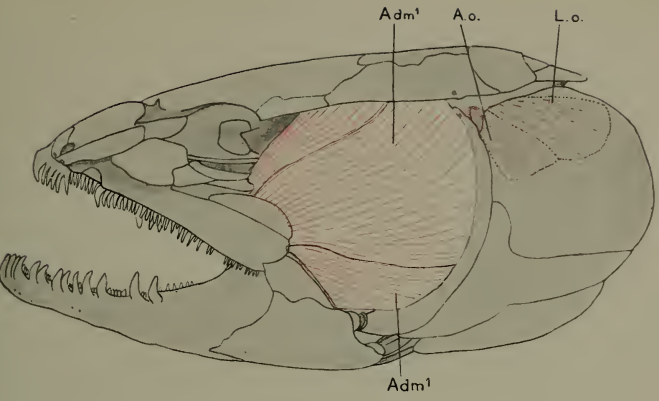
In the Holostei and Teleostei the adductor mandibulæ and levator maxillæ superioris of selachians are subdivided into numerous muscles all lying in front of the hyomandibular and innervated by V_3; while the $C._2$sd. group behind the hyomandibular, which is innervated by VII, includes three muscles (*Ad. hy., A. o., L. o.*). The levator arcus palatini (*L. a. p.*) and the dilator operculi (*D. o.*) belong to the $C._1$sd. series and appear to represent the protractor hyomandibularis of the sturgeon (Pl. I, Fig. 3). The levator maxillæ superioris (*L. m. s.*) includes several slips of which only one is shown. The first division of the adductor mandibulæ (Adm_1) covers the cheek behind the eye and runs from the preoperculum to the mandible. The fourth division (Adm_4) is lodged in the Meckelian fossa of the mandible. The dilator operculi (*D. o.*) passes through a groove or depression in the hyomandibular and is inserted by tendon into the operculum.

Fig. 3.—*Lepidosteus.*

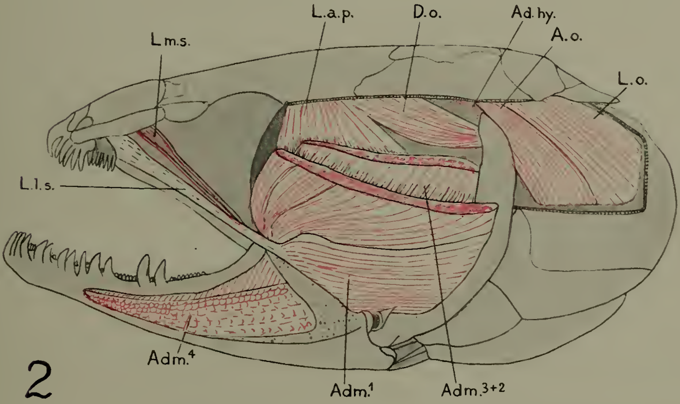
In correlation with the anteroposterior elongation of the head the jaw muscles are nearly horizontal instead of vertical. This oblique insertion gives great speed but low power in the closing of the jaw. The protractor hyomandibularis (*P. hy.*), as in *Acipenser* (Plate I, Fig. 3), runs from behind the eye to the anterior border of the hyomandibular. The second slip of the adductor is now above the eye instead of behind it.

Figs. 4 and 5.—*Anguilla* sp.

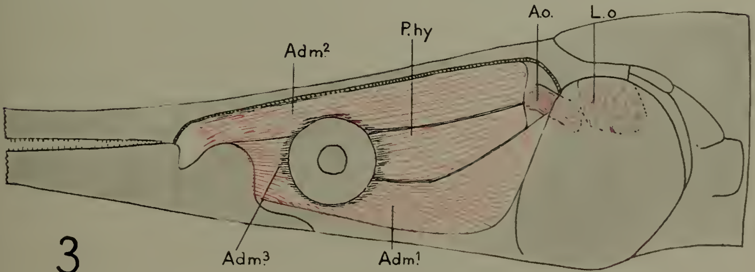
In this peculiar teleost the adductor mandibulæ is greatly enlarged and has spread out upon the top of the skull after the fashion of the capiti-mandibularis of certain Amphibia. The large dilator (*D. o.*) and levator operculi (*L. o.*) muscles assist in the strong respiratory movements of the branchial region.


Adm^1
A.o.
L.o.
Adm^1

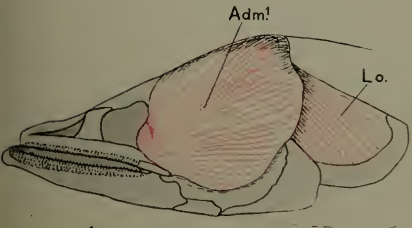
1


L.m.s.
L.a.p.
D.o.
Ad.hy.
A.o.
L.o.
L.l.s.
Adm.^{4}
Adm.^{1}
Adm.$^{3+2}$

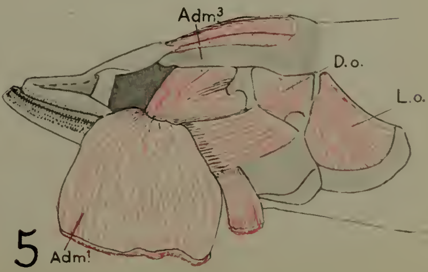
2


A.o.
L.o
P.hy
Adm^2
Adm^3
Adm^1

3


Adm^1
L.o.

4


Adm^3
D.o.
L.o.
Adm^1

5

EXPLANATION OF PLATE III.

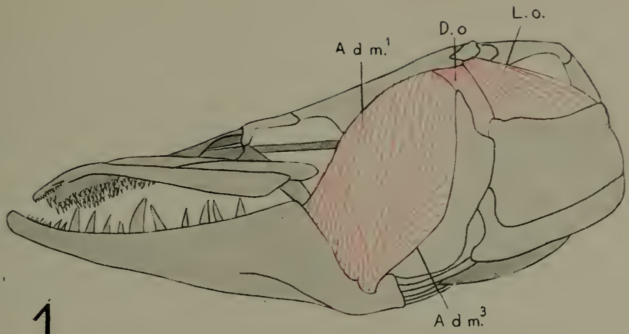
Jaw muscles of *Esox*, representing the Teleostei Haplomi, and of *Palinurichthys*, representing the Teleostei Acanthopterygii

FIGS. 1 and 2.—*Esox*. (Muscles mainly after Vetter.)

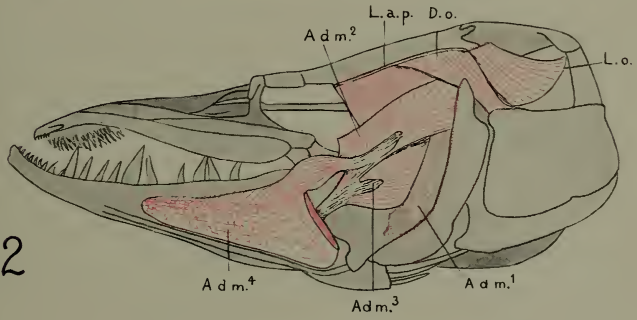
The superficial muscles are shown in Fig. 1, and the deep muscles in Fig. 2. In this rather primitive teleost the divisions of the adductor are substantially the same as in *Amia* (Pl. II, Figs. 1, 2). The protractor hyomandibularis is either absent or not separate from the levator arcus palatini (*L. a. p.*). The fourth branch of the adductor fills the Meckelian fossa of the mandible. The dilator operculi (*D. o.*) passes above the hyomandibular and the preoperculum in the normal manner.

FIGS. 3–5.—*Palinurichthys*. (Identification of muscles after Vetter in *Perca*.)

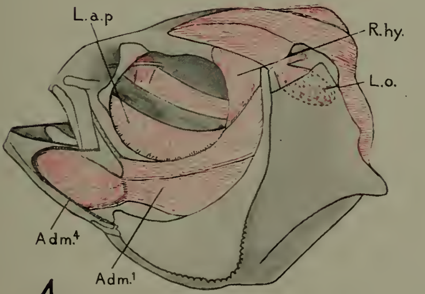
These are the jaw muscles of a highly evolved teleost. The protractor hyomandibularis (*P. hy.*) is distinct from the well developed levator arcus palatini (*L. a. p.*). The retractor hyomandibularis (*R. hy.*), the levator operculi (*L. o.*) and the so-called trapezius of the pectoral girdle are extended forward above the orbit, on either side of the sagittal crest.


L.o.
D.o
Adm.^{1}
Adm.^{3}

1

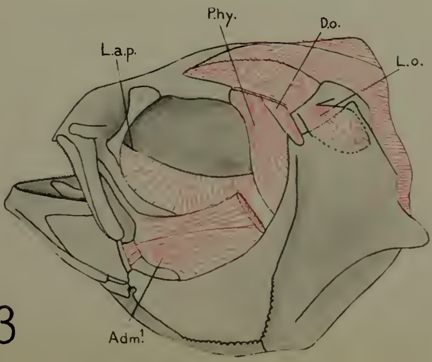

L.a.p.
D.o.
Adm.^{2}
L.o.
Adm.^{4}
Adm.^{3}
Adm.^{1}

2


L.a.p
R.hy.
L.o.
Adm.^{4}
Adm.^{1}

4

5


P.hy.
D.o.
L.a.p.
L.o.
Adm.^{1}

3

EXPLANATION OF PLATE IV

Jaw muscles of *Polypterus*, representing the Crossopterygii, and of *Neoceratodus*, representing the Dipnoi

FIGS. 1 and 2.—*Polypterus*. (Muscles mainly after Pollard.)

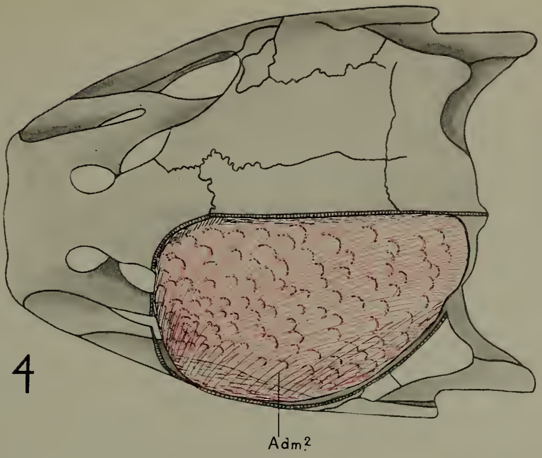
The deep muscles are shown in Fig. 1, after the removal of the preoperculum, and the superficial muscles in Fig. 2.

The superficial layer of the adductor mandibulæ (*Adm.*^{1}) extends from the enlarged hyomandibular to the ascending ramus of the mandible. The deep branches (*Adm.*^{2}, *Adm.*^{3}) run nearly at right angles to the outer branch and arise from the side of the skull. This arrangement foreshadows the differentiation of the jaw muscles in amphibians into masseter, temporal and pterygoid branches (Pollard). The levator maxillæ superioris (*L. m. s.*) is closely associated with the protractor hyomandibularis (*P. hy.*) as in elasmobranchs. A small slip of the latter muscle runs dorsad to the spiracular ossicle. The dilator operculi (*D. o.*) seems to be absent. In Fig. 1 the hyomandibular is seen with the area of origin of the adductor mandibulæ on its anterior border. The levator operculi (*L. o.*) is closely associated with the adductor hyomandibularis (*Ad. hy.*).

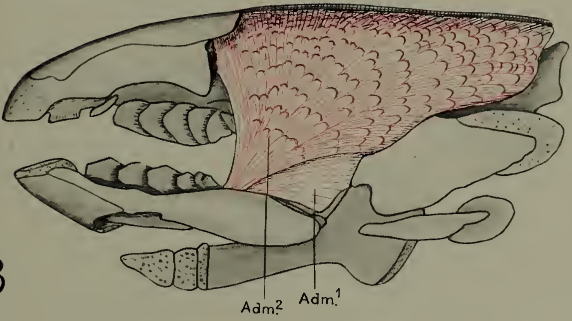
FIG. 3.—*Neoceratodus*. Side view of jaw muscles.

The superficial layer of the adductor is fastened posteriorly to the opercular region. The middle layer (*Adm.*^{2}) runs over the top of the massive chondrocranium and separates the dermal skull roof from it. This part of the adductor is divided into numerous small fascicles interspersed with connective tissue.

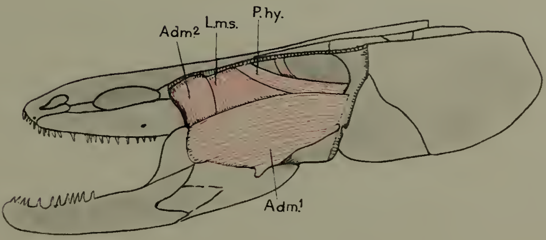
FIG. 4.—*Neoceratodus*. Viewed from above.


Adm.²

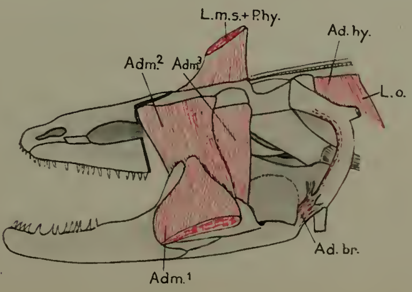
4


Adm.²
Adm.¹

3


Adm.²
L.m.s.
P.hy.
Adm.¹

2


L.m.s.+P.hy.
Ad.hy.
Adm.²
Adm.³
L.o.
Ad.br.
Adm.¹

1

EXPLANATION OF PLATE V

Jaw muscles of *Rana*, representing the Anura, and of *Cryptobranchus japonicus*, *Amphiuma* and *Amblystoma*, representing the Urodela

In all modern Amphibia, owing to the loss of most of the derm bones covering the occiput and temporal region, the jaw muscles lie immediately beneath the skin and extend above the parietals. The muscles are divided into a pretrematic group, in front of the squamosal and quadrate, innervated by V_3, and a posttrematic group behind the squamosal and quadrate, innervated by VII.

FIGS. 1 and 2.—*Rana.* (Muscles after Ecker and Wiedersheim.)

The superficial muscles after the removal of the maxilla are shown in Fig. 1, and the deep muscles in Fig. 2.

The adductor mass of fishes is now represented by the capiti-mandibularis (*C. m.*), which is divided into anterior and posterior slips running respectively from the squamosal and quadrate to the mandible. The deep part runs from the under side of the squamosal to the mandible. The pterygoideus anterior (*Pt. ant.*) probably represents the deepest part of the adductor mass. The depressor mandibulæ (*D. m.*) lies entirely behind the otic region and is innervated by the 7th nerve; it may have been derived from the retractor hyomandibularis of fish (Pollard).

FIG. 3.—*Cryptobranchus japonicus.* (Muscles mainly after Humphrey.)

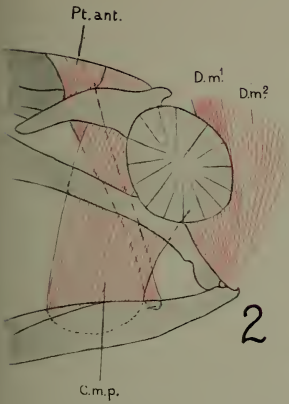
The deep anterior part of the adductor mass of fish is here represented by the much-enlarged pterygoideus anterior, the outer part by the capiti-mandibularis superficialis (*C. m. s.*), while the levator maxillæ superioris may be represented by the capiti-mandibularis profundus (*C. m. p.*) and pterygoideus posterior. The depressor mandibulæ is divided into two parts, of which the anterior is large.

FIG. 4.—The same seen from above.

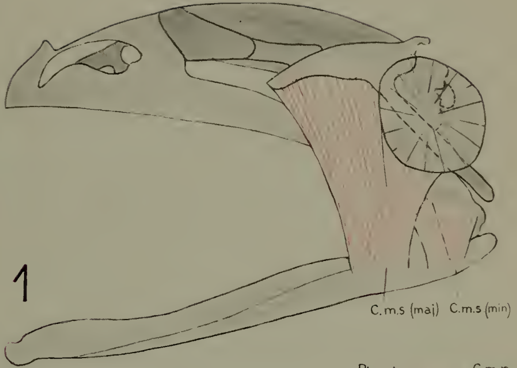
FIG. 5.—*Amphiuma.* (Muscles mainly after Drüner.)

FIGS. 6 and 7.—*Amblystoma.* (Muscles mainly after Drüner.)

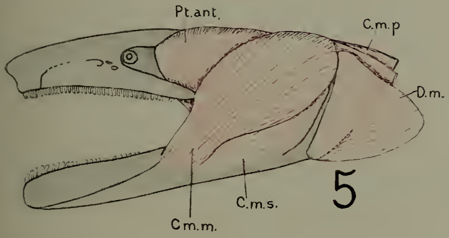
The superficial and middle layers of the jaw muscles are seen in Fig. 6, and the deep muscles after the reflection of the capiti-mandibularis in Fig. 7.


Pt.ant.
D.m.¹
D.m.²
C.m.p.

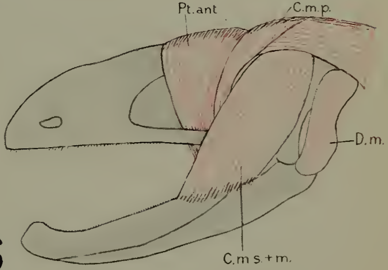
2


C.m.s (maj)
C.m.s (min)

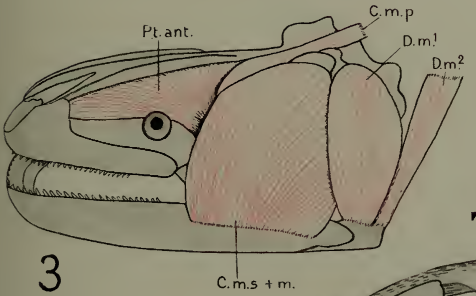
1


Pt.ant.
C.m.p
D.m.
C.m.m.
C.m.s.

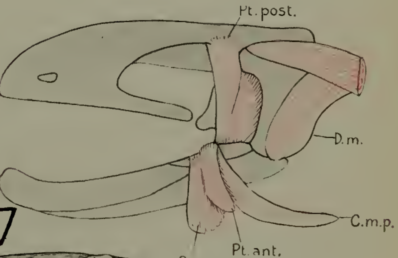
5


Pt.ant
C.m.p.
D.m.
C.m.s.+m.

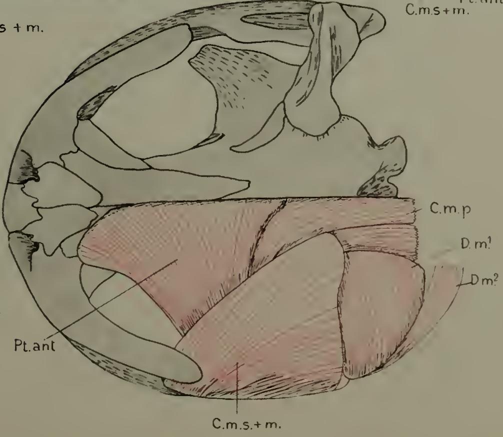
6


C.m.p
Pt.ant.
D.m.¹
D.m.²
C.m.s + m.

3


Pt.post.
D.m.
C.m.p.
Pt.ant.
C.m.s+m.

7


C.m.p
D.m.¹
D.m.²
Pt.ant
C.m.s.+m.

4

EXPLANATION OF PLATE VI

Jaw muscles of monimostylic reptiles: *Chelydra*, *Sphenodon*, and *Alligator*. The pretrematic muscles (innervated by V_3) are seen in front of the auditory region, the posttrematic muscles (innervated by VII) are seen behind it

FIGS. 1 and 2.—*Chelydra.*

The deep muscles are shown in Fig. 1, and the superficial in Fig. 2.

The capiti-mandibularis (*C. m.*) has penetrated the dermal skull roof and after passing through the posttemporal opening is attached to the long sagittal crest. The pterygoideus anterior runs obliquely across the capiti-mandibularis (*C. m. s.; C. m. m.*). These two muscles coöperate in closing the jaw. The depressor mandibulæ (*D. m.*) arises from the posterior border of the squamosal behind the auditory region and is inserted into the posterior process of the mandible. The extreme simplicity of the jaw muscles in the Chelonia is associated with the rigid fixation of the upper jaw.

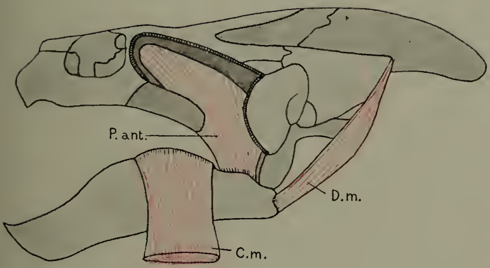
FIGS. 3 and 4.—*Sphenodon.* (Mainly after Osawa.)

The superficial muscles are shown in Fig. 3, and the deep muscles in Fig. 4.

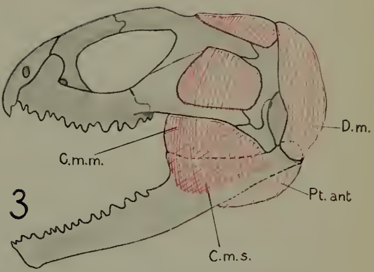
The fibres of the superficial (masseter) layer of the capiti-mandibularis (*C. m. s.*) cross those of the middle layer nearly at right angles. The middle layer (*C. m. m.*) arises around the borders of the supratemporal fenestra. The lateral temporal fenestra affords space for the expansion of this muscle. The deep layer (*C. m. p.*) arises from the lower borders of the supratemporal fenestra and from the side of the brain-case in the auditory region. The pterygoideus anterior (*Pt. ant.*) is inserted around the lower posterior border of the mandible.

FIGS. 5 and 6.—*Alligator.*

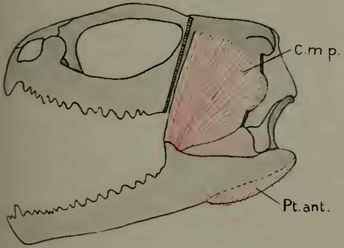
The capiti-mandibularis (*C. m. s.; C. m. m.*) is inserted into the Meckelian fossa of the mandible. The middle slip runs up to the small supratemporal fenestra. The pterygoideus anterior (*Pt. ant.*) is extended forward beneath and in front of the orbit. The pterygoideus posterior (*Pt. post.*) wraps around the posterior end of the mandible.


P. ant.
D.m.
C.m.

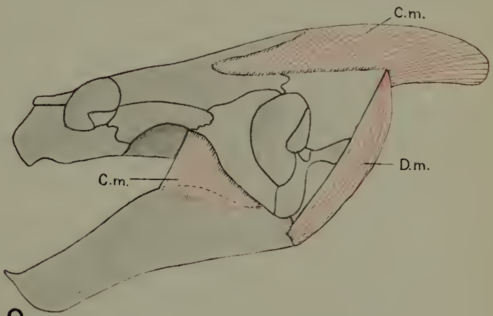
1


D.m.
C.m.m.
Pt. ant
C.m.s.

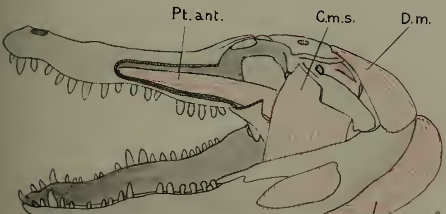
3


C.m p.
Pt. ant.

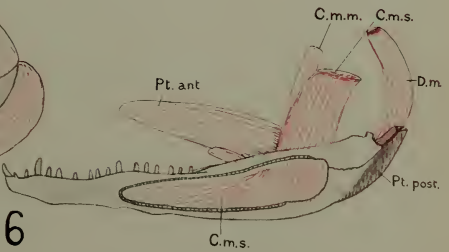
4


C.m.
C.m.
D.m.

2


Pt. ant.
C.m.s.
D.m.
Pt. post

5


C.m.m.
C.m.s.
D.m.
Pt. ant
Pt. post.
C.m.s.

6

EXPLANATION OF PLATE VII

Jaw muscles of streptostylic reptiles: *Iguana* and *Varanus*

FIGS. 1 and 2.—*Iguana.* (Muscles mainly after Mivart.)

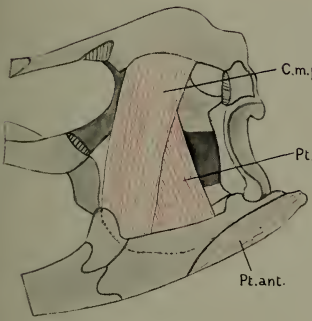
The superficial muscles are shown in Fig. 1, and the deep muscles in Fig. 2.

The capiti-mandibularis is divided into three layers, which have the same arrangement as in *Sphenodon.* The pterygoideus anterior (*Pt. ant.*) differs from that of *Alligator* in being confined to the posterior part of the skull.

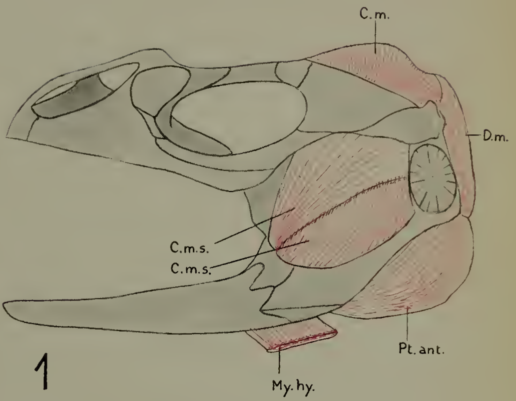
FIGS. 3-5.—*Varanus.* (Muscles mainly after Watkinson.)

The superficial muscles are shown in Fig. 3, the middle layers in Fig. 4, and the deep layers in Fig. 5.

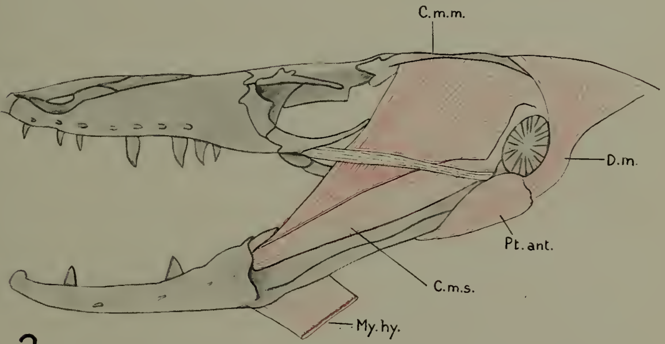
In correlation with the extreme mobility of the jaws the pterygoid muscles are differentiated into four distinct elements, pterygoideus anterior (*Pt. ant.*), pterygoideus posterior (*Pt. post.*), pterygo-sphenoidalis (*Pt. s.*), and pterygo-parietalis (*Pt. pa.*). These are probably all derived from the primitive adductor mass and along with the three divisions of the capiti-mandibularis are innervated by V_3.


C.m.p.
Pt.ant.
Pt.ant.

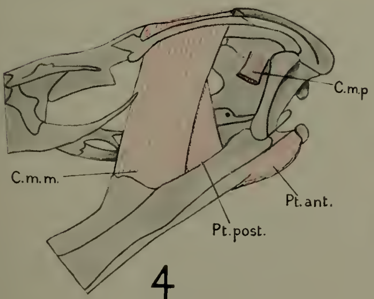
2


C.m.
D.m.
C.m.s.
C.m.s.
Pt.ant.
My.hy.

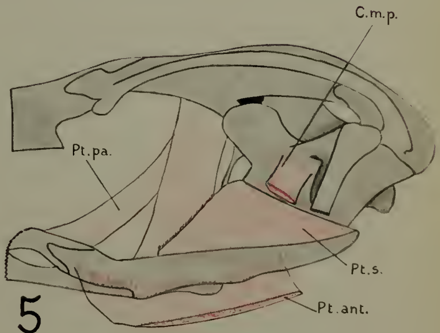
1


C.m.m.
D.m.
Pt.ant.
C.m.s.
My.hy.

3


C.m.p
C.m.m.
Pt.ant.
Pt.post.

4


C.m.p.
Pt.pa.
Pt.s.
Pt.ant.

5

EXPLANATION OF PLATE VIII

Jaw muscles of a typical bird: *Gallus*

FIG. 1.—*Gallus*. Superficial muscles.

The capiti-mandibularis is divided into a superficial layer, analogous with the masseter of mammals, and a deep layer, analogous with the temporalis. The capiti-mandibularis superficialis (*C. m. s.*) is attached to the quadrate.

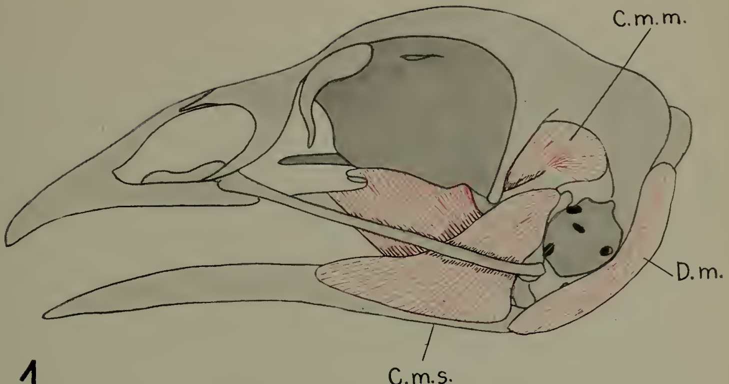
FIG. 2.—*Gallus*.

Deep muscles after removal of the capiti-mandibularis superficialis et medius.

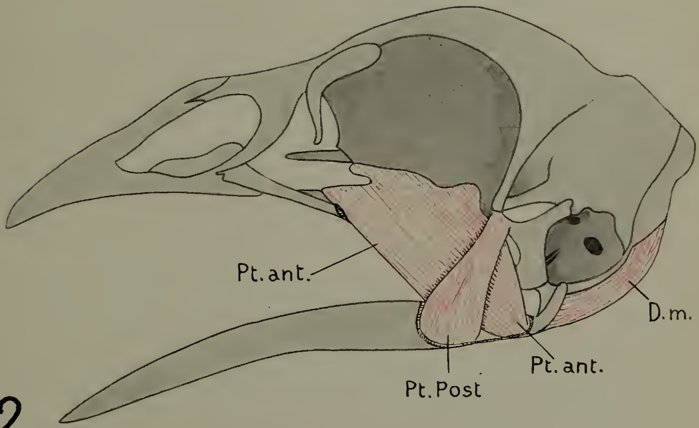
The pterygoideus anterior (*Pt. ant.*) has the normal reptilian relations. The pterygoideus posterior (*Pt. post.*) perhaps is attached to the quadrate. The depressor mandibulæ (*D. m.*) is of normal reptilian type.

FIG 3.—*Gallus*.

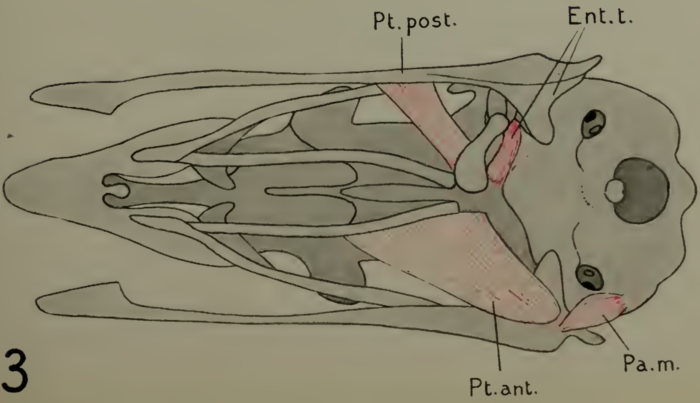
Deep muscles as seen from below. The entotympanicus (*En. ty.*) muscle is a remnant of the adductor mass of lower vertebrates. The parieto-mandibularis (*Pa. m.*) seems to represent a part of the depressor mandibulæ of reptiles.



1



2



3

Explanation of Plate IX

Jaw muscles of monotremes: *Ornithorhynchus*, *Echidna*. After Schulman

The jaw muscles of monotremes as well as their skulls exhibit peculiar specializations along with certain very ancient characters not found in other mammals.

Fig. 1.—*Ornithorhynchus*. Superficial muscles. (Muscles mainly after Schulman.)

The capiti-mandibularis of reptiles is now represented by the masseter (*Mas.*), temporalis (*Tem.*), and pterygoideus externus. The masseter is subdivided into several muscles of which the detrahens mandibulæ (*Det. m.*) simulates the depressor mandibulæ or reptiles, but is innervated by the mandibular nerve and not by the facialis. The digastric is not present as such.

Fig. 2.—*Ornithorhynchus*. Deep muscles. (Muscles mainly after Schulman.)

The anterior end of the temporalis (*Tem.*) is attached to a strong ligament running from the postorbital region of the skull to the coronoid process of the mandible. Beneath the zygomatic branch of the masseter the pterygoideus externus (*Pt. ext.*) is seen.

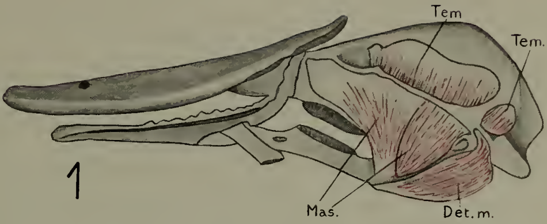
Fig. 3.—*Ornithorhynchus*.

Mandible seen from below, showing the attachments of the jaw muscles.

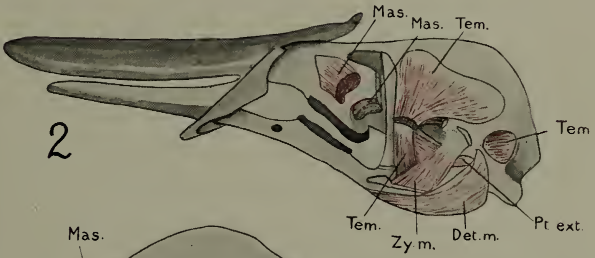
Fig. 4.—The same seen from above.

Figs. 5–7.—*Echidna*. (Muscles mainly after Schulman.)

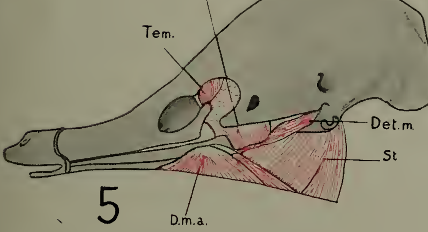
In correlation with the edentulous condition and great reduction of the jaws the temporalis (*Tem.*) and masseter (*Mas.*) muscles are rather feeble. The arrangement of the muscles, however, is fundamentally the same as in *Ornithorhynchus*. The posterior belly of the digastric of mammals is probably represented by the anterior part of the stylohyoideus (*St.*), innervated by VII, while the anterior belly is probably represented by the detrahens mandibulæ anterior (*D. m. a.*), which is innervated by V_3, and is related to the mylohyoid (Parsons).


Tem
Tem.
Mas.
Det. m.

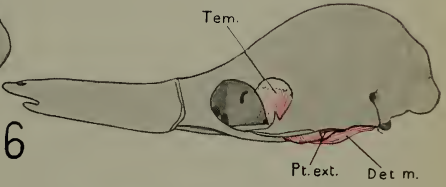
1


Mas.
Mas.
Tem.
Tem
Tem.
Zy. m.
Det. m.
Pt. ext.

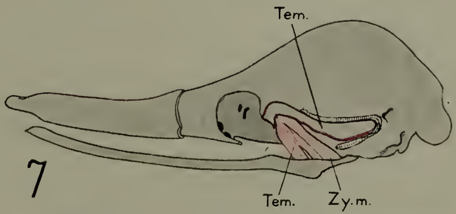
2


Mas.
Tem.
Det. m.
St
D. m. a.

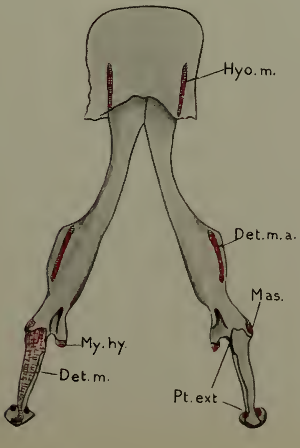
5


Tem.
Pt. ext.
Det m.

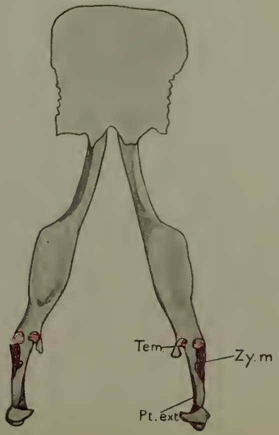
6


Tem.
Tem.
Zy. m.

7


Hyo. m.
Det. m. a.
Mas.
My. hy.
Det. m.
Pt. ext

3


Tem.
Zy. m
Pt. ext.

4

EXPLANATION OF PLATE X

Jaw muscles of typical mammals: *Didelphys*, *Solenodon*, *Mus*, and *Homo*

In mammals the jaw muscles in front of the auditory meatus are derived from the capiti-mandibularis of reptiles and are innervated by the nerve V_3. The depressor mandibulæ of the reptiles has disappeared and is functionally replaced by the digastric which is originally a compound muscle characteristic of marsupials and placentals. The posterior belly of the digastric (*Dig. p.*) probably represents a separate slip of the stylohyoideus, both muscles being innervated by closely associated branches of the seventh nerve. The anterior belly (*Dig. a.*) belongs with the ventral throat muscles and is innervated by the mylohyoid branch of V_3.

FIG. 1.—*Didelphys.* Superficial muscles.

In correlation with the carnivorous habits and orthal jaw motion the temporalis and masseter are both powerfully developed, while the external pterygoid (Fig. 2) is relatively small. The anterior and posterior bellies of the digastric (*Dig. a.*, *Dig. p.*) are in the normal mammalian position.

FIG. 3.—*Solenodon.* Superficial muscles.

The masseter is considerably enlarged and its principal attachment is not on the slender zygomatic arch, but on the masseteric tubercle of the maxillary beneath the orbit. This is often the case in animals with piercing front teeth. The jaw muscles as a whole are of the carnivorous type.

FIG. 4.—*Solenodon.*

Deep muscles, showing the weak external pterygoid (*Pt. ext.*).

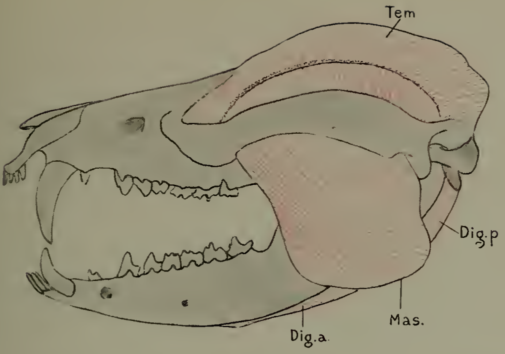
FIG. 5.—*Mus.* Superficial muscles.

The masseter is extended forward beneath the zygomatic arch in front of the orbit, crossing the temporalis nearly at a right angle.

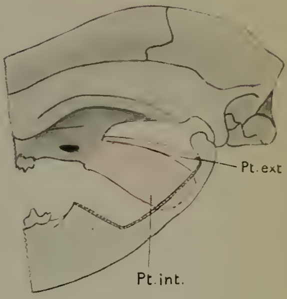
FIG. 6.—*Mus.* Deep muscles.

FIG. 7.—*Homo.* Superficial muscles.

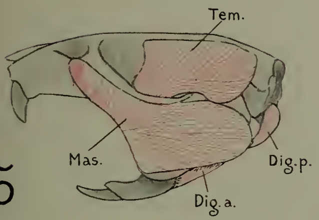
FIG. 8.—*Homo.* Deep muscles.


Tem
Dig.p
Mas.
Dig.a.

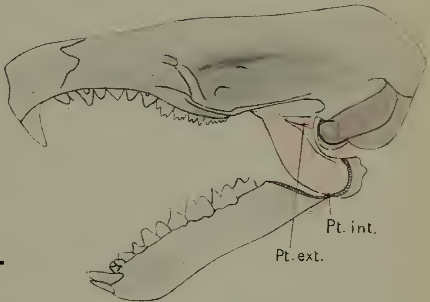
1


Pt.ext
Pt.int.

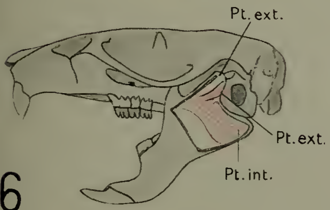
2


Tem.
Mas.
Dig.p.
Dig.a.

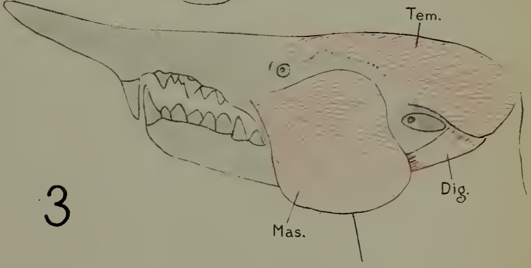
5


Pt.int.
Pt.ext.

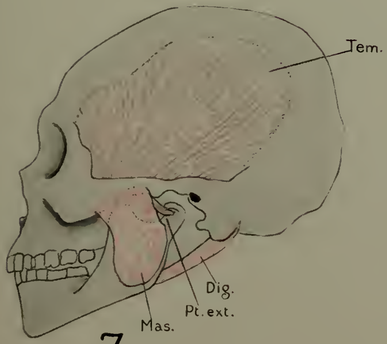
4


Pt.ext.
Pt.ext.
Pt.int.

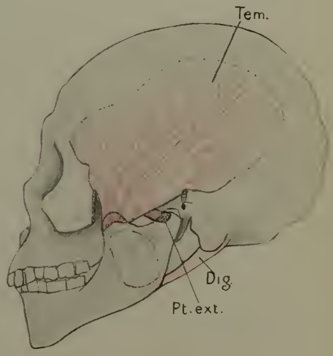
6


Tem.
Dig.
Mas.

3


Tem.
Dig.
Pt.ext.
Mas.

7


Tem.
Dig.
Pt.ext.

8

EXPLANATION OF PLATE XI

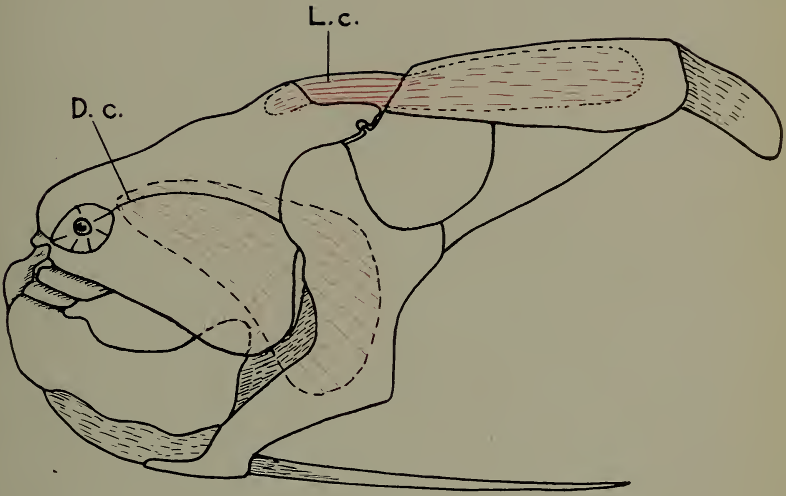
Partial reconstruction of the jaw muscles of *Dinichthys*, representing the Arthrodira

FIG. 1.—*Dinichthys.*

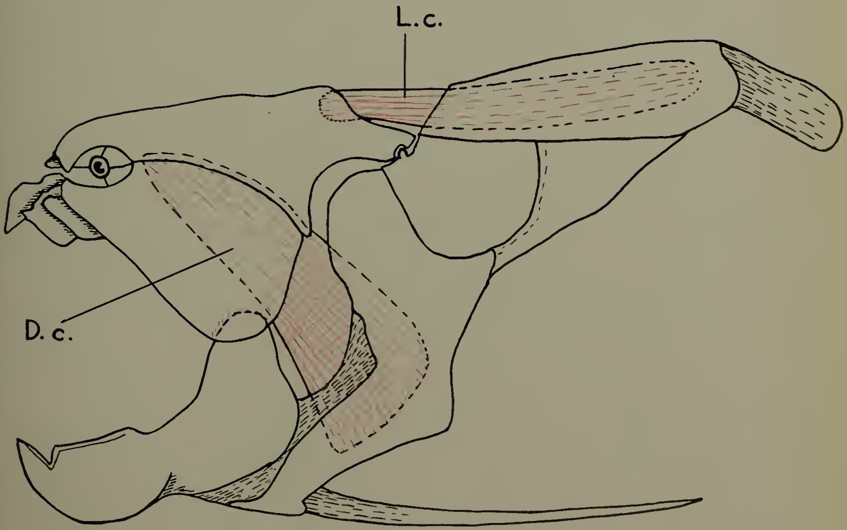
Jaws closed, depressor capitis (*D. c.*) contracted, levator capitis (*L. c.*) extended.

FIG. 2.—*Dinichthys.*

Jaws open, depressor capitis extended, levator capitis contracted.



1



2

Explanation of Plate XII

Restoration of the jaw muscles of *Eryops*, representing the Temnospondyli, and of *Labidosaurus*, representing the Cotylosauria

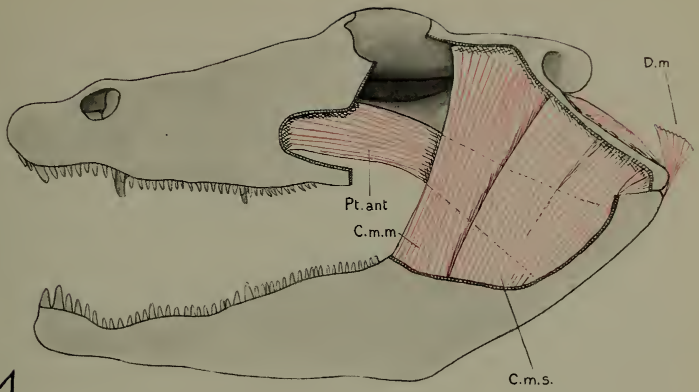
Fig. 1.—*Eryops*. Superficial muscles.

Very probably the jaw muscles of this form were fundamentally similar to those of modern amphibians and include superficial, middle and deep layers of the capiti-mandibularis (*C. m.*). The pterygoideus anterior (*Pt. ant.*) very probably had the normal course and crossed the capiti-mandibularis on the inner side. The jaw was doubtless depressed by the depressor mandibulæ (*D. m.*) lying behind the quadrate.

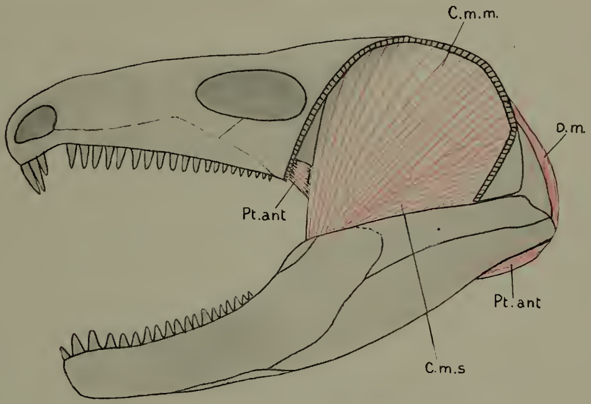
Figs. 2–4.—*Labidosaurus*.

As in the Temnospondyli (Fig. 1) the jaw muscles were entirely beneath the dermal skull roof. The capiti-mandibularis was probably differentiated into three layers and was inserted into the Meckelian fossa of the mandible, and the pterygoideus anterior probably crossed beneath these, being inserted on the back of the mandible.

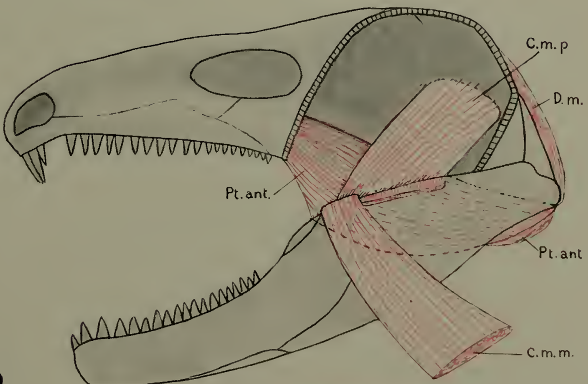
ang. = angular
art. = articular
cor. = coronoid
d. = dentary
pa. = prearticular
sp. = splenial


D.m
Pt.ant
C.m.m
C.m.s.

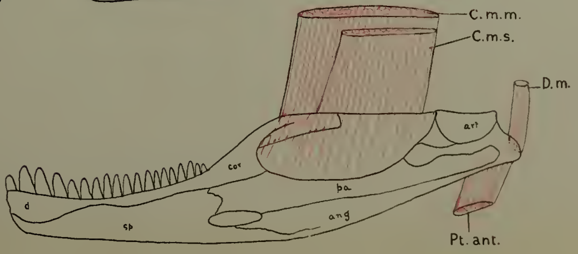
1


C.m.m.
D.m.
Pt.ant
Pt.ant
C.m.s

2


C.m.p
D.m.
Pt.ant.
Pt.ant
C.m.m.

3


C.m.m.
C.m.s.
D.m.
art
cor
ba
d
sp
ang
Pt.ant.

4

EXPLANATION OF PLATE XIII

Restoration of the jaw muscles of *Tyrannosaurus*, representing the Dinosauria Theropoda, and of *Cynognathus*, representing the Therapsida

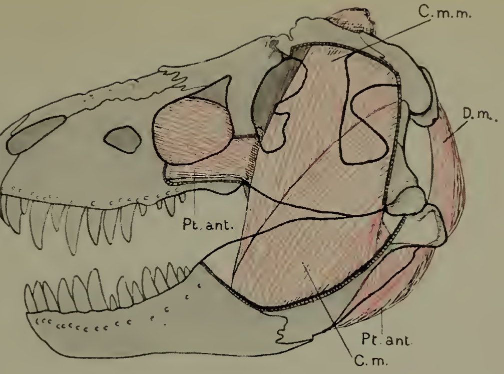
FIG. 1.—*Tyrannosaurus.* Superficial muscles.

As in many other reptiles, the capiti-mandibularis (*C. m. s.*) was probably differentiated into three layers, the more superficial layer of which (*C. m.*) is analogous with the masseter of higher types of mammals. The supratemporal fenestra was probably filled by the middle and deep layers. The pterygoideus anterior may have filled the space beneath the preorbital fenestra.

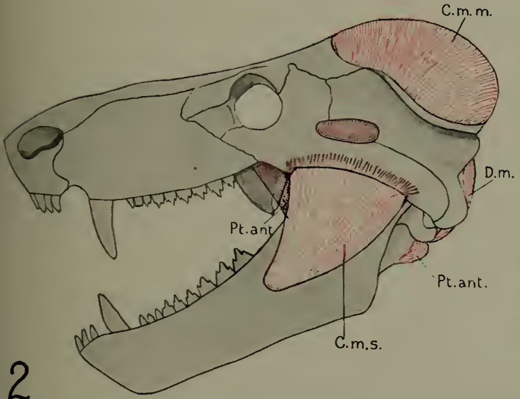
FIGS. 2–5.—*Cynognathus.* Jaw muscles.

A distant approach to mammalian conditions is seen in the reduction of the posterior jaw elements and in the enlargement of the ascending ramus of the dentary. Very probably the outer layer of the capiti-mandibularis was attached to the lower border of the zygomatic arch in the position of its homologue, the mammalian masseter. The middle and deep layers fill the temporal fossa as in mammals. *Cynognathus* probably still retained the reptilian pterygoideus anterior which does not appear to be homologous with either of the pterygoid muscles of mammals, but may possibly be represented by the tensor tympani. The capiti-mandibularis was in a better position to give rise to these muscles. A true depressor mandibulæ (*D. m.*) was doubtless present and the general arrangement of the muscles was reptilian in type.

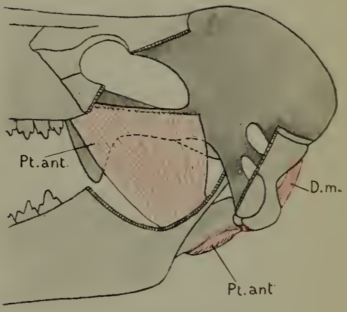
A. = articular (inside)
Ang. = angular
Art. = articular (outside)
Cr. = coronoid
D. = dentary
P. art. = prearticular
Sur. a. = surangular


C.m.m.
D.m.
Pt.ant.
Pt.ant.
C.m.

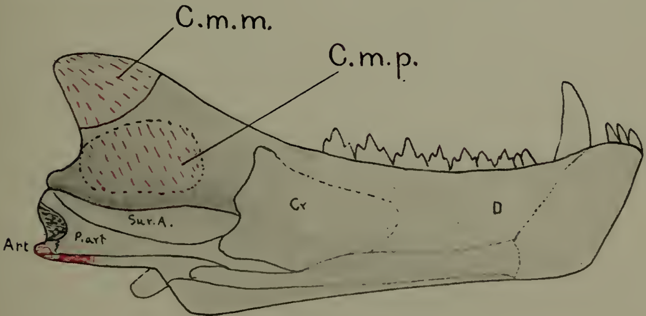
1


C.m.m.
D.m.
Pt.ant
Pt.ant.
C.m.s.

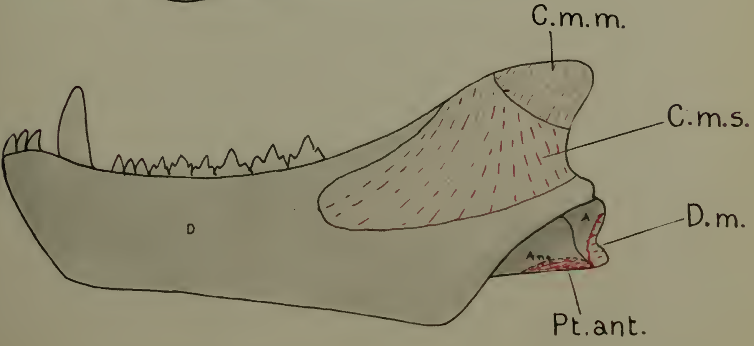
2


Pt.ant.
D.m.
Pt.ant

3


C.m.m.
C.m.p.
Cr
D
Sur.A.
P.art
Art

5


C.m.m.
C.m.s.
D.m.
A
Ang
D
Pt.ant.

4

ANNALS OF THE NEW YORK ACADEMY OF SCIENCES
Vol. XXVIII, pp. 167-200

Editor, Ralph W. Tower

CONTRIBUTIONS TO THE HERPETOLOGY OF PORTO RICO

BY

Karl Patterson Schmidt

NEW YORK
PUBLISHED BY THE ACADEMY
8 September, 1920

THE NEW YORK ACADEMY OF SCIENCES

(LYCEUM OF NATURAL HISTORY, 1817-1876)

OFFICERS, 1920

President—EDWARD L. THORNDIKE
Vice-Presidents—WILLIAM J. GIES, CHARLES L. BRISTOL,
ISAIAH BOWMAN, ROBERT S. WOODWORTH
Corresponding Secretary—HENRY E. CRAMPTON
Recording Secretary—RALPH W. TOWER
Treasurer—JOHN TATLOCK
Librarian—RALPH W. TOWER
Editor—RALPH W. TOWER

SECTION OF ASTRONOMY, PHYSICS AND CHEMISTRY

Chairman—WILLIAM J. GIES
Secretary—WALTER H. EDDY

SECTION OF BIOLOGY

Chairman—CHARLES L. BRISTOL
Secretary—ROBERT C. MURPHY

SECTION OF GEOLOGY AND MINERALOGY

Chairman—ISAIAH BOWMAN
Secretary—CHARLES C. MOOK

SECTION OF ANTHROPOLOGY AND PSYCHOLOGY

Chairman—ROBERT S. WOODWORTH
Secretary—ROBERT H. LOWIE

The sessions of the Academy are held on Monday evenings at 8:15 o'clock from October to May, inclusive, at The American Museum of Natural History, 77th Street and Central Park, West.

[ANNALS N. Y. ACAD. SCI., Vol. XXVIII, pp. 167-200. 8 September, 1920]

CONTRIBUTIONS TO THE HERPETOLOGY OF PORTO RICO

BY KARL PATTERSON SCHMIDT

As a part of the Scientific Survey of Porto Rico inaugurated by the New York Academy of Sciences and carried on with the coöperation of The American Museum of Natural History and other institutions, it was my good fortune to conduct the first herpetological field-work in the summer of 1919. For this purpose Mrs. Schmidt and I spent the period from August 3 to October 8 on Porto Rico and the adjacent islands, which are under the same political jurisdiction.

For cordial assistance in furthering our work, I am especially grateful to Mr. and Mrs. B. A. Wall, of San Juan; Mr. E. M. Bruner, Forester of Porto Rico; Mr. Marc Lejeune, of Mayaguez, who made possible the trip to Mona Island, and to Colonel George A. Shanton, Chief of the Insular Police.

The exceptionally thorough and exhaustive "Herpetology of Porto Rico" by Dr. Leonhard Stejneger is available as a handbook of the reptiles and amphibians, making it possible to identify the species in the field and thus facilitating the study of habits and habitat associations. Dr. Stejneger has given an excellent résumé of herpetological work on Porto Rico previous to his own. The herpetological papers which have appeared since 1902 relating to the fauna under consideration are given in the bibliography at the close of this paper.

Collections were made on the islands of Porto Rico, Mona, Vieques and Culebra. Notes on the relation between the distribution of the species and the types of habitat will be found below under the discussion of individual species. The addition of six species of *Eleutherodactylus* to the Porto Rican fauna, five of which are here described as new, is an unexpected result of the expedition. All but one of these were captured with the aid of an electric hand-lamp while they were singing at night. This method of stalking is well known to those who have studied the notes of amphibians. The voices of *Eleutherodactylus,* as of other frogs and toads, are useful characters for distinguishing the species.

The expedition secured over twelve hundred specimens, comprising thirty-one species. To this collection are added more than a hundred specimens obtained by previous expeditions of the survey (H. E. Anthony, T. H. Jones, F. E. Lutz, R. W. Miner, J. T. Nichols), making the total number of specimens, on which this report is based, much larger than any previously made in Porto Rico and equaling in completeness that of the National Museum.

The present paper is preliminary to the general account of the herpetology of Porto Rico to be published by the New York Academy of Sciences in the volumes embodying the results of the Scientific Survey of Porto Rico and the Virgin Islands.

AMPHIBIA

Bufo Laurenti

Bufo lemur (Cope)

This species, five specimens of which were collected at Coamo Springs, has previously been known from the north side of Porto Rico; the only exact locality being given as Arecibo by Stejneger. Its occurrence at Coamo Springs, nearly at the opposite side of the island, proves that it is widely distributed.

The five half-grown specimens are so nearly uniform and were found in so circumscribed an area that they probably are members of a single brood. They agree in coloration with the juvenile specimen described by Stejneger (1904, p. 572) and all show the hour-glass shaped dark mark on the shoulders. The dimensions of one of these specimens may be compared with those of an adult recorded by Stejneger:

	A. M. N. H. No. 10151	U. S. N. M. No. 27148
Tip of snout to vent	37 mm.	83 mm.
Tip of snout to posterior edge of tympanum	12 "	29 "
Greatest width of head	13 "	32 "
Foreleg from axilla	21 "	51 "
Hind leg from vent	37 "	99 "

The stomach contents of these specimens included ant remains, beetle wings, an insect larva, and segments of a small millipede.

Leptodactylus Fitzinger

Leptodactylus albilabris (Günther)

The following localities are represented by sixty-three specimens in the collections: Adjuntas, Aibonito, Bayamon, Caguas, Coamo Springs, Maricao, San Turce, Utuado, El Yunque, and Culebra Island.

This species exhibits a great variability in coloration, with a relative uniformity in structural characters. Fowler (1918, p. 3, Fig. 1) has figured the extremes of color pattern in Porto Rican specimens. Of fifty specimens in the present series, seven have the broad median stripe on the back, the others varying chiefly in the distinctness of the dorsal V-shaped markings. The measurements of the largest specimen and of one apparently recently transformed are as follows:

	A. M. N. H. No. 10182	A. M. N. H. No. 10036
Tip of snout to vent	49 mm.[1]	16 mm.
Tip of snout to posterior edge of tympanum	18 "	7.5 "
Greatest width of head	17 "	7 "
Foreleg from axilla	29 "	10 "
Hind leg from vent to tip of longest toe	78 "	24 "

Eight of twenty-five stomachs examined were empty. Four contained land snails; two contained spiders (one a large lycosid spider and egg sack); two contained ants; two contained beetles; two contained bugs; two contained flies (Muscidæ); one a small moth; one a large caterpillar; one a medium-sized cockroach; and seven the remains of an unidentifiable insect.

The nest of this species was observed by Stejneger (1904, p. 579) under a flat stone in a stream. Peters (1877, Monatsber. Akad. Wiss. Berlin, 1876, p. 709) records one observed by Gundlach in a "wet burrow." At Coamo Springs, on the terrace behind the bath-houses of the hotel, the water of some of the springs forms a permanent rivulet at the base of the cliff. *Leptodactylus albilabris* was abundant on the terrace, beneath loose stones. Under a large stone at the edge of the creek, on August 27, 1919, I found a shallow, rounded excavation, 6 or 7 cm. in diameter and about 3 cm. deep, filled with a mass of white foam, in which were the small tadpoles of this species (12 mm. in length, body 3–4 mm.). There were between seventy-five and one hundred tadpoles in the foam-mass, and not confined to the central hollow, as described by Stejneger. The bottom of the excavation was about 3 cm. above the water level. Two similar excavations, though empty, were discovered in the immediate vicinity, in the same relative position with reference to the water. On August 29, near Bayamon, a small mass of foam, between 3 and 4 cm. in diameter, containing similar tadpoles, was found under a stone on a hilltop, with no water whatever in the neighborhood. On October 1, near the Forester's cabin, on El Yunque, at about 1200 feet, a nest of this species was observed under a rotten log, beside a pool of standing water (also at a slightly higher level than that of the water). This nest contained between 150 and 200 eggs uniformly distributed

---

[1] 144 mm., given by Stejneger (1904, pp. 576, 578), is obviously a misprint.

through the foam and with no central hollow. It was somewhat larger than those previously observed, measuring 8 cm. in diameter. The eggs are light yellow, and measure 2.5 mm. to 3 mm. in diameter. The smallest tadpoles taken, swimming at large, measure 6 mm. in body length, which probably represents their maximum size at the time they escape from the foam. It is evident that the tadpoles usually will be washed from the nest into the adjacent water by a flood or heavy rain. The small nest isolated from water was probably a mistake on the part of the frog, and the nest described by Stejneger under water probably had been covered by a rise in the creek after the deposition of the eggs. The largest larvæ, nearly ready to transform, measure 13 mm. from snout to vent. The V-shaped dorsal markings are already evident in the tadpoles at this stage. The median dorsal white line is probably an adult character.

Eleutherodactylus Duméril and Bibron

Eleutherodactylus auriculatus (Cope)

The following localities are represented by two hundred and seven specimens in the collection: Adjuntas, Aibonito, Alto Manzano, Cataño, Coamo Springs, Jayuya, Maricao, Rio Piedras, San Turce, Vega Baja, and El Yunque. *Eleutherodactylus auriculatus* occurs in Santo Domingo and Cuba as well as in Porto Rico, the type locality being Cuba. It appears to be rare in Cuba and Santo Domingo, while in Porto Rico it is exceeded in abundance only by the ubiquitous *Leptodactylus albilabris.* Its closest relative appears to be the *E. martinicensis* of the Lesser Antilles.

E. auriculatus is remarkable for its color variation, with a comparatively stable structure, but a considerable variation in measurements. A specimen in the collection of Prof. G. E. Johnson, of the University of Porto Rico, collected by him in the Luquillo Forest, is remarkable for its size, but it apparently is a giant individual of *E. auriculatus.* The maximum size in over three hundred specimens in the National Museum and the present collection is 44 mm. from snout to vent, while Professor Johnson's specimen measures 52 mm. Its measurements compared with the largest in the present series are as follows:

	A. M. N. H. No. 10241	Johnson coll.
Tip of snout to vent	44 mm.	52 mm.
Tip of snout to posterior edge of tympanum	18 "	20 "
Greatest breadth of head	19 "	23 "
Foreleg from axilla	29 "	35 "
Hind leg from vent	69 "	80 "

The most frequent coloration is a grayish brown of varying shade, sometimes reddish, sometimes nearly black, which may be uniform or mottled. In the lighter specimens there is nearly always a dark interorbital mark, and in a few the snout is white in front of this, either with a broad transverse white band or completely light to the tip of the snout. There is usually also a dark subcanthal mark, interrupted by the eye, and continued over the ear for a short distance. In a few cases the dorsum is spotted irregularly with vivid white spots. Of one hundred and ninety-four examined, eighteen have a light line beginning at the snout and passing over the edge of the eyelid to the ear, continuing as a broader light dorsolateral band to the thigh. In nineteen specimens there is a sharp median white stripe (compare Fowler, 1918, Fig. 2). Five have a broad median light band, about four times as broad as the more common narrow line. The hind legs are occasionally distinctly barred, more usually indistinctly barred or uniform. The concealed surfaces of the thighs are often bright pink or red. The venter is usually light and unspotted, occasionally spotted with groups of dark-brown punctuations. In no specimen were the concealed surfaces of the thighs reticulated with the fine or coarse dark network of *E. antillensis*.

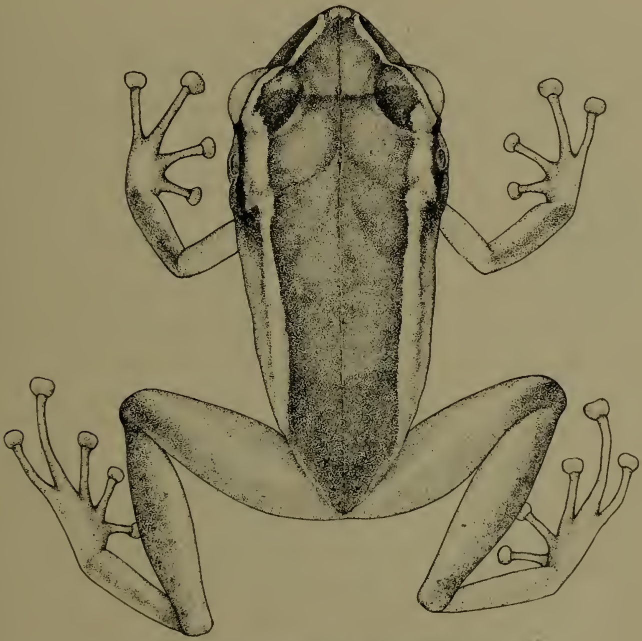


FIG. 1.—*Eleutherodactylus auriculatus* (Cope), ♂
A. M. N. H. No. 10249. A common phase of coloration. Twice natural size.

Persistent search about the banana plants, under the leaves of which adults hide during the day, failed to discover the eggs of this species, and it was not until the writer visited the Luquillo Forest that a single egg-mass was discovered in a basal leaf of an air plant, just at the surface of the water in the lower part of the leaf. A large *E. auriculatus* in the same plant, but not on the same leaf as the eggs, escaped. There are thirty-six eggs, with well-advanced embryos, adhering in an oval mass from which individual eggs are easily detached. The eggs measure 6–8 mm. in greatest diameter, being somewhat elongated in the axis of the embryo.

The young of this species are extraordinarily abundant, and it is difficult to understand why the eggs are so infrequently observed. It is possible that at the time of my visit (August to October) the height of the breeding season had passed. The only previously recorded date of breeding is that observed by Gundlach, May 24 (Peters, 1877, Monatsber. Akad. Wiss. Berlin, 1876, p. 709). Professor Johnson found a mass of eggs on July 8, with embryos at about the same stage as the writer's, in the same bunch of moss in which the giant female specimen, mentioned above, was collected. Gundlach (loc. cit.) also observed a female sitting on the egg-mass received by him, while Bello y Espinosa (Martens, 1871, Zoöl. Garten, XII, p. 351) records that in the case observed by him the parent frog remained in the neighborhood of the eggs "as if to guard them." From these several observations it appears not unlikely that the female does remain in the neighborhood of the eggs until they are hatched, but further observations on this point are desirable. Ruthven (1915, Occas. Papers, Mus. Zoöl. Univ. Michigan, No. 11), observing the breeding habits of *E. cruentus* (Peters) in Colombia, found no evidence of such a habit.

FIG. 2.—Embryo of *Eleutherodactylus auriculatus*
A. M. N. H. No. 10302. Four times natural size.

Eleutherodactylus gryllus, new species

Sixteen specimens from Maricao and El Yunque were collected.

Diagnostic Characters

Distinguished from *Eleutherodactylus auriculatus* by a shorter snout, less granulate venter, and its minute size.

Range

Taken at El Yunque and Maricao, probably confined to the coffee belt and the wet rain forests above it.

Type

A. M. N. H. No. 10307, ♂, El Yunque, near the Forester's cabin (about 1300 feet), September 30, 1919, Karl P. Schmidt.

Description of Type

Habitus of *Eleutherodactylus auriculatus,* but with a distinctly shorter snout, its length equal to the diameter of the eye (in *E. auriculatus* the diameter of the eye equals its distance from the nostril), and to the interorbital space; canthus rostralis rounded; nostril one-third the distance from tip of snout to eye; tympanum scarcely distinct, one-fourth the diameter of the eye, its distance from the eye equal to its diameter; toes without vestige of web; digital disks well developed; first toe as long as the second; an inner and outer metatarsal fold; vomerine teeth in two oblique patches behind and within the choanæ; tongue large, slightly nicked behind; skin smooth above, but apparently much more glandular than in *E. auriculatus;* venter strongly granulate; a large subgular vocal sac.

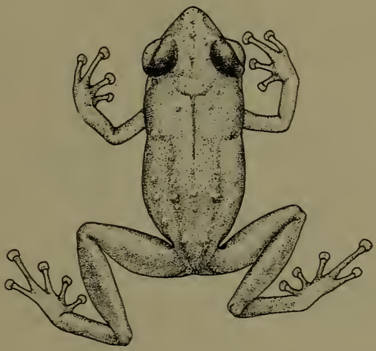


FIG. 3.—*Eleutherodactylus gryllus,* new species
A. M. N. H. No. 10226. Twice natural size.

Middle of the back, beginning with an interorbital line, dark gray, enclosing a light spot on the occiput; sides and snout lighter, the darker color everywhere consisting of minute black punctations, especially evident on the limbs and throat; venter light.

Measurements

Tip of snout to vent	16	mm.
Tip of snout to posterior border of tympanum	5.5	"
Greatest breadth of head	6	"
Foreleg from axilla	11	"
Hind leg from vent	24	"
Tibia	8.5	"

Notes on Paratypes

The type is a male, taken singing at night, with the usual pale night coloration. Specimens taken in the daytime (concealed under moss) are very dark in color and exhibit considerable variation in pattern, two having a light median dorsal line. In a specimen taken in an air plant (No. 10291) the dorsal dark area is cinnamon brown and the sides bright pale green, the legs with dark bars; this coloration has been described by Stejneger (1904, Rept. U. S. Nat. Mus., 1902, p. 586) as a variant coloration of juvenile *E. auriculatus.* The darker specimens have narrow light crossbands on the limbs. The granulation of the venter in the female specimens is faint, though still evident.

This species was found very numerous at Maricao and on El Yunque, singing frequently from trees, at least ten feet from the ground. On El Yunque specimens were collected in air plants, near the peak, and under moss on the rocks of the peak itself.

The note is a rapid succession of shrill clicks, very insect-like; the chorus sounding not unlike the rapid clicking of a telegraphic instrument. Were it not for the minute size of the singers and the extremely distinct note, this species might well be considered the young of *E. auriculatus.* I am unable to agree with Stejneger's supposition that its note is made by juvenile males of the latter species. The gonads, at any rate, appear to be those of an adult in the specimens examined, differing in form and pigmentation from those of young *E. auriculatus* of similar size.

Eleutherodactylus locustus, new species

A single specimen from El Yunque, just above the Forester's cabin, collected September 30, 1919.

Diagnostic Characters

Size small, snout obtuse, nostril much nearer to the end of the snout than to the eye; tympanum small, indistinct, one-fourth the diameter of the eye, separated from the eye by a little more than its diameter;

vomerine teeth in two oblique series, behind and within the choanæ; toes free; digital disks well developed; tibiotarsal articulation reaching the posterior border of the eye; heels overlapping when the legs are placed at right angles to the body; skin rugose above, with scattered round tubercles, especially on the eyelid; venter smooth; inner face of thighs finely rugose.

Range

Known only from the type locality.

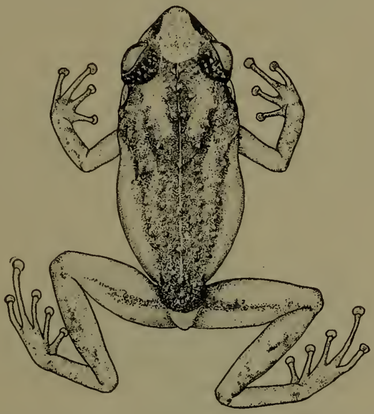


FIG. 4.—*Eleutherodactylus locustus*, new species
A. M. N. H. No. 10240, type. Twice natural size.

Type

A. M. N. H. No. 10240, ♂, El Yunque, near the Forester's cabin (about 1300 feet), Luquillo Forest Reserve, Porto Rico, September 30, 1919, Karl P. Schmidt.

Description of Type

Head slightly longer than broad, slightly narrower than the body; snout moderately obtuse, its length anterior to the eye exceeding the interorbital space; nostrils one-fourth the distance between eye and tip of snout from the latter; tympanum scarcely distinct, one-fourth the diameter of the eye, separated from the eye by a little more than its diameter; canthus rostralis rounded; elbow and knee pressed along the side, overlap; heels overlap when the legs are placed vertically to the axis of the body; tibiotarsal articulation reaching the posterior border of the eye; disks of fingers and toes well developed; toes without vestige of web; inner and outer metatarsal tubercles present; no tarsal fold; first toe as long as the second; vomerine teeth in two linear oblique patches, converging posteriorly, well separated on the median line, behind and within the choanæ by about the diameter of the choana; tongue large, slightly nicked behind; skin rugose above, with rounded tubercles; a well-marked mid-dorsal ridge from snout to vent; eyelid strongly rugose; venter smooth (faintly rugose under the lens); thighs slightly rugose; male with a large subgular vocal sac.

Dorsum gray, mottled with grayish brown; a well-defined interorbital dark band; sides of canthus with a dark mark, interrupted by the eye, extending over the tympanum, legs not barred, with dusky markings; venter uniform, light.

Measurements

Tip of snout to vent	19	mm.
Tip of snout to posterior border of tympanum	7	“
Greatest breadth of head	6.5	“
Foreleg from axilla	12	“
Hind leg from vent	29	“
Tibia	9	“

This species was discovered by accident, singing on a leaf some three feet from the ground. Its note is the most distinctive of any observed in Porto Rico, beginning with a shrill continuous note almost at the limit of audibility, which is followed by a succession of clicks. So closely does this note resemble a familiar type of note produced by long-horned grasshoppers that the writer neglected to search for the author of the sound, and watched the present specimen repeat the song several times before being convinced that it really proceeded from an *Eleutherodactylus*.

It is closely related to *E. auriculatus*, from which it is well distinguished by its small size and smooth venter. Even more closely related to the still smaller new species, *E. gryllus*, it is still readily distinguished by its smooth venter and more rugose dorsum, as well as by its song.

Eleutherodactylus cramptoni,[2] new species

Three specimens from the peak of El Yunque, September 30, 1919.

Diagnostic Characters

Size small, habitus stout; hind legs short; snout very obtuse, canthus rostralis rounded; dorsum very rugose with rounded tubercles; vomerine

---

[2] Named for Prof. Henry E. Crampton, whose active interest and investigation have greatly furthered the zoölogical work of the Survey.

teeth in two oblique linear series, extending laterally as far as the inner border of the choanæ; digital disks large; uniform dark brown above, light brown beneath.

Range

Known only from the type locality.

Type

A. M. N. H. No. 10305, ♂, peak of El Yunque, September 30, 1919, Karl P. Schmidt.

Description of Type

Habitus stout, compact; snout short, obtuse, canthus rostralis rounded; nostril one-third the distance from tip of snout to eye; heel reaching the anterior border of the orbit; heels meet but do not overlap when the legs are placed at right angles to the body; both anterior and posterior limbs notably stout, nearly twice as thick as those of *E. auriculatus* of the same body length; vomerine teeth in two linear, oblique series, extending laterally as far as the choanæ; tympanum small, distinct; dorsum covered with rounded tubercles, extending onto the eyelids and snout; venter finely granular; digital disks large; first toe as long as the second; no subgular vocal sac.

FIG. 5.—*Eleutherodactylus cramptoni,* new species
A. M. N. H. No. 10305, type. Twice natural size.

Color uniform brown above; lighter brown below and slightly variegated with lighter punctations.

Measurements

Tip of snout to vent	19	mm.
Tip of snout to posterior border to tympanum	6.5	“
Greatest breadth of head	7	“
Foreleg from axilla	12	“
Hind leg from vent	29	“
Tibia	9	“

Notes on Paratypes

The two paratypes are similar in every respect to the type, with the single exception that one of them is slightly more mottled with light and has the hind legs indistinctly barred.

The three small tree frogs described above were taken under moss in the crevices of the rocks on the peak of El Yunque. The species is a well-differentiated one, characterized by the stoutness of its limbs, the obtuseness of the snout, and the extreme rugosity of the dorsum.

Eleutherodactylus antillensis (Reinhardt and Luetken)

The following localities are represented by thirty specimens in the collection: Aibonito, Bayamon, Maricao, San Turce, and Culebra Island. This species has previously been known only from St. Thomas (type

FIG. 6.—*Eleutherodactylus antillensis* (Reinhardt and Lütken), ♂
A. M. N. H. No. 10019. Twice natural size.

locality), Tortola, and Vieques. The present records add Culebra and Porto Rico to its range. Since it was discovered at widely distant points in Porto Rico, it probably is indigenous to that island. In San Turce, along the railroad and trolley embankments north of the Hotel Eureka, it is more abundant than *Eleutherodactylus auriculatus.*

The single specimen from Culebra agrees closely with the Porto Rican series. In coloration this species is less variable than *E. auriculatus,* but the median white dorsal line may be present or absent. It is developed in twelve of the present specimens. The usual color is grayish brown, with faint dusky markings, and a sharply defined black canthal line which extends over the ear and a short distance beyond it, outlined above in most cases by a very narrow white line on the canthus extending over the eyelid. The concealed surfaces of the legs are reticulated with black, which affords a fairly good character for distinguishing this species in the field from *E. auriculatus.* One specimen, No. 10001, ♂, was violet-red above, with a very heavy black canthal and supra-auricular mark, and with the concealed surfaces of the legs black with sharply defined white spots. When compared directly with *E. auriculatus,* this species is seen to be distinguished by the much heavier granulation of the venter and the much smaller digital disks, in addition to the difference in proportions noted by Stejneger. The measurements of the largest specimens of each sex follow:

	No. 10117 ♂	No. 10082 ♀
Tip of snout to vent	24 mm.	33 mm.
Tip of snout to posterior border of tympanum	10 "	13 "
Greatest breadth of head	11 "	14 "
Foreleg from axilla	16 "	19 "
Hind leg from vent	38 "	48 "

Eleutherodactylus brittoni,[3] new species

Four specimens of this species were collected at Maricao and El Yunque, near the Forester's cabin.

Diagnostic Characters

Derived from *Eleutherodactylus antillensis,* from which it is distinguished by its small size, its sharp canthus rostralis, which is continued as a dorsolateral angle some distance behind the ear, and its more posteriorly placed nostril.

---

[3] Named for Dr. Nathaniel L. Britton, chairman of the Committee on the Scientific Survey of Porto Rico of the New York Academy of Sciences.

Range

Known from Maricao and El Yunque, it is probably confined to the coffee belt and the moist forests above it.

Type

A. M. N. H. No. 10318, ♂, El Yunque, near the Forester's cabin (about 1300 feet), September 30, 1919, Karl P. Schmidt.

Description of Type

Habitus slender, head narrower than the body, legs rather short, snout sharp, pointed; nostril two-fifths the distance from the end of the snout to the orbit; canthus rostralis sharp; interorbital space broader than the eyelid; heel reaching the anterior border of the orbit; heels meeting but not overlapping when the legs are at right angles to the body; top of snout flat, as is the anterior half of the back behind the eyes, the side of the body being vertical anteriorly; vomerine teeth in two small rounded patches, behind and within the choanæ; tympanum indistinct, separated from the eye by less than its diameter; dorsum smooth, venter coarsely granulate; digital disks small, as long as wide; a well-defined tarsal fold; a well-developed subgular vocal sac. Dorsum light grayish brown, venter lighter. Two black spots between the eyes, one on the middle of the back, and three posteriorly on the back, above the groin; legs with a single faint darker bar on the femur; concealed surfaces of the femur not reticulated; a black subcanthal streak, continued below the dorsolateral angle behind the eye.

FIG. 7.—*Eleutherodactylus brittoni,* new species
A. M. N. H. No. 10318, type. Twice natural size.

Measurements

Tip of snout to vent	16	mm.
Tip of snout to posterior border of tympanum	6	"
Greatest breadth of head	6	"
Foreleg from axilla	9	"
Hind leg from vent	23	"
Tibia	8	"

Notes on Paratypes

The three paratypes are closely similar in size and structural characters to the type. Two have the black subcanthal and shoulder mark outlined with white above. One lacks the dorsal black spots.

The specimen from Maricao was taken singing in herbage along the roadside, together with *E. auriculatus* and *E. antillensis.* Two were taken singing on El Yunque, likewise in low herbage, and the last was found by accident in collecting *E. wightmanæ.*

The note of this species is a succession of clicks, less shrill and less rapid than in *E. gryllus.*

This species stands in the same relation to *E. antillensis* as *E. gryllus* does to *E. auriculatus.*

Eleutherodactylus wightmanæ,[4] new species

Thirteen specimens of this species were collected at Maricao and El Yunque, near the Forester's cabin.

Diagnostic Characters

Size small, snout pointed; nostril much nearer to the tip of the snout than to the eye; tympanum small, distinct, separated from the eye by about its own diameter; vomerine teeth in two straight series, in the same line, extending as far laterally as the choanæ, and about the diameter of a choana behind them; toes free, digital disks well developed; tibiotarsal articulation reaching the anterior border of the eye; heels overlapping when the legs are placed at right angles to the body; skin rugose above, with elongate folds and ridges; venter rugose; thighs granular.

Range

Luquillo Forest to Maricao, probably confined to the coffee belt and the wet forests above it.

---

[4] Named for the author's wife, Margaret Wightman Schmidt, whose loyal assistance contributed largely to the success of the work in Porto Rico.

Type

A. M. N. H. No. 10317, ♂, El Yunque near the Forester's cabin (about 1300 feet), Luquillo Forest Reserve, Porto Rico, September 30, 1919, Karl P. Schmidt.

Description of Type

Head as long as broad, narrower than the body; snout pointed, its length anterior to the eyes once and a half the interorbital width; nostrils one-third the distance between eye and tip of snout from the latter; tympanum distinct, small, about one-third the diameter of the eye, separated from the eye by a little more than its own diameter; canthus rostralis sharp; elbow and knee pressed along sides overlap; heels overlap when the legs are placed at right angles to the body; tibiotarsal articulation reaching the anterior border of the eye; disks of fingers and toes well developed; digits slender, free; first toe distinctly shorter than the second; no tarsal folds; vomerine teeth in two straight series, separated in the median line, extending laterally as far as the outer border of the choanæ, and about the diameter of a choana behind them; tongue large, slightly nicked behind; skin rugose above, with longitudinal lines or folds, the most distinct of which originate behind the orbits and extend backward about two-thirds the length of the back; a less distinct mid-dorsal ridge from snout to vent; venter and outer face of thighs rugose; a subgular vocal sac.

FIG. 8.—*Eleutherodactylus wightmanæ*, new species

A. M. N. H. No. 10220. Twice natural size.

Brown above, with a black subcanthal line extending over the ear half way along the sides; a black spot on each side of the back over the groin; venter uniformly light; a single dark cross-band on the radius; one on the femur, tibia, and tarsus (in line when the legs are folded), and a dark spot on the metatarsus; anterior and posterior faces of the thighs dusky.

Measurements

Tip of snout to vent	20	mm.
Tip of snout to posterior border of tympanum	7.5	"
Greatest breadth of head	7.5	"
Foreleg from axilla	11	"
Hind leg from vent	30	"
Tibia	10	"

Notes on Paratypes

In structural characters the twelve paratypes agree closely with the type. Two specimens are light gray, instead of brown, with only indications of the black spots; in most specimens the postocular dark streak is broken up into a series of spots; one specimen is light brownish gray on each side, the area between sharply darker; the bars on the legs are distinct in all specimens.

The plaintive, diminuendo note of this small species is one of the most characteristic sounds in the amphibian chorus of the Luquillo forest. Its song consists of a series of six or eight whistled notes, each slightly louder in pitch and a little fainter than the last. It sings habitually on the ground or in the lowermost leaves of plants. It is particularly difficult to locate its position from its song, partly because it is usually well concealed, partly on account of the peculiar ventriloquy of its voice.

Eleutherodactylus richmondi Stejneger

Eleven specimens of this species were collected at El Yunque, between the Forester's cabin and the peak. This species is probably distributed throughout the virgin forest of the Luquillo Reserve. It should be looked for in the high forest south of Jayuya. Its relations with *E. lentus* of St. Thomas and *E. weinlandi* of Hispaniola add to the evidence of former land connections of the Virgin Islands and Hispaniola with Porto Rico.

Like the larger series examined by Stejneger, the present specimens are extremely uniform in structural characters and in coloration. The only variation noted is the occasional lightening of the chestnut color of the dorsal area between the light dorsolateral lines. The proportions are quite different in this species from the other Porto Rican species of the genus:

	No. 10233
Tip of snout to vent	32 mm.
Tip of snout to posterior border of tympanum	13 "
Greatest breadth of head	12 "
Foreleg from axilla	21 "
Hind leg from vent	51 "

Fig. 9.—*Eleutherodactylus richmondi* Stejneger

A. M. N. H. No. 10237. Twice natural size.

Two extremely small specimens, measuring 9 and 11 mm. respectively, probably are recently transformed. They are colored like the adults.

REPTILIA

Sphærodactylus Wagler

Sphærodactylus macrolepis Günther

Sphærodactylus macrolepis monensis Meerwarth, 1901, Mitt. Naturh. Mus. Hamburg, XVIII, p. 20.

Sphærodactylus monensis Stejneger, 1904, Rept. U. S. Nat. Mus., 1902, p. 607. Barbour, 1914, Mem. Mus. Comp. Zoöl., XLIV, p. 270.

Sphærodactylus grandisquamis Stejneger, 1904, Rept. U. S. Nat. Mus., 1902, p. 602, figs. 46-52. Barbour, 1914, Mem. Mus. Comp. Zoöl., XLIV, p. 270.

The following localities are represented by forty-five specimens in the collection: Aibonito, Bayamon, Cataño, Coamo Springs, Ensenada, Maricao, El Yunque, and Mona Island. This species is found on Mona Island, throughout Porto Rico, and on most of the Virgin Islands (Vieques, St. Thomas, St. Croix, Tortola, Virgin Gorda, Anegada). Stejneger, with specimens from only two localities in Porto Rico (Luquillo and Ponce), described the Porto Rican and Vieques specimens as distinct from the Virgin Island form, as well as from that of Mona Island. He surmised that it was confined to the lowlands, whereas the present series proves that it reaches an altitude of at least two thousand feet.

Barbour (1917, p. 98), after examining a considerable series of *Sphœrodactylus macrolepis* from the Virgin Islands, expresses a measure of doubt as to the distinctness of *S. grandisquamis*. Stejneger separates *S. grandisquamis* and *S. monensis* from *S. macrolepis* solely on the size of the scales, which he gives as 34-38 about the body in *S. grandisquamis*. 46-48 in *S. monensis*. In the series from Porto Rico under consideration the variation is as follows:

Scales about the body............	32—	36—	40—	44—	48—	52—	56
Number of specimens............	2	8	3	4	5	6	2

In five specimens from Mona Island the number of scales varies from 44-52. As *S. macrolepis* is intermediate between *S. grandisquamis* and *S. monensis,* it is evident that the variation in the present series includes all three supposed forms. There is probably a somewhat different range of variation on the several islands, but the extremes are certainly included in that of the Porto Rican series. Reproduced tails have a much widened series of median ventral scales.

An egg, probably of this species, was found under a log at Aibonito, August 21, 1919. It is white, discolored by stains, with a hard and smooth shell, 6 x 4.5 mm.

Anolis Daudin

Anolis cuvieri Merrem

Eleven specimens of this species were collected at Aibonito. *Anolis cuvieri* has been taken at Aibonito, Catalina Plantation (El Yunque), Humacao, Luquillo, Mayaguez, and Utuado. It is probably not found in the arid southwestern corner of the island, but ranges quite generally over the remaining part of Porto Rico. It is recorded from Vieques and

Tortola of the Virgin Islands. Its absence from the other Virgin Islands is probably due to difference in the habitat conditions. It is nearly allied to *Anolis ricordii* of Hispaniola.

There is little variation in this series. In No. 13234 the tail crest is unusually high, fully as high as in *A. ricordii* of Hispaniola, but the scale characters which distinguish *cuvieri* from *ricordii* are perfectly constant.

Seven out of eight stomachs examined contained the remains of large beetles; one, a large phasmid; one, remains of heteropterous bugs; and one, a mass of skin of *Anolis cuvieri* (doubtless its own). The boys say that it eats berries and fruits, and in the coffee plantations it is said to eat coffee berries. It seems probable that vegetable matter forms only a small proportion of its food, as in *Anolis cristatellus.*

Anolis cristatellus Duméril and Bibron

The following localities are represented by three hundred specimens in the collection: Adjuntas, Aibonito, Bayamon, Cataño, Coamo Springs, Ensenada, Maricao, Mayaguez, Salinas, San Truce, Desecheo Island, Mona, Vieques, and Culebra. This species ranges everywhere in Porto Rico. It occurs also on Mona and Desecheo Island, to the west, and extends through the entire Virgin group to the east. I do not regard the records of this species from Santo Domingo as valid. A nearly allied form is found in the Turk's Islands (*Anolis albipalpebralis* Barbour).

Stejneger regarded the *Anolis* of Mona Island as a species distinct from *A. cristatellus,* differing in having larger scales on the head; hence fewer loreals and fewer scales between the occipitals and the semicircles; in having a much higher tail crest, and a somewhat peculiar coloration. I cannot agree in this separation. Specimens from Ensenada and Coamo Springs agree exactly with those from Mona, while *A. cristatellus* from Culebra Island has an even higher caudal crest than those from Mona. The coloration of the Mona specimens taken on limestone is not ordinarily seen in Porto Rican *cristatellus,* but specimens taken on limestones at Ensenada, Salinas, and Coamo Springs are similarly colored. Ordinary *cristatellus* with low tail crests occur in the same area, and it is obviously impossible to separate them. The species does differ somewhat on the various islands, but the variation curves overlap too greatly to warrant even subspecific distinction. The number of scales between the occipital and the semicircles varies as follows in forty specimens respectively from Vieques and Mona Islands:

Number of scales between occipital and semicircles	1	2	3	4
Number of specimens, Mona Island	14	18	8	0
Number of specimens, Vieques	5	16	12	7

The vertical rows of loreals in the same series are as follows:

Loreals	5	6	7
Mona Island	27	11	2
Vieques	12	22	8

In the present series of Porto Rican specimens, adult males which wholly lack the tail "fin" are frequent, and such specimens are even more frequent in Vieques. Thus, of thirty-nine males collected in Vieques, none have a high continuous "fin" like those of Culebra or Mona, twenty-seven have a low serrated crest, about one-third as high as the diameter of the tail, and twelve lack the crest entirely, having merely a compressed tail with a denticulate row of dorsal scales. This is evidently the condition referred to by Reinhardt and Luekten (1863, Vidensk. Med. naturh. For. Kjøbenhavn, p. 249), whose comment was inexplicable to Stejneger (1904, p. 640) because he lacked a sufficient series from Vieques. In going from Vieques to Culebra, the difference between the tail crests of the males is very striking, and if they were not linked by Porto Rican specimens they would certainly be regarded as distinct forms. Thus, out of twenty Culebra males, only four have a crest as low as the highest found in the Vieques specimens, and in the remaining sixteen it varies from a height equal to the vertical diameter of the tail to twice the diameter. Evidently we have an excellent example of the beginning of the process of differentiation through isolation on islands of this plastic species. The specimens from Desecheo present no peculiarities.

Anolis cristatellus reaches an altitude of at least two thousand five hundred feet, being associated with *Anolis pulchellus* on the deforested hills near Maricao. It is evident that the differences in the distribution of this species and *A. gundlachi* are due not to altitude, but to habitat conditions, of which light seems to be one of the determining factors, *A. cristatellus* being the species of open fields and roadsides, *A. gundlachi* of the thickly planted coffee plantations and of the forests.

The examination of one hundred stomachs yields the following information as to food habits: Empty, 22; unidentified insect remains, 15; beetle remains, 20 (larva and adults; a species of *Diaprepes* very abundant); Orthoptera, 16 (cockroaches, grasshoppers, and a single cricket and mantis); ants, 10; caterpillars, 9; bugs, 5 (mostly heteroptera, one large cicada); flies, 3; spiders, 3; vegetable matter, 9 (mostly brightly colored seeds); vertebrates, 2 (*Anolis* sp.).

The eggs are two or three in number, about 10 x 6 mm., uniformly oval, the surface white and striate. They are frequently found under the edges of logs or stones, or in debris about the base of banana plants.

Anolis gundlachi Peters

Forty-eight specimens of this species were collected at the following localities: Adjuntas, Aibonito, Maricao, and El Yunque. This species is very distinct from *A. cristatellus,* but is obviously directly related to that species. Its range and habitat are much more restricted and the amount of variation is accordingly smaller. In the present series the height of the tail crest (at its highest point) reaches a maximum of three times the diameter of the tail at the same point.

Anolis stratulus Cope

The following localities are represented by fifty-eight specimens of this species in the collection: Aibonito, Coamo Springs, Ensenada, Maricao, El Yunque, and Vieques and Culebra Islands. The distribution of *Anolis stratulus* is closely similar to that of *Anolis cristatellus,* occurring on Porto Rico, Vieques, Culebra, St. Thomas, Tortola, and Jost Van Dyke. It is not found on Mona Island, and has not been recorded from St. Croix, where it might logically be expected to occur.

The series under examination shows only slight variation. The majority of specimens have the supraocular semicircles in contact. One (No. 13282) has only a single row of scales between the occipital and the semicircles. In recently hatched specimens the dorsal markings are invariably indistinct.

The examination of twenty-five stomachs indicates that ants form a much larger proportion of the food than in *A. cristatellus.* The contents are classified as follows: Empty, 3; unidentifiable insect remains, 4; ant remains, 12; beetle remains, 5; spiders, 2; cockroach, 1; earwig, 1; flies, 1; lizard skin (doubtless its own), 1.

Anolis evermanni Stejneger

The following localities are represented by thirty-seven specimens in the collection: Adjuntas, Aibonito, Maricao, and El Yunque. This species is confined to Porto Rico and does not appear to be especially related to the green *Anolis* of Hispaniola (*A. chlorocyanus*). It appears to be closely related to *Anolis mayeri* Fowler of the Virgin Islands. In Porto Rico it is most abundant in the coffee belt, but reaches the coastal plain at Rio Piedras and doubtless occasionally elsewhere.

As in *A. stratulus,* the scale between the supraciliaries and the supraorbital semicircles, anterior to the supraorbital granules, is remarkably constant. It is double on one side in only one specimen out of thirty-one examined. The semicircles may be broadly in contact (3 specimens), narrowly in contact (9), or separated by a single row of scales (19). The scales between the semicircles and the occipital vary from two to four.

Anolis mayeri from the Virgin Islands was compared in the original description with *Anolis cuvieri* and *Anolis cristatellus* (Fowler, 1918, Papers Dept. Marine Biol., Carnegie Inst., XII, p. 8, Fig. 4), chiefly because of the presence of small granular scales interspersed between the larger dorsal scales. On examination with sufficient magnification, both *A. cristatellus* and *A. evermanni* prove to exhibit this character. *A. mayeri* is therefore not particularly related to *A. cuvieri* and is in fact intermediate between *A. cristatellus* and *A. evermanni,* having the two scales bordering the supraocular granules anteriorly of *A. cristatellus,* while it is closely allied to *A. evermanni* by its habitus (especially the form of the head and tail), the larger scales, and the uniform (green) coloration. It is remarkable that no other specimens of this species have appeared in the numerous collections from the Virgin Islands.

The results of the examination of the contents of twenty stomachs are as follows: Empty, 3; beetle remains, 11; wasps, 2; ants, 1; caterpillars, 1; spiders, 1; skin of *Anolis* (doubtless its own), 2; juvenile *Anolis evermanni,* 1.

Anolis pulchellus Duméril and Bibron

The following localities are represented by eighty-seven specimens in the collection: Aibonito, Cataño, Coamo Springs, Ensenada, Maricao, Mayaguez, San Turce, Culebra and Vieques Islands.

Anolis pulchellus is recorded from nearly all of the Virgin Islands, including Anegada and St. Croix. Except for its absence from Mona Island, it has therefore the same distribution as *Anolis cristatellus.*

The number of loreal scales in a vertical row is usually four (five or six in *A. krugi*); in eighty-five specimens, sixty-nine have four loreal rows, fifteen have five, and one has six. The scales separating the occipital from the supraorbital semicircles number one in one specimen, two in twenty-nine specimens, three in fifty-one, and four in four. The semicircles are in contact in seventeen specimens, separated by one scale row in sixty-six, and by two scale rows in two.

Stejneger supposed that *Anolis pulchellus* was confined to the coastal plain area, rarely going above five hundred feet in altitude. In the course of the present survey it was found to be abundant everywhere, up to an altitude of at least two thousand feet, but strictly confined to open fields.

Anolis krugi Peters

The following localities are represented by sixty-two specimens in the collection: Adjuntas, Aibonito, Coamo Springs, Maricao, and El Yunque. *Anolis krugi* is confined to Porto Rico. In Porto Rico it is confined largely to the coffee belt, extending beyond it only where similar habitat conditions occur. It is directly related to the more widely distributed *Anolis pulchellus* and is probably derived from it. The specimens recorded from Guanica by Fowler (1918, Papers Dept. Marine Biol., Carnegie Inst., XII, p. 11) prove on re-examination to be *A. pulchellus.*

In sixty specimens, the number of loreal scales in a vertical row is four in one specimen, five in thirty-four, six in twenty-three, and seven in two. The number of scales between the occipital and the supraorbital semicircles varies from one to six—one in one specimen, two in eighteen, three in twenty-five, four in thirteen, five in two, and six in one. The supraorbital semicircles are in contact in two specimens, separated by a single scale row in thirty-four, by two scales rows in nineteen, and by three in five. This species is often difficult to distinguish from *A. pulchellus* without direct comparison; the color of the dewlap in life, orange instead of crimson, is distinctive. In alcoholic specimens the narrower band of enlarged dorsal scales is the most satisfactory character for separating the two. Other characters are at best comparative, useful only for a series of specimens.

Stejneger distinguished *Anolis krugi* as characteristic of the intermediate altitudes, from five hundred to fifteen hundred feet. The specimens in the present series from Coamo Springs are from an altitude of less than three hundred feet, while specimens from Aibonito reach an altitude of at least two thousand feet. The specimens from Coamo Springs supply the clue to the determining factor in the distribution of the species, for at that locality it was abundant among the ferns and vines of the moist, dark gorge back of the bath-houses and was found nowhere else. At Aibonito and Maricao, *Anolis pulchellus* was found on the bare hilltops or in open fields, while a few steps within the borders of the coffee plantations only *A. krugi* was to be found. Moisture and shade, therefore, are the habitat requirements of *Anolis krugi. Anolis cristatellus* and *Anolis gundlachi* have an exactly parallel distribution.

Anolis pencensis Stejneger

Thirty-eight specimens of this species were collected at Coamo Springs and Ensenada. This very distinct species of *Anolis* is confined to Porto Rico, and specifically to the arid southwestern area from Coamo Springs to Ensenada (and probably to Cabo Rojo).

Anolis poncensis is a highly unique species, not only in its lepidosis, but in the extremely small size of its throat fan, scarcely one-third as large as that of *A. pulchellus* or *A. krugi* when extended. There is little variation in the present series, which is much the largest hitherto examined. The coloration described by Stejneger is characteristic and constant. The females invariably have a broad mid-dorsal band. The loreal rows in a vertical line are three in eighteen specimens, four in twenty. The scales between the occipital and the supraorbital semicircles are none in two specimens, one in twenty-one, and two in fourteen. The scale rows separating the supraorbital semicircles are none in thirty-two specimens, one in six. This species was found associated with *Anolis cristatellus* and with a rare *A. pulchellus,* at both Coamo Springs and Ensenada. Broadly speaking, it replaces *A. pulchellus* in the southwestern part of the island, inhabiting fences and grazing land much as *A. pulchellus* does in the remaining part of the island. A few specimens were found on the arid cactus-covered hilltops about Ensenada. Near Coamo Springs this species occurred in colonies, sometimes a mile or more apart.

Cyclura Harlan

Cyclura stejnegeri Barbour and Noble

One specimen of this species was collected on Mona Island. This single specimen is a very old male with the irregular development of the large tubercular scales of the head characteristic of old specimens of this group. The nasal is separated from the rostral on one side by a space filled with very small scales; on the other by a large tubercular shield. A third "comb" is plainly distinguishable on the third toe. The scales of the reproduced tip of the tail are not arranged in verticils.

The measurements as as follows:

Total length (tail reproduced)	910	mm.
Body	470	"
Length of head	127	"
Breadth of head	79	"
Foreleg	173	"
Hind leg	260	"

In spite of the separation of the nasal shield from the rostral, I have retained the name *stejnegeri,* as it may well be the case that the young of the three related species, *cornuta, nigerrima,* and *stejnegeri,* are well distinguishable, while in the adults the characters are obscured. In other respects it accords well with the previously described specimens from Mona. Additional material of *cornuta,* however, is required to establish satisfactorily the status of the forms on Mona and Navassa.

Celestus Gray

Celestus pleii (Duméril and Bibron)

Seven specimens were collected at Aibonito. This species is confined to Porto Rico, where it is apparently rare and of local distribution.

The present series is so uniform in scale characters as to suggest that they are directly related. The proportion of the length of the forelimb to that of the body varies between 12:100 and 15:100. The scales about the body are 34 in one, 35 in one, 36 in four, and 38 in one.

The two female specimens contain respectively one and three well advanced embryos. The egg measures 18 x 11 mm. The completely formed embryo rests on a very large yolk mass. The head and legs of the embryo are proportionately larger than in the adult, while the tail is shorter.

Ameiva Meyer

Ameiva exsul Cope

The following localities are represented by fifty-two specimens in the collection: Coamo Springs, Ensenada, Palo, Seco Point, San Truce, and Culebra Island. This species reaches a large size, apparently much exceeding half a meter, but the larger specimens are exceptionally wary and I was unable to secure them. The largest seen was on Culebra Island. In nearly all the specimens examined an additional row of ventral plates on each side is enlarged to a varying degree, in some cases to such an extent that there are distinctly twelve longitudinal rows of ventrals.

The common report in Porto Rico that the "iguana" eats the shoots of young corn appears to be supported to a degree by an examination of stomach contents. Of twenty stomachs examined, one was empty; eleven contained vegetable matter, chiefly large numbers of red-coated seeds; five, unidentifiable insect remains; two, crickets; three, small crabs; three, eggs of a lizard; one, tail of a large *Anolis cristatellus;* and six, parasitic worms.

Ameiva alboguttata Boulenger

Forty-two specimens were collected on Mona Island. This species is confined to Mona Island, where it is abundant on the low terrace to the west and south.

Ameiva alboguttata is extremely close to *Ameiva exsul,* but may be distinguished by the more spotted dorsum. The Mona Island form does not exhibit the tendency to enlargement of an additional row of ventral plates, one specimen having only eight longitudinal rows of ventrals (No. 13739).

The results of the examination of twenty stomachs are as follows: Empty, 4; vegetable matter (chiefly red-coated seeds), 8; unidentifiable insect remains, 3; beetles, 3; crickets, 2; land snails, 2; *Anolis cristatellus* (juv.), 1.

Ameiva wetmorei Stejneger

Twenty-seven specimens were collected from Ensenada. This species, hitherto known only from two specimens, appears to be confined to the region near Ensenada. It probably ranges westward toward Cabo Rojo and eastward toward Ponce, on the limestone hills. *Ameiva lineolata,* its relative in Hispaniola, appears to be similarly confined to the more arid parts of that island, and arid or semiarid conditions prevail also on Great Inagua and St. Croix, each of which is inhabited by a related species. These four species form a highly interesting group of Ameivas, characterized by the oblique scales of the tail, a distinctive habitus, and a lineolate type of coloration.

In the present series the prefrontals are broadly in contact in twenty-one specimens, meet at a point in one, and are separated by a suture between the frontal and frontonasal in three. The number of supraciliaries varies from five to seven; normally six. The interparietal is horizontally divided in one specimen. There are usually two or three transversely enlarged postoccipitals. On the whole, there is a remarkably small degree of variation.

The measurements of a male and female specimen are:

	A. M. N. H.			
	No. 13821 ♂		No. 13828 ♀	
Total length (tail reproduced at tip)	169	mm.	147	mm.
Body	52	"	45	"
Length of head	12.5	"	11	"
Breadth of head	8.5	"	6.5	"
Foreleg	16	"	14	"
Hind leg	30	"	26	"

This species was found only on or near the tops of the limestone hills back of Ensenada, associated with a few *Ameiva exsul.*

Amphisbæna Linné

Amphisbæna cæca Cuvier

Eighteen specimens of this species were collected at Aibonito, Bayamon, and Rio Piedras. This species is confined to Porto Rico, with a related species in the Virgin Islands (*A. fenestrata*) and another in Hispaniola (*A. manni*).

The variation in the present series falls well within the limits established by Stejneger. One specimen has a small supraocular plate on each side. When killed in formalin, the head is bent abruptly to one side, indicating apparently a special development of the muscles of the neck, which doubtless is of advantage to the animal in burrowing. The largest specimen measures 233 mm.; tail, 18 mm.

All of the specimens were found burrowing in the ground, most of them uncovered by cultivation. One was found about three inches beneath an ant's nest, under a log, while digging up the eggs of *Leimadophis.* Three eggs were found—one beneath a termite nest, the other two under the log where the above-mentioned adult was dug up. The largest egg measured 42 x 11 mm.

Mabuya Fitzinger

Mabuya sloanii (Daudin)

The following localities are represented by seven specimens in the collection: Bayamon, Ensenada, and Mona and Culebra Islands. This species ranges from Mona Island through Porto Rico and the Virgin Islands. Barbour (1916, p. 219) refers two specimens from Turk's Island, in the southern Bahamas, to this species, and it seems probable that the *Mabuya* of Hispaniola is also referable to the same species.

With seven specimens before me—three from Culebra, three from Porto Rico, and one from Mona—I am unable to find differences corresponding to the separate localities, other than the difference in color described below. In all specimens there are two pairs of chin shields in contact behind the unpaired postmental. The prefrontals are narrowly or widely separated by a suture between the frontal and the frontonasal. The supraoculars are three on one side in one specimen. One specimen has three large occipitals on one side. The scales about the body are thirty-two in the specimens from Culebra and Mona and in one from Porto Rico, thirty in the remaining two.

The coloration is highly interesting. The three specimens from Porto Rico agree with the description of Stejneger (1904, p. 611) in the presence of a narrow black border above the dorsolateral light line. In the specimens from Culebra this is increased anteriorly to include the whole of the head, neck, and shoulders, leaving, however, a sharply defined median light line from the frontal to the shoulders, where it merges into the dorsal color. This pattern is approximated also in the specimen from Mona Island. It is evident that the type of *Euprepes semitæniatus* Wiegmann described by Stejneger (1904, p. 610) corresponds accurately with the Culebra specimens. It is therefore possible that the Porto Rican form may be sufficiently distinguishable to merit specific or subspecific designation, in which case *sloanii* would be restricted to the form in the Virgin Islands (including Vieques and Culebra) and *M. nitida* Garman would be applicable to the Porto Rican and Santo Domingan form. In view of the close approach of the Mona specimen to those from Culebra, I prefer to retain, for the present, the use of *sloanii* for the entire series.

The measurements of the only specimen with a complete tail are as follows:

	A. M. N. H. No. 14007
Length	180 mm.
Body	67 "
Length of head	15 "
Breadth of head	10 "
Foreleg	17 "
Hind leg	25 "

The largest specimen (from Culebra) measures 90 mm. from snout to vent.

Typhlops Oppel

Typhlops richardii Duméril and Bibron

Typhlops richardii Duméril and Bibron, 1844, Erpetol. Gen., VI, p. 290.

Typhlops lumbricalis Stejneger, 1904, Rept. U. S. Nat. Mus., 1902, p. 684, figs. 141-144.

Typhlops lumbricalis (part) Barbour, 1914, Mem. Mus. Comp. Zoöl., XLIV, p. 322.

Nineteen specimens of this species were collected at Bayamon.

The common species of *Typhlops* in Porto Rico has been referred to *T. lumbricalis* by all authors since the publication of Boulenger's "Catalogue of Snakes" (1893). The large series now before me appear to warrant a distinction of the Porto Rican form, for which I have used the name applied by Duméril and Bibron to the *Typhlops* from St. Thomas, on the ground that it is logically likely to be conspecific with the Porto Rican form. In its more elongate form and greater number of scales from snout to vent, the description of *T. richardii* applies fairly well to the series from Porto Rico. *Typhlops lumbricalis* is reported from all of the Greater Antilles and from a large number of the Lesser Antilles. Being unable to examine specimens from the Lesser Antilles, I am unable to form an opinion as to the status of the form found there. The Linnean description of *T. lumbricalis* is said by Duméril and Bibron to be taken from the Jamaican *Amphisbœna argenta* of Browne. Not having Jamaican specimens for comparison, I have compared the Porto Rican series with the specimens from Cuba in The American Museum of Natural History.

In fourteen specimens examined in detail, the total length varies from 216 to 310 mm.; average, 266 mm. The largest specimen available from Cuba measures 244 mm., the average length of nine specimens is 203 mm., and the specimen selected by Barbour for description in the "Herpetology of Cuba" (Barbour and Ramsden, 1919, Mem. Mus. Comp. Zoöl., Cambridge, XLVII, p. 185) measures only 182 mm. It appears, therefore, that the Porto Rican and Cuban *Typhlops* are distinctly different in adult size. The ratio of the body diameter to total length is only slightly different in the two series, 34 to 44 in the Porto Rican, 27 to 38 in Cuban. The number of scales about the body is 22-20-20 in seven specimens, 22-20-18 in seven, in the Porto Rican series; the reduction to 20 scale rows occurring only a little anterior to the middle of the body. In the Cuban series the scale formula is 20-20-18 in six, 20-18-18 in three specimens. The number of scales counted on the mid-dorsal line from snout to tail spine ranges from 365 to 415 in the Porto Rican specimens and from 270 to 325 in the Cuban. (The Cuban specimen described by Barbour has been reëxamined at my request by Mr. Emmett R. Dunn and is found to have between 320 and 325 scales on the mid-dorsal line.) In spite of the relatively small series of Cuban specimens at my disposal, it seems unlikely that the range of variation of a larger number would be greatly different.

The Porto Rican specimens are darker in color, and, with a single exception, the tail is marked with a white ring. In the specimen described by Stejneger (1904, p. 685), as well as in the exception here noted, the white ventral color forms a prominent notch on the side of the tail, indicating the existence of the tendency to form a ring. No such notch or ring is found in Santo Domingan or Cuban specimens.

The differences, then, between the Porto Rican and the Cuban *Typhlops* may be summarized as follows:

	Porto Rican	Cuban
Average length of adult......	Greater than 250 mm.	Less than 250 mm.
Scales about the body.......	22-20-20 or 22-20-18	20-20-18 or 20-18-18
Scales from snout to tail spine.	365-415	270-325
Tail.........................	With white ring or notch	Without white ring or notch

The specimens of the present series were found during cultivation on the farm of Mr. B. A. Wall. The single specimen secured by me personally was burrowing in the loose earth around an old stump, in which both *Typhlops* and *Leimadophis* eggs were found.

Three eggs of this species were found in the soil about the same stump, containing well-developed embryos. The egg is elongated, like a slightly bent cylinder with rounded ends, with a perfectly smooth, white surface. The embryo measures 98 mm. in length and 3 mm. in diameter. The smallest hatched specimens found measure 114 mm.

Three of the smallest specimens in the collection are in every way like the adults, except that they are pale grayish white. This appears on examination to be caused by the opacity of the skin, which is nearly ready to be shed, probably for the first time. An adult Cuban specimen in the collection has the same appearance, and the underlying skin proves to be normally colored. Some of the cases of supposed albinism in *T. lumbricalis* may be due to this appearance.

Typhlops rostellatus Stejneger

Eleven specimens of this species were collected at Aibonito and Bayamon. This species is confined to Porto Rico, where it proves to be widely distributed.

It is readily distinguished from *T. lumbricalis* by its nearly uniform coloration above and below and the sharply defined white subcaudal spot. There is little variation in the present series. The scales about the body number twenty in ten specimens, eighteen in one.

The measurements of the largest specimen are as follows:

	A. M. N. H. No. 13345
Total length..	205 mm.
Tail..	5 "
Greatest diameter..................................	4.5 "

Leimadophis Fitzinger

Leimadophis stahli Stejneger

Twenty-four specimens of this species were collected at Aibonito, Bayamon, and Ensenada. *Leimadophis stahli* is confined to Porto Rico, replaced by a vicarious form, *L. exiguus*, in the Virgin Islands, and closely related to the Hispaniolan *L. parvifrons*.

The range in number of ventral plates is slightly greater in this series than in Stejneger's—146-166 in twenty-three specimens. The subcaudals range from 83-94. The sexes are scarcely distinguishable by these characters. The tail length varies from .29 to .34 of the total length (.29-.31 in ♀, .32-.34 in ♂ specimens). The scales about the body are uniformly 19-19-17. The lower labials are nine (eight in the original description). Freshly hatched specimens show the color pattern most distinctly, especially the median black marking on the head. The largest specimen, a female, measures 580 mm.; tail, 178 mm.

Eggs of this species were found in three places: under a log in a pasture and under an old termite nest in a coffee plantation at Aibonito and in the loose soil under a stump at Bayamon. One lot contained seven eggs, one thirteen, and one forty. Six well-developed eggs were found in the adult female staying with the largest number. The eggs in this place were in three lots: eighteen old and discolored, in two clusters; six loose, somewhat different in appearance; and two clusters of six and ten eggs very fresh and white. Examination of the eggs showed that they contained embryos at at least three stages, the fresher eggs having scarcely begun development, the oldest containing embryos nearly ready to hatch. The eggs found under the termite nest were also in two clusters—one of seven eggs, with advanced embryos, the other of six, with no apparent development. The older eggs are slightly larger, ranging from 21 to 25 mm. in length and from 12 to 15 mm. in diameter. The surface is finely striate, very white in the fresher specimens. It appears that the adult females of this species take up a location from which they do not wander far, and in which they lay successive batches of eggs, from six to eighteen (?) in number. The largest "nest" contained the remains of still older eggs, which were either infertile or from which the young had hatched. The eggs are laid in clusters of six to ten, the individual eggs adhering firmly to the mass. The rate of reproduction is evidently fairly rapid.

Alsophis Fitzinger

Alsophis antillensis (Schlegel)

Alsophis anegadæ Barbour, 1917, Proc. Biol. Soc. Wash., XXX, p. 102.

Two specimens were collected at Coamo Springs. This species has not hitherto been recorded from Porto Rico, although there is an older, questionable record from Haiti. Its presence in Porto Rico, together with that of *Eleutherodactylus antillensis,* diminishes the difference between the Porto Rican fauna and that of the Virgin Islands.

The identification of these two specimens with this species removes the element of geographical distinctness from the allied *A. portoricensis.* The male specimen has only seventeen scale rows, and so might be identified with *A. portoricensis,* were it not that the coloration of both is nearly typical of *A. antillensis,* while the female has nineteen scale rows at mid-body. In view of the higher number of ventral plates and the distinct coloration, I prefer to retain *portoricensis* and *antillensis* as distinct species.

These specimens agree closely in coloration with the color variety described by Barbour from Anegada, and as I do not wish to admit of a discontinuous distribution of *A. anegadæ,* it seems best to include both Porto Rican and Anegadan specimens with *A. antillensis.*

The measurements and scale characters are as follows:

	A. M. N. H. No. 13305 ♂	 No. 13306 ♀
Length	707 mm.	820 mm.
Tail	245 "	270 "
Tail length	.35 "	.33 "
Ventral plates	184 "	185 "
Subcaudals	134 "	132 "
Dorsal scales	17-17-15 "	17-19-15 "

Alsophis portoricensis Reinhardt and Luetken

Four specimens of this species were collected, at Adjuntas and on Mona Island. This species is confined to Porto Rico and Mona Island, its nearest relatives being *A. melanichnus* in Hispaniola and *A. antillensis* in Porto Rico and the Virgin Islands.

The two specimens from Adjuntas are perfectly typical in coloration, the dorsal scales and ventral plates being heavily bordered with black. In the two Mona Island specimens the black is arranged as irregular transverse markings, not confined to the borders of the scales. There does not seem to be any scale character distinguishing them from typical *portoricensis.* The four specimens fall within the limits of variation established by Stejneger in every respect. The two from Adjuntas have the dorsal scale formula of 17-17-14 instead of 17-17-15, as in the Mona Island specimens.

The stomach of one of the specimens from Mona contained the remains of two *Ameiva alboguttata,* and that of the other contained a tail of the same species.

LITERATURE

BARBOUR, THOMAS

1914. A contribution to the zoögeography of the West Indies, with especial reference to amphibians and reptiles. Mem. Mus. Comp. Zoöl., XLIV, pp. 209-359, Pl. I, text-fig. 1.

1915. Recent notes regarding West Indian reptiles and amphibians. Proc. Biol. Soc. Wash., XXVIII, pp. 71-78.

1916. Additional notes on West Indian reptiles and amphibians. Proc. Biol. Soc. Wash., XXIX, pp. 215-220.

1917. Notes on the herpetology of the Virgin Islands. Proc. Biol. Soc. Wash., XXX, pp. 97-104.

1919. Herpetological notes. Notes on *Celestus.* Proc. New England Zoöl. Club, VII, pp. 11-13.

1919*a.* A new rock iguana from Porto Rico. Proc. Biol. Soc. Wash., XXXII, pp. 145-148, Pl. I.

BARBOUR, THOMAS, and NOBLE, G. KINGSLEY

1915. A revision of the lizards of the genus *Ameiva.* Bull. Mus. Comp. Zoöl., LX, pp. 139-164, Pls. I-XV.

FOWLER, HENRY W.

1918. Some amphibians and reptiles from Porto Rico and the Virgin Islands. Papers Dept. Marine Biol., Carnegie Inst.. XII, pp. 1-15, Pl. I, text-figs. 1-6.

STEJNEGER, LEONHARD

1904. The herpetology of Porto Rico. Rept. U. S. Nat. Mus., 1902, pp. 549-724, Pl. I, text-figs. 1-197.

1913. A new lizard from Porto Rico. Proc. Biol. Soc. Wash., XXVI, pp. 69-72.

GENERAL INDEX TO VOLUME XXVIII