UNIVERSITY OF CALIFORNIA PUBLICATIONS

IN

ZOÖLOGY

VOLUME XLVI
1941–1943

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
1943

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
CALIFORNIA

CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

PRINTED IN THE UNITED STATES OF AMERICA

CONTENTS

THE NATURAL HISTORY AND CLASSIFICATION OF THE MOUNT LYELL SALAMANDER, HYDROMANTES PLATYCEPHALUS

BY

LOWELL ADAMS

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOÖLOGY
Volume 46, No. 2, pp. 179–204, plates 21–22, 9 figures in text

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
1942

THE NATURAL HISTORY AND CLASSIFICATION OF THE MOUNT LYELL SALAMANDER, HYDROMANTES PLATYCEPHALUS

BY

LOWELL ADAMS

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY AND LOS ANGELES
1942

UNIVERSITY OF CALIFORNIA PUBLICATIONS IN ZOÖLOGY
EDITORS (Berkeley): J. F. DANIEL, HAROLD KIRBY, S. F. LIGHT, A. H. MILLER
Volume 46, No. 2, pp. 179–204, plates 21–22, 9 figures in text
Submitted by editors July 1, 1940
Issued May 2, 1942
Price, 35 cents

UNIVERSITY OF CALIFORNIA PRESS
BERKELEY, CALIFORNIA

CAMBRIDGE UNIVERSITY PRESS
LONDON, ENGLAND

PRINTED IN THE UNITED STATES OF AMERICA

THE NATURAL HISTORY AND CLASSIFICATION OF THE MOUNT LYELL SALAMANDER, HYDROMANTES PLATYCEPHALUS

BY

LOWELL ADAMS

(Contribution from the Museum of Vertebrate Zoölogy of the University of California)

INTRODUCTION

THE MOUNT LYELL SALAMANDER was discovered and named in 1916 by Camp, who recognized its close resemblance to *Oedipus* (*Spelerpes*) of Mexico, and accordingly placed it in that genus. Later, Dunn (1923) transferred it to the genus *Hydromantes*. This genus is at present composed of only two full species, *Hydromantes genei* of Sardinia and the mainland of Italy, and *Hydromantes platycephalus* of the Sierra Nevada of California. *Hydromantes italicus* has been reduced to subspecific status under *H. genei* by Wolterstorff (1925), and Pomini (1936) was unable to verify the existence of *ferrugineus*, which Lazzarini (1930) assigned to the genus *Hydromantes*. The zoögeographic significance of the discontinuous distribution of *Hydromantes* is emphasized by Dunn: "The most startling discovery made in the United States since Stejneger announced the finding of a discoglossal toad in the Olympic Mountains was that of *Spelerpes platycephalus* in the Yosemite by Camp." Dunn's reference of *platycephalus* to the genus *Hydromantes* was based on examination of only two specimens. An understandable reluctance on Dunn's part to dissect any of the then few known specimens and thus destroy certain external characters would explain why he did not cite many features of internal structure in support of his generic identification. This omission, especially in view of the importance ascribed to the identification, led me to undertake an independent appraisal of the relationships of the Mount Lyell salamander. With more specimens available, selected parts of the internal anatomy were investigated to provide a wider basis for judging the animal's affinities.

My interest in the Mount Lyell salamander dates from 1935, when I was rearranging the study collections of the Yosemite Museum. About 25 specimens were then in the collections—probably three-fourths of all the known material. These formed the nucleus for the present study.

For many helpful suggestions and criticisms I am indebted to Professor E. Raymond Hall, under whose supervision this work has been done, and to Professor Charles L. Camp, Professor Alden H. Miller, and Dr. Jean M. Linsdale. Mr. James E. Cole aroused my initial interest in the problem, and lent specimens from the Yosemite Museum. Other specimens came from the California Academy of Sciences, Stanford University, and Wilbur V. Henry, who graciously lent me the specimens which he himself had planned to use in a similar study. I did most of the present work at the Museum of Vertebrate Zoölogy through the kindness of the late Professor Joseph Grinnell. Mr.

Thomas L. Rodgers has assisted with the staining of skeletons, and Professor E. O. Essig has kindly identified insects recovered from the stomachs of the salamanders. To these persons, and others, I wish to express my gratitude for their assistance and coöperation.

CLASSIFICATION

Genus **Hydromantes** Gistel

Hydromantes Gistel, Naturgesch. Thierr., 1848, p. XI (first use of name known to me).

Diagnosis.—Tongue boletoid; two premaxillae; a fontanelle; septomaxilla present or absent; maxilla normal; prefrontal absent; vomerine and parasphenoid series not continuous; internal nares a slit in prevomer; atlas normal; eyes functional; no aquatic larval stage; males with swollen snout and with enlarged premaxillary (sometimes also maxillary) teeth; tail not constricted at base; toes 4–5, half-webbed; terminal phalanges T-shaped; no palmar tubercles; 2 species.

Classification of the genera of plethodontids has been based largely on characters of the skull. Dunn (1926) used the following skull characters in diagnosing genera: premaxillae, fused or unfused; fontanelle, present or absent; septomaxillae, present or absent; maxillae, normal or edentulous; prefrontals, present or absent, bordering or not bordering nares; internal nares, notch or slit in prevomer; vomerine and parasphenoid teeth, continuous or discontinuous; condyles, sessile or stalked; atlas, normal or with transverse collar; other characters used by Dunn are: tongue, boletoid or attached at margin; eyes, functional or nonfunctional; sexual dimorphism, present or absent; tail constriction at base, present or absent; number of toes; amount of webbing between toes; shape of terminal phalanges; palmar tubercles, present or absent.

Piatt (1935), in an attempt to trace the ancestry of *Hydromantes,* has used characters of the hyobranchial apparatus and throat musculature. Noble (1927) and Dunn (1926) have pointed out the value of life history data in studies of phylogeny.

On the basis of the characters listed, these authors have agreed that *Hydromantes* is more closely related to *Oedipus* than to any other genus, and that both are well differentiated from other genera of plethodontids. Piatt (1935), relying on the hyobranchial apparatus and throat musculature, concluded that the *Oedipus* group developed from a *Plethodon* ancestry. Dunn (1926) assumed that *Oedipus* and *Hydromantes* arose from some terrestrial form, but made no attempt to trace their ancestry among the known terrestrial plethodontids. Noble (1931) pointed out the resemblance of the *Oedipus* group to both *Eurycea* and *Plethodon,* but reached no final conclusion regarding the immediate ancestors.

Hydromantes platycephalus (Camp)
Mount Lyell salamander

Spelerpes platycephalus Camp (1916, p. 11)
Hydromantes platycephalus, Dunn (1923, p. 40)
Eurycea platycephala, Stejneger and Barbour (1917, p. 20)

External characters (pl. 21, fig. *b*).—Adult male (Yosemite Mus., no. 171, Half Dome, 8852 feet, Mariposa County, California): 11 costal grooves; appressed toes of fore and hind feet overlap a distance of one costal fold; head width 19.6 per cent of length from tip of snout to posterior end of vent; length of head from tip of snout to gular fold, 23.9 per cent of length from tip of snout to posterior end of vent; snout not appreciably more swollen than in females at hand; eye longer than its distance from tip of snout; mouth curved upward at the angle; angle of jaw behind posterior angle of eye; teeth on upper jaw long, irregular in size and spacing, protruding beneath upper lip, 12 on right maxilla and premaxilla; upper eyelid fitting over lower in front and behind; a groove from eye to gular fold; bulge on side of head between posterior angle of eye and angle of mouth, larger than in females at hand; limbs slightly smaller in proportion to body than those of

TABLE 1

MEASUREMENTS OF TOTAL LENGTH AND HEAD WIDTH (IN MILLIMETERS)

Description	Number of specimens	Range	Average length	Standard deviation
Males, length	23	71.7–98.1	82.9 ± 1.4	6.8 ± 1.0
Females, length	26	71.4–97.5	79.8 ± 1.5	7.6 ± 1.0
Males, head width	23	8.7–12.6	10.1 ± 0.2	1.0 ± 0.2
Females, head width	26	8.2–10.8	9.6 ± 0.1	0.7 ± 0.1

TABLE 2

MEASUREMENTS OF SKULLS (IN MILLIMETERS)

Description	*H. gensi* MVZ no. 27301		*H. gensi* MVZ no. 11188		*H. platycephalus* MVZ no. 32221	
	Dimensions	Per cent of skull length	Dimensions	Per cent of skull length	Dimensions	Per cent of skull length
Premaxillae to ventral lip of foramen magnum	11.1	100.0	12.3	100.0	9.5	100.0
Premaxillae to posterior-median tip of vomerine tooth row	4.7	42.3	5.6	45.5	3.8	40.0
Width across frontals at narrowest point	2.5	22.5	2.9	24.4	2.6	27.4
Width across parietals	3.7	33.3	4.3	35.0	3.7	39.0
Width across otic capsules	6.4	57.7	7.4	60.2	5.7	60.0
Depth of skull back of vomerine tooth row	1.6	14.4	2.1	17.1	1.4	14.7
Depth of skull anterior to otic capsules	2.5	22.5	2.9	23.6	1.4	14.7
Length of premaxillary spine[a]	3.1	28.0	3.6	29.3	1.7	17.9
Length of parasphenoid tooth row	4.2 (right) 3.9 (left)		5.4 (right) 5.0 (left)		2.9 (right) 3.5 (left)	

[a] Extends to frontal in *H. gensi*. Separated 0.7 mm. from frontals in *H. platycephalus*.

Triturus torosus; fingers in order of length are 3, 2, 4, 1, webbed at base; toes in order of length, 3, 4, 2, 5, 1, webbed to next to last joint; toes and fingers slightly flattened, enlarged at tips; tail circular in cross section, not constricted at base, shorter than body; cloacal lips smooth, gaping; vomerine tooth rows not continuous with tooth patches on parasphenoids, separated from each other by the width of the nares and from tooth patches of parasphenoids by 8 times that distance; teeth of parasphenoids in two distinct patches, broadest and farthest from each other near the posterior end. Color, of specimens preserved in 65 per cent alcohol: middle of back, top of head, tail and legs obscurely mottled with dark gray and dark brown, becoming lighter brown on ventral surfaces; no lichenlike markings; these are present, however, in other specimens at hand.

Variations.—Adult female (Yosemite Mus., no. 159, Half Dome): Appressed toes fail to meet by one-half costal fold; head width 18.8 per cent of length from tip of snout to posterior tip of vent; head length 23.1 per cent of length from tip of snout to posterior tip

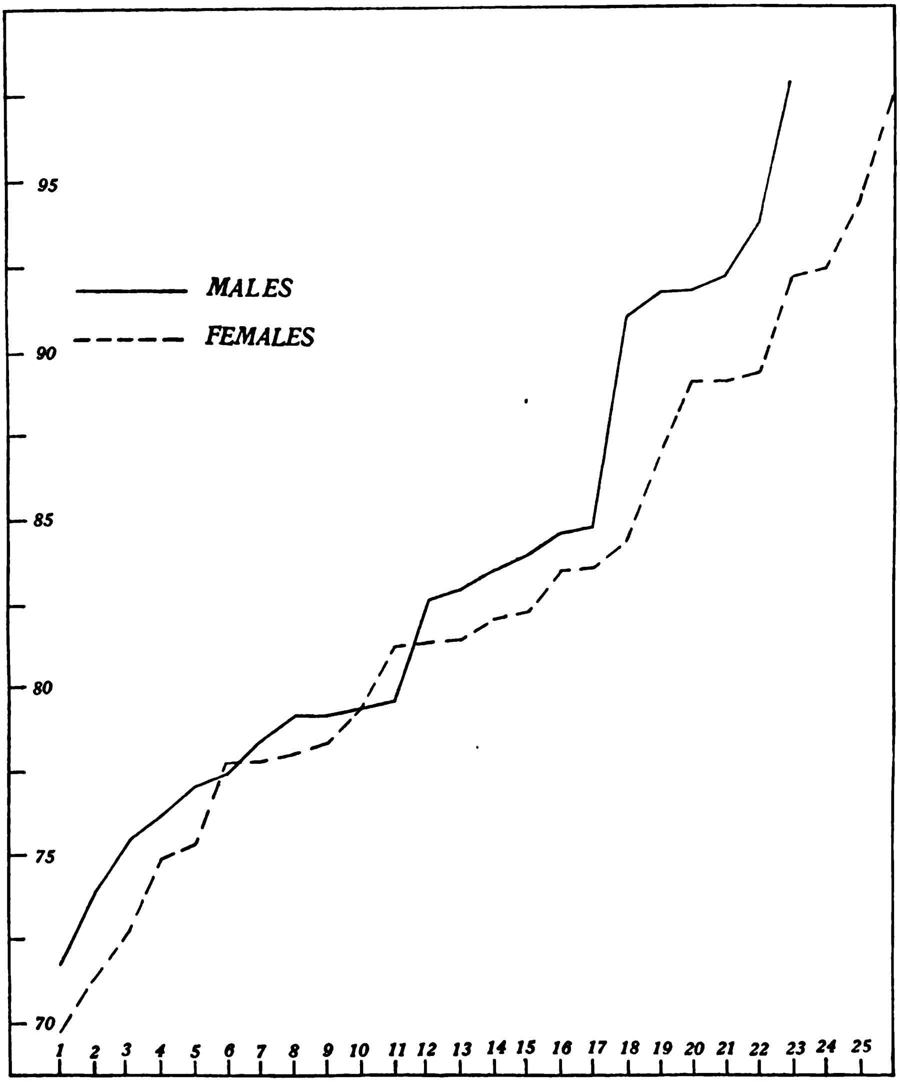


Fig. 1. Differences in total length between males and females of the Mount Lyell salamander. Numbers on ordinate indicate total length in millimeters. Salamanders numbered (shown on abscissa) in an ascending series based on size.

of vent; mouth not curved upward at the angle; teeth on upper jaw not long as in males; bulge on side of head between posterior angle of eye and angle of mouth, smaller than in males at hand; cloacal lips not gaping.

Yearling (Yosemite Mus., no. 166, Half Dome): the appressed toes overlap for a distance of one-half costal fold; head width 18.5 per cent of length of body from tip of snout to posterior tip of vent; head length 24.4 per cent of length of body from tip of snout to posterior tip of vent; head not as flat in proportion to its width as in adults; mouth not curved upward at angle; teeth on upper jaw not long as in males; tail slightly compressed laterally along distal half; cloacal lips not gaping; color, darker brown on under parts than in adults.

Young-of-the-year (Yosemite Mus., no. 178, Half Dome): Appressed toes meet; width of head 20.5 per cent of length of body from tip of snout to posterior tip of vent; length of head 25.6 per cent of length of body from tip of snout to posterior tip of vent; snout less swollen than in intermediate sizes and adults; nostrils larger than in intermediates and

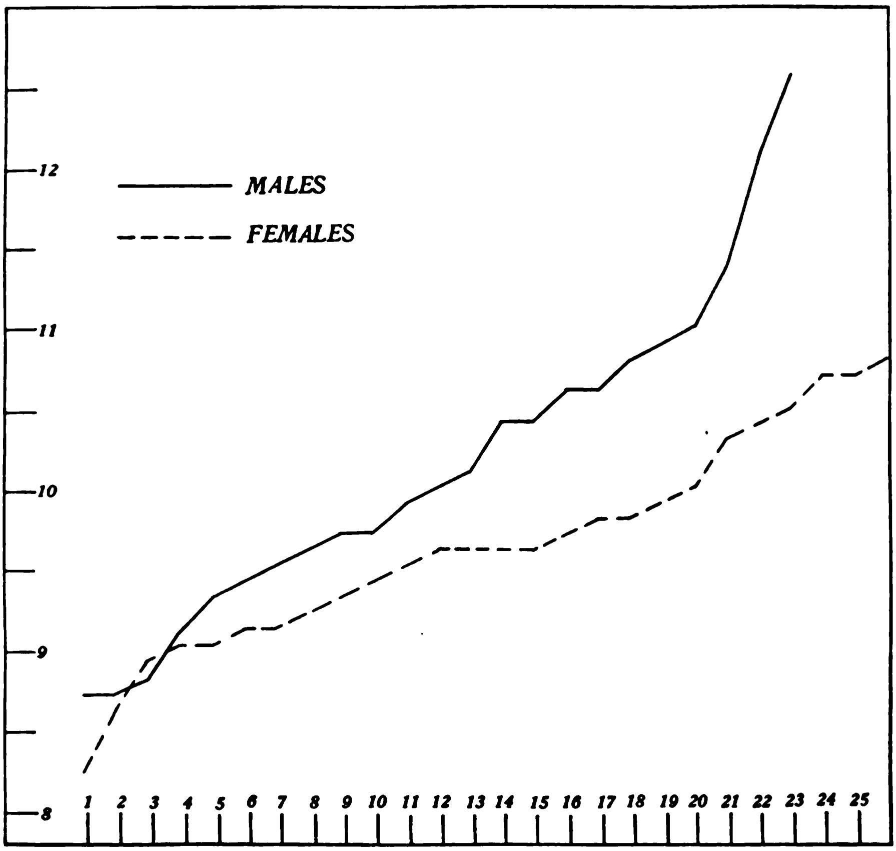


Fig. 2. Differences in head width between males and females of the Mount Lyell salamander. Numbers on ordinate indicate head widths in millimeters. Salamanders numbered (shown on abscissa) in an ascending series based on size.

adults; mouth not curved upward at the angle; teeth on upper jaw not enlarged as in adult males; no bulge at sides of head; neck as wide as head; head not as flat in proportion to its width as in adults; toes in order of length, 4, 3, 2, 5, 1; tail slightly constricted laterally in distal half; cloacal lips not gaping; brown of underparts darker than in adults.

Secondary sexual differences.—Enlarged maxillary and premaxillary teeth present in male only, and can be easily detected by rubbing fingertips across the mouth. The gaping cloaca in the male contrasts with the closed lips of the cloaca of females in all the preserved specimens examined.

In general appearance (size, color, proportions) the sexes are indistinguishable when individual specimens are considered. Nevertheless, the accompanying graphs (see figs. 1, 2) and table 1 indicate that the males average slightly larger than the females, and the difference is disproportionately greater in the group of larger animals. Blanchard (1928)

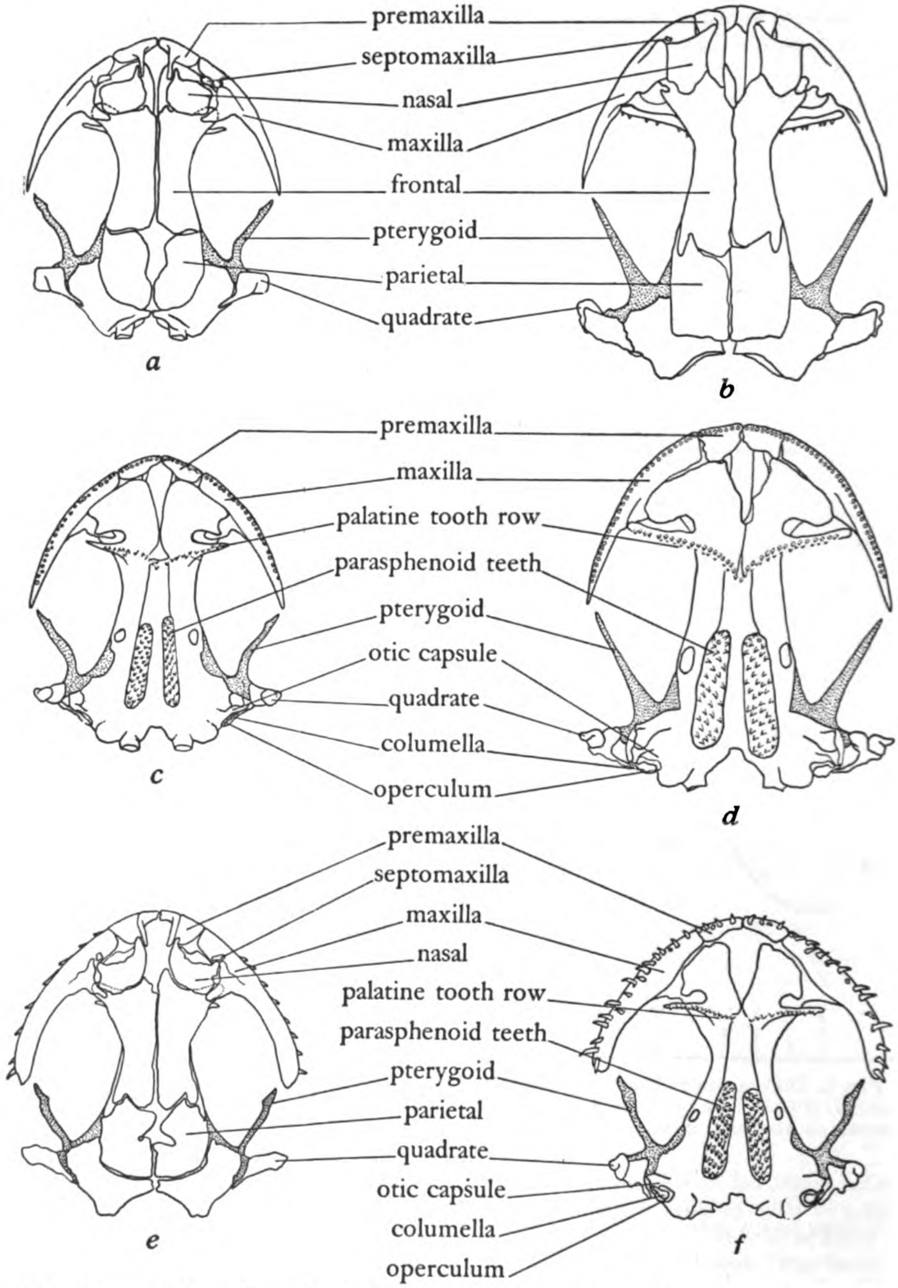


Fig. 3. Dorsal views of crania of females: (*a*) *Hydromantes platycephalus* and (*b*) *H. genei;* (*c*), (*d*) ventral views of same; (*e*) dorsal and (*f*) ventral views of male *H. platycephalus;* × 3.5.

found that in *Plethodon cinereus cinereus* the difference is just the reverse, the females being larger than the males. The difference seems slightly greater in *Plethodon*.

Skulls.—Measurements of the skulls of *Hydromantes genei* and *H. platycephalus* are given in table 2 (see also figure 3). For purposes of these comparisons skulls of two *Hydromantes genei genei* and two *H. platycephalus* were stained with alizerine red. Measurements were made with calipers calibrated to 0.1 millimeter on a vernier scale.

As shown by these measurements, the skull of an adult female of *Hydromantes platycephalus*, compared to that of *H. genei*, is shorter and more nearly flat; the brain case, relative to length of skull, is wider anteriorly and of about equal width posteriorly; ossification of

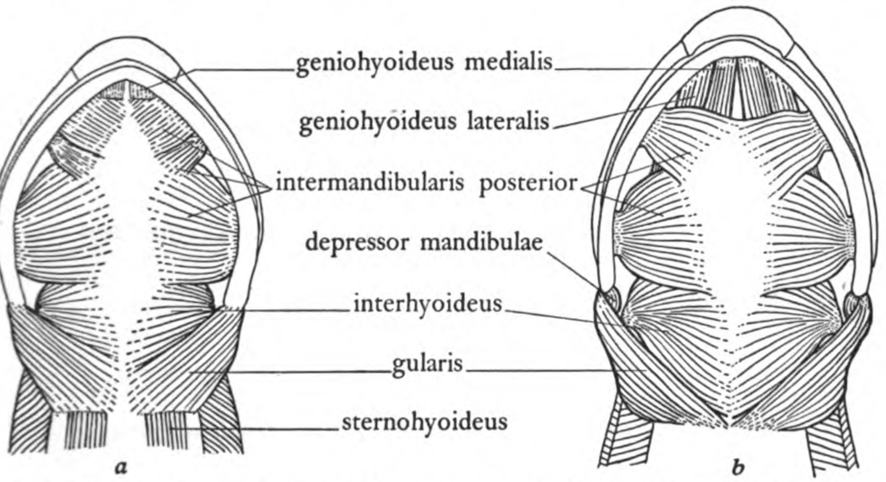


Fig. 4. Ventral view of head, with skin removed to show transverse muscles of throat and floor of mouth; (*a*) *H. platycephalus* and (*b*) *H. genei*, × 3.5.

the skull is less extensive and premaxillary spines are shorter and weaker; the vomerine tooth row, which extends laterally to the maxillae in *genei*, is considerably shorter in *platycephalus*. Other differences in size and proportion are apparent but in generic characters mentioned on page 180 the two species are alike, and the descriptions given by Dunn, Piatt, and Noble (*op. cit.*) are fully applicable to the specimens which I examined.

Muscles of Head Region

Further evidence of the close resemblance of *H. platycephalus* and *H. genei* is apparent upon examination of the muscles of the head region. The following descriptions and illustrations (figs. 4–7, incl.) are based on my own dissection of the muscles in four specimens of *platycephalus* and one of *genei*. Each muscle is described for *platycephalus*, and any marked differences in origins and insertions which distinguish the muscles in *genei* from those in *platycephalus* are noted.

Wiedersheim (1875) has described the musculature of the European *Hydromantes*. Piatt (1935) used the characters of the muscles of the throat in tracing the phylogeny of the Plethodontidae. Other authors (Humphrey, 1872; Druner, 1901; Lubosch, 1914; Smith, 1920; Eaton, 1936) have described and traced the phylogeny and ontogeny of the muscles of the head in various forms of salamanders. The names of muscles here employed are those used by Smith (1920) and Eaton (1936).

TRANSVERSE MUSCLES OF FLOOR OF MOUTH

M. intermandibularis posterior (Druner, 1901; Eaton, 1936) (figs. 4, 5, 6).—Thin layer of paired muscles covering most of the area between mandibles; origin along dorsal inner edge of mandibles; insertion on median fascia; divided into anterior and posterior slips

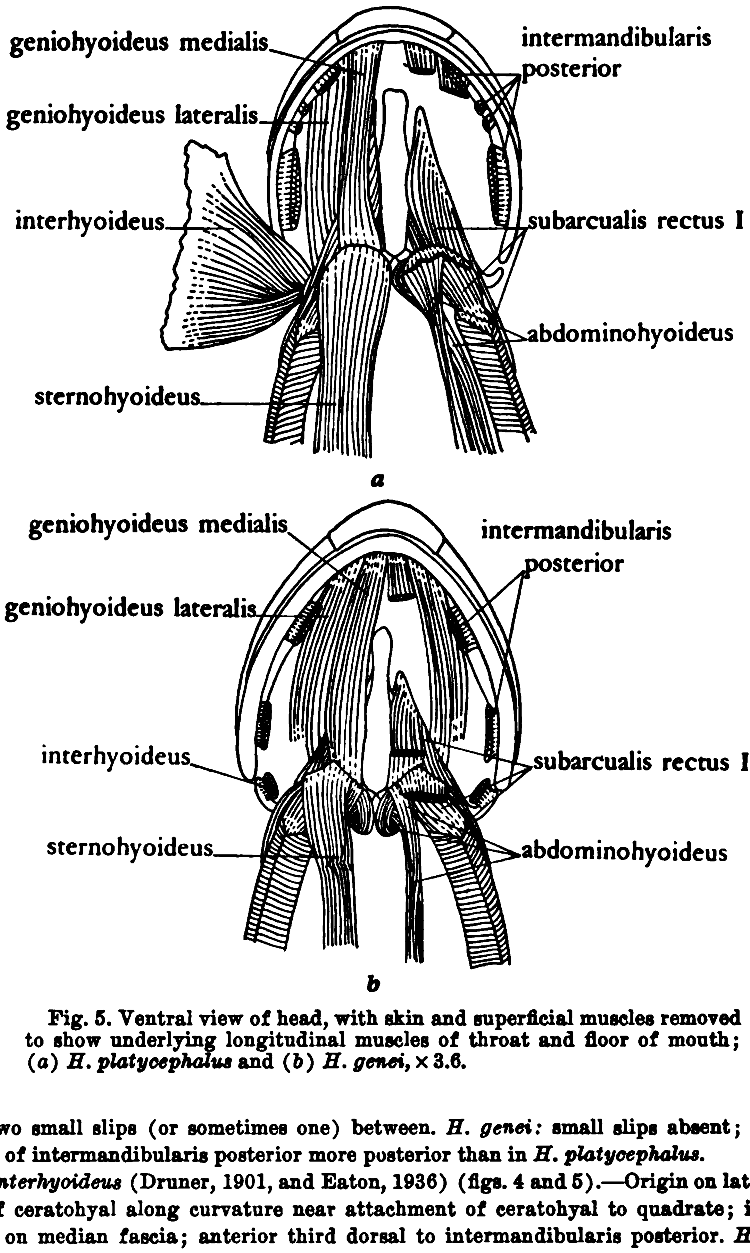


Fig. 5. Ventral view of head, with skin and superficial muscles removed to show underlying longitudinal muscles of throat and floor of mouth; (*a*) *H. platycephalus* and (*b*) *H. genei*, × 3.6.

with two small slips (or sometimes one) between. *H. genei:* small slips absent; anterior border of intermandibularis posterior more posterior than in *H. platycephalus*.

M. interhyoideus (Druner, 1901, and Eaton, 1936) (figs. 4 and 5).—Origin on lateral surface of ceratohyal along curvature near attachment of ceratohyal to quadrate; insertion broad, on median fascia; anterior third dorsal to intermandibularis posterior. *H. genei:* origin on ceratohyal near attachment to quadrate, not extending to curvature of ceratohyal.

M. gularis (Smith, 1920) (figs. 4 and 7).—The origin is on tip of mandible, on quadrate and along horizontal fold of skin posterior to eye; skin insertion marked externally by

horizontal postocular fold; insertion, anterior half on median fascia, posterior half on gular fold of skin. *H. genei:* Origin of dorsal portion not on skin but on fascia, which in turn attaches to quadrate and otic capsule (fig. 7); insertion on gular fold only.

LONGITUDINAL MUSCLES OF THE FLOOR OF THE MOUTH

M. subarcualis rectus I **(Edgeworth, 1920; Eaton, 1936) (figs. 5, 6, 7).—Origin on anterior and lateral margins of ceratohyal; insertion double, medially on tendinous sheath enclos-**

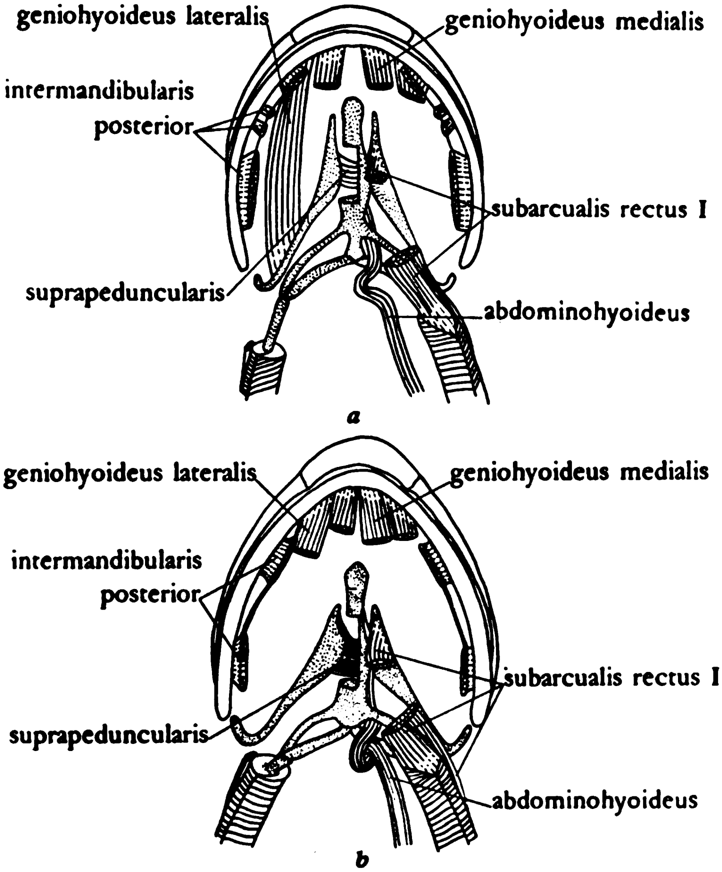


Fig. 6. Ventral view of head, showing origins and attachments of muscles of throat and floor of mouth; (*a*) *H. platycephalus* and (*b*) *H. genei*, × 3.6.

ing first epibranchial; laterally, fibers intermingle with fibers of muscular sheath of first epibranchial. *H. genei:* same.

This muscle contracts to eject the tongue. Smith (1920) suggests that it spirals around the first epibranchial in *Eurycea* to form a closed bulb which, when contracted, squeezes the epibranchial cartilage out. Apparently this mechanism is more specialized in *Hydromantes* than in *Eurycea* and, although I do not yet understand in detail how the muscle operates, I think Smith's hypothesis explains inadequately the functioning of the subarcualis rectus I in *Hydromantes*.

M. geniohyoideus lateralis **(Smith, 1920) (figs. 4, 5, 6).—Origin on posterior margin of mandible lateral to origin of geniohyoideus medialis; insertion midway between ends of ceratohyal on its lateral margin. *H. genei:* lateral half of geniohyoideus lateralis inserts on membrane of mouth anterior to ceratohyal.**

M. geniohyoideus medialis (Smith, 1920) (figs. 4, 5, 6).—Origin on posterior margin of mandible lateral to symphysis; insertion on the inscriptio tendinae, a connective tissue vestige of the os thyroideum. *H. genei:* same.

The os thyroideum has been lost in *Hydromantes.* Its place and function as an organ for muscular attachments has been taken by a paired mass of connective tissue, the inscriptio

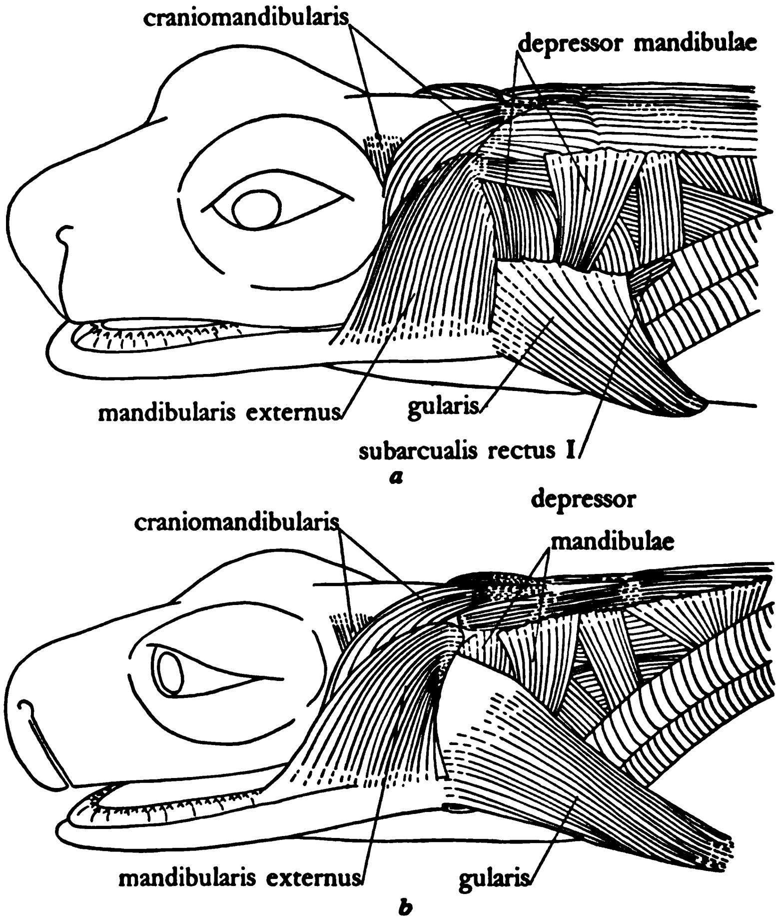


Fig. 7. Side view of head, showing jaw muscles; (*a*) *H. platycephalus* (× 2.8) and (*b*) *H. genei* (× 2.6).

tendinae (Weidersheim, 1875). These structures lie obliquely across, and attached to, the belly of the subarcualis rectus I at about its middle. The muscles that attach to the os thyroideum in other salamanders attach to the ligamentous vestiges in *Hydromantes.* The position of these vestiges in relation to other organs is different from the position of the os thyroideum illustrated by Smith (1920) in *Eurycea,* in which the bone lies directly medial to the posterior tip of the second ceratobranchial when the tongue is withdrawn into the mouth. In *Hydromantes* the inscriptio tendinae lie directly medial to the anterior tip of the second ceratobranchial.

M. sternohyoideus (Smith, 1920) (figs. 4, 5).—Anterior continuation of musculature of ventral wall of body; insertion on inscriptio tendinae and on ventral side of belly of subarcualis rectus I. *H. genei:* same.

In *Eurycea* (Smith, 1920) this muscle does not originate on the sternum. Apparently in *platycephalus* the muscle is a forward growth of the abdominal musculature of the body wall, as shown by the myocommata, which are serially arranged through the length of the abdominal musculature and continued forward in the sternohyoideus.

M. abdominohyoideus (Smith, 1920) (figs. 5, 6).—Origin on pelvic girdle; extends along body wall and into neck region parallel and dorsal to sternohyoideus, passing ventral to ceratobranchial 2, dorsal to ceratobranchial 1; inserts near tip of basibranchial; slip branching from level of pectoral girdle inserts on inscriptio tendinae dorsal and medial to insertion of sternohyoideus, opposite insertion of median half of geniohyoideus medialis. *H. genei:* same.

In contrast to the condition described in *Eurycea* by Smith (1920), the abdominohyoideus is not crossed by myocommata in *Hydromantes.*

MUSCLES OF THE JAW

M. craniomandibularis (Lubosch, 1914, and Eaton, 1936) (fig. 7).—Two parts, sublimus anterior and sublimus posterior; origin of sublimus anterior, anterolateral part of parietal bone behind supraorbital crest; insertion on membrane of mouth at base of pterygoid cartilage; origin of sublimus posterior, crest of first cervical vertebra; insertion on mandible by fusion with tendon of mandibularis externus. *H. genei:* same.

The sublimus profundus is not present in *Hydromantes,* nor are the sublimus anterior and sublimus posterior as intimately associated as in *Dicamptodon* (Eaton, 1936). Neither muscle has the origin or insertion in common with the other muscle, and the muscles do not lie parallel.

M. mandibularis externus (Lubosch, 1914, and Eaton, 1936) (fig. 7).—Origin on dorsolateral face of quadrate and on otic capsule; insertion on dorsal surface of mandible from posterior tip to angle of mouth. *H. genei:* same.

M. depressor mandibulae (Humphrey, 1872, and Eaton, 1936) (fig. 7).—Origin on lateral face of quadrate; origin of posterior slip on skin of neck and aponeurosis of dorsal muscles of neck; insertion on posterior tip of mandible. *H. genei:* No origin on aponeurosis of dorsal muscles of neck.

As indicated by the foregoing descriptions of the muscles of the head region, there is a marked similarity in these parts between *H. platycephalus* and *H. genei.* The variations in the insertion, origin, shape, and position of the muscles in the two species, and the differences noted in other structural features, indicate full specific rank for the two forms, and at the same time seem to show that the two are congeneric. These findings agree with Dunn's (*op. cit.*) conclusion that *platycephalus* and *genei* are distinct species of the genus *Hydromantes.*

NATURAL HISTORY

Distribution (see map, fig. 8).—The seven localities from which Mount Lyell salamanders are known are in the Sierra Nevada of California: near Mount Lyell, at 10,800 feet, Yosemite National Park, Tuolumne County, 8 specimens (Camp, 1916; Slevin, 1928). Silliman Gap, 10,000 feet, Sequoia National Park, Tulare County, 1 specimen (Adams, 1938). Sonora Pass, approximately 9500 feet, Alpine County, 8 specimens (Myers, 1938). Peeler Lake, 9500 feet, Mono County, at least 2 specimens (Adams, 1938). Half Dome, 8852 feet, Yosemite National Park, 100–200 specimens (Adams, 1938; Myers, 1938). Tenaya Canyon, 5800 feet, Yosemite National Park, 1 specimen (Adams, 1938). Upper Yosemite Fall, 5140 feet, Yosemite National Park, 1 specimen (Adams, 1938).

Habitat.—The geologic history of the region where the salamanders occur has been described by Matthes (1930). The rugged topography of the habitat

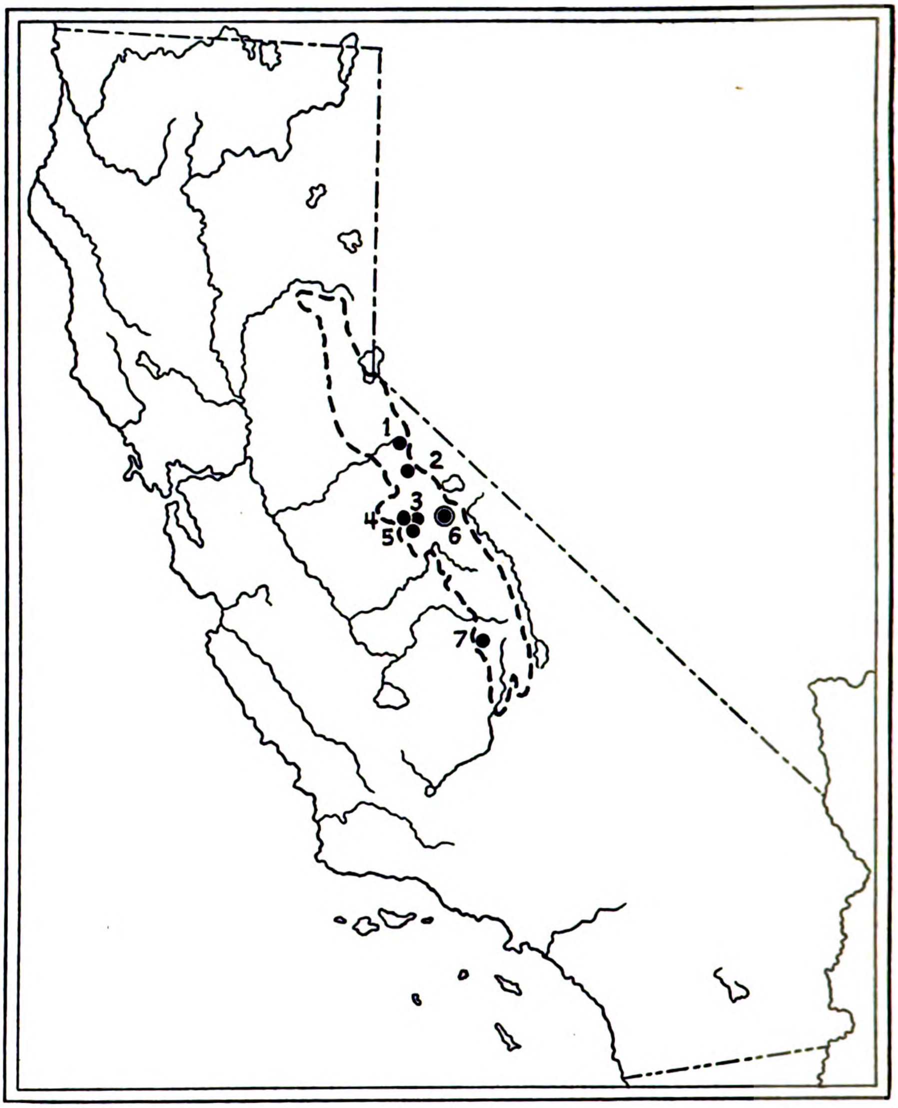


Fig. 8. Localities where Mount Lyell salamanders have been collected: (1) Sonora Pass, (2) Peeler Lake, (3) Tenaya Canyon, (4) upper Yosemite Fall, (5) Half Dome, (6) Mount Lyell, type locality, (7) Silliman Gap. The hypothetical range—the Boreal Zone in the Sierra Nevada—is outlined.

of the Mount Lyell salamander and the reclusive habits of the animal account for the comparatively recent discovery of this species and the paucity of preserved specimens.

The soil at the localities where the salamanders have been collected is remarkably similar. In the two localities with which I am personally acquainted, Half Dome and Yosemite Falls, the soil is almost entirely decomposed granite with little humus. Half Dome (pl. 21, figs. *a, b*) is topped with a veneer of flat exfoliation shells of granite under which salamanders retire in the day. What little humus exists is furnished by a sparse vegetation composed of lichens, grasses, *Caryx* sp., *Eriogonum lobbii, E. marifolium, E. ovalifolium, E. wrightii, E. nudum, Sedum yosemitense, Stellariopsis santolinides, Gilia pungens, Pentstemon menziesii, Achillaea millefolium* var. *lanulosa,* and *Hieracium horridum* (Presnall, 1932). Only six scrubby trees grow on the entire 13-acre expanse of the dome's top—four lodgepole pines (*Pinus contorta murrayana*), one Jeffrey pine (*P. Jeffreyi*), and one white-bark pine (*P. albicaulis*).

In Tenaya Canyon there is much more plant growth, but even so the soil is largely mineral. Moss, lichens, and dwarfed azalea were present where a specimen was taken in Tenaya Canyon. The first two grow on the surface of granite boulders, but azalea usually grows along wooded stream banks. The type locality, north of Mount Lyell, is in terrain characterized by outcrops of granite, with occasional deposits of decomposed granite along the streams and lakes. These deposits usually support a variety of vegetation including grasses, alpine willow, heather, and scrubby white-bark pine. Camp, in his field notes dated July 18, 1915, describes the type locality as "... a large rock outcropping in a patch of heather (100 ft. in dia.) on a steep hillside (east-facing slope) above the Donohue Pass trail at 10,800 ft.... Although this heather patch lies directly in the sun almost all day, there is still snow about it and it is practically surrounded by rockslides on a bare rocky slope."

Myers's (1938) report of the Sonora Pass locality indicates edaphic conditions similar to that at Mount Lyell. He does not mention humus-producing plants.

Until the summer of 1938 all Mount Lyell salamanders had been taken at high altitudes which, according to the life-zone map of this region (Grinnell and Storer, 1924), were above the lower border of the Hudsonian. Accordingly, this salamander was thought to have been restricted to places high in the Boreal life zone. On June 18, 1938, Robert Wiegel of the Yosemite Junior Nature School found an immature salamander in Tenaya Canyon at the base of Clouds Rest. Near this locality western yellow pines, Douglas firs, and other indicators of the Transition life zone are plentiful. The salamander was found near a large deposit of avalanche snow, which remains until late in the summer, and may bring about conditions that are nearly Canadian in nature. Only a mile downstream is an island of Upper Sonoran zone which is possibly due to south exposure and reflection from the bare granite walls.

A second low-altitude find was made by me on July 29, 1938, at the base of Upper Yosemite Fall, 5140 feet. This is well within the upper border of the Transition zone. Each winter a large ice cone accumulates at the base of the fall, and this area is drenched with spray until late summer, the region thus being kept moist and cool. So many unique climatic factors exist in the immediate vicinity of the fall that they may produce there a tiny island of Canadian zone.

Thus, the Mount Lyell salamanders have been recorded from the upper border of the Transition zone upward to the upper border of the Hudsonian. The absence of records from the Arctic-Alpine zone may result from lack of intensive effort to collect there. Far more specimens have been taken from the top of Half Dome than from all other localities combined, but this, far from being evidence that the animal is most abundant here, is a measure of the easy accessibility of the place and popular knowledge of the station. However, the dearth of recorded occurrences in the Transition life zone indicates absence of the salamanders from such low altitudes. Chance occurrences at low elevations in Yosemite may result from some salamanders falling or crawling off the edges of precipitous places and thus becoming "distributed" to lower stations, such as in Tenaya Canyon and at Yosemite Falls.

Within this salamander's range the climate (Martin, 1930) is characterized by well-defined wet and relatively dry seasons. The wet season is in winter and most of the precipitation is in the form of snow, which is most abundant from 7000–8000 feet. By July all the snow melts away at most localities below 8000 feet. On the highest peaks some snow usually remains all summer. A negligible amount of precipitation occurs as rain in the summer months.

Moisture conditions are strikingly similar at the several places where *H. platycephalus* has been found. The type locality is near a stream issuing directly from a snowfield. The stone under which 7 salamanders were found at Sonora Pass was wet by the splash of a small stream from a snowbank. A snowbank was reported near the station of occurrence at Silliman Gap. Although no spray was produced there, the salamander was found in the late evening when the relative humidity was presumably higher than in the daytime. Barren rocks and melting snow were described where salamanders were collected at Peeler Lake. On Half Dome there is a snowfield, the water from which flows over the sheer side and is caught by a strong updraft and blown back on top in a cold, drenching spray. Again, in Tenaya Canyon the gravel was kept wet by melting snow. The ice cone at Yosemite Falls was gone when the specimen was taken there, but spray was furnished in great abundance by the fall. The evidence indicates that high humidity is an important factor in the habitat of *H. platycephalus*.

With the exception of Yosemite Falls and Tenaya Canyon, the localities where Mount Lyell salamanders have been found are all well within the Boreal zones. Habitats of the kind described occur at many localities in these zones between Plumas County to the north and the southern part of Inyo and Tulare counties to the south. It would seem most profitable to look for *Hydromantes* in favorable habitats within these zones, namely the Canadian and Hudsonian life zones.

Cycles of activity.—The Mount Lyell salamander is nocturnal. Of the 45 individuals that I have observed in the field, only two were abroad in the daytime. One was moving about on top of Half Dome in bright sunlight; the other was crawling on a boulder in a dark recess beneath Upper Yosemite Fall. The other 43 animals were under rocks. This is in agreement with the findings of other collectors, for some 28 specimens in the Yosemite Museum taken on Half Dome, presumably in daytime, were found "under rocks in snow water," and the specimens from Sonora Pass were found in the daytime under a rock. The specimen from Silliman Gap was seen actively abroad in the late evening, and the type specimen and one other with it, were taken at night in a mouse-trap "set in front of a small hole running into the moist soil beneath some rocks." Therefore, it seems that the salamanders remain in seclusion during the day and come out at night.

These salamanders have been found as early as May 1, and as late as August 22. Probably factors of temperature and moisture determine the period of activity. Although the salamanders are out until the latter part of August on Mount Lyell, where the snow lasts until late summer, they may aestivate much earlier on Half Dome, probably when the snow disappears in early July. On September 4, 1938, I spent several hours in fruitless search for salamanders at the base of the Upper Yosemite Fall, where I had found two on my previous visit on July 29. Water was still coming over the fall but the volume had decreased so much that areas which would otherwise have afforded suitable habitats were subject to intervals of drying as the fall was blown back and forth. A period of activity possibly occurs again in autumn when rains increase the volume of water. The salamanders may push farther and farther down into the substrata as their summer environment becomes dry, and then be brought out again by an overabundance of water seeping into their retreats in the autumn and again in the spring.

Food habits.—Remains of the following animals were found in the stomachs of two adult salamanders: 2 centipedes, 8 spiders, 1 termite (*Zoötermopsis nevadensis*), 1 rove beetle (Family Staphylinidae), 6 antlike flower beetles (*Anthicus* sp.), 1 click beetle (Family Elateridae), 1 ladybird beetle (*Hyperaspis* sp.), 1 leaf beetle (*Diabrotica soror* Lec.), 2 maggots of crane flies (Family Tipulidae), 1 maggot of a fly (Family Muscidae), and 7 adult flies of unidentified species.

A yearling salamander's stomach contained 2 spiders, 3 adult and 19 larval fungus gnats (Family Mycetophilidae), and 1 fly (Family Muscidae).

The stomach of a young-of-the-year contained one Sminthurid (*Sminthurus* sp.), and 10 adult and 11 larval fungus gnats (Family Mycetophilidae).

Most of the food items were ground-dwelling forms, as would be expected in these terrestrial salamanders. The immature salamanders seem more limited than the adults in their choice of food; only small insects and spiders were found in the stomachs of the immature salamanders, which probably cannot capture and swallow the larger insects that constitute the diet of the adults. Small particles of granite were also found in the stomachs.

Size groups.—The 84 salamanders from Half Dome were collected over a period of several years, all between June 14 and 29; they comprise three well-defined size groups (fig. 9 and pl. 22, fig. *a*). The small individuals are probably the young of the year, those of middle size are "yearlings," and those in the largest group are adults. The middle group is smallest because, as Blanchard and Blanchard (1931) have pointed out in a similar study of *Hemidactylium scutatum*, "there has been a year for their numbers to be thinned out by such vicissitudes as enemies, accidents, weather, winter and diseases; and the individuals are more scattered from their year of wanderings." The adult group is largest because it is made up of survivors from the intermediate groups from an indeterminate number of years; it represents all the survivors of the first two years of growth.

The male secondary sexual characters, enlarged maxillary and premaxillary teeth, may mark sexual maturity. If so, they are a guide to the age at

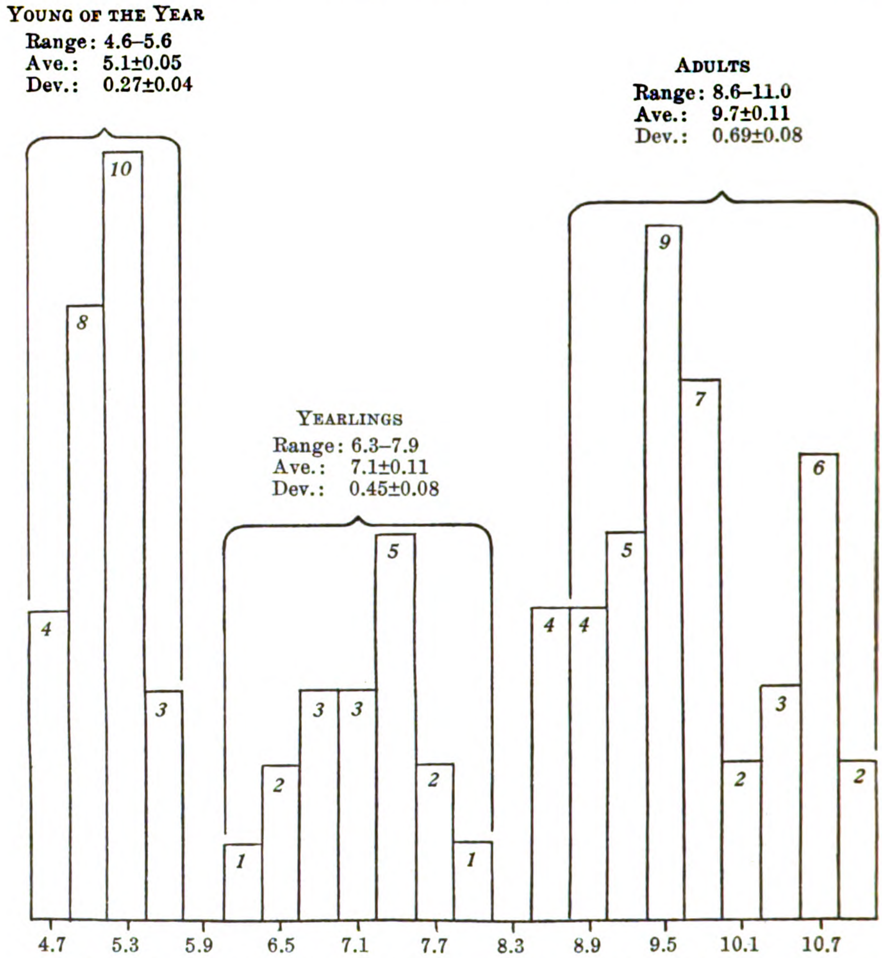


Fig. 9. Head widths, in millimeters, of salamanders collected on Half Dome. Measurements are grouped into intervals of 0.3 mm.; figures on columns show number of individuals in each class.

which breeding occurs. Although the teeth are absent in the yearlings, they are found in the smallest members of the adult group (8.7 mm. head width), which are judged to be approximately two and a half years of age.

Because the 84 specimens used were taken at the same time each year, the range of size within any one age group is small. Males and females were included in one frequency polygon because the secondary sexual difference in average size (see figs. 1 and 2) is too slight to obscure the grouping by age. A grouping like that based on head width was obtained with the other measurements of total length, head length, body length, and tail length.

SUMMARY

An examination of the skull and all muscles of the head region verifies Dunn's reference of *Spelerpes platycephalus* Camp to the genus *Hydromantes,* and separates it from *H. genei*. *H. platycephalus* occurs in the Boreal regions of the Sierra Nevada. It is found in granitic soil largely lacking in humus, and is active from the first of May until the last of August, while the soil is kept wet by melting snow. It is nocturnal, its food consisting mostly of ground-dwelling insects, spiders, and centipedes. Specimens from Half Dome collected from July 14 to 29 can be segregated on the basis of size into three age groups: young of the year, animals between one and two years old, and animals more than two years old.

LITERATURE CITED

Adams, L.
1938. The Mt. Lyell salamander. Yos. Nat. Notes, 17:138–139.

Blanchard, F. N.
1928. Topics from the life history and habits of the red-backed salamander in southern Michigan. Am. Naturalist, 62:156–164, 4 figs. in text.

Blanchard, F. N., and Blanchard, F. C.
1931. Size groups and their characteristics in the salamander *Hemidactylium scutatum* (Schlegel). Am. Naturalist, 65:149–164, 4 figs. in text.

Camp, C. L.
1916. *Spelerpes platycephalus*, a new alpine salamander from the Yosemite National Park, California. Univ. Calif. Publ. Zoöl., 17:11–14, 5 figs. in text.

Druner, L.
1901. Studieren zur Anatomie der Zungenbein-, Kiemenbogen- und Kehlkopfmuskulatur der Urodelen. I Theil. Zoöl. Jahrb. Abt. für Anat., 15:435–622, Taf. 25–31.

Dunn, E. R.
1923. Mutanda herpetologica. Proc. N. Eng. Zoöl. Club, 8:39–40.
1926. The salamanders of the Family Plethodontidae. Smith College Fiftieth Ann. Publ., viii + 441 pp., 86 figs. in text, 1 pl., frontisp.

Eaton, T. H.
1936. The myology of salamanders with particular reference to *Dicamptodon ensatus*. Jour. Morph., 60:31–76, 5 figs. in text, 1 pl.

Edgeworth, F. H.
1920. On the development of the hyobranchial and laryngeal muscles in Amphibia. Jour. Anat., 54:125–162, 15 pls.

Grinnell, J.
1935. A revised life-zone map of California. Univ. Calif. Publ. Zoöl., 40:327–329, 1 pl.

Grinnell, J., and Storer, T. I.
1924. Animal life in the Yosemite. Univ. Calif. Press, xviii + 669 pp., 65 figs. in text, 62 pls.

Humphrey, G. M.
1872. The muscles and nerves of *Cryptobranchus japonicus*. Jour. Anat. and Phys., 6: 1–61.

Lazzarini, G.
1930. Una nuova specie d'Urodolo terrestre, *Spelerpes ferrugineus*. Udine, Porretti. (Not seen by me.)

Lubosch, W.
1914. Vergleichende Anatomie der Kaumuskeln der Wirbeltiers, im fünf Teilen. I Teil: Die Kaumuskeln der Amphibien. Zeitschr. Nat., 53:15–188, 5 Taf.

Martin, R. J.
1930. United States, Department of Agriculture, Weather Bureau, Climatic summary of the United States, 1, Section 17, Central California, pp. 1–64.

Matthes, F. E.
1930. Geologic history of the Yosemite Valley. U. S. Geol. Surv., Prof. Paper 160.

Myers, G. S.
1938. *Hydromantes platycephalus* in Sonora Pass, California. Copeia, 1938, p. 91.

Noble, G. K.
1927. The value of life history data in the study of the evolution of the Amphibia. Ann. N. Y. Acad. Sci., 30:31–128.
1931. Biology of the Amphibia. McGraw-Hill, xiii + 577 pp., 174 figs. in text, frontisp.

Piatt, J.
1935. A comparative study of the hyobranchial apparatus and throat musculature in the Plethodontidae. Jour. Morph., 57:213–242, 4 pls.

POMINI, F.
1936. Osservazioni sistematiche ed ecologiche sugli Anfibi del Veneta. Arch. Zoöl., 23: 241–272, 1 fig. in text.
PRESNALL, C. C.
1932. Skyland. Yos. Nat. Notes, 2: 10, pp. 7–8.
SLEVIN, J. R.
1928. The amphibians of western North America. Occas. Papers Calif. Acad. Sci., 16: 1–152, 23 pls.
SMITH, L.
1930. The hyobranchial apparatus of *Spelerpes bislineatus*. Jour. Morph., 33:527–583, 3 figs. in text, 16 pls.
STEJNEGER, L., and BARBOUR, T.
1917. A check list of North American amphibians and reptiles. Harv. Univ. Press, ed. 1, iv + 125 pp.
WIEDERSHEIM, R.
1875. *Salamandrina perspicillata* und *Geotriton fuscus*. Genoa, Druck des Instituts der Sordo-muti, 207 pp., 17 pls.
WOLTERSTORFF, W.
1925. Katalog der Amphibien-Sammlung in Museum für Natur- und Heimatkunde zu Magdeburg. I Teil: Apoda, Caudata. Mus. Natur- und Heimatkunde, 4:231–310.

PLATES

PLATE 21

Fig. *a*. The top of Half Dome, Yosemite National Park, showing habitat of the Mount Lyell salamander; photograph taken April 12, 1939. (Arrow indicates a man at the brink of the sheer face.)

Fig. *b*. Typical habitat on Half Dome, under flat rocks at the foot of a melting snowbank.

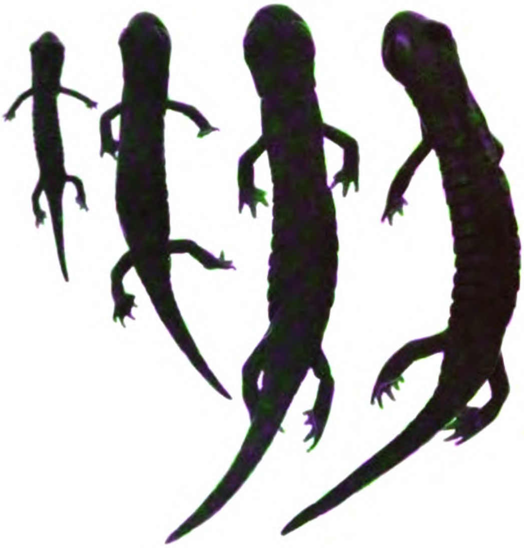
a

b

PLATE 22

Fig. a. Mount Lyell salamanders, × 1. From left to right: small young-of-the-year, yearlings, adult female, and adult male, showing difference in size and head-shape of male and female, and of the three size groups.

Fig. *b*. Live Mount Lyell salamander, male, slightly enlarged. Photo by Ralph Anderson.



a

b