Comparative Osteology of the Plethodontid Salamander Genus *Aneides*

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The genus *Aneides* is one of 26 genera of highly specialized lungless salamanders in the family Plethodontidae. Within the family, members of the genus have been considered specialized and advanced by virtue of their loss of the aquatic larval stage and their climbing and arboreal tendencies. This report is an attempt to present information concerning osteological variation within the species of *Aneides*, to make detailed osteological comparisons of the species, and to compare the genus with closely related genera.

Of the five species of *Aneides*, three occur in far western North America: *Aneides ferreus*, *Aneides flavipunctatus*, and *Aneides lugubris*. *Aneides hardii* occurs at high elevations in south-central New Mexico, and *Aneides aeneus* is found in the Appalachian highlands of eastern United States.

Recently a trend has developed in the direction of comparative osteological studies of salamanders. The study of the family Ambystomatidae by Tihen ('58), Baird's ('51) anatomical study of the plethodontid genus *Pseudoeurycea*, and the osteological approach used by Hansen and Tanner ('58) in studying several species of the plethodontid genus *Bolitoglossa* are examples of such work. No previous comparative studies have dealt with *Aneides*, however, and none have considered all of the species of a genus.

Some information concerning the osteology of *Aneides* may be found in the published works of Wiedersheim (1877), Cope (1889), Dunn ('26), and Hilton ('45). These studies contain no information concerning inter-specific variation and it is apparent that *lugubris* was the species studied. Lowe ('50) utilized some osteological characters in delimiting the genus. His characters are also those used by Cope, Dunn, and Bishop ('43) and include: premaxillae fused, maxilla with posterior portion knife-edged and edentulous, and terminal phalanges Y-shaped. These have remained the major characters differentiating *Aneides* from its close plethodontid relatives *Plethodon* and *Ensatina*.

In the following account each bone is described in detail for the genus *Aneides* and comparisons are made with the condition seen in the related genera *Plethodon* and *Ensatina*. A discussion of evolutionary relationships of the various species of *Aneides* and of the phylogenetic position of the genus within the family Plethodontidae has been prepared on the basis of the analysis presented here, and will be published elsewhere.

MATERIALS AND METHODS

Skeletonized, cleared and stained, and x-ray radiographed specimens were utilized. Prepared salamander skeletons alone, whether intact or disarticulated, are not suitable for a detailed osteological study. Observations recorded here were made primarily on cleared and stained material. The advantages of clearing and staining over other methods of preparation are two: retention of cartilaginous parts, and clarification of articulations. While cleared and stained material formed the basis for the descriptive portions of this paper, comparisons were made with skeletonized and radiographed material, and preserved specimens were sometimes dissected in order to study cartilaginous structures in greater detail. The material was studied under a stereoscopic dissecting microscope with magnifications of 10 to 75 diameters. Specimens utilized in the study are as follows (data in the following order: species, number cleared and stained, number skeletonized, state or province where collected): *Aneides aeneus* 10, 3, Kentucky, West Virginia, North Carolina; *A. ferreus* 23, 3, Oregon, British Columbia; *A. flavipunctatus* 13, 2, California; *A. hardii* 11, 0, New Mexico; *A. lugubris* 12, 1, California; *Ensatina eschscholtzii* 7, 3, California; *Plethodon cinereus* 4, 2, Virginia, North Carolina; *P. dorsalis* 3, 0, Alabama; *P. dunni* 4, 1, Oregon; *P. elongatus* 9, 2, Oregon; *P. glutinosus* 11, 2, Virginia, Texas; *P. jordani* 9, 3, Virginia, North Carolina; *P. larselli* 1, 0, Washington; *P. longicrus* 1, 0, North Carolina; *P. neomexicanus* 1, 0, New Mexico; *P. ouachitae* 1, 0, Arkansas; *P. richmondi* 7, 0, West Virginia, Virginia; *P. vandykei* 7, 0, Washington, Idaho; *P. vehiculum* 8, 1, Washington; *P. wehrlei* 1, 0, Virginia; *P. welleri* 6, 0, Virginia, North Carolina; *P. yonahlossee* 10, 1, Virginia, North Carolina. Cleared and stained or skeletal material has also been available for the following genera: *Desmognathus, Leurognathus, Batrachoseps, Hemidactylium, Stereochilus, Gyrinophilus, Pseudotriton, Eurycea, Manculus, Typhlotriton, Typhlomolge, Haideotriton, Pseudoeurycea, Parvimolge, Thorius, Lineatriton, Bolitoglossa, Oedipina, Chiropterotriton, Hydromantes, Salamandra, Taricha, Diemyctylus, Ambystoma, Rhyacotriton, Dicamptodon, Cryptobranchus, Amphiuma, Necturus, Hynobius*, and *Siren*. In addition radiographs of the following have been available: *Pleurodeles, Euproctus, Chioglossa*, and *Salamandrina*. Males, females, and juveniles were available for all *Aneides* and *Ensatina*, and for many *Plethodon*.

OSTEOLOGICAL ANALYSIS

Preliminary investigations revealed that the closest relatives of *Aneides* were to be found among members of the genera *Plethodon* and *Ensatina*. In the following section, a comparative study of the skeleton in the five species of *Aneides* is presented. In addition each skeletal element of *Aneides* is compared with the corresponding element in *Plethodon* and *Ensatina*. Comments on intraspecific and interspecific variation are limited to *Aneides*, with a few exceptions.

Cranium

The typical plethodontid cranium of *Aneides* consists of the primordial skeleton (of endochondral ossifications and cartilage) and the dermal investing bones. Francis ('34) recognized four regions of the primordial cranium: ethmoidal, orbitotemporal, otic capsular, and palatoquadratic. The ethmoidal region consists of the entirely cartilaginous nasal capsules and their connectives, and is almost entirely enclosed by dermal bones. The anterior portions surrounding the external nares and the posterior portions, the antorbital cartilages, are the only regions visible externally in undissected cleared and stained specimens. The region has been studied in some detail in *Salamandra* by Francis ('34) and no significant differences were noted in the species studied. The orbitotemporal region is represented by the orbitosphenoid, an endochondral ossification. The large ossified occipito-otic complex includes the otic capsular region. The large, complex cartilaginous palatoquadrate proper and a distal endochondral ossification, the quadrate, are the remnants of the palatoquadratic region. All elements of the primordial skeleton are paired, with the exception of certain fused portions of the ethmoidal region.

Included among the investing bones are the dorsally paired maxillae, nasals, septomaxillae, prefrontals, frontals, parietals, and squamosals, and the fused premaxillae; and the ventrally paired prevomers and the unpaired parasphenoid.

The crania of *A. aeneus, A. ferreus, A. flavipunctatus, A. hardii, A. lugubris, E. eschscholtzii*, and *P. dunni*, are figured in figures 1–4.

Premaxilla. The primitively paired premaxillae are fused to form a single element in all species of *Aneides*. The resultant structure is a toothed bar from which a thin and narrow shelf proceeds posteriorly, and two flattened spines, embracing a fontanelle, proceed dorsally. Three general regions are recognizable: the toothed portion (*pars dentalis*), forming the anterior border of the upper jaw; the palatal portion (*pars palatina*), a small flattened plate appressed to the posterior margin of the *pars dentalis;* and the paired frontal

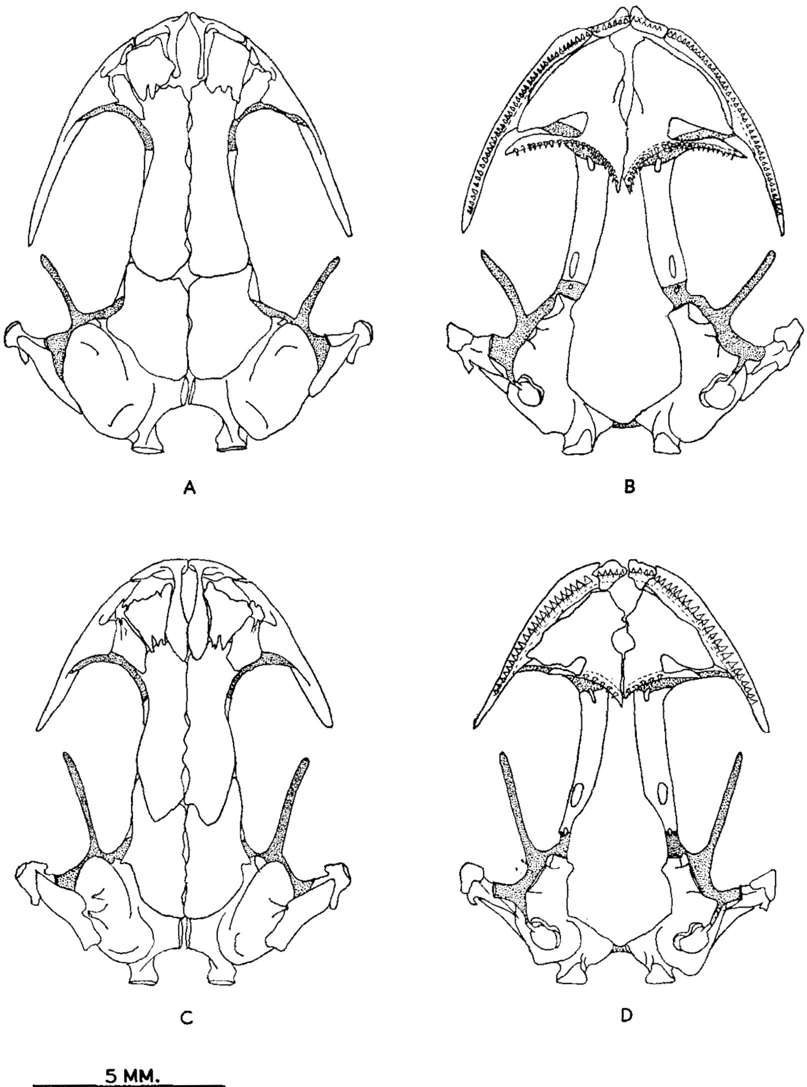

Fig. 1 Dorsal and ventral views of male crania. Posterior prevomerine tooth patches removed. Cartilage stippled. A & B, *Ensatina eschscholtzii;* C & D, *Plethodon dunni.*

processes (*partes frontales*), ascending dorsally from the *pars dentalis.* The toothed and palatal portions have fused medially with their bilateral counterparts. All portions are subject to ontogenetic variation, generally increasing in all dimensions with increasing age, and the frontal processes exhibit considerable interspecific and individual variation.

Pars dentalis relatively smooth and uncurved, approximately quadrangular in transverse section; variable in length but extending, in general, to point below medial border of external nares; longest in *aeneus,* shortest in *hardii;* articulates laterally by means of dorsal and anterior surfaces with *pars dentalis* of maxilla. Amount of overlap by maxilla variable, virtually absent in *lugubris* where bones articulate squarely. *Pars dentalis* relatively largest in *lugubris,* massive with a greater dorsoventral dimension than in other species. *Pars palatina* same length as *pars dentalis,* shares lateral articulation

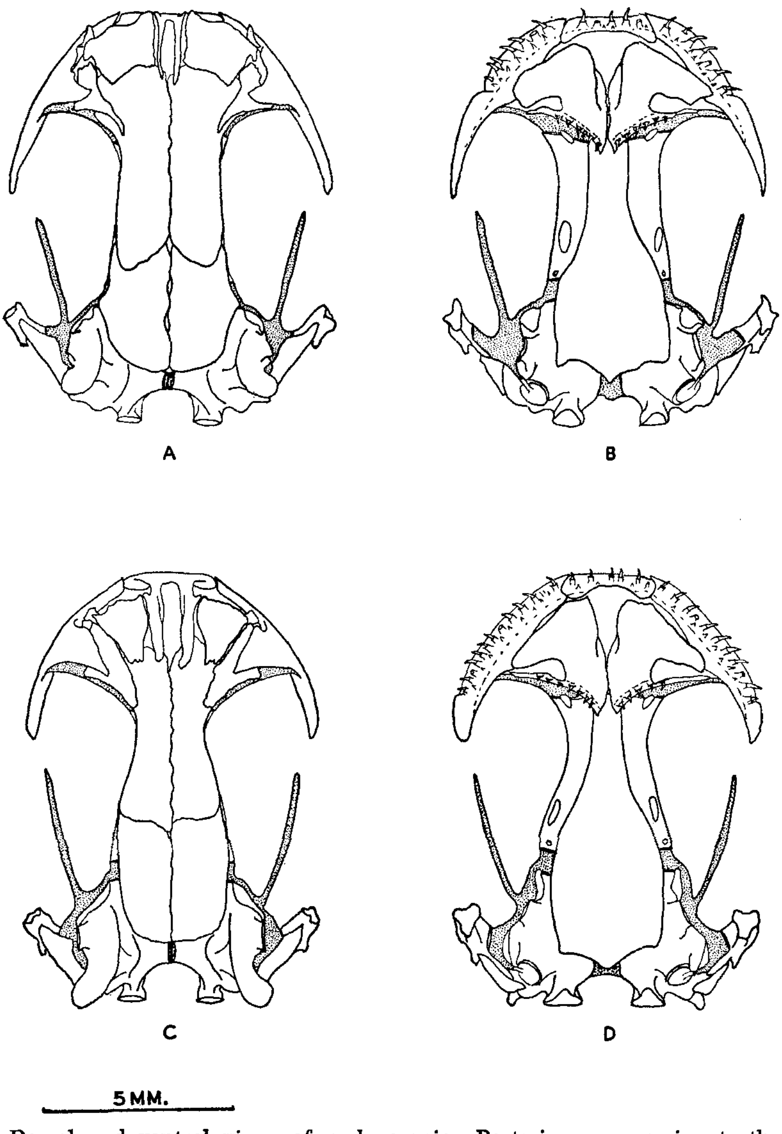

Fig. 2 Dorsal and ventral views of male crania. Posterior prevomerine tooth patches removed. Cartilage stippled. A & B, *Aneides aeneus;* C & D, *Aneides hardii.*

in which overlapped dorsally by maxilla; extends dorsoposteriorly from *pars dentalis* as narrow and thin shelf; greatest posterior extension always lateral; medial portion always narrow and often indistinguishable from *pars dentalis;* articulates posteriorly on either side by means of lateral portions with body of either prevomer; subject to ontogenetic variation, virtually absent in young of all species, most highly developed in adult *lugubris.* *Pars frontalis* a flat blade in young; with increasing age a vertically oriented septum-like process directed ventrally appears along medial border similar to septum described by Tihen ('58) in ambystomatid subgenus *Ambystoma* (*Linguaelapsus*). Septum most obvious in adult *lugubris* in which definite dorsoventrally oriented process forms lateral wall of internasal fontanelle and occasionally articulates ventrally with small dorsal process of pre-

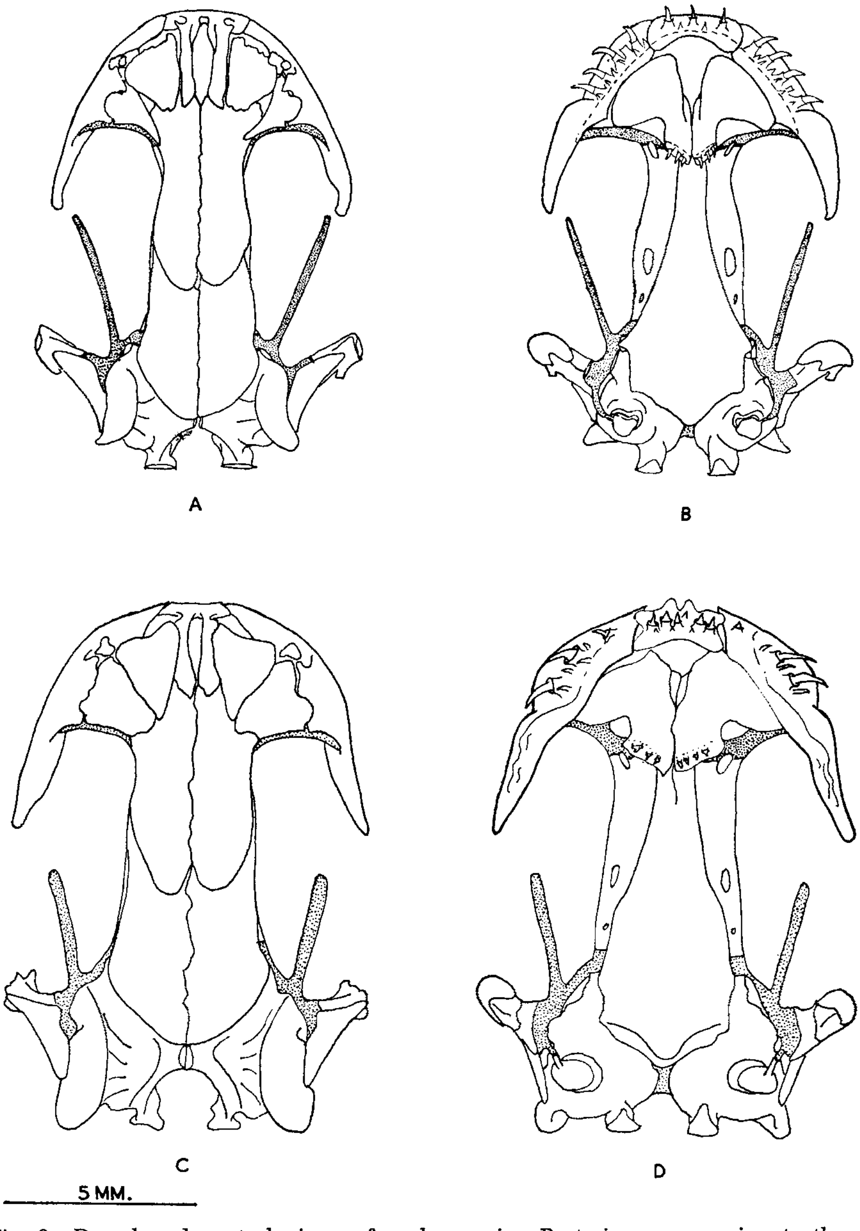

Fig. 3 Dorsal and ventral views of male crania. Posterior prevomerine tooth patches removed. Cartilage stippled. A & B, *Aneides ferreus;* C & D, *Aneides flavipunctatus.*

vomer. *Pars frontalis* bears anterolaterally directed process at anterior dorsal angle of snout directly below septum, but above and separated from *pars dentalis.* Paired *partes frontales* arise from dorsal portion of *pars dentalis* and ascend dorsally, then arch dorsoposteriorly with abruptness of change in direction subject to interspecific variation, angle most abrupt in *lugubris,* approaching 90° in adults. Each *pars frontalis* articulates almost squarely with nasal laterally; overlaps frontal posteriorly with ventral surface articulating with grooves in dorsal surface of frontal;

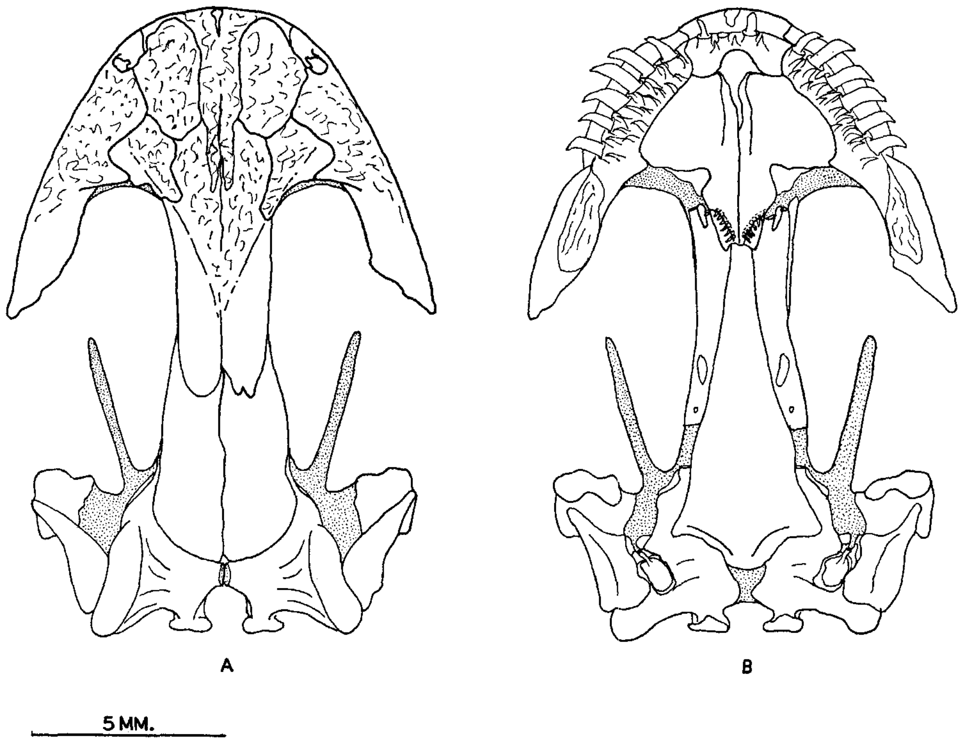

Fig. 4 Dorsal and ventral views of male cranium. Posterior prevomerine tooth patches removed. Cartilage stippled. A & B, *Aneides lugubris.*

frontal articulation subject to ontogenetic and individual variation, absent or limited in young, increasing in adults; frontal articulation extensive in *lugubris* with frontal broadly overlapped. Frontal processes embrace internasal fontanelle that is widest in *aeneus,* becoming narrower and smaller in *hardii, ferreus, flavipunctatus,* and *lugubris* in that order, but size subject to considerable individual variation; fontanelle length subject to individual as well as ontogenetic variation, becoming relatively shorter with increasing age. Frontal processes never articulate with one another behind fontanelle in *aeneus* and *hardii,* occasionally in *ferreus,* usually in *flavipunctatus,* and always for considerable distance in adult *lugubris.* Frontal processes shortest in *aeneus,* often falling short of posterior border of fontanelle; longer in *hardii* and *ferreus,* terminating at or near posterior border of fontanelle. Relation of frontal processes to neighboring elements variable; posterior tips fall anterior to orbital margin and anterior to posterior tips of nasals in majority of *aeneus;* posterior tips usually extend beyond nasals to level of orbital margin in *hardii, ferreus,* and *flavipunctatus;* posterior tips extend well beyond orbit margin and nasals in *lugubris.* Frontal processes laterally dilated posteriorly in *flavipunctatus* and *lugubris,* rarely in other species; rarely completely fused to one another in *lugubris.* Frontal processes heavily ornamented with dense osseous accretions in *lugubris;* bone appears massive as result; ornamentation almost completely roofs over internasal fontanelle leaving only small anteriorly directed opening directly adjacent to dorsal surface of *pars dentalis,* or completely covering fontanelle with bony roof; ornamentation subject to ontogenetic variation, entirely absent in very young, increasing with age.

The premaxillae of *Plethodon* are characteristically paired. Occasionally, however, variant individuals are found. In one specimen of *vandykei* the premaxillae are joined by a very slender ventrally located osseous bridge that is much narrower than either *pars dentalis*. The bridge, apparently a tooth pedicel that has fused to either premaxilla, bears a single tooth. In normal specimens a median tooth is often borne on a medial extension of either premaxilla, and the situation in the exceptional individual is apparently simply a more extreme condition. In one *neomexicanus* a small triangular medial plate bearing two teeth is present between the two primary toothed portions. The length of the *pars dentalis* in *Plethodon* is subject to interspecific variation but, in general, the length of the two portions is about equal to or slightly greater than the length of the single element in *Aneides*. The palatal portion is not as well-developed in most *Plethodon* as in *Aneides*, but in some species (*dunni, neomexicanus, yonahlossee*) it is well-developed and may articulate with the prevomer. The frontal processes proceed posterodorsally from their origin in contrast to the situation in *Aneides*. In the western *Plethodon* (especially *dunni, larselli, elongatus*) a septum is present on the frontal processes and the processes narrow at that point. The septum is absent in the eastern species of *Plethodon*. In most species of *Plethodon* the frontal processes extend to the posterior end of the fontanelle or beyond, but the length is subject to interspecific variation and in some species (e.g. *dorsalis*) the processes are very short. The frontal processes normally reach the level of the orbit or beyond but in *yonahlossee* the processes fall short. In most of the species the posterior tips of the frontal processes are dilated to some extent, but dilation is greatest in such western species as *dunni* and *elongatus*. In certain species (*dorsalis, welleri*) the processes are very narrow posteriorly. The relationship of the posterior extent of the frontal processes compared to that of the nasal is rather variable. The posterior portions of the processes consistently articulate with one another posterior to the internasal fontanelle only in *dunni* and *elongatus*, with such an articulation occurring occasionally in *glutinosus* and *yonahlossee*.

The paired premaxillae of *Ensatina* are similar to those of *Plethodon*. The length of the paired toothed portions is proportionately greater than that of any *Plethodon* or than the single element of any *Aneides*. The *pars palatina* of *Ensatina* is somewhat more shelf-like than in either *Plethodon* or *Aneides*, with less evident lateral processes. The frontal processes extend initially in a slightly anterodorsal direction, gradually reversing and arching posterodorsally. The frontal processes are narrow but are slightly dilated posteriorly. Only rarely do the short frontal processes extend past the internasal fontanelle and never beyond the nasal. The frontal processes never articulate with one another beyond the internasal fontanelle.

Maxilla. The upper jaw of *Aneides* is formed by the premaxilla and the paired maxillae. Each maxilla consists of three portions: the toothed portion (*pars dentalis*), articulating with the premaxilla anteriorly; the facial process (*pars facialis*), arising from the toothed portion and extending across the side of the face from the external nares to the orbit; and the palatal portion (*pars palatina*), a thin shelf extending dorsomedially from its origin on the *pars dentalis*. The maxilla is subject to ontogenetic and interspecific variation. Individual variation is seen in the degree of articulation with neighboring elements.

Pars dentalis largest portion of maxilla; extends anteriorly to articulate with premaxilla; greatest anterior extension ventral, extending to point directly ventral to cutaneous opening of external nares; anterior projection often anteriormost point of skull. *Pars dentalis* extends posterolaterally in gentle arc, posterior portion partially following curve of eyeball; extreme posterior tip directed posteriorly or slightly posteromedially. Posterior tip connected with palatoquadrate and quadrate by means of jugal ligament; attached to pterygoid portion of palatoquadrate cartilage by short ligaments, tip not touching pterygoid. *Pars dentalis* proportionately longest in *aeneus*, extending slightly beyond eyeball to about level of anterior margin of optic fenestra; extends to posterior edge of eyeball in *ferreus* and *flavipunctatus;* falls just short of posterior limit of eyeball in *lugubris;* extends no farther posteriorly than two-thirds of distance through eyeball in *hardii.* Posterior portion of maxilla toothless in most adult specimens; hatchet-shaped from posterior tip to teeth in most adult specimens, wedge-shaped with ventral knife-edged alveolar surface; thickened and rugose in adult *lugubris.* Dorsoventrally expanded portion originates at anterior margin of orbit and extends posteriorly in *ferreus, flavipunctatus, lugubris,* and *aeneus* (males); originates at anterior margin of eyeball in female *aeneus;* at anterior margin of eyeball or slightly posterior in male *hardii;* as far posterior as center of eyeball in female *hardii. Pars dentalis* as much as 70% toothless in *flavipunctatus,* 50 to 60% in *ferreus* and *lugubris,* 44 to 50% in *aeneus,* 20 to 40% in *hardii;* toothless portion usually somewhat more extensive in males than in females. Dorsal surface of toothless portion broad and rounded, rod-like in *lugubris,* with laterally compressed process extending ventrally. Dorsoventral depth of toothless portion greatest in *lugubris,* depth less in *ferreus, flavipunctatus, aeneus,* and *hardii* in approximately that order. Dorsal surface of toothless portion closely follows curvature of orbit; portions of dorsal surface may lie ventral to ventral surface of toothed portion, especially in *lugubris.* Ventral extent of toothless portion usually corresponds with tips of maxillary teeth. Toothless portion broadly expanded dorsoventrally in male *hardii* as in both sexes of other species; more limited in extent with dorsoventral expansion virtually absent in female *hardii.* Toothless portion subject to ontogenetic variation in all species, always best developed in old adults; subject to considerable individual and sexual variation in *hardii,* and, to much lesser extent, in *aeneus. Pars facialis* variable in shape and articulations; arises from middle one-third of *pars dentalis;* articulates firmly and extensively anterodorsally with nasal in *lugubris,* slight or limited articulation with nasal in *aeneus,* normally no articulation with nasal in other species. Posterior margin of *pars facialis* somewhat curved, forming lateral anterior border of orbit; articulates ventrally with antorbital cartilage. *Pars* *facialis* somewhat curved, forming lateral anterior border of orbit; articulates ventrally with antorbital cartilage. *Pars facialis* reaches greatest dorsal extent in *aeneus,* closely followed by *hardii,* usually extending dorsally beyond middle of eye; shorter in *ferreus* and *lugubris,* shortest in *flavipunctatus* where process rarely extends beyond lower one-third of eye. *Pars facialis* massive and heavily ornamented in *lugubris. Pars facialis* distinctly triangular in *aeneus* and *hardii* with apex located dorsoposteriorly; extensively overlaps and articulates ventrally with large posterolateral portion of prefrontal (figs. 5c, 5d). *Pars facialis* trapezoidal with apex dorsoposterior in *ferreus, flavipunctatus,* and *lugubris;* articulation with prefrontal firm, complex and interlocking; triangular dorsoposterior portion overlapped by prefrontal, dorsoanterior portion of process overlaps anterolateral portion of prefrontal; articulation most exaggerated in *ferreus* where large oval process of prefrontal overlaps maxilla; overlappings not so extensive in *flavipunctatus* and *lugubris* (figs. 5e, 5f, 5g). Small anteriorly directed extension originates at anterior margin of *pars facialis* just dorsal to *pars dentalis,* present in all species but *lugubris;* usually articulates loosely on medial border with septomaxilla. *Pars palatina* thin, shelf-like, similar to corresponding structure of premaxilla; width at anterior end approximately equal to width of *pars palatina* of premaxilla; width gradually increases, reaching greatest extent at point opposite greatest lateral extension of prevomer; greatest width in *ferreus, flavipunctatus,* and *lugubris* at same level as last maxillary tooth, greatest width posterior to that point in *aeneus* and *hardii.* Palatal shelf rapidly narrows posterior to greatest width and terminates, in most specimens, well anterior to tip of *pars dentalis. Pars palatina* articulates anteriorly with *pars palatina* of premaxilla; articulates medially from premaxilla to point of greatest width with body of prevomer. Palatal shelf width subject to ontogenetic variation, very narrow and minute in juveniles, best developed in old adults.

The maxilla of *Plethodon* differs from the *Aneides* pattern in some details. The *pars facialis* is generally trapezoidal, triangular, or quadrangular in shape and is usually rounded dorsally. The *pars facialis* overlaps the prefrontal at least slightly in all species (fig. 5a). The prefrontal never overlaps the *pars facialis*. An occasional slight anterodorsal articulation with the nasal is present in some species, but no anteriorly directed extension is present and the septomaxilla is not overlapped. The *pars facialis* generally arises from the second one-fourth of the *pars dentalis*. The *pars dentalis* usually extends almost to the posterior border of the eye, falling short of the anterior margin of the optic fenestra. The posterior tip is directed posterolaterally and the toothless portion is small, rather spinelike, not expanded dorsoventrally, and not wedge-shaped. Of all the *Aneides*, only female *hardii* has a similar posterior *pars dentalis*. In *P. dunni* the maxilla may be as much as 18% edentulous but teeth always extend past the center of the eye. The extent of toothlessness is usually much less in the other species of *Plethodon*. The *pars palatina* is similar to that of *Aneides* but may be narrow in some. The greatest width of the palatal shelf usually coincides with the position of the last maxillary tooth.

The maxilla of *Ensatina* is very different from that of *Aneides* and *Plethodon*. The triangular *pars facialis* is very small and arises from the central one-fifth of the *pars dentalis*, ascending dorsally to terminate in a small point that may overlap the prefrontal slightly (fig. 5b). No anteriorly directed extension is present and the anterior margin is widely separated from the septomaxilla. The *pars facialis* never articulates with the nasal. The *pars dentalis* of *Ensatina* is longer than that of any species of the other two genera, although approached in length by *A. aeneus*, and extends about to the level of the anterior margin of the optic fenestra. The posterior tip is directed posterolaterally and is similar to the condition in *Plethodon*. The maxilla is less than 10% edentulous and teeth extend well beyond the middle of the eyeball. The palatal portion is similar to that of *Plethodon*.

Septomaxilla. Embedded in the cartilaginous anterior ethmoidal region on either side of the skull is a tiny septomaxilla. The bone consists of an exposed anteromedial portion and a deep posterolateral portion, and lies in the osseous nasal aperture. The osseous nasal aperture, bordered by the premaxilla, nasal,

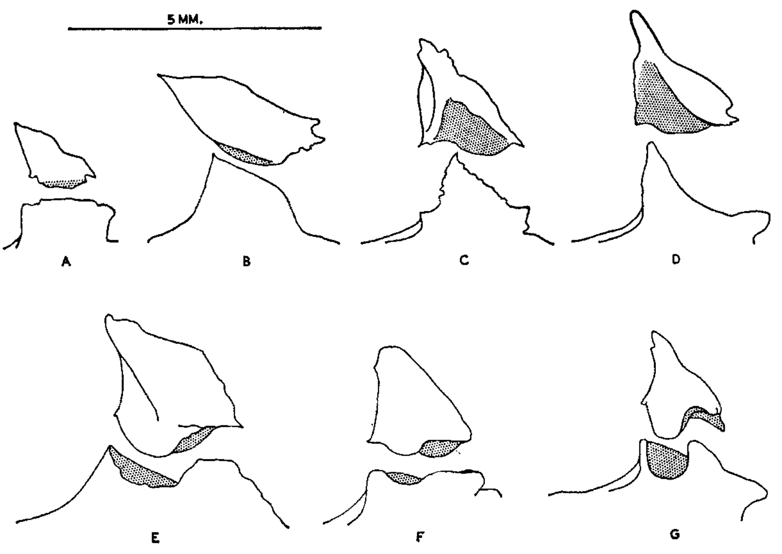

Fig. 5 Detail of articulation of prefrontal with maxilla. *Pars facialis* only portion of maxilla illustrated. Lateral view. Overlapped portions stippled. A, *Plethodon dunni;* B, *Ensatina eschscholtzii;* C, *Aneides hardii;* D, *A. aeneus;* E, *A. lugubris;* F, *A. flavipunctatus;* G, *A. ferreus*. Anterior to right.

maxilla, and, in all but *lugubris* and *aeneus*, by the prefrontal, does not correspond with the actual cutaneous opening of the external naris which is enclosed in the cartilaginous nasal capsule and lies medial to the septomaxilla.

Septomaxilla shaped rather irregularly; largest in *aeneus*, smallest in *lugubris;* articulates dorsally with nasal, ventrally with *pars dentalis* of maxilla, posteriorly with *pars facialis* of maxilla (except in *lugubris*), and posterodorsally with prefrontal (except in *lugubris* and *aeneus*). Two processes may be present, one arising from anterior border and extending anteroventromedially, the other arising from dorsal border of exposed portion. Second process small and pointed in *ferreus*, broader in *flavipunctatus*, absent in other species. Nasolacrimal duct passes posteromedial to second process, proceeds across dorsal edge of exposed portion of septomaxilla. In one specimen of *flavipunctatus* a partially closed groove, apparently for the passage of the nasolacrimal duct, is present on the dorsal surface.

The septomaxilla of *Plethodon* is more exposed and slightly larger than that of *Aneides*. Articulation of the septomaxilla with the *pars facialis* of the maxilla is present only in *elongatus* and *dunni* and is very limited. The processes are less evident than in *Aneides* and a depression may be located in the position of the dorsal projection of *Aneides*. The depression, together with portions of the nasal, prefrontal, and *pars facialis* of the maxilla, form a "foramen" for the nasolacrimal duct.

The septomaxilla of *Ensatina* is similar to that of *Plethodon*. The bone is overlapped broadly by the nasal, slightly by the prefrontal, but not at all by the *pars facialis* of the maxilla. Only the anterior process is evident.

Nasal. Located above the cartilaginous nasal capsule on either side is an irregularly shaped nasal that lies lateral to the frontal process of the premaxilla. The nasal is subject to a considerable amount of ontogenetic and individual variation in *Aneides*. In young individuals the nasal is small and amorphous with articulations limited in extent or completely absent. A characteristic shape is gradually attained with age in each species and the articulations become increasingly firm and extensive. The bone is occasionally anomalous. Splitting or doubling occurs infrequently (*ferreus*).

Nasal triangular in *lugubris, ferreus,* and *flavipunctatus* with greatest angle anterolateral, approaching 90°, anteromedial angle about 60°, posterior angle about 30°; triangular in *hardii*, nearly isoceles; almost quadrangular in *aeneus;* occasionally pentagonal in all species. Nasal longer than broad in all but *aeneus*, reaching greatest length in *lugubris* and *flavipunctatus;* about as broad as long in *aeneus*, but often either slightly shorter or slightly longer than broad. Nasal slightly arched lateromedially. Anteromedial extension extends forward almost to tip of snout in all species; least evident in *hardii* and *aeneus*. Anterior margin of nasal slants posterolaterally, slant greatest in *ferreus, flavipunctatus,* and *lugubris*, less in *hardii*, least in *aeneus*. Posterior tip acute in *flavipunctatus*, becoming obtuse in *hardii, ferreus,* and *lugubris*, truncate in *aeneus;* apex usually entire, but occasionally divided, especially in *hardii*. Nasal articulates medially with frontal process of premaxilla, either bone being slightly overlapped by other or meeting squarely; articulates posteroventrally with depressions in dorsal portion of frontal, articulation limited in *hardii*, extremely limited in *aeneus;* articulates extensively laterally with prefrontal in *flavipunctatus* and *hardii*, less extensively in *ferreus* and *lugubris*, slightly in *aeneus;* articulates anterolaterally firmly and rather extensively with *pars facialis* of maxilla in *lugubris*, slightly in most *aeneus*, slightly in some *hardii*, but never in *ferreus* or *flavipunctatus*. Separated from septomaxilla by nasolacrimal duct that passes dorsal to small, anterolateral process, then passes between nasal and maxilla, nasal and prefrontal, over or through prefrontal to orbit; occasional slight indentation in lateral border of nasal seemingly related to position of duct. Dorsal surface heavily ornamented in adult *lugubris*.

The nasal of *Plethodon* is similar to that of *Aneides* but is somewhat more irregular in shape. The basic triangular or pentagonal pattern is usually present, but occasionally the bone is almost square. The angles are not as evident and the posterior margin is often a gentle curve which may be notched once or twice. The anterolateral angle is often projected into a lateral process that may occasionally articulate slightly with the *pars facialis* of the maxilla. Such a situation is also present in many *A. aeneus* and rarely in the other species of *Aneides*. The nasal is usually longer than broad and the articulations are similar to those of *A. ferreus* and *A. hardii*. No ornamentation is present.

The nasal of *Ensatina* is rather amorphous but is usually somewhat quadrangular, often very wide posteriorly with little or no indication of a posteriorly directed apex. The bone is proportionately larger than in either of the other genera. The anterolateral process is normally better established and more evident than in the other genera. Articulation with the facial portion of the maxilla is absent, and the posterior articulation with the frontal is very limited. In other respects the bone resembles that of *Plethodon*.

Prefrontal. The dorsal portion of the medial one-half of the anterior orbital margin is formed by a pair of roughly triangular prefrontals. The shape and articulations are subject to ontogenetic and individual variation.

Prefrontal approximately a right triangle with right angle located posterolaterally. Dorsal angle truncate in *lugubris*, acute in *flavipunctatus* and *hardii*, almost spine-like in *ferreus*, drawn into long spinous process in *aeneus*. Anterior angle truncate in *lugubris*, sharply acute in other species; extends to anterior margin of nasal in most *ferreus*, *flavipunctatus*, and *hardii*, falls short in *aeneus*, only rarely extends beyond midpoint of nasal in *lugubris;* occasionally notched to form part of nasolacrimal "foramen." Notch may continue as dorsal groove extending posteriorly, serving for passage of nasolacrimal duct; duct passes through special anteroposteriorly oriented foramen present in posterior portion of prefrontal in *lugubris*. Lateral border of prefrontal complex in *ferreus*, *flavipunctatus*, and *lugubris;* consists of large oval posteriorly located superficial projection, and smaller anteriorly located deep projection in *ferreus;* projections present but less well defined in *flavipunctatus* and *lugubris*. Lateral border simple with deep and superficial projections reversed and only slightly, if at all, indicated in *aeneus* and *hardii*. Articulates with *pars facialis* of maxilla laterally; overlaps antorbital cartilage posterolateroventrally; articulates medially with nasal. Nasal articulation extensive in *flavipunctatus* and *hardii*, less extensive in *ferreus* and *lugubris*, only slight in *aeneus*. Prefrontal usually slightly smaller than nasal and rather thin; loses triangular shape in adult *lugubris*, in which bone is thickened and heavily ornamented.

The prefrontal of *Plethodon* is usually smaller than the nasal and is club-shaped with the widest portion located posteriorly. The prefrontal extends to the anterior margin of the nasal in only about one-half of the species and does not extend as far posteriorly as in *Aneides*. The prefrontal may be fused to the nasal in rare instances. Such a situation was observed on one side in a small individual of *vandykei*. Dunn ('26) was incorrect in stating that the prefrontals border on the external nares in *Plethodon*, and his statement that the prefrontals do not border the external nares in *Aneides* holds true only for *lugubris* and some *aeneus*. A notch is usually present in the extreme anterior angle of the nasal in *Plethodon*. No ornamentation is present.

The prefrontal in *Ensatina* is longitudinally elongate and very small, usually less than one-half the size of the nasal. The prefrontal extends to the anterior margin of the nasal and is relatively broad. No ornamentation is present.

Prevomer. The dorsal and anterior portion of the roof of the oral cavity is formed by the paired prevomers. Each of the thin bones consists of four portions in the primitive *Aneides* condition: the body, an expanded concave portion located anterior to the internal nares; the posterior projection of the body, located medial to the internal nares; the preorbital process, arising from the posterior section and located posterior to the internal nares; and the isolated posterior prevomerine patch (parasphenoid tooth patch of many authors, paravomerine tooth patch of others) attached to the ventral surface of the parasphenoid. The articulations with the premaxilla and maxilla are subject to ontogenetic variation, becoming increasingly more extensive with age. The preorbital process is variously developed within the genus and is subject to interspecific and individual variation. The posterior prevomerine patch was demonstrated to be a portion of the prevomer by Wilder ('20).

Concave body of prevomer forms roof of mouth; arches anteroventrally and lateroventrally from center of concavity towards margins; reaches greatest width at or near point of greatest width of *pars palatina* of maxilla; reaches greatest length at or near point of articulation with lateroposterior extension of *pars palatina* of premaxilla. Paired prevomer bodies embrace internasal space that is located directly ventral to internasal fontanelle. Medial wall of body often bears septum-like dorsal extension bordering internasal space; septum may proceed dorsally to articulate with frontal processes of premaxillae; septum subject to ontogenetic variation, best developed and most consistently present in adult *lugubris*. Body articulates with bilateral counterpart along medial border from midpoint, directly posterior to internasal space, nearly to posterior tip of bone; articulates by means of curved lateral, and anterior margin with *pars palatina* of maxilla; articulates slightly, in adults, with *pars palatina* of premaxilla. Posterior extension proceeds from body between medial border of internal nares and midline. Extension trapezoidal in shape; posterior edge reaches greatest posterior extent medially, slants sharply anterolaterally from that point forming angle of from 30° (*lugubris*) to 45° (*aeneus*) with midline. Width of posterior extension 50% length of prevomer proper (excluding posterior patch) in *aeneus*, 30–35% in other species. Posterior border of posterior extension bears dentigerous bony ridge that may be essentially straight following slant of posterior border (*lugubris, ferreus, flavipunctatus*) or gently and concavely curved (*hardii, aeneus*). Preorbital process, present only in *hardii* and *aeneus*, arises as slender lateral continuation from slanting posterior border of posterior extension; forms osseous posterior border of internal nares; unites dorsally with antorbital cartilage; longer and more highly developed in *hardii* than in *aeneus*, falling just short of lateral margin of prevomer body; always present but smaller in *aeneus*. Preorbital process completely absent in *ferreus, flavipunctatus,* and *lugubris*. Preorbital process bears teeth to level of middle of internal nares in *hardii*, to level of medial border of internal nares in *aeneus*. Posterior prevomerine patch isolated from prevomer proper; attached to ventral surface of parasphenoid; tear-drop shaped, broad posteriorly near posterior margin of parasphenoid, narrowing to tiny point anteriorly. Patch consists of numerous tooth sockets that have fused to one another; new teeth develop along lateral margins; old teeth, as well as old sockets, shed medially. Bilateral patch counterparts do not articulate with each other medially.

The prevomer of *Plethodon* is similar to that of *A. aeneus* and *A. hardii*, but the body is proportionately larger. The tooth-bearing preorbital process is always present and well-developed, often extending as far as the lateral border of the body. The length of the preorbital process and the number of teeth borne on it are subject to ontogenetic variation, both increasing with age.

The prevomer of *Ensatina* is larger than that of either *Aneides* or *Plethodon*. The preorbital process is very well-developed, extending beyond the lateral border of the prevomer body and bearing teeth almost to the tip. The anterior tooth series is deeply concave and extends far posteriorly. In one very young specimen (23.1 mm, snout-vent length) the anterior tooth series is continuous with the teeth of the posterior patch. The posterior patches are more widely separated from each other than in either *Plethodon* or *Aneides*.

Frontal. The paired frontals, together with the adjoining paired parietals, form the roof of the brain case proper. The anterior articulations are subject to considerable ontogenetic and individual variation. Articulation with the anterior cranial elements is very limited in juveniles but becomes increasingly more firm in adults. The frontals of old adult *lugubris* tend to fuse.

Elongate frontal extends from point posterior to eye to anterior margin of *pars facialis* of maxilla; narrow posteriorly and for most of length, becoming dilated and laterally expanded anterior to orbit. Posterior portion forms dorsomedial border of orbit; widest posteriorly, narrowest near anterior margin of orbit. Disproportion between widest and narrowest points least in *aeneus*, greater in *flavipunctatus*, greatest in *ferreus, lugubris*, and *hardii*. Margin of expanded anterior portion eroded and irregular. Anterior portion reaches posterior border of internasal fontanelle in all species but *lugubris;* forms extreme posterior border of fontanelle in *ferreus* and *hardii;* forms somewhat more of posterior border in *aeneus;* forms variable but usually slight amount of fontanelle border in *flavipunctatus*, depending on extent of development of frontal processes of premaxillae. Ornamentation extensive on anterior portion in *lugubris*, covering portion anterior to line that extends obliquely from anterior margin of orbit posteriorly to about level of center of eye on midline; raised oblique line marks anterior-most extent of cranial musculature and is clearly evident only in *lugubris*. Frontal articulates anteriorly by means of depressions in dorsal surface with prefrontal, nasal, and *pars frontalis* of premaxilla; articulates anteroventrally with antorbital cartilage; articulates medially with bilateral counterpart for virtually entire length; articulates laterally by means of ventral surface with orbitosphenoid; articulates posteriorly by means of ventral surface with parietal. Greatest extension of posterior margin lateral in position in *aeneus*, medial in all other species. Small diamond-shaped fontanelle may be present between frontals and parietals along midline; subject to ontogenetic variation, becoming increasingly smaller with age and disappearing in old adults.

The frontal of *Plethodon* is, in general, similar to that of *Aneides*. The anterior interorbital area is usually noticeably pinched but seldom to such a degree as in *A. lugubris, A. hardii*, or *A. ferreus*. The posterior projection is usually slightly lateral to the center of the bone although the position is somewhat variable. When the projection is medial, a small lateral projection is often present as well. A diamond-shaped posterior fontanelle is not uncommon in adults. No ornamentation is present.

A proportionately much broader frontal than in either *Aneides* or *Plethodon* is found in *Ensatina*. The posterior projection is usually at about the center of the bone. A diamond-shaped fontanelle of considerable size is usually present, but it is larger in small individuals.

Parietal. Much of the posterior cranial roof is formed by a pair of large parietals that are of about the same area but are slightly shorter than the frontals. In old adults, especially in *lugubris, flavipunctatus*, and male *ferreus* and *hardii*, a median ridge forms and in adult *lugubris* the two parietals may fuse together. The anterior articulation of the parietal is subject to some ontogenetic variation, becoming increasingly firm and extensive with age.

Parietal broad, about three times as long as wide in all species but *aeneus* in which bone is shorter and wider; borders posterior portion of medial margin of orbit. Greatest anterior extension lateral; medial anterior projection often present, usually very small but normally projecting anterior beyond posterior margin of frontal. Parietal extensively overlapped anteriorly by frontal although overlapping somewhat confined to lateral margin in *aeneus*. Parietal articulates medially with counterpart; articulates laterally by means of ventral surface with orbitosphenoid, ascending process of palatoquadrate, and anteromedial portion of occipito-otic; articulates posteriorly with occipito-otic. Lateral margin shaply curved ventrally in area of orbitosphenoid, becoming flattened posteriorly. Posterior portion broadly rounded bordering anterior margin of raised portion of occipito-otic.

The parietal of *Plethodon* is broader than in *Aneides* and the length is only slightly more than twice the width. Two anteriorly directed processes may be present and well-developed, one lateral overlapped by the frontal and the other medial overlapping the frontal. The overlapping by the frontal is not so extensive as in *Aneides* and is more extensive laterally than medially. The parietal is usually very broadly rounded posteriorly. No median ridge or fusion is present.

The situation in *Ensatina* is generally similar to that of *Aneides* but the parietal is less than twice as long as broad and is much shorter than the frontal. The parietal is very broadly rounded and almost squared posteriorly. The width of the two parietals combined is greater in proportion to the total skull length than in either *Plethodon* or *Aneides*. No median ridge or fusion is present.

Orbitosphenoid. The vertically oriented paired orbitosphenoids are endochondral ossifications that form the lateral sides of the brain case. Some individual and interspecific variation is seen, particularly in the position of the oculomotor foramen.

Orbitosphenoid rectangular in outline; surface smooth laterally; convex medially with convexity flattening anteriorly; thin, but thickening anteriorly and dorsally. Orbitosphenoids meet ventrally and anteriorly in adult *lugubris*, nearly meet in *ferreus*, more widely separated in other species; diverge from one another during dorsolateral ascent. Orbitosphenoid articulates dorsally with ventral surface of frontal and lateral margins of parietal by a medially expanded shelf of varying width; articulates ventrally with parasphenoid that may slightly overlap lateral margin of orbitosphenoid; articulates anteriorly with antorbital cartilage; articulates posteriorly with ascending process of palatoquadrate cartilage. Orbitosphenoid pierced by three openings. *Foramen orbitonasale mediale*, serving for passage of branch of fifth cranial nerve, perforates anterior margin of orbitosphenoid; not enclosed in bone but bordered posteriorly by orbitosphenoid, that sends a small anterior projection of bone dorsal and ventral to the foramen, and anteriorly by the antorbital cartilage. Optic fenestra very large, considerably larger than optic nerve; located in posterior one-third of orbitosphenoid; enclosed in bone; posterior margin at about level of posterior margin of frontal. *Foramen oculomotorium*, for passage of third cranial nerve, lies posterior to optic fenestra; small and variable in position; usually entirely enclosed in bone and located some distance anterior to posterior margin of orbitosphenoid in *ferreus;* usually entirely enclosed in bone and located near posterior margin of orbitosphenoid in *hardii* and *aeneus;* partially or wholly enclosed in bone and located at posterior margin of orbitosphenoid in *flavipunctatus* and *lugubris;* when not enclosed in bone, posterior margin of oculomotor foramen formed by ascending process of suspensorium.

The orbitosphenoids of *Plethodon* are similar to those of *Aneides* but are usually more widely separated from each other ventrally. The optic fenestra is located somewhat more posteriorly than in *Aneides*. The oculomotor foramen is usually enclosed partially in bone and partially in cartilage, but in adults of larger species (*yonahlossee*) may be entirely enclosed in bone.

The orbitosphenoids of *Ensatina* are widely separated from one another ventrally. The optic fenestra is located very close to the posterior margin of the bone. The orbitosphenoid forms no more than the extreme anterior margin of the oculomotor foramen, that is primarily enclosed in cartilage. The angle between the orbitosphenoid and the frontal is less than in *Aneides* or *Plethodon*.

Parasphenoid. The posterior roof of the oral cavity is formed by the elongate median parasphenoid. The bone is unpaired and essentially bilaterally symmetrical. Proportions and shape of the structure are subject to individual and interspecific variation.

Parasphenoid truncate posteriorly, becoming very narrow and almost pointed anteriorly; falls short of anterior orbit margin anteriorly; U-shaped in cross section with greatest concavity at *sella turcica* in posterior portion. Anterior portion very narrow in *lugubris*, *ferreus*, and *hardii*, somewhat broader in *flavipunctatus* and *aeneus;* rarely bifurcate at tip; bone rapidly broadens posterior to anterior one-third. Small paired lateral projection borne somewhat posterior to midpoint in adults of *ferreus*, *flavipunctatus*, and *lugubris;* absent in *aeneus* and *hardii*. Carotid canals evident about three-fourths of distance behind anterior tip at lateral border, especially in adult *lugubris*. Parasphenoid thickened posteriorly with thickened margin serving as insertion of subvertebral muscles; eroded along posterior margin with erosion proceeding anteromedially into thickened portion, particularly in adults of all species. Parasphenoid articulates ventrally at anterior tip with prevomer; articulates dorsally with orbitosphenoid by means of lateral margins; articulates dorsally with ascending process of palatoquadrate cartilage by means of posterior lateral margins; articulates dorsally with occipito-otic by means of broad posterior portion. Posterior prevomerine tooth patches cover as much as two-thirds of ventral surface of parasphenoid.

The parasphenoid of *Plethodon* is, in general, somewhat wider and flatter anteriorly than in *Aneides*. The lateral projections are not evident and the posterior margin is thickened only in adults of such large species as *yonahlossee*. The shape of the posterior portion is subject to much interspecific variation.

The parasphenoid of *Ensatina* is similar to that of *Plethodon*, although the anterior portion is somewhat wider proportional to the length.

Occipito-otic complex. The posterior portion of the skull is dominated by a pair of large irregular endochondral ossifications. Each consists of a large bulbous otic capsule and a small exoccipital region. Laterally and ventrally the complex supports the jaw suspensorium, while posteriorly the complex articulates with the first element of the vertebral column. Medially the complex forms the posterior portion of the cranial cavity. In general little variation is seen in proportions of the complex intragenerically, but crests borne on the otic capsule are subject to individual, ontogenetic, and interspecific variation.

Otic capsule posterolateral in position, very large, broadest posteriorly, becoming gradually narrower anteriorly; narrows abruptly anteriorly in *aeneus* in which capsule is more bulbous than in other species. Membranous labyrinth of auditory system enclosed within capsule; route of three semicircular canals revealed by dorsally located anterolaterally and posterolaterally oriented elevations, and dorsolaterally located anteroposteriorly oriented elevations of the otic capsule. Well-developed wing-like crest borne on dorsal surface of capsule, often extending posteriorly beyond capsule; most highly developed in *lugubris*, rising sharply above capsule with height equal to depth of capsule; well-developed in *hardii* males, *ferreus*, and *flavipunctatus;* poorly developed in *aeneus* and female *hardii.* Crest absent in very young individuals of all species, increases in height with age; posterior projection of crest virtually only portion present in young of all species and in adult female *hardii*, but projection is poorly developed even in adult *aeneus*. Crest serves as origin of enlarged *adductor mandibulae* muscle masses that characterize adult *Aneides*. Capsule articulates anterodorsomedially with ventral surface of parietal, anteriorly by means of two articulating surfaces with ascending process of palatoquadrate cartilage, anteroventromedially with dorsal surface of parasphenoid, ventrolaterally by means of small anteriorly directed raised articulating surface with basal process of palatoquadrate cartilage, laterally by means of small slightly raised articulating surface with otic process of palatoquadrate cartilage, laterally by means of small ridge (*crista muscularis*) with dorsomedial surface of squamosal. Exoccipital region formed by thin narrow dorsal and ventral projections from medial border of otic capsule; forms one-half of occipital ring; paired exoccipitals surround *foramen magnum*, unite to each other dorsal and ventral to foramen. Occipital condyles large and sessile, posterior in position; arise as cylindrical extensions of exoccipital at lateral margins of *foramen magnum;* convex posteriorly, capped with thin sheath of cartilage. Exoccipitals joined dorsomedially by means of cartilaginous *tectum synoticum*, joined ventromedially by means of small square hypochordal commissure; articulate anterodorsally with parietals; articulate posteriorly by means of occipital condyles and lateral walls of *foramen magnum* with condylar facets and with lateral borders of odontoid process of atlas, respectively; articulate ventrally with parasphenoid. Occipito-otic complex perforated by many foramina including: *foramen magnum*, surrounded by ring-like exoccipital elements, serving for passage of spinal nerve cord; foramen of trigeminal nerve, enclosed on three sides by anteromedial projection from capsule near posteromedial border of orbit, serving for passage of fifth cranial nerve, branch of seventh cranial nerve, and possibly sixth cranial nerve; facial foramen, penetrating ventrolateral portion of brain cavity wall ventral to capsule, proceeding from recess and bifurcating at ventral exterior surface of bone with anterior (palatal) foramen bearing palatal branch of seventh cranial nerve and posterior (facial) foramen bearing remainder of nerve; acoustical foramina, double interior foramina lying anterior to facial recess, bearing branches of eighth cranial nerve; perilymphatic foramen, situated internally near base of capsule posterior to acoustic foramina; tiny endolymphatic foramen, situated internally slightly anterior and considerably dorsal to perilymphatic foramen; post-otic foramen, bearing ninth and tenth cranial nerves and passing from posterolateral wall of cranial cavity through exoccipital, emerging anterolateral to occipital condyle; vestibular fenestra, large posterolateral opening in ventral portion of capsule, covered ventrally by opercular plate.

The oocipito-otic complex of *Plethodon* is similar to that of *Aneides* as far as articulations, foramina, and basic structure are concerned. The capsule is proportionately larger in *Plethodon* and is broad anteriorly, terminating abruptly at the anterior border of the element. A well-defined *crista muscularis* is not evident in *Plethodon* and in most species the articulation with the squamosal is by means of a groove-like depression in the dorsal surface of the capsule. When such a depression is present a small cylindrical process is normally present immediately anterior to the squamosal on the dorsal surface of the capsule. Such a situation is seen in *cinereus, dunni, glutinosus, jordani, longicrus, ouachitae, richmondi, vehiculum, wehrlei, welleri,* and *yonahlossee*. In *glutinosus* a secondary process may be present near the anterior margin of the capsule at the dorsolateral border. The depression and the groove are poorly defined or absent in *dorsalis, larselli, neomexicanus,* and *vandykei*. Although the wing-like crest so evident in most *Aneides* is absent in *Plethodon,* an entirely different type of crest is present in *elongatus,* extending mediolaterally across the anteromedial border of the capsule. The crest is subject to ontogenetic variation and appears at an early age, increasing in height with age. In adults the crest is rather high and well-developed. The squamosal is enlarged in *elongatus* and although the groove-like depression is absent a hook-like portion of the squamosal fits behind the posteriorly sloping crest between the crest and the surface of the capsule. The crest may be notched and at least in one instance a small process of the squamosal extends anteriorly through the notch.

Ensatina resembles *Plethodon* more than *Aneides* in the shape of the occipito-otic complex. The capsule is proportionately larger than in any *Aneides* or *Plethodon,* and ends abruptly anterolaterally, then proceeds slightly posteromedially. In most individuals the capsule is smooth, lacking crests and projections, but in very large individuals a low crest unlike any seen in *Aneides* or *Plethodon* may be present on the elevation marking the position of the anterior vertical semicircular canal.

Opercular plate. The ossified structures concerned with sound reception are located near the vestibular region of the occipito-otic complex and have been described anatomically, embryologically, and functionally in considerable detail in various representatives of the family Plethodontidae by Kingsbury and Reed ('09) and Reed ('20). Briefly, the situation in all *Aneides, Plethodon,* and *Ensatina* is as follows. The cavity of the vestibular fenestra is covered by a small circular flattened plate. The plate is a composite structure representing both the operculum, derived from otic capsular tissue, and the columella, a structure believed to be homologous with the primitive hyomandibula. The vertically oriented plate is attached to the fenestral wall by a membranous connection in the genera studied. Opercular material forms the entire plate according to Reed ('20) and the columella is represented solely by a tiny cylindrical projection, the *stylus columellae*, fused to the anterior border of the plate. The stylus, or stapedial rod, proceeds anterolaterally and is continuous with a tiny cylindrical posterior projection of the palatoquadrate portion of the suspensorium. No direct connection of the stylus to either the fenestral wall or squamosal is present.

Suspensorium. The posterior margins of the orbits and the suspensorial apparatus of the mandibles are formed by a pair of irregularly shaped structures that are attached tripod-like to the anterolateral portion of the otic capsules. Each structure consists of five regions: ascending, otic, basal, pterygoid, and quadrate. The first four regions are cartilaginous and are collectively termed the palatoquadrate cartilage. The quadrate is an endochondral ossification that is a direct lateral continuation of the basal region and extends ventro-obliquely at almost right angles to the longitudinal axis of the skull. Study of the entire structure is hampered by absence of ossification of most regions, but the element is similar in all species of *Aneides*. Massiveness and extent of ossification of the quadrate region are subject to ontogenetic variation.

Basal region ventrolateral in position; acts as base for otic, ascending, and pterygoid processes; ossifies distally to form quadrate; articulates by means of basal process with well-developed elevated articulating surface on ventrolateral portion of otic capsule. Tiny cylindrical process arises from proximal posterior margin of basal region and becomes continuous distally with *stylus columellae*. Otic process dorsal in position; joined to basal process ventrally; articulates proximally with raised articulating surface on lateral margin of otic capsule, dorsally with squamosal; overlain almost entirely by squamosal. Ascending region joins basal region to lateral skull wall; arises from basal region as slender cylindrical bridge-like process that extends to enlarged quadrangular portion inserted in lateral skull wall and bounded by parasphenoid, orbitosphenoid, occipito-otic, and parietal; enlarged portion forms anterior margin of trigeminal foramen. Pterygoid process arises from bridge-like ascending process near juncture with basal region; forms posterolateral border of orbit; proceeds anterolaterally almost to posterior tip of maxilla; connected to maxilla by short tendons. Quadrate massive, roughly cylindrical, wholly continuous with basal region; bears flattened dorsomedial extension; element thicker and more massive than squamosal but similar in overall length; small posteriorly directed process arises from distal portion of quadrate, connected by short ligaments to elongate curved posterior portion of ceratohyal. Quadrate articulates dorsally with squamosal, distally with articular of mandibular arch by means of large cartilage-lined anteroventrally directed fossa. Suspensorium joined to posterior tip of *pars dentalis* of maxilla by two large jugal ligaments that arise primarily from quadrate but also from basal region. Basal region and basal, ascending, and otic processes enclose cavity (*antrum petrosum laterale*) lying between area of juncture of processes and otic capsule.

The suspensorium of *Plethodon* is essentially similar to that of *Aneides*. The proximal flattened portion of the quadrate is not as long, however, and the element is not as massive as in *Aneides*.

The basic structure of the suspensorium of *Ensatina* is similar to that of *Plethodon* and *Aneides*, but the pterygoid is shorter than in either genus.

Squamosal. The suspensorium is overlain by a pair of flattened, vertically oriented squamosals. The squamosals lie lateral to the occipito-otics and are directed anteroventrally. Shape and extent of development of the posterior crest are subject to individual and interspecific variation.

Squamosal roughly triangular with definite longitudinal axis; lies splint-like over dorsal surface of quadrate and palatoquadrate; posterior portion of dorsal margin passes ventral to posterior projection of occipito-otic crest. Squamosal becomes thickened and relatively massive in adult *lugubris*, bearing well-developed wing-like posteriorly directed crest along posterodorsal margin; crest becomes continuous with ventral margin of posterior projection of occipito-otic crest; squamosal somewhat thickened in adults of other species, occasionally bearing poorly developed dorsoposterior projection or ridge in *ferreus* or *flavipunctatus*. Squamosal articulates dorsally with otic capsule just dorsal to position of horizontal semi-circular canal near *crista muscularis* by means of narrowest side of triangle; articulates with otic process of suspensorium and with quadrate lateral to occipito-otic by means of ventromedial surface.

In *Plethodon* the squamosal is smaller, more elongate and less triangular than in *Aneides*. The posteriorly directed projection found in some *Aneides* is absent, although the element may become thickened along the posterior border in adults of the large species such as *yonahlossee*. The longitudinal axis of the element is directed somewhat more horizontally than in *Aneides*. Articulation with the occipito-otic has been discussed previously and, in general, is less firm than in *Aneides*.

The squamosal of *Ensatina* is similar to that of *Plethodon* but is slightly more triangular and the longitudinal axis is directed vertically as in *Aneides*. No posterior projection or crest is present and no thickening is observed even in adults.

Mandible

The mandibular arch includes a pair of mandibular rami. Each ramus consists of: a persistent Meckel's cartilage; an articular, a proximal replacing ossification of the cartilage; and two investing bones, the dentary and prearticular. The coronoid height of the prearticular is subject to ontogenetic variation and increases with age.

Meckel's cartilage extends full length of mandibular ramus; exposed posteriorly and, for a short distance anterior to prearticular, medially; tapers anteriorly to tiny cartilaginous rod with no evidence of mentomeckelian replacing ossification at mandibular symphysis; becomes considerably broadened and partially ossified posteriorly to form articular.

Articular primarily cartilaginous, located at posterior end of ramus; articulates with quadrate posterodorsally; remains cartilaginous posteriorly on articulating surface; articulates and partially fuses medially with prearticular; articulates laterally with dentary; becomes exposed dorsally and posteriorly.

Dentary, principal element, extends almost entire length of ramus; C-shaped in transverse section with medial border partially open; contains Meckel's cartilage within cavity of C; becomes O-shaped anteriorly, entirely enclosing cartilaginous rod; expands funnel-like to form broad articulating surface at anterior symphysis. Triangular elevation of variable proportions arises from dorsal surface of dentary just posterior to midpoint; very well-developed in adult *lugubris* in which height is only slightly lower than greatest height of prearticular; dorsal apex of elevation always anterior to apex of prearticular; elevation laterally expanded, especially in *lugubris*, serving as insertion for mandibular muscles. Dentary becomes thin, narrow, and elongate posteriorly, terminating at or slightly anterior to posterior tip of articular; teeth borne on medial side of dorsal portion of dentary with well-developed pedicels which, although deciduous, contribute considerably to substance of bone; tooth-bearing area occupies slightly less than one-half of ramus length in female *hardii;* area becomes progressively less in *aeneus*, male *hardii*, *lugubris*, *ferreus*, and *flavipunctatus* approximately in that order; as little as anterior one-fourth of ramus bears teeth in *flavipunctatus*.

Prearticular forms medial border of posterior portion of ramus; occupies more than one-half of total mandibular length; widest ventrally where it extends ventral to articular; becomes expanded and very compressed dorsally; well-developed coronoid portion arises from dorsal region, inflected medially just anterior to articular; inflection forms shelf-like structure on which insert enlarged *adductor mandibulae* muscles; height of coronoid roughly proportional to length of mandibular ramus, increasing as ramus increases in length; both ramus length and coronoid height increase with age. Prearticular narrows in height anteriorly and terminates in sharp point in middle of open portion of dentary C anterior to midpoint of ramus; bone perforated posteromedially by two foramina for branch of seventh cranial nerve and blood vessels.

The dorsal extension of the dentary of *Plethodon* is smaller than in *Aneides* and often not triangular. The dorsal extension may or may not be slightly expanded laterally. The tooth-bearing area occupies more than one-half but less than two-thirds of the total ramus length. The prearticular is proportionately shorter than in *Aneides* and often occupies slightly less than one-half of the total ramus length.

In *Ensatina* the tooth-bearing portion of the dentary occupies about three-fourths of the total ramus length. Only a slight dorsal extension of the dentary is present posterior to the tooth-bearing portion. The prearticular is small and the coronoid process is proportionately shorter than in either *Plethodon* or *Aneides*. Slightly to considerably less than one-half of the total ramus length is occupied by the prearticular.

Hyobranchial apparatus

The hyobranchial apparatus consists of a pair of distally expanded ceratohyals, a single median basibranchial I bearing a pair of anteriorly located cornua, paired ceratobranchials I, paired ceratobranchials II, a pair of epibranchials, and a tiny median basibranchial II. All elements but basibranchial II are entirely cartilaginous with the exception of an occasional calcified basibranchial I. The element has been accurately figured by Hilton ('45).

Ceratohyal attached to skull posteriorly, free anteriorly; anterior portion flattened and dilated, contributes extensively to floor of mouth; becomes cylindrical posteriorly and hooks dorsally and laterally to connect by means of short strong hyoquadrate ligament to process of quadrate, portions of basal region of palatoquadrate, and in some cases with portions of squamosal. Basibranchial I rather elongate, slightly flattened dorsoventrally; bears attenuate anteriorly directed process that normally lacks terminal knob; bears two laterally directed cornua that extend into distal portion of tongue and articulate with basibranchial at base of anterior process; articulates near posterior end with proximal portions of ceratobranchials I; becomes narrower posterior to articulation with ceratobranchial I and articulates with ceratobranchials II at posterior tip; basibranchial I normally shortest of articulated branchial skeletal elements. Ceratobranchial I cylindrical, somewhat sigmoid shaped; convex anteriorly becoming concave posteriorly; articulates proximally with basibranchial I; appressed to ceratobranchial II along medial margin for distal one-third of length; articulates distally with epibranchial; larger with greater diameter than ceratobranchial II; longest of branchial skeletal elements. Ceratobranchial II cylindrical, slightly sigmoid shaped; concave anteriorly becoming slightly convex posteriorly; appressed to bilateral counterpart medially for short distance near proximal articulation with basibranchial I; well-separated from ceratobranchial I anteriorly but becomes appressed to that structure posteriorly as far as distal articulation with epibranchial; shorter than ceratobranchial I but longer than basibranchial I and epibranchial. Epibranchial elongate, relatively robust proximally, drawn into point distally; extends dorsally so that tip is located dorsolaterally near insertion of forelimb; shorter than ceratobranchial I and ceratobranchial II, longer than basibranchial I, occasionally shorter than basibranchial I in some, especially *lugubris*. Basibranchial II does not articulate with any other structure; represented by tiny ossification of irregular shape located medially at about level of proximal tip of epibranchial; embebbed in and serving as insertion for ventral musculature; swollen medially with tiny lateral process on either side; poorly developed in young, present as tiny dot of ossified tissue.

The structure of the hyobranchial skeleton is essentially the same in all species of *Aneides* with only minor variation in the shape of the cornua and of the anterior process of basibranchial I. Piatt ('35) said basibranchial I remains cartilaginous in *Aneides* but I find the structure calcified in five of nine specimens of *hardii* and one specimen of *flavipunctatus*.

The hyobranchial skeleton of *Plethodon* is essentially similar to that of *Aneides* but the various elements are subject to some variation. The cornua are smaller than in *Aneides*. The anterior extension of basibranchial I is usually well-developed and knob-like. Basibranchial II is usually somewhat larger than in *Aneides* and bears a ventrally directed medial process as well as more elongate lateral processes. Piatt ('35) said that basibranchial I was ossified (calcified?) in *Plethodon*. Fully calcified basibranchials I are found in *dorsalis, glutinosus, jordani, ouachitae, wehrlei, welleri,* and *yonahlossee*. The structure is calcified in all of the specimens examined of *dorsalis* (3), *ouachitae* (1), and *wehrlei* (1), but is calcified only in adults or near adults in the other species. In *yonahlossee* the structure is calcified only in specimens of more than 70 mm snout-vent length. One (an adult) of eight *vandykei* has a partially calcified basibranchial I. I have not seen a calcified basibranchial in any of the following: *cinereus, dunni, elongatus, larselli, longicrus, neomexicanus, richmondi,* and *vehiculum*.

In *Ensatina* the anterior extension of basibranchial I is absent or reduced to a small point. The cornua arise from the tip of the element and basibranchial I is never calcified. The epibranchial is the same length as or slightly longer than ceratobranchial I and is the longest element. Basibranchial I is the shortest articulated element as in *Aneides* and *Plethodon*. Basibranchial II is elongate and larger than in either *Aneides* or *Plethodon*. Basibranchial II is shaped somewhat like an inverted flattened V.

Dentition

Teeth are borne on four elements in *Aneides:* premaxilla, maxilla, dentary, and prevomer. Shape, position, and number of teeth is subject to considerable ontogenetic, individual, sexual, and interspecific variation. Premaxillary, maxillary, and dentary teeth are pleurodont and deciduous. The teeth are comprised of two distinct parts, a crown and a pedicel, separated by a ring of fibrous tissue (see Parsons and Williams, '62). In tooth replacement the crown is lost first, followed by gradual disintegration of the pedicel. Tooth replacement is continuous in all groups of teeth, and teeth of all sizes and stages of development are observed in the toothed regions. It is well known that numbers of teeth are ontogenetically variable in salamanders. In most species tooth number increases with increasing size and age. I have not had sufficient material available to thoroughly investigate variation in tooth number. However, it appears that the number of maxillary and prevomerine teeth tends to increase with increasing age while the number of premaxillary and dentary teeth remains relatively constant or decreases slightly. The absolute number of maxillary and dentary teeth present in sexually mature individuals appears to be significant and these figures are presented in table 1. Tooth counts are based on ankylosed teeth. In *Aneides* the primitive tooth apparently is bicuspid with a prominent sharp-pointed lingual cusp that is often hooked slightly to the posterior and a small

TABLE 1

Variation in maxillary and dentary dentition (totals per individual)

Species	Sample size	Maxillary		Dentary	
		Range	Mean	Range	Mean
Aneides					
ferreus	18	5–11	8	6–16	11
flavipunctatus	13	8–15	11	6–18	11
lugubris	11	9–16	13	9–19	15
aeneus					
males	4	7–17	11	12–19	15
females	5	12–21	16	22–25	24
hardii					
males	4	14–22	19	17–32	23
females	6	28–36	31	31–49	39
Plethodon					
16 species		17–55		27–70	
Ensatina					
eschscholtzii	6	56–73	61	82–96	88

inconspicuous labial cusp that may be sharp-pointed or blunt-tipped. Maxillary, premaxillary, and dentary teeth of *hardii*, young *aeneus*, young *flavipunctatus*, and young *ferreus* are at least slightly bicuspid with poorly to well-developed labial cusps. The three groups of teeth are definitely bicuspid in adult *hardii* but only the premaxillary teeth are bicuspid in the adults of *ferreus*, *aeneus*, and *flavipunctatus*. Occasionally a developing maxillary or dentary tooth of the latter three may be bicuspid but only a slight indication of a labial cusp is ever found in mature teeth and such a situation is encountered relatively infrequently. I have not seen the slightest indication of a bicuspid tooth in *lugubris*, in which the teeth are bizarre and highly specialized. The maxillary and dentary teeth of *lugubris* are formidable appearing sabre-like unicuspid teeth that are elongate and compressed and in close contact with neighboring teeth. The premaxillary teeth of *lugubris* are long spine-like unicuspid structures that curve anteriorly at their distal tips to pierce the upper lip. Such a situation is particularly evident in old adult males but is also present to a lesser extent in adult females and young adult males. Noble ('31) also reported the loss of a cusp and the direct development of unicuspid teeth in *lugubris*.

Premaxillary teeth short conical structures in young, becoming somewhat longer with age and reaching greatest length in adult male *lugubris* in which teeth become spine-like; always shorter than longest maxillary teeth; variable in number in all species, numbering two to ten.

Maxillary teeth variable as to shape, length, and number; short conical structures in young and in female *hardii* and female *aeneus*, somewhat longer and conical but distally recurved in male *hardii*, slightly longer, conical and distally recurved but spine-like in male *aeneus*, longest and distally recurved in *flavipunctatus*, *ferreus*, and *lugubris;* great lateral compression in *ferreus* and *lugubris*, usually conical or only slightly compressed in *flavipunctatus* with greatest compression in adult males, no compression in *aeneus* and *hardii;* shortest among adults in female *hardii*, longest in *lugubris;* variable in number, most numerous in female *hardii*, decreasing in number in male *hardii, aeneus, lugubris, flavipunctatus*, and *ferreus* in that order (table 1); sexual dimorphism marked only in *hardii*, present to lesser extent in *aeneus*.

Dentary teeth variable as to shape, length, and number; short conical structures in young; short and conical in *hardii* females, slightly longer in *hardii* males; rather spine-like in *aeneus*, longer than in *hardii;* rather spine-like and somewhat longer in *flavipunctatus* and *ferreus*, reaching greatest length in *lugubris;* slightly compressed in *flavipunctatus* with somewhat more compression in adult males; greatly compressed in *ferreus* and *lugubris;* distally recurved in all species; teeth closely adjoined to one another in *ferreus* and *lugubris*, large gaps occasionally present between teeth in other species; a few tiny conical teeth often present near mandibular symphysis; considerable variation in number but most numerous in female *hardii*, fewer in male *hardii, aeneus, lugubris, flavipunctatus* and *ferreus* in that order (table 1); sexual dimorphism marked only in *hardii*, present to lesser extent in *aeneus*, only slight in other species.

Prevomerine teeth located in two positions: anteriorly along preorbital process (when present) and posterior margin of posterior extension of prevomer, and posteriorly in patch borne under parasphenoid. Anterior prevomerine teeth tiny and conical with recurved distal hook; teeth in series borne on elevated ridge of bone; variable in number, averaging highest in number in *hardii*, lower in *aeneus, lugubris, flavipunctatus*, and *ferreus* in that order, numbering from two to ten per bone in all species. Posterior prevomerine teeth extremely small, located in paired patches that appear to consist of no more than fused tooth sockets; separated from anterior prevomerine teeth by disjunction in prevomer; teeth lost medially with new teeth added laterally; distally recurved; variable in number in all species, more numerous in adults, numbering between 45 and 115 per patch.

The teeth of *Plethodon* are, in general, very similar to those of female *A. hardii*. Premaxillary, maxillary, and dentary teeth are bicuspid in all 16 species examined although very weakly bicuspid in *vehiculum* and *dunni*. Only the developing teeth are bicuspid in *dunni*. Other western species, notably *vandykei* and *elongatus*, have strongly bicuspid teeth. The teeth usually are slightly recurved distally. In general the western species and the smaller eastern species have larger teeth relative to the size of the maxilla than do the larger eastern species, particularly *yonahlossee*, *longicrus*, *glutinosus*, *ouachitae*, and *jordani*, but in none are the teeth relatively as large as in any *Aneides*. Sexual dimorphism appears to be present in many species with the teeth in males generally longer and fewer in number. The total number of premaxillary teeth is somewhat higher than in *Aneides* with a range of 5 to 16. The maxillary and dentary teeth average much higher than in *Aneides* (maxillary totals: 17–55, dentary totals: 27–70). Numbers of prevomerine teeth are similar in the two genera. The teeth of *Ensatina* are conical, bicuspid structures that are very tiny and are usually not distally recurved. Sexual dimorphism is not evident. Premaxillary teeth are much more numerous than in either *Plethodon* or *Aneides* and average 18 (range: 13–21). Maxillary and dentary teeth average much higher than in either *Plethodon* or *Aneides* (table 1). Anterior prevomerine teeth average 20, with a range of 14–29.

Vertebral column

The vertebral column consists of one cervical, a variable number of trunk, normally a single sacral, and a variable number of caudal vertebrae. The number of trunk and caudal vertebrae is subject to interspecific and individual variation. Caudal vertebrae apparently increase in number with age, within limits. A more or less continual reduction in vertebral size occurs from anterior to posterior in both trunk and caudal vertebrae.

Cervical vertebra. The atlas, the only cervical vertebra, bears both odontoid and condylar processes. Ontogenetic and individual variation is seen in the degree of fusion of the pedicels at the mid-dorsal suture and the boss that forms at the suture is subject to interspecific variation.

Atlas bears well-developed odontoid process ventral to neural canal; process concave dorsally, convex ventrally, concave along anterior margin; bears two convex, anteroventrolateral articulating surfaces that articulate with walls of *foramen magnum*. Two very large anteriorly directed concave condylar facets are borne on pair of laterally expanded condylar processes that project wing-like from anterior margin of neural arch pedicels; located just posterior and dorsal to articulating surfaces of odontoid process; well separated from one another by large odontoid process; articulate cranially with occipital condyles. Centrum of atlas small, limited to posterior end of vertebra; slopes conically anteriorly and becomes indistinguishable at about vertebral midpoint; becomes conically hollow posteriorly (centrum articular cavity) with cavity containing anterior one-half of intervertebral cartilage; ventral margin of centrum articular cavity proceeds farther posteriorly than dorsal margin and is convex posteriorly; ventral margin thickened in old adults, particularly *lugubris*. Neural arch high; bears pair of well-developed postzygapophyses posteriorly; posterior margin of arch ascends sharply posterodorsally exposing large surface to which are attached main fiber masses of *m. interspinalis;* arch pedicels not fused dorsally with one another in juveniles, leaving mid-dorsal gap; pedicels become fused in adults with well-developed thickened boss appearing with increasing age mid-dorsally. Boss usually rounded anteriorly, becomes broader posteriorly and terminates abruptly, broadest point coinciding with posterior margin of neural arch; boss well-developed in *hardii*, very wide anteriorly and retaining width posteriorly forming large dorsal rectangular plate; narrower but very well-developed in *ferreus* and *lugubris;* narrow and elongate in *flavipunctatus;* least well-developed, triangular in shape and more or less limited to anterior portion of arch with apex anterior in *aeneus*. Neural arch perforated laterally just posterior to dorsal surface of condylar facets for emergence of first spinal nerve; evacuated posteriorly by large intervertebral fenestra that includes dorsal anterior extension that serves as passage for second spinal nerve. Vertebra perforated ventrally by two pair of foramina, one at about midpoint, other along dorsolateral margins of centrum; foramina may coalesce at ventral surface; allow passage of blood vessels.

In many species of *Plethodon* the atlas is similar to that of *Aneides* with the exception that the mid-dorsal suture is not completely ossified. In *yonahlossee*, *jordani*, *longicrus*, and *glutinosus*, however, the suture is completely ossified and a narrow dorsal boss is developed.

In *Ensatina* the neural arch is incompletely ossified except in very large individuals. The atlas differs from that of *Aneides* and *Plethodon* in that the pedicels are convex and proportionately higher. A dorsal boss is developed poorly if at all and is very narrow, not extending as far posteriorly as in *Aneides*. The foramen for the second spinal nerve is less evident and the anterior margin of the odontoid process is less concave than in either of the other genera.

Trunk vertebrae. The number of trunk vertebrae varies in *Aneides* as follows (number of specimens in parentheses): *aeneus*, 15 (2), 16 (10), 17 (4); *hardii*, 15 (1), 16 (18); *lugubris*, 16 (13), 17 (1); *ferreus*, 16 (2), 17 (18), 18 (5); *flavipunctatus*, 16 (1), 17 (13), 18 (1). In one of the *ferreus* with 16 vertebrae, one vertebra bears two ribs on one side and is obviously abnormal, apparently representing two vertebrae fused in a very inexact manner. Each normal trunk vertebra consists of two portions, the centrum and neural arch, together with their associated structures. Normally all but the last bear ribs but in many cases even the vertebra immediately preceding the sacral bears abbreviated ribs. The vertebrae are subject to interspecific variation and certain structures, including the neural spine, may be serially and ontogenetically variable as well.

The vertebrae of *Aneides*, *Plethodon*, and *Ensatina* are structurally amphicoelous and the centrum in younger individuals of all species is hollow, forming a notochordal canal. The articular cavities are filled by intervertebral cartilages that attach into the anterior cavity of each centrum. Nomenclature of plethodontid vertebral structure has been a source of some confusion. Soler ('50) discussed the structure of the vertebral centrum of several species and proposed terms to replace amphicoelous and opisthocoelous, terms he considered to be inappropriate for salamanders. Soler suggested the following: "holocoelous" for a condition in which material enclosed in the notochordal canal is neither calcified nor ossified; "hemicoelous" for a condition in which the posterior half of the notochordal canal is hollow and the anterior half is solid bone including a condyle that projects from the solid bony portion; "pseudocoelous" for a condition in which the notochordal canal itself is hollow, yet covered at its anterior end by an ossified cap. I have examined sagittal sections of vertebrae of dried skeletons and cleared and stained skeletons of *Desmognathus* and *Leurognathus*, the two genera for which the term "hemicoelous" was proposed, *Pseudotriton* and *Gyrinophilus*, genera that are said to have "pseudocoelous" vertebrae, and *Plethodon*, a genus said to have "holocoelous" vertebrae. In addition I have studied sagittal sections of the vertebrae of *Aneides*, *Ensatina*, and *Taricha*, and whole vertebrae for all members of the family Plethodontidae with the exception of *Phaeognathus*. Soler apparently underestimated the significance of the intervertebral cartilage and changes that occur ontogenetically in that structure. In young *Aneides* the intervertebral cartilage is spindle-shaped and composed of an almost gelatinous-like cartilage. The cartilage shrivels upon drying and may be found attached to the anterior articular cavity of dried preparations. The cartilage becomes fibrous and increasingly firm with increasing age of the organisms and in old adults (at least in *lugubris* and *hardii*) is firmly and intimately associated with the bony portion of the centrum, filling the entire anterior cavity. Upon drying the cartilage protrudes as a bone-like condyle from the anterior cavity. The condylar cartilage may be partially calcified as is indicated by the affinity of the structure for alizarin red-S in some old *lugubris* and *hardii*.

Examination of an ontogenetic series of *Desmognathus quadrimaculatus* and *Desmognathus ochrophaeus* is instructive in clarifying the problem of progressive changes in vertebral articulation. In dried preparations of old individuals of both species the condyle formed at the anterior end of the centrum appears to be bony. In young individuals, however, it is evident that the condyle is a portion of the intervertebral cartilage which has become fibrous at a very early age. The condyle in larvae and young individuals may be separated from the bony borders of the centrum. In older individuals of *Desmognathus* the cartilage is dense and fibrous and is closely adherent to, but separable from, the borders of the centrum. In large adult *D. quadrimaculatus* (81.2 mm snout-vent length) no indication of ossification is seen and only small amounts of calcification are present as shown by the low affinity for alizarin red-S in cleared and stained preparations. When the condyle is dissected and stained separately the stain is taken up in the granulated pattern of calcified cartilage, not the relatively homogeneous pattern of bone. I have not had extremely large *Pseudotriton* or *Gyrinophilus* available to me but on the basis of examination of large series of both, as well as the comments of Moore ('00), it seems apparent that a process similar to that in *Aneides* occurs in the two genera. In *Thorius, Parvimolge*, and some *Pseudoeurycea* a well-developed condyle having a high affinity for alizarin red-S stain is present. The stain pattern is similar to that seen in heavily calcified cartilage and I think the condition, considered an example of "pseudocoely" by Soler, is an extension of the trend seen in other plethodontids towards solidification and calcification of the intervertebral cartilage. It is true that the condyle, especially in *Thorius*, is more protrusive than in most other plethodontids. A salamandrid, *Taricha*, was also considered to be "pseudocoelous" by Soler but it has ossified condyles that are coextensive with the centrum and represents a condition I consider to be opisthocoely. The condition in *Thorius* evidently parallels that in *Taricha* and the salamandrids but the origin of this condition has developed through different routes in the two groups.

Auffenberg ('61), in describing a new fossil salamander, discussed the terms proposed by Soler and apparently accepted them. He admitted the possibility that a well-developed condyle on the anterior articular cavity need not necessarily be bone to be preserved in a fossil without shrinkage. On the basis of the information presented above concerning the progressive solidification of the intervertebral cartilage to a condition superficially identical with bone, it seems that it would be difficult to determine whether a fossil condyle was originally bony as in the salamandrids, or a solid fibrous, partially calcified cartilage as in *Desmognathus* and several other plethodontids.

In the plethodontid salamanders there appears to be a trend from a primitive amphicoelous type of vertebra to an opisthocoelous condition. Vaillant (1885, 1886) demonstrated long ago that the vertebrae of *Aneides* may be considered functionally or physiologically opisthocoelous although anatomically amphicoelous. Moore ('00) demonstrated that a single process accounts for the varying conditions of the vertebral articulation in *Desmognathus, Pseudotriton*, and *Plethodon* and that the vertebrae in all are of the same basic type. Taylor ('44) discussed vertebral structure in plethodontid salamanders including some information on ontogenetic changes in intervertebral articulation. He stated that misleading conclusions might be reached unless size and age of a given specimen are taken into account. He would, however, place considerable systematic importance on the intervertebral articulation since he believes there is as great specific and generic constancy in vertebral articulation of large adults as in any other character. I do not wish to enter into a discussion of constancy of the character throughout the various members of the family Plethodontidae at this time, but rather point out that the various conditions of vertebral articulation found in plethodontid salamanders (including *Desmognathus* and relatives) are the results of attainment of various levels of development within a single process. The terms introduced by Soler connote basic differences that do not seem to be present in the character among plethodontids. I believe the adult condition to be of less significance than indicated by Soler and consider his terminology to be both unnecessary and confusing.

Apparently a gradual change occurs during the life of an organism in regard to the condition of the intervertebral cartilage. Young individuals have vertebral centra that are "holocoelous" according to the definition of Soler, while older individuals of the same species must be considered "hemicoelous" since the posterior half of the notochordal canal is hollow and the anterior half is filled by a projecting condyle that, although not ossified, is solidified and at least partially calcified.

The following description is based on a detailed study of the seventh and eighth trunk vertebrae of both sexes of all species of *Aneides* (see fig. 9).

Vertebral centrum well-developed and elongate, 0.7 to 0.8 times pre- to postzygapophyseal length; round to oval in transverse section anteriorly, oval posteriorly, broader than high; tapers conically from both ends and becomes narrowly constricted near mid-point; universally amphicoelous with conical articular cavity at either end each bearing portion of intervertebral cartilage that is firmly attached to anterior end of centrum; slightly shorter than neural arch, anterior extremity craniad to anterior margin of neural arch. Hypophyseal ridge present on ventral surface of centra of anterior one to three vertebrae in large *lugubris*, absent in young and in other species; ridge divides sagittally on succeeding vertebrae and two low ridges separate and flatten posteriorly, becoming heavily eroded and interrupted. Ventral surface of centrum usually smooth and unridged, imperforate in all but *lugubris;* slight ridging occasionally present in old adults of other species; one to two pairs of foramina, often large and well defined, pass dorsally through thickened walls of centrum on either side of narrow notochordal canal, open into neural arch. Neural canal formed by neural arch, surrounds spinal cord; rather triangular with very broad rounded apex and convex ventral floor; presents impression of inverted deep crescent with rounded tips. Paired wing-like prezygapophyses extend anterolaterally from margins of neural arch, bear tear-drop shaped articulating facet dorsally; anterior tips widely divergent, extending well anterior to deeply concave anterior margin of neural arch. Paired postzygapophyses extend posterolaterally from posterior lateral margin of neural arch; lateral extent about equal to that of prezygapophyses; bear ventral articulating surfaces. Well-developed zygapophyseal ridge extends from prezygapophyses to postzygapophyses along dorsolateral margin of neural arch, especially marked in *aeneus*. Posterior margin of neural arch originates from dorsal surface of postzygapophyses, extends posterodorsally; vertically thickened dorsoposteriorly, hollow, often bearing pair of recesses from which arise portions of the intervertebral muscles; dorsoposterior margin of neural arch entire on anterior vertebra, becoming increasingly bipartite and projecting posteriorly as paired hyperpophyses. Hyperpophyses most strongly developed in *flavipunctatus* in which posterior tips extend well posterior to postzygapophyses; less well-developed in *lugubris, ferreus, aeneus,* and *hardii* in that order, posterior tips extending about to level of postzygapophyses or falling short of that point; serially variable, becoming increasingly well-developed as one proceeds posteriorly along vertebral column. Paired diaphophyses arise from lateral margin of neural arch near midpoint of vertebra, proceed laterally and somewhat posteriorly. Paired parapophyses arise from centrum directly ventral to diapophyses, are of about same length as diapophyses: may be slightly anterior to diapophyses, especially in *aeneus*. Diapophyses and parapophyses extend to point just beyond lateral margins of zygapophyses; at least partially fused to each other proximally by means of thin plate-like portion of bone which is perforated by small foramina; processes separate from one another distally, become cylindrical and bear concave tips that articulate with bicipital ribs; processes fused almost to tips in *lugubris.* Diapophyses of ribless posterior trunk vertebrae become reduced while parapophyses become elongate and bear wing-like alar processes. Parapophyses of adult *lugubris* supported by dorsoventrally compressed plate-like shelf that arises from ventrolateral surfaces of anterior and posterior margins of centrum and extends to distal tip of parapophyses; shelf results in diamond-shaped appearance of vertebrae when viewed ventrally; shelf poorly developed or absent in other species. Neural arch evacuated posteriorly to form intervertebral foramen; spinal nerves do not emerge from intervertebral foramina but from special foramina just posterior to each backward-swept diapophysis; neural arch perforated by several foramina for passage of blood vessels just anterior to diapophyses. Neural spine arises from low anterior dorsal midline of neural arch and attains height usually not greater than posterior margin of arch; continuous from anterior origin of spine to posterior margin of arch in *lugubris*, *ferreus*, and *flavipunctatus*, occasionally interrupted; less well-developed in *hardii* and *aeneus*, low in both species and limited to anterior portion of vertebra in *aeneus;* best developed on anterior vertebrae of all species, becoming increasingly lower posteriorly.

The trunk vertebrae of *Plethodon* differ somewhat from those of *Aneides*. Considerable interspecific variation is seen in number and in the shape of the centrum and neural arch. The number of vertebrae varies from 14 to 23 in the various species. In addition considerable intraspecific variation may be found in certain species. In *cinereus* for example the number varies from 18 to 23 with geographic as well as intrapopulational variation (Highton, '60). An elongate centrum, shaped like that of *Aneides*, is present, but accessory basipophyseal processes, only faintly indicated in *Aneides*, are at least slightly developed on either side of the posterior edge of the centrum in nine species (*cinereus*, *dorsalis*, *elongatus*, *glutinosus*, *longicrus*, *neomexicanus*, *ouachitae*, *wehrlei*, and *welleri*) and are probably found in some individuals of other species as well. Centrum length is considerably more than twice the anterior diameter of the centrum. The distance between the tips of the prezygapophyses is interspecifically variable but is, in general, less than in *Aneides*. Diapophyses arise from the midpoint of the neural arch, as in *Aneides*, or slightly posterior to that point. Parapophyses are situated slightly anterior to the diapophyses and are not fused to the diapophyses to nearly as great an extent as in *Aneides*. The distal tips of the two transverse processes are widely separated. Hyperpophyses are poorly developed on the anterior vertebrae but are well-developed posteriorly. In general the hyperpophyses extend to about the level of the posterior tips of the postzygapophyses. A small keel-like crest is found on the anterior portion of the first trunk vertebra in all species. Similar, although often much lower, crests are found at least as far as the midbody vertebrae in all but *dunni* and *neomexicanus*. In some species (*larselli*, *vehiculum*, *welleri*) the crest at midbody may be simply a low but definite ridge. In others (*jordani*, *longicrus*, *yonahlossee*) the crest at midbody is high, discrete, and well-developed. Occasionally a low ridge is found on the ascending posterior portion of the neural arch. Crests become increasingly less well-developed as one proceeds posteriorly along the vertebral column.

The trunk vertebrae of *Ensatina* number 14 (22 individuals) or 15 (3 individuals). The dorsal roof of the neural arch is broader and flatter than in *Plethodon* or *Aneides*. Fusion of the diapophyses and parapophyses is almost complete to the distal tips and the two processes extend further laterally than in *Plethodon* or *Aneides*. The prezygapophyses are widely divergent and the anterior margin of the neural canal is more broadly concave than in either *Plethodon* or *Aneides*. A crest is present on the more anterior vertebrae but it becomes ridge-like on succeeding vertebrae and is virtually absent at midbody and posteriorly. The dorsoposterior margin of the neural arch is thickened and is broadly cylindrical in shape. The posterior margin is entire in all but the last two or three trunk vertebrae in which the margin becomes divided and gives rise to two cylindical hyperpophyses that point dorsoposteriorly. Ribs are never present on the last vertebra, the last two often lack ribs, and occasionally the last three vertebrae lack ribs.

Sacral vertebrae. The sacral vertebra is essentially a well-developed trunk vertebra bearing modified ribs for articulation with pelvic girdle elements. Both diapophyses and parapophyses are present and extend laterally, lateroposteriorly, or they may be swept considerably posteriorly. The ilia are usually located posterior to the sacral vertebra. In all *Aneides* and *Ensatina* examined there is only one sacral vertebra and it bears a pair of short stubby ribs. In *Plethodon* (one *welleri,* one *yonahlossee,* one *vandykei*) a variant condition may be present in which the sacral rib articulates with one vertebra on one side of the organism and with the following vertebra on the opposite side. Similar situations have been reported by Highton ('57) and unsymmetrical sacral vertebrae probably also occur in *Aneides.* Rarely two sacral ribs issue from two successive vertebrae on the same side of an organism. This condition is present in one *A. hardii* and one *P. vehiculum.* In both cases, one rib is present on one side of the organism and two on the opposite side in the sacral region. The second rib is borne on a postsacral vertebra.

Caudo-sacral vertebrae. The three (usually) vertebrae immediately posterior to the sacral vertebra are morphologically and functionally distinct from the caudal vertebrae that follow them. These vertebrae are incapable of autotomy even in forms in which autotomy occurs because they are functionally part of the trunk of the salamander. The posterior edge of the cloacal slit is located ventral to the third postsacral vertebra in most individuals and only posterior to that point can the vertebrae be called caudal vertebrae. The caudo-sacral veterbrae are transitional in structure between the posterior trunk vertebrae and the anterior caudal vertebrae. Both ribs and well-developed hemal arches are absent. The transverse processes are very long, longer than on any other vertebrae in the body, and bear well-developed wing-like alar processes, especially on the first vertebra of the series. The last of the series bears on the ventral surface of the centrum an attenuate hemal arch and a relatively low hypapophyseal keel. The Y-shaped hemal complex extends posteroventrally, terminating ventrally to the first one-third of the succeeding vertebra, and is thickened and much expanded laterally on the posterior border. Forming the basis of the expanded portion are a pair of processes that arise anterior to the vertebral midpoint on either side of the hemal arch and proceed ventroposteriorly and slightly latero-obliquely, becoming, at their termination, the greatest ventral, posterior, and lateral portion of the hemal complex. The processes are joined to each other and, by their commissure, to the hypapophyseal keel. Occasionally the central of the three vertebrae bears low projections that represent the walls of the hemal arch. Rarely the arch itself may be present, but the hemal complex is always very poorly developed. The hemal complex of the caudal vertebrae is similar to that described above but is more fully developed and the angle of the paired processes to the neural canal is considerably greater in the caudal than in the caudo-sacral vertebrae. Hyperpophyses are well-developed.

Caudal vertebrae. Caudal vertebrae vary from 30 to 45 in number in the various species. Many tails are broken and accurate data concerning vertebral number are not available. The vertebrae are serially and interspecifically variable and the number of vertebrae is subject to individual, ontogenetic, and interspecific variation. Tail autotomy apparently does not occur in *Aneides,* but breaks may occur any place in the series. Broken and regenerated tails are most common in *flavipunctatus* followed by *hardii.* Tail autotomy is rare in the remaining species but occurs more often in *ferreus* than in *aeneus* or *lugubris.* Transverse processes are present on most vertebrae but are more well-developed on the anterior than on the posterior members of the series. The transverse processes arise near the midpoint of the vertebra and extend laterally and posteriorly. In *aeneus, hardii,* and *ferreus,* the transverse processes are long and slender, in *flavipunctatus* relatively somewhat shorter, and in *lugubris* the processes are short and stout. In *lugubris* in particular, but in the other species to a lesser extent, the transverse process is expanded and dilated dorsoventrally. A well-developed zygapophyseal ridge is present in *ferreus* and *lugubris* but in the other species the ridge is less developed. Neural spines are present in all species and generally increase in height relative to vertebral size until near the end of the vertebral series. The spines are very low and almost absent in *hardii,* and are low in the rest of the species but become higher posteriorly. Of the remaining species the spines are most weakly developed in *aeneus*, followed by *flavipunctatus.* In both the spine is short basally. The hemal complex is similar to that described for the last caudo-sacral vertebrae with the modifications mentioned above. Posteriorly the caudal vertebrae become very simple and lose all processes until they consist of no more than a centrum with neural and hemal elements, the final vertebrae consisting of centrum only. Hyperpophyses are well-developed.

The caudal vertebrae of *Plethodon* are very similar to those of *Aneides*. In general, fewer vertebrae bear transverse processes and the processes are directed somewhat more posteriorly than in *Aneides.* A well-developed zygapophyseal ridge is present in *jordani, glutinosus, longicrus, ouachitae, wehrlei,* and *yonahlossee* and in these species the vertebrae are noticeably broader than the other species examined as a result. The same six species appear to have relatively lower neural spines than the remaining members of the genus.

The caudal vertebrae of *Ensatina* differ considerably from those of the other two genera. The first vertebra is considerably shorter than either the last caudo-sacral or the second caudal vertebrae. The area of the shortened vertebra corresponds with the obvious tail constriction noted in living and preserved specimens. Tail autotomy occurs in *Ensatina* when the organisms are subjected to conditions that cause considerable stress and the break occurs most commonly at the point of constriction between the last caudo-sacral and first caudal vertebrae. Transverse processes are present on most of the caudal vertebrae but have undergone considerable modification. The first vertebra bears modified processes that arise from the anterior portion of the vertebra and proceed anteriorly and laterally. Distally these processes are dorsoventrally dilated and expanded. The succeeding vertebrae bear smaller processes that are located almost at the anterior edge of each vertebra and proceed nearly directly anteriorly and only slightly laterally. The processes are very different from any that occur in either *Plethodon* or *Aneides.* Neural spines are present only on the vertebrae of large adults and are always very low. Hyperpophyses are well-developed. Marked sexual dimorphism is noted in the number of caudal vertebrae. Males may have as many as 45 vertebrae while females have less than 35.

Ribs. The ribs of *Aneides* are essentially the same in all species and are Y-shaped structures articulating by means of two heads with the diapophyses and parapophyses of the rib-bearing trunk vertebrae and the sacral vertebra. The rib heads are more divergent in *Plethodon* and *Ensatina* than in *Aneides.* The distal tips of the ribs remain cartilaginous, and, in the first two pairs of ribs, have become expanded for articulation with pectoral girdle elements (suprascapula). The first pair of ribs are almost X-shaped, bifurcating both proximally and distally. Posteriorly the ribs become shorter and smaller. The sacral ribs, however, are relatively massive although rather short, and articulate distally by means of a cartilaginous portion with cartilaginous portions of the ilia.

Pectoral girdle

The pectoral girdle of *Aneides* consists of a single skeletal element that is the result of a fusion of the scapula, procoracoid, and coracoid. The structure is primarily cartilaginous and is ossified only in the region of the glenoid fossa. The amount of ossification is subject to individual and ontogenetic variation. Little or no interspecific variation is noted.

Scapula arises from dorsal portion of glenoid region, forms dorsolateral portion of girdle. Proximal osseous portion (scapula proper) narrowest at point of origin in glenoid region, becoming compressed and longitudinally dilated dorsally. Large fan-shaped cartilaginous distal portion (suprascapula) relatively thick ventrally, becoming very thin and compressed dorsally; attached by muscles and connective tissue to first rib. Ventral procoracoid arises from glenoid region; proceeds anteriorly almost to level of occipital condyles. Osseous proximal portion of procoracoid forms major portion of glenoid fossa. Spatulate distal portion of procoracoid cartilaginous, slightly concave dorsally. Procoracoid and coracoid regions separated by deep notch in cartilaginous portion and supracoracoid foramen in osseous portion. Foramen sometimes entirely enclosed in bone, sometimes partially in bone, partially in cartilage, with location apparently related to amount of proximal ossification which in turn increases with age. Coracoid largest portion of pectoral girdle, extends medially from glenoid region across ventral midline and overlaps, or is overlapped by, bilateral counterpart; thicker proximal portion ossified; very large expanded cartilaginous distal portion becomes increasingly thinner distally; coracoid slightly concave dorsally. Glenoid region formed primarily by portions of procoracoid and coracoid, but scapula also involved; posterior border of cavity formed by thick cartilage; cartilaginous head of humerus almost fills fossa.

The pectoral girdle of *Plethodon* and *Ensatina* is similar to that of *Aneides*. In *Plethodon* the supracoracoid foramen is entirely enclosed in bone more often than not, at least in adults. In all adult *Ensatina* the supracoracoid foramen is entirely enclosed in bone. In one old *Ensatina* (70 mm snout-vent length) the foramen is reduced to a tiny puncture. In a very young *Ensatina* (23 mm snout-vent length) the foramen is large and located entirely in cartilage.

A small somewhat rhomboidal cartilaginous sternal plate is present in *Aneides, Plethodon,* and *Ensatina*. The sternum is located on the ventral midline between the posterior tips of the coracoid elements.

Fore limb

The fore limb consists of a humerus, radius, and ulna together with carpal, metacarpal, and phalangeal elements. Limb length is subject to interspecific variation. The length of the humerus and radius combined is less than that of the femur and tibia combined in all species of *Aneides*, and is greatest in *aeneus*, becoming increasingly shorter in *lugubris, ferreus, hardii,* and *flavipunctatus* in that order (fig. 8). The length of the humerus and radius combined is less than that of the length of the femur and tibia combined in *Plethodon* but greater in *Ensatina*. Cartilaginous caps form the articulating surfaces of all of the long bones of the fore limb and the carpal elements are entirely cartilaginous.

Humerus. The humerus is the longest bone in the fore arm and is surpassed in length only by the femur. The proximal element of the fore limb is very similar in all species of *Aneides, Ensatina,* and *Plethodon*, but is relatively longest in *Ensatina*.

Humerus, a long bone on straight axis; articulates by means of large cartilaginous almost hemispherical head with glenoid cavity of pectoral girdle; well defined short massive process (*crista ventralis humeri*) arises from anteroventral portion of shaft, fits into special notch in glenoid cavity wall; smaller hook-like process (*crista dorsalis humeri*) arises from posterodorsal portion of shaft; both processes serve as insertions for muscles. Shaft round in central transverse section, expands dorsoventrally proximally and anteroposteriorly distally. Distal cartilaginous condylar portion virtually double; preaxial radial condyle large, rounded; postaxial ulnare condyle considerably smaller; ventral groove (*fossa cubitalis ventralis*) present in condylar portion for articulation with proximal tip of radius; dorsal olecranon fossa located distally in cartilaginous area, small and indefinite.

Radius. The radius is essentially the same in all species of *Aneides, Plethodon,* and *Ensatina*.

Radius preaxial in position; constructed on relatively straight axis; expanded proximally and distally, larger distally; articulates proximally with humerus, distally with radiale and intermedium of carpus, has slight proximal articulation with ulna.

Ulna. The ulna is a slender bone, shorter and smaller than the radius, and is essentially the same in all species of *Aneides, Plethodon,* and *Ensatina*.

Ulna postaxial in position; constructed on relatively straight axis; bears poorly defined olecranon process on large proximal articulating surface; articulates proximally with humerus, distally with ulnare and intermedium of carpus.

Manus. The manus consists of the carpus, metacarpus and phalanges. Seven or eight cartilaginous elements form the carpus of *Aneides*. Primitively the carpus consists of the following: a proximal series of three elements, ulnare, intermedium, and radiale; four centrally located centralia; and five distal carpals. The situation is modified in more advanced urodeles and the homologies of the various elements have been discussed by Gregory, Miner, and Noble ('23). In *Aneides* the intermedium apparently represents a fusion of the primitive intermedium, centrale 3, and centrale 4. The central element is probably composed of centrale 2 only. Distal carpals 1 and 2 have fused to form a single element and distal carpal 5 has been lost. In *hardii* a further fusion has taken place and the ulnare has become completely fused with the intermedium. This condition is found elsewhere in the specimens examined only in one carpus of one young specimen of *ferreus* from Vancouver Island. Perhaps the most significant feature of the carpus of *Aneides* is the articulation of all of the elements with the centrally located centrale 2. With the exception of the fusion noted above, the carpus is similar in all species of *Aneides*. The carpi of *A. lugubris* and of *Plethodon dunni* are figured (fig. 6a, 6b).

Rectangular intermedium largest element of tarsus; located centrally and proximally; articulates proximally with ulna and radius, distally with centrale 2, postaxially with ulnare, preaxially with radiale; separated from ulnare by small gap ("foramen") for passage of blood vessels; intermedium-ulnare of *hardii* exceptionally large relative to size of other carpal elements, almost square. Rectangular ulnare slightly smaller than intermedium; postaxial in position; normally articulates with centrale 2, but, when separated, located in very close proximity to centrale 2; articulates distally with carpal 4, proximally with ulna. Radiale smallest of proximal series, smaller than centrale 2; preaxial in postion; articulates postaxially with intermedium and centrale 2, proximally with radius, distally with centrale 1. Thickened centrale 2 relatively large, irregularly-shaped structure; located postaxially and medially; articulates with all elements of carpus. Irregularly-shaped centrale 1 located preaxially; smaller than centrale 2; articulates postaxially with centrale 2, proximally with radiale, distally with distal carpal 1 and 2; limited articulation with metacarpal 1. Distal carpal 1 and 2 intermediate in size between large distal carpal 4 and small distal carpal 3; articulates with centrale 1, centrale 2, distal carpal 3, and proximal tips of metacarpals 1 and 2. Distal carpal 3 small and triangular, often smallest element of carpus; articulates with distal carpal 1 and 2, centrale 2, distal carpal 4, and metacarpal 3. Rounded distal carpal 4 relatively very large, occasionally larger than centrale 2; articulates with distal carpal 3, centrale 2, ulnare, and metacarpal 4; limited articulation with intermedium occurs rarely.

The carpus of *Plethodon* differs from that of *Aneides* in several regards. The smaller, less dominant intermedium usually articulates rather broadly with distal carpal 4 and eliminates the ulnare from articulation with centrale 2. Centrale 2 is a smaller element than in *Aneides*, but distal carpal 3 is larger. Distal carpal 4 is much larger than the other carpals. The articulations of the various elements are subject to some interspecific and intraspecific variation.

The carpus of *Ensatina* closely resembles that of *Plethodon*. The articulation of the intermedium with distal carpal 4 is extensive and the ulnare is thus eliminated from any articulation with centrale 2. In one large adult male a remarkable reduction had taken place in both mani with only four large elements remaining: a very large proximal element, a smaller proximal element, and two distal elements. In a single radiographed specimen of an adult *Ensatina* the intermedium, ulnare, carpals 1 and 2, 3, and 4 are calcified. In addition there is indication of lesser amounts of calcium deposition in centrale 2.

Four metacarpal elements are present in all *Aneides*. Each metacarpal is rather

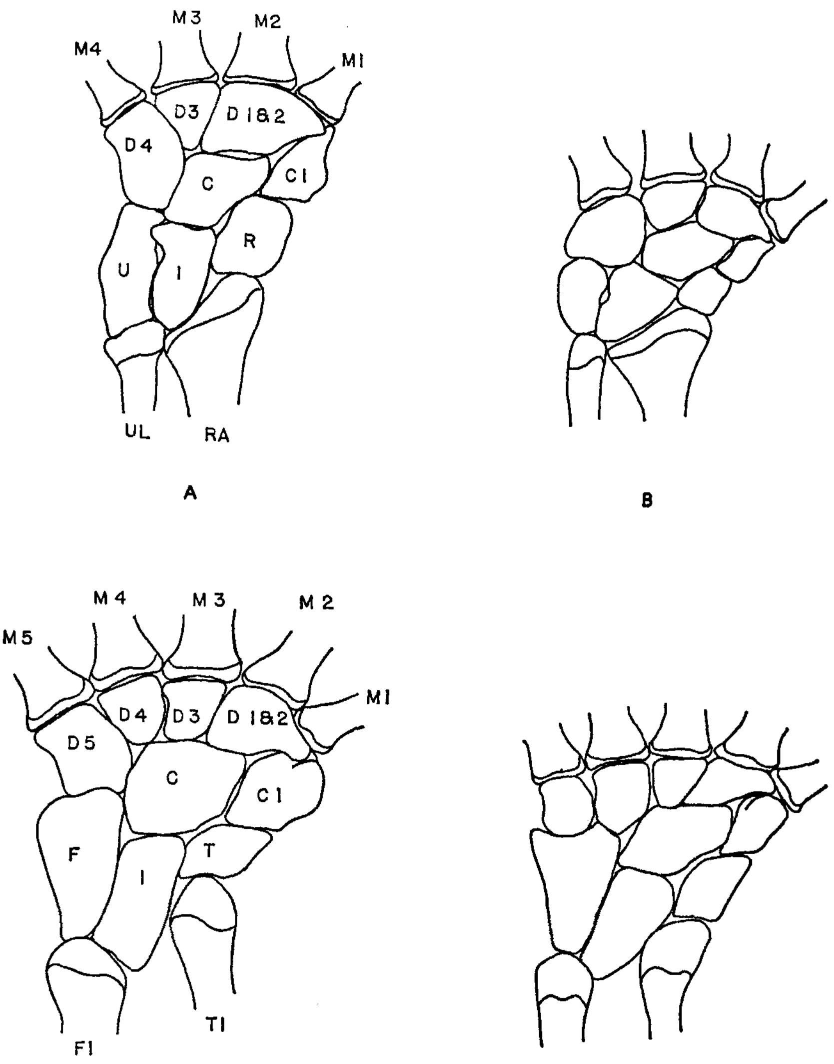

Fig. 6 Dorsal views of carpi and tarsi. A, carpus of *Aneides lugubris;* B, carpus of *Plethodon dunni;* C, tarsus of *A. lugubris;* D. tarsus of *P. dunni.* Symbols for carpus: UL, ulna; RA, radius; U, ulnare; I, intermedium plus centralia 3 and 4; R, radiale; C, centrale 2; C 1, centrale 1; D 1 & 2, distal carpals 1 and 2; D 3, distal carpal 3; D 4, distal carpal 4; M 1–M 4, metacarpals 1–4. Symbols for tarsus: FI, fibula; TI, tibia; F, fibulare; I, intermedium plus centrale 4; T, tibiale; C, centrale 2 and 3; C 1, centrale 1; D 1 & 2, distal tarsals 1 and 2; D 3, distal tarsal 3; D 4, distal tarsal 4; D 5, distal tarsal 5; M 1–M 5, metatarsals 1–5.

dumbbell-shaped, narrow in the center of the shaft but expanded at either end. Both ends are capped with cartilage. The first metacarpal is always the shortest, but the others are of about equal length. Metacarpal 1 articulates proximally with distal carpal 1 and 2, and less extensively, with centrale 1. Metacarpal 2 articulates proximally with distal carpal 1 and 2, metacarpal 3 with distal carpal 3 and metacarpal 4 with distal carpal 4. Distally all of the metacarpals articulate with phalangeal elements. The metacarpals are shortest in *hardii* and increase in length in *flavipunctatus, lugubris* or *ferreus,* and *aeneus* approximately in that order. The metacarpals of *flavipunctatus* and *hardii* are notably shorter than those of the other three species.

The metacarpal elements of most *Plethodon* resemble those of *A. hardii* but may be shorter. None have the elongate appearance of the elements of *A. aeneus.*

The metacarpals of *Ensatina* are much larger than those of *Plethodon.* Metacarpals of large adult *Ensatina* may be longer and more massive, but less elongate, than the metacarpals of *Aneides.*

The phalangeal formula of all *Aneides* is 1-2-3-2. The first digit consists of a single minute conical phalanx. The first digit is notably reduced in all species but the reduction is most evident in the long-fingered *aeneus* and *ferreus.* The digits are longest in *aeneus* and *ferreus,* slightly shorter in *lugubris,* considerably shorter in *flavipunctatus,* and shortest in *hardii.* A typical phalanx resembles a miniature metacarpal and is dumbbell-shaped with cartilaginous knobs at either end. In those species possessing long digits the phalanges are correspondingly elongate. The central phalanx of the third digit is normally the longest. The peculiar terminal phalanges are similar to those of the pes and will be considered in detail in a following section.

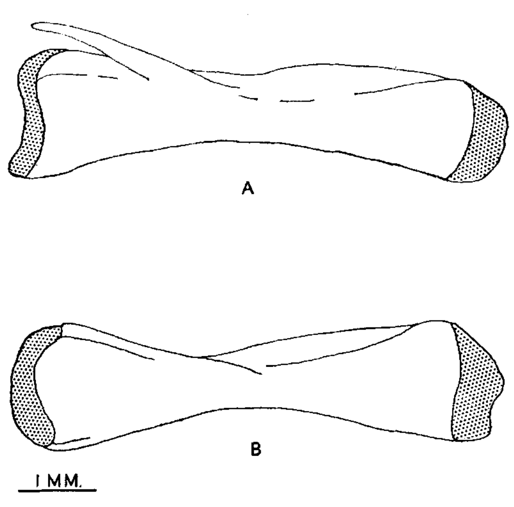

Fig. 7 Preaxial views of tibia. Cartilage stippled. A, *Aneides lugubris;* B, *Ensatina eschscholtzii.*

The phalangeal formula of all *Plethodon* is 1-2-3-2. The digits are short for the most part, resembling those of *A. hardii.* The phalanges are usually short and stubby.

The phalangeal formula of *Ensatina* is 1-2-3-2. The phalanges, other than the terminal phalanges, resemble those of *Aneides* in most respects and are relatively long and massive. The proximal phalanx of the third digit is as long as, or longer than, the central phalanx. The digits are long and are similar in length to those of *A. lugubris.*

Pelvic girdle

The solid arch-like pelvic girdle is attached dorsally to the vertebral column by means of the sacral ribs. The girdle proper consists of two pairs of elements, the vertically oriented ilia located laterally and the horizontally oriented pubo-ischia located medioventrally. The structure is essentially similar in all species of *Aneides, Plethodon,* and *Ensatina.*

Slightly elongate ilium laterally compressed; ascends dorsally and slightly laterally from acetabular region; cartilaginous ventrally at articulation with pubo-ischium. Dorsal extremity of ilium somewhat more compressed than remainder of bone, cartilaginous; firmly attached by medial border to lateral surface of ventrolateral extension of sacral rib. Large irregularly-shaped plate-like pubo-ischium articulated mid-ventrally with counterpart. Posterior (ischial) portion of plate ossified except at symphysis; bears well-developed cylindrical ischial spine that projects posteriorly from lateral margin of plate; often partially eroded along posterior margin, between spine and plate proper. Anterior (pubic) portion of plate usually cartilaginous, occasionally with spots of calcification; perforated latero-ventrally by small obturator foramen for passage of obturator nerve. Pubes present rather pointed appearance anteriorly; reaching greatest anterior extension mid-ventrally. Acetabulum formed by dorso-ventrally expanded, lateral margins of pubo-ischium and posteroventrolateral portion of ilium; borders of large acetabular cavity formed of cartilage, calcified cartilage, and bone; cavity receives largely cartilaginous head of femur that attaches firmly by means of two ligaments.

Hind limb

The hind limb consists of a femur, fibula, and tibia, together with tarsal, metatarsal, and phalangeal elements. The length of the femur and tibia combined is relatively longest in *aeneus*, becoming shorter in *lugubris*, *ferreus*, *hardii*, and *flavipunctatus* in that order (fig. 8). Cartilaginous caps form the articulating surfaces of all of the long bones of the hind limb and the tarsals are entirely cartilaginous.

Femur. The femur is the longest bone of the body in *Aneides*. It is roughly 75% longer than the tibia in adult *aeneus*, 67% in *hardii*, 50% in *lugubris*, 33% in *ferreus*, and 30% in *flavipunctatus* (fig. 8). The femur is from 2 to 14% longer than the humerus.

Femur articulates with acetabulum by means of rounded cartilaginous head; bears robust hook-shaped trochanter, enclosing crescent-shaped concavity, on ven-

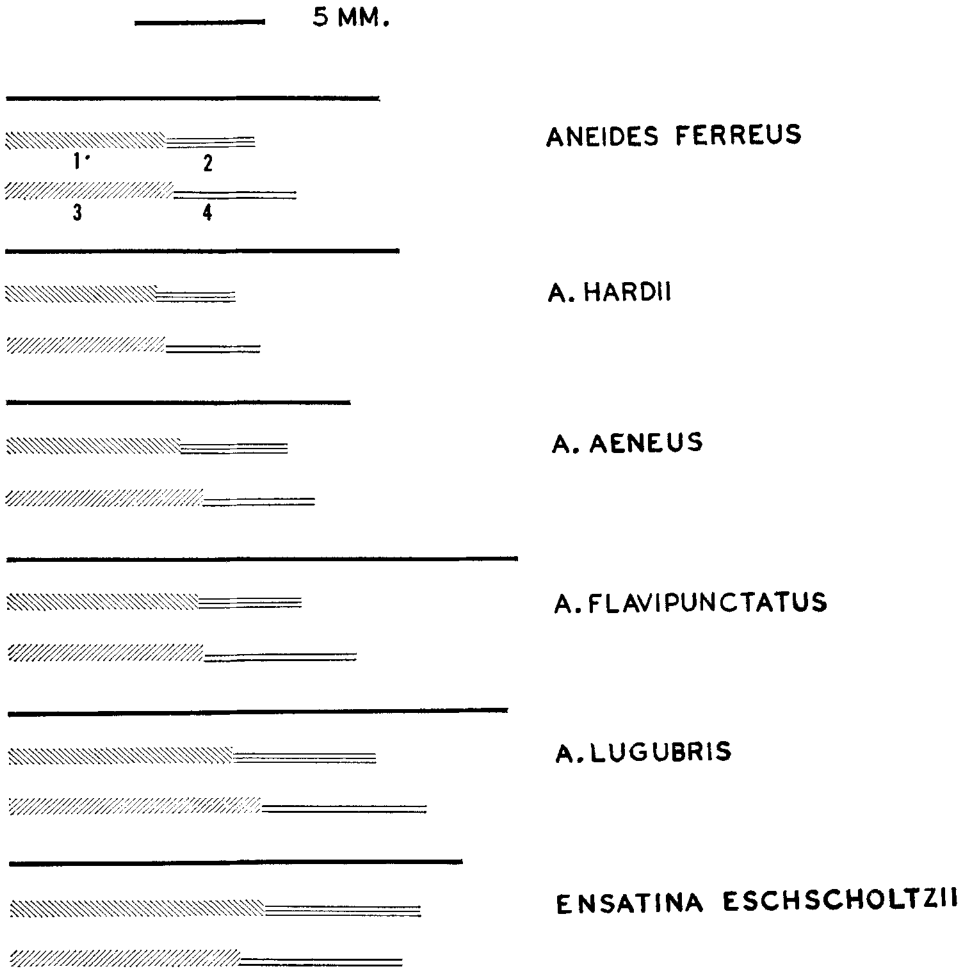

Fig. 8 Absolute proportions of limb elements based on average large adult organisms. Solid line represents one-fourth distance from tip of snout to posterior end of vent. 1, humerus; 2, radius; 3, femur; 4, tibia.

tromedial surface; roughly triangular in transverse section proximally, becoming almost round near midpoint, broadly ovate distally; narrows to smallest diameter at point slightly proximal to midpoint, dilates rapidly distally; somewhat dorsoventrally compressed distally, with slightly concave ventral surface. Two cartilaginous articulating surfaces present distally; large (preaxial) surface articulates with tibia; smaller (postaxial) surface articulates with fibula.

The femur of *Plethodon* is very similar to that of *Aneides*. Some variation is evident in the relative proportions of the bone which is long in some of the large species (*jordani, yonahlossee*), moderate in length in many species, and very short in some species (*elongatus*).

Although the femur of *Ensatina* is similar in general structure to that of *Aneides* and *Plethodon* it differs in that it is shorter than the humerus by about 10%, at least in adults. The femur is about 40% longer than the tibia.

Fibula. The fibula is slenderer than the tibia and is essentially the same in all species of *Aneides, Plethodon,* and *Ensatina.*

Fibula simple bowed structure; postaxial in position; articulates proximally with postaxial condyle of femur and partially with proximal portion of tibia, distally with fibulare and intermedium of tarsus; approximately round in transverse section; least diameter at point slightly proximal to midpoint.

Tibia. The tibia is a relatively straight, sturdy bone and is usually slightly longer than the fibula. The structure of the tibial crest and spine is subject to individual, sexual, and interspecific variation.

Tibia straight structure; preaxial in position; articulates proximally with preaxial condyle of femur and with portion of fibula, distally with tibiale and intermedium of tarsus; round in transverse section near midpoint, becoming broadly ovate toward either end; least diameter usually located distal to midpoint. Prominent tibial crest arises from dorsomedial surface of bone near distal tip; becomes free from surface of bone proximally and proceeds dorsally as spinous process; crest and spine well-developed in *lugubris, ferreus,* and *flavipunctatus* with spine usually extending beyond distal limit of ossification (fig. 7a); crest not so well-developed in *aeneus* but spine well-developed, extending beyond distal limit of ossification; crest present in *hardii* but spine not well-developed, rarely extending as far as limit of ossification and often falling far short; spine subject to sexual variation in *hardii,* considerably longer in males than females; sexual variation noted to lesser extent in *lugubris* and *ferreus,* not apparent in other species.

The tibia of *Plethodon* is very similar to that of *Aneides.* The structure of the tibial spine is subject to interspecific variation. The spine is a short, almost massive structure falling short of the limit of ossification in some species. In other species the spine resembles that of *Aneides* and is variable in length, sometimes falling short, sometimes equaling, and sometimes extending beyond the distal limit of ossification.

In *Ensatina* the tibia bears a very broad structure which is not at all crest-like as in the other genera, but appears as a more or less poorly defined ridge (fig. 7b). The spinous process is absent.

Pes. The pes comprises the tarsus, metatarsus, and phalanges. The tarsus of a primitive Labyrinthodont, for example *Trematops,* consisted of the following elements: a proximal series of three elements, tibiale, intermedium, and fibulare; four centrally located centralia; five distal tarsals; and a distal pretarsal (Schaeffer, '41). The situation has been but little modified in the more primitive living salamander families, such as the Hynobiidae, but is considerably modified in the plethodontids. Nine tarsal elements are present in *Aneides.* The intermedium and centrale 4 have evidently fused to form a single structure, centrale 2 and centrale 3 have apparently fused, distal tarsals 1 and 2 have fused, and the pretarsal has been lost. The most significant feature of the tarsus of *Aneides* is the large size of distal tarsal 5 and its articulation with centrale 2 and 3. All of the elements remain cartilaginous. The tarsi of *A. lugubris* and of *P. dunni* are figured (fig. 6c, d).

Fibulare largest element of tarsus; elongately triangular in shape; postaxial in position; articulates proximally with fibula, preaxially with intermedium and centrale 2 and 3, distally in extensive articulation with distal tarsal 5. Intermedium rectangular, elongate; slightly shorter but considerably less massive than fibulare; articulates proximally with tibia and fibula, preaxially with tibiale, postaxially with fibulare, distally with centrale 2 and 3. Tibiale about one-half size of fibulare, much smaller than intermedium; preaxial in position; irregular in shape; articulates proximally with tibia, postaxially with intermedium, distally with centrale 2 and 3 and with centrale 1. Centrale 2 and 3 second in size only to fibulare; medial in position; irregular in shape; dorsoventrally thickened; articulates at least to some extent with all tarsal elements. Centrale 1 small, about same size as tibiale; preaxial in position; thin and irregular in shape; articulates proximally with tibiale, postaxially with centrale 2 and 3, distally with distal tarsal 1 and 2; overlapped by distal tarsal 1 and 2; slight articulation with metatarsal 1 usually present. Distal tarsal 1 and 2 large, usually exceeded in size by distal tarsal 5; serves as base and articulates distally with metatarsal 1 and metatarsal 2; articulates with centrale 1, centrale 2 and 3, and distal tarsal 3. Distal tarsal 3 small, about same size or smaller than distal tarsal 4; triangular in shape; articulates with distal tarsal 1 and 2, centrale 2 and 3, distal tarsal 4 and metatarsal 3. Distal tarsal 4 small, triangular in shape; usually slightly larger than distal tarsal 3; articulates with distal tarsal 3, centrale 2 and 3, distal tarsal 5 and metatarsal 4. Distal tarsal 5 usually largest of distal elements; extensively articulates with fibulare and with centrale 2 and 3; articulates with distal tarsal 4 and metatarsal 5.

The tarsus of *Plethodon* differs considerably from that of *Aneides*. Distal tarsal 5 never articulates with centrale 2 and 3. Distal tarsal 1 and 2 is normally the largest but distal tarsal 4 is occasionally as large or slightly larger. Distal tarsal 5 is usually the smallest of the distal elements. The fibulare appears almost bifurcate distally; one portion articulates with distal tarsal 5 and the other with distal tarsal 4. Metatarsal 1 appears to articulate with centrale 1 to a greater extent than in *Aneides*, but the primary articulation remains with distal tarsal 1 and 2.

The tarsus of *Ensatina* is similar to that of *Plethodon*. Distal tarsal 5 does not articulate with centrale 2 and 3. The tibiale is larger than centrale 1, but the intermedium is very small, only about one-half the size of the fibulare. The fibulare articulates with both distal tarsal 5 and distal tarsal 4.

Five metatarsal elements, which resemble the metacarpals in general structure, are present in *Aneides*. The first metatarsal is always the shortest and metatarsal 5 may be slightly shorter than metatarsals 2, 3, or 4. The metatarsals are shortest in *hardii* and increase in length in *flavipunctatus*, *lugubris*, *ferreus*, and *aeneus* in that order. Metatarsal 1 articulates with distal tarsal 1 and 2, metatarsal 3 with distal tarsal 3, metatarsal 4 with distal tarsal 4, and metatarsal 5 with distal tarsal 5.

The metatarsal elements of *Plethodon* resemble those of *A. hardii*, in general.

The metatarsals of *Ensatina* resemble those of *Plethodon* but are longer and more massive than in any species of *Plethodon*.

The phalangeal formula of all species of *Aneides* is 1-2-3-3-2. The phalanges, with the exception of the terminal ones, appear to be minatures of the metatarsals: dumbbell-shaped with cartilaginous knobs at either end. In those digits comprised of three phalanges the central is the longest. The first digit is notably shorter than the remaining digits and the third digit is normally the longest. The digits are longest in *aeneus*, *ferreus*, and *lugubris*, shorter in *flavipunctatus*, and shortest in *hardii*. Considerable taxonomic significance has been placed on the structure of the terminal phalanx by Lowe ('50). The terminal phalanx of all but the first digit of both manus and pes is a relatively short bone, round in transverse section and relatively massive proximally. The least diameter of the phalanx is just distal to the midpoint. A relatively large process arises from about the midpoint of the ventral surface and becomes increasingly deeper proximally. The process terminates abruptly before the limit of ossification of the phalanx is reached. The large, dorsoventrally oriented surface formed by the abrupt termination of the process serves as the insertion of digital muscles. Distally the phalanx becomes recurved, broadly expanded, and flattened. The tip usually becomes bipartite and the phalanx appears to possess two ventrally recurved, hook-like processes on either margin. Lowe ('50) has called such a phalanx Y-shaped. However, the term Y-shaped phalanx does not apply to all *Aneides*. It is true that the terminal phalanges of *flavipunctatus*, *ferreus*, and *lugubris* are often Y-shaped, but the tips are also occasionally scalloped. In *aeneus* the distal margin of the phalanx is often scalloped with the deepest indentation centrally located and all projecting points of about equal length. The tip of the phalanx is not so recurved in *hardii* as in other species but in other features the bone most closely resembles that of *aeneus*. Only in some cases is a terminal phalanx of *hardii* or *aeneus* truly Y-shaped. The terminal phalanx of the first digit of both pes and manus of all species is often reduced to a small knob bearing a small terminal point.

The terminal phalanx in *Plethodon* is normally very different from that of *Aneides*. The ventral process is very small and often absent. The tip is rounded and not as expanded as in *Aneides*. The expanded tip may appear as a rounded bony knob in some species; in others the tip is somewhat more flattened and bears small wing-like processes on either side. When the latter situation prevails the distal margin of the phalanx may be even and the phalanx appears I-shaped. Occasionally a depression is present in the midpoint of the distal margin and the margin appears hooked on either side. Lowe ('50) has stated that the terminal phalanx of *Plethodon* is I-shaped, but I have found this not to be the case in many instances.

In *Ensatina* the terminal phalanx bears a small ventral process which is better developed than in *Plethodon* but not nearly so well-developed as in *Aneides*. The tip usually consists of a partially flattened knob, but occasionally two small processes are present. These processes are never recurved.

The phalangeal formula for *Plethodon larselli* and for *P. neomexicanus* is 1-2-3-3-1. The phalangeal formula for all other *Plethodon*, *Ensatina*, and *Aneides* is 1-2-3-3-2.

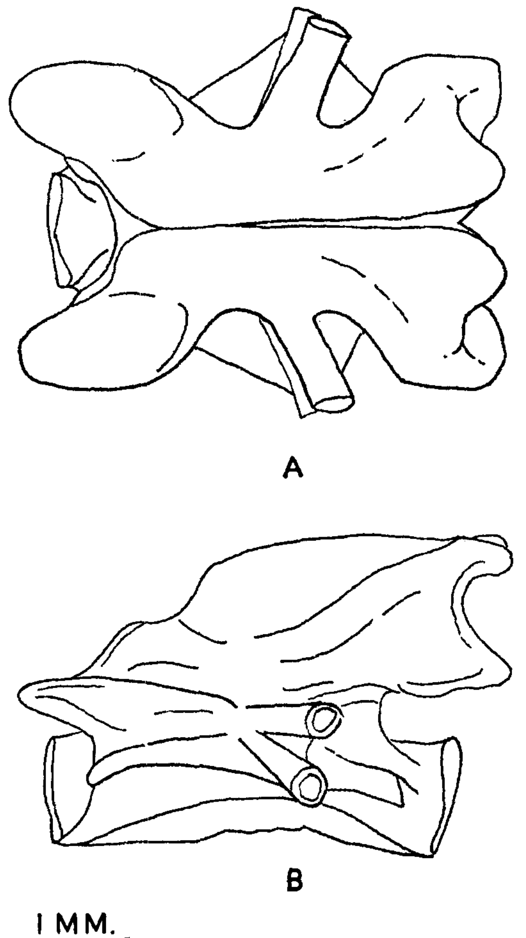

Fig. 9 Seventh trunk vertebra of adult *Aneides lugubris*. A, dorsal view; B, lateral view.

SYNOPSIS OF DIAGNOSTIC CHARACTERS

In order to assist those using this paper for taxonomic purposes, I have prepared a synopsis of those characters that I consider to have the greatest diagnostic value. In addition, the primary osteological defining characters are outlined for the three genera and for the species of *Aneides*.

Genus *Aneides* Baird

Diagnosis. Salamanders differing from *Plethodon* and *Ensatina* in having a single premaxilla and articulation of all tarsal elements with the central element; differing from all other plethodontid salamanders in the combination of the following: lack of an aquatic larva, possession of five toes, a normal atlas, and a tongue that is attached in front.

Definition. (1) One premaxilla with unfused frontal processes and an internasal fontanelle; (2) septomaxilla present; (3) maxilla not toothed posteriorly, usually dorsoventrally expanded; (4) prefrontals present, articulation with maxilla complex; (5) preorbital process of provomer present or absent; (6) anterior and posterior prevomerine tooth series not continuous; (7) occipito-otic crest usually well-developed, longitudinally oriented; (8) occipital condyles sessile; (9) opercular plate bearing well-developed columella; (10) anterior process of basibranchial I present, well-developed; (11) basibranchial II relatively short; (12) teeth bicuspid or unicuspid; (13) relatively low numbers of maxillary and dentary teeth; (14) mandibular tooth-bearing area less than one-half mandibular ramus length; (15) prearticular relatively large; (16) atlas normal, lacking enlarged dorsal process on neural arch; (17) neural arch of trunk vertebrae relatively high and arched; (18) tail not constricted at base, no shortened anterior caudal vertebra; (19) transverse processes of anterior caudal vertebrae arising from midpoint of vertebrae; (20) most caudal vertebrae bearing transverse processes; (21) ulnare of carpus articulating with centrale 2; (22) tibial spine present; (23) distal tarsal 5 large, articulating with centrale 2 and 3; (24) toes 4-5, not joined by web; (25) terminal phalanx recurved, flattened, and expanded distally. Five species, all North American. Assigned species: *Aneides aeneus* (Cope and Packard), *Aneides ferreus* Cope, *Aneides flavipunctatus* (Strauch), *Aneides hardii* (Taylor), *Aneides lugubris* (Hallowell).

Aneides aeneus (Cope and Packard)

Diagnosis. Salamanders differing from all other *Aneides* in the shape of the nasals which are normally as broad as, or broader than, long; differing from *A. ferreus*, *A. flavipunctatus*, and *A. lugubris* in having a preorbital process on the prevomer and a relatively simple articulation of the maxilla with the prefrontal; differing from *A. hardii* in having broad frontals and parietals and relatively much longer limbs.

Definition. (1) Frontal processes of premaxilla not articulating posterior to fontanelle, fontanelle large; (2) frontal processes of premaxilla not dilated posteriorly; (3) *pars facialis* of maxilla triangular; (4) prefrontal extensively overlapped by *pars facialis* of maxilla; (5) nasal quadrangular, about as broad as long; (6) posterior angle of nasal truncate; (7) articulation of nasal with maxilla not extensive or firm; (8) dorsal angle of prefrontal a long spinous process; (9) preorbital process of prevomer present; (10) interorbital area only slightly narrower anteriorly than posteriorly; (11) posterior extension of frontal lateral in position; (12) anterior cranial elements not ornamented with osseous accretions; (13) parietal not elongate but relatively broad; (14) no lateral projection present on parasphenoid; (15) occipito-otic crest poorly developed; (16) maxillary and dentary teeth medium to short, conical, often spine-like; (17) dorsal boss of atlas small and triangular, poorly developed posteriorly; (18) subvertebral plate absent; (19) limbs relatively long; (20) ulnare not fused with intermedium of carpus; (21) tibial spine long, usually extending beyond limit of ossification of tibia; (22) digits relatively long; (23) sexual dimorphism not marked.

Aneides ferreus Cope

Diagnosis. Salamanders differing from *A. aeneus* and *A. hardii* in absence of a preorbital process on the prevomer, and presence of a complex articulation of the maxilla with the prefrontal; differing from *A. flavipunctatus* in having longer limbs and in absence of an extensive articulation of the nasal with the prefrontal; differing from *A. lugubris* in absence of a firm and extensive articulation of the nasal with the maxilla, and in presence of short frontal processes on the premaxilla.

Definition. (1) Frontal processes of premaxilla usually not articulating posterior to fontanelle, fontanelle medium to large; (2) frontal processes of premaxilla not dilated posteriorly; (3) *pars facialis* of maxilla trapezoidal; (4) *pars facialis* of maxilla overlapped by prefrontal; (5) nasal triangular or pentagonal, longer than broad; (6) posterior angle of nasal obtuse; (7) articulation of nasal with maxilla normally absent; (8) dorsal angle of prefrontal spine-like; (9) preorbital process of prevomer absent; (10) interorbital area much narrower anteriorly than posteriorly; (11) posterior extension of frontal medial; (12) anterior cranial elements not ornamented with osseous accretions; (13) parietal elongate; (14) lateral projection present near midpoint of parasphenoid; (15) well-developed occipito-otic crest; (16) maxillary and dentary teeth long and compressed; (17) dorsal boss of atlas broad, well-developed; (18) subvertebral plate absent or poorly developed; (19) limbs relatively long; (20) ulnare not normally fused with intermedium of carpus; (21) tibial spine long, usually extending beyond limit of ossification of tibia; (22) digits relatively long; (23) sexual dimorphism not marked.

Aneides flavipunctatus (Strauch)

Diagnosis. Salamanders differing from *A. aeneus* and *A. hardii* in absence of a preorbital process on the prevomer, and presence of a complex articulation of the maxilla with the prefrontal; differing from *A. ferreus* in having a much smaller internasal fontanelle, posteriorly expanded premaxillary frontal processes, an extensive articulation of the prefrontal with the nasal, and shorter limbs; differing from *A. lugubris* in absence of a firm and extensive articulation of the nasal with the maxilla, and presence of shorter limbs.

Definition. (1) Frontal processes of premaxilla usually articulating posterior to fontanelle, fontanelle small; (2) frontal processes of premaxilla dilated posteriorly; (3) *pars facialis* of maxilla trapezoidal; (4) *pars facialis* of maxilla overlapped by prefrontal; (5) nasal triangular, much longer than broad; (6) posterior angle of nasal acute; (7) articulation of nasal with maxilla normally absent; (8) dorsal angle of prefrontal acute; (9) preorbital process of prevomer absent; (10) interorbital area somewhat narrower anteriorly than posteriorly; (11) posterior extension of frontal medial; (12) anterior cranial elements not ornamented with osseous accretions; (13) parietal elongate; (14) lateral projection present near midpoint of parasphenoid; (15) well-developed occipito-otic crest; (16) maxillary and dentary teeth long and somewhat compressed; (17) dorsal boss of atlas elongate; (18) subvertebral plate absent or poorly developed; (19) limbs relatively short; (20) ulnare not fused with intermedium of carpus; (21) tibial spine long, usually extending beyond limit of ossification of tibia; (22) digits relatively short; (23) sexual dimorphism not marked.

Aneides hardii (Taylor)

Diagnosis. Salamanders differing from all other *Aneides* in having fused ulnare and intermedium in the carpus; differing further from *A. ferreus, A. flavipunctatus,* and *A. lugubris* in having a preorbital process on the prevomer and a relatively simple articulation of the maxilla with the prefrontal; differing from *A. aeneus* in the shape of the nasal which is triangular and longer than broad.

Definition. (1) Frontal processes of premaxilla not articulating posterior to fontanelle, fontanelle medium; (2) frontal processes of premaxilla not dilated posteriorly; (3) *pars facialis* of maxilla triangular; (4) prefrontal extensively overlapped by *pars facialis* of maxilla; (5) nasal triangular, longer than broad; (6) posterior angle of nasal obtuse; (7) articulation of nasal with maxilla usually absent; (8) dorsal angle of prefrontal acute; (9) preorbital process of prevomer present, well-developed; (10) interorbital area much narrower anteriorly than posteriorly; (11) posterior extension of frontal medial; (12) anterior cranial elements not ornamented with osseous accretions; (13) parietal elongate; (14) no lateral projection present on parasphenoid; (15) well-developed occipito-otic crest in males, poorly developed in females; (16) maxillary and dentary teeth short and conical; (17) dorsal boss of atlas large and broad, often quadrangular; (18) subvertebral plate absent; (19) limbs relatively short; (20) ulnare fused with intermedium of carpus; (21) tibial spine short, falling short of limit of ossification of tibia; (22) digits relatively short; (23) sexual dimorphism marked in regards to occipito-otic crest, shape of maxilla, and shape and number of maxillary and dentary teeth.

Aneides lugubris (Hallowell)

Diagnosis. Salamanders differing from all species of *Aneides* in having a firm and extensive articulation of the nasal with the maxilla and a well-developed subvertebral plate; differing from *A. aeneus* and *A. hardii* in absence of a preorbital process on the prevomer; differing from *A. ferreus* in presence of an articulation of the frontal processes of the premaxilla posterior to the internasal fontanelle; differing from *A. flavipunctatus* in possession of greatly compressed maxillary and dentary teeth and longer limbs.

Definition. (1) Frontal processes of premaxilla long, articulating posterior to very small fontanelle; (2) frontal processes of premaxilla dilated posteriorly; (3) *pars facialis* of maxilla trapezoidal; (4) *pars facialis* of maxilla overlapped by prefrontal; (5) nasal triangular or pentagonal, longer than broad; (6) posterior angle of nasal obtuse; (7) articulation of nasal with maxilla extensive and firm; (8) dorsal angle of prefrontal truncate; (9) preorbital process of prevomer absent; (10) interorbital area much narrower anteriorly than posteriorly; (11) posterior extension of frontal more medial than lateral; (12) anterior cranial elements heavily ornamented with osseous accretions; (13) parietal elongate; (14) lateral projection present near midpoint of parasphenoid; (15) well-developed occipito-otic crest; (16) maxillary and dentary teeth long and greatly compressed; (17) dorsal boss of atlas large and broad, yet often elongate; (18) subvertebral plate well-developed and extensive; (19) limbs relatively long; (20) ulnare not fused with intermedium of carpus; (21) tibial spine long, extending beyond limit of ossification of tibia; (22) digits relatively long; (23) sexual dimorphism not marked.

Genus *Plethodon* Tschudi

Diagnosis. Salamanders differing from *Aneides* in having two premaxillae; differing from *Ensatina* in having a tibial spine; differing from all other plethodontid salamanders in the combination of the following: lack of an aquatic larva, possession of five toes, a normal atlas, and a tongue that is attached in front.

Definition. (1) Two premaxillae with unfused frontal processes and internasal fontanelle; (2) septomaxilla present; (3) maxilla normally toothed, not dorsoventrally expanded posteriorly; (4) prefrontals present, articulation with maxilla simple; (5) preorbital process of prevomer present; (6) anterior and posterior prevomerine tooth series not continuous; (7) occipito-otic crest absent or poorly developed, directed transversely when present; (8) occipital condyles sessile; (9) opercular plate bearing well-developed columella; (10) anterior process of basibranchial I present; (11) basibranchial II of relatively moderate size; (12) teeth bicuspid; (13) relatively moderate to high numbers of maxillary and dentary teeth; (14) mandibular tooth-bearing area more than one-half mandibular ramus length; (15) prearticular relatively small; (16) atlas normal, lacking enlarged dorsal process on neural arch; (17) neural arch of trunk vertebrae relatively high and arched; (18) tail not constricted at base, no shortened anterior caudal vertebra; (19) transverse processes of anterior caudal vertebrae arising from midpoint of vertebrae; (20) many caudal vertebrae bearing transverse processes; (21) ulnare of carpus not articulating with centrale 2; (22) tibial spine present; (23) distal tarsal 5 small, not articulating with centrale 2 and 3; (24) toes 4–5, not joined by web; (25) terminal phalanx straight, not flattened and only slightly expanded distally. Seventeen species, all in North America north of Mexico. Assigned species: *Plethodon caddoensis* Pope and Pope, *Plethodon cinereus* (Green), *Plethodon dorsalis* Cope, *Plethodon dunni* Bishop, *Plethodon elongatus* Van Denburgh, *Plethodon glutinosus* (Green), *Plethodon jordani* Blatchley, *Plethodon larselli* Burns, *Plethodon longicrus* Adler and Dennis, *Plethodon neomexicanus* Stebbins and Riemer, *Plethodon ouachitae* Dunn and Heintze, *Plethodon richmondi* Netting and Mittleman, *Plethodon vandykei* Van Denburgh, *Plethodon vehiculum* (Cooper), *Plethodon wehrlei*

Fowler and Dunn, *Plethodon welleri* Walker, *Plethodon yonahlossee* Dunn.

Genus *Ensatina* Gray

Diagnosis. Salamanders differing from *Aneides* in possession of two premaxillae; differing from *Plethodon* in absence of a tibial spur; differing from all other plethodontid salamanders in the combination of the following: lack of an aquatic larva, possession of five toes, a normal atlas, and a tongue that is attached in front.

Definition. (1) Two premaxillae with unfused frontal processes and an internasal fontanelle; (2) septomaxilla present; (3) maxilla normally toothed, not dorsoventrally expanded posteriorly; (4) prefrontals present, articulation with maxilla simple; (5) preorbital process of prevomer present, very elongate; (6) anterior and posterior prevomerine tooth series continuous only in very small individuals; (7) occipito-otic crest normally absent; (8) occipital condyles sessile; (9) opercular plate bearing well-developed columella; (10) anterior extension of basibranchial I absent or poorly developed; (11) basibranchial II elongate; (12) teeth bicuspid; (13) relatively high numbers of maxillary and dentary teeth; (14) mandibular tooth-bearing area more than two-thirds mandibular ramus length; (15) prearticular relatively small; (16) atlas normal, lacking enlarged dorsal process on neural arch; (17) neural arch of trunk vertebrae relatively broad and flattened; (18) tail constricted near base, constriction correlated with one or two shortened anterior caudal vertebrae; (19) transverse processes of anterior caudal vertebrae arising from anterior edge of vertebrae; (20) transverse processes borne only on a few anterior caudal vertebrae; (21) ulnare of carpus not articulating with centrale 2; (22) tibial spine absent; (23) distal tarsal 5 small, not articulating with centrale 2 and 3; (24) toes 4–5, not joined by web; (25) terminal phalanx straight, not flattened, slightly expanded and knoblike distally. One species in western North America west of the Cascade-Sierra Nevada mountain system. Assigned species: *Ensatina eschscholtzii* Gray.

DISCUSSION

The five species of *Aneides* form three species groups. The *hardii* group contains only *hardii*, the *aeneus* group contains only *aeneus*, while the *lugubris* group contains *ferreus*, *flavipunctatus*, and *lugubris*.

The *lugubris* group can be distinguished from the other groups by two important characters: (1) the preorbital process of the prevomer is either absent or represented by a minute projection, while the process is universally present in the other groups, and (2) the maxilla articulates with the prefrontal by means of a complex interlocking arrangement, while the articulation is relatively simple and overlapping in the other groups. Other characters supporting recognition of the group include the increasingly firm and extensive skull articulations of the three species, presence of paired parasphenoid lateral projections, and the decreased numbers of maxillary and dentary teeth.

The *aeneus* group is distinguished from the *hardii* group by its broader skull, relatively shorter and broader nasals and parietals, poorly developed occipito-otic crests, broader interorbital area, fewer numbers of maxillary and dentary teeth, poorly developed dorsal boss of the cervical vertebra, long tibial spine, relatively much longer limb and digital elements, and carpus with separate ulnare and intermedium.

The relationships of the species are reflected in the geographic distribution of the species groups. Each group is widely separated geographically from each of the other groups; *aeneus* is found in the Appalachian Mountains of eastern United States, *hardii* in the mountains of New Mexico, and the *lugubris* group in far western North America.

Many of the characters of *Plethodon* appear more generalized and primitive than those of *Aneides*, yet the overall similarity of the two genera indicates a fairly close relationship. The generalized characters of *Plethodon* include shapes and relations of skull elements, large numbers of teeth, non-fusion of premaxillae, relatively short limb elements and digits, and generalized carpal and tarsal patterns. From the above detailed analysis it is readily seen that *hardii* resembles *Plethodon* more than do any of the other species of *Aneides,* and on the basis of this resemblance, it appears that *hardii* is the most primitive species of *Aneides.* The distribution of *hardii* in the mountains of New Mexico is an example of a relict distribution pattern as pointed out by Lowe ('50), and such a pattern is not unusual for a primitive species.

Within the genus *Aneides* a trend is seen in the direction of morphological specialization. The generalized condition is usually found in *hardii,* with increased specialization in both of the more advanced groups. The trend is illustrated by increasing limb length, increasing digital length, decreasing numbers of teeth, loss or reduction of prevomerine processes, and increasing complexity of skull element articulations, in the more advanced species. On the basis of complete loss of the preorbital process of the prevomer, presence of a highly specialized maxilla-prefrontal articulation, and enlarged teeth of greatly reduced numbers it seems evident that the *lugubris* group is the most advanced in the genus.

The specialized *aeneus* group appears to be more closely related to the *hardii* group than to the *lugubris* group. *Aeneus* and *hardii* share generalized and presumably primitive characters such as presence of preorbital process of the prevomer, relatively simple articulation of the maxilla with the prefrontal, and relatively high numbers of teeth.

On the basis of similarity of skull shape, shape and articulation of individual skull elements, and vertebral similarities, *hardii* appears more closely related to the *lugubris* group than to *aeneus.*

In summary, three evolutionary lines are apparent within the genus *Aneides.* Close to a presumed generalized ancestral stock is *hardii,* the Rocky Mountain relict. This ancestral stock has given rise to the *aeneus* group in the East in one direction, and in the other to the *lugubris* group in the West. The relationships and biogeography of the species are discussed more fully in a report by the author to be published at a later date.

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