

OSTEOLOGY OF *DACTYLOSCOPUS TRIDIGITATUS* (DACTYLOSCOPIDAE: BLENNIOIDEI)

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ABSTRACT

The osteology of the common Caribbean sand stargazer *Dactyloscopus tridigitatus* (Dactyloscopidae: Blennioidei) is reviewed. Twenty-eight cleared and stained specimens were examined, ranging in standard length from 28.2 to 65.5 mm. The infraorbital bones, suspensorium, hyoid arch, pectoral girdle, and caudal skeleton exhibit considerable variation between specimens. In contrast, the neurocranium, branchial arches, and pelvic girdle were relatively conservative regions. Emphasis is placed on documenting variation that is potentially discrete. Such variation may reveal characters that are inappropriate indicators of phylogenetic relationship.

Sand stargazers (Percomorpha: Blennioidei: Dactyloscopidae) are small, sand-dwelling fishes restricted to tropical and warm temperate New World waters. In a series of papers reviewing the alpha-level taxonomy of these fishes, Dawson (1974, 1975, 1976, 1977, 1982) recognized 41 dactyloscopid species in nine genera. The phylogenetic affinities of the Dactyloscopidae have until recently been poorly understood. Most authors (e.g., Gosline, 1968; Greenwood et al., 1966) followed traditional practices in allying the sand stargazers with the electric stargazers of the family Uranoscopidae. The latter are currently recognized to belong to the percomorph suborder Trachinoidei (Pietsch and Zabetian, 1990). George and Springer (1980) formulated the current conception of the Blennioidei, and included the Dactyloscopidae in that suborder. Springer (1993) further delineated the monophyly of the blennioid fishes, and discussed current evidence regarding their interrelationships. At present, the only hypotheses of the interrelationships of the Blennioidei are the molecular analyses of Stepien et al. (1993), which did not consider the Dactyloscopidae, and Stepien et al., (1997), which only examined a single dactyloscopid taxon.

The osteology of dactyloscopids has received little attention since the work of Starks (1923), although Springer (1993) documented variation in several characters among blennioid taxa. A review of the osteology of a common dactyloscopid (*Dactyloscopus tridigitatus* Gill, 1859) is useful not only for reference purposes, but also for the estimation of levels of osteological variation between members of the same species. Extensive variation may suggest either species-level morphological plasticity, population differentiation, or a combination of both. Furthermore, variation may preclude the usefulness of certain characters in the estimation of the phylogeny of the Dactyloscopidae (Doyle, 1998).

MATERIALS AND METHODS

Specimens were in general dissected using modifications of the techniques presented by Weitzman (1974). All cleared specimens examined were double-stained for bone and cartilage, employing modifications of the methods of Dingerkus and Uhler (1977) and Taylor and Van Dyke (1985). Figures were drawn using a camera lucida. Some figures were inverted to illustrate structures in left lateral perspective. Institutional acronyms follow Leviton et al. (1985). Familial membership fol-

lows Eschmeyer and Bailey (1990) and Nelson (1994). Myological terminology follows Winterbottom (1974).

SPECIMENS EXAMINED.—Specimens are listed by taxon, followed by catalog number, number of specimens, and individual specimen standard length in mm. Lengths are measured to the nearest 0.1 mm.

Dactyloscopus tridigitatus—ANSP 142881, 3: 59.0 (f), 63.5 (m), 65.5 (f); GCRL 3009, 1: 49.5(f); ROM 1528CS, 6: 30.2 (?), 33.5 (?), 33.9 (?), 38.8 (?), 42.3 (?), 59.5 (m); ROM 1532CS, 1: 38.3 (?); ROM 1534CS, 1: 45.5 (f); ROM 1536CS, 1: 51.2 (?); ROM 1538CS, 1: 28.2 (?); ROM 1589CS, 3: 38.1 (?), 39.0 (?), 49.0 (?); ROM 1590CS, 8: 30.6 (?), 32.0 (?), 34.3 (?), 41.8 (?), 43.2 (?), 51.0 (f), 57.0 (m), 58.5 (m); ROM 1591CS, 1: 49.5 (m); USNM 318998, 2: 36.0 (?), 37.0 (?).

Twenty-eight specimens of *D. tridigitatus* were dissected, ranging from 28.2 mm SL to 65.5 mm SL. Osteological descriptions are primarily based on three specimens, a 57.0 mm SL male (ROM 1590 CS), a 45.5 mm SL female (ROM 1534 CS), and a 49.0 mm SL female (ROM 1589 CS). Where possible, variation is discussed after the osteological description; however, for some structures widespread variation (especially ranges of discontinuous variables) precluded any meaningful description of osteology without discussion of variation. Representative variation discussed in the text is referred to the appropriate figure by an asterisk and an integer (e.g., “see Figure 2, *1”).

ABBREVIATIONS

ANG, anguloarticular	META, metapterygoid
ANT, anterohyal	METH, median ethmoid
ASC, accessory supraoccipital crest	NS, neural spine
BASO, basioccipital	OP, opercle
BB1-3, basibranchials 1-3	PAL, palatine
BH, basihyal	PARA, parasphenoid
CB1-5, ceratobranchials 1-5	PARI, parietal
CF, foramen for caudal vessels	PB3, pharyngobranchial 3
CL, cleithrum	PMAX, premaxilla
COR, coracoid	POP, preopercle
DENT, dentary	POST, posterohyal
DHH, dorsal hypohyal	PRO, prootic
DPCL, dorsal postcleithrum	PTT, posttemporal
DPR, dorsal procurrent rays	PU2, preural centrum 2
EB1-4, epibranchials 1-4	PU3, preural centrum 3
ENDECT, fused endo- and ectopterygoid	QUAD, quadrate
EP1, epural 1	R1, pectoral radial 1
EP2, epural 2	RET, retroarticular
EPIO, epioccipital	SCAP, scapula
EXO, exoccipital	SCL, supracleithrum
FR, frontal	SO, supraoccipital
HB1-3, hypobranchials 1-3	SOP, subopercle
HS, haemal spine	SPH, sphenotic
HYO, hyomandibula	SR1, first segmented pectoral fin-ray
IH, interhyal	SYM, symplectic
INT, intercalar	TSC, transverse supraoccipital crest
IO1, infraorbital 1 (lacrymal)	UC, first ural centrum, hypurals 1-4 and parhypural
IO5, infraorbital 5	V, vomer
IOP, interopercle	VHH, ventral hypohyal
LETH, lateral ethmoid	VPCL, ventral postcleithrum
MAX, maxilla	VPR, ventral procurrent rays

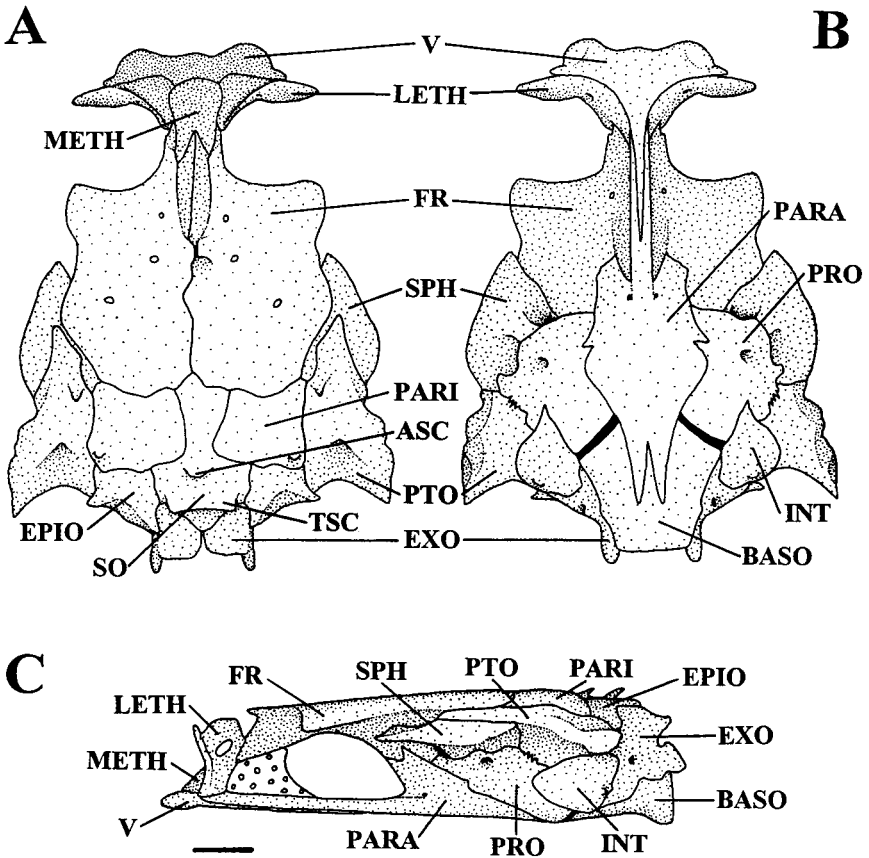


Figure 1. Neurocranium of *D. tridigitatus* (ROM 1590CS, SL 57.0 mm) in (A) dorsal view; (B) ventral view; and (C) left lateral view. Scale bar is 1 mm.

OSTEOLOGY AND VARIATION

NEUROCRANIUM.—*Osteology* (Fig. 1).—In ventral view, the median, edentate vomer overlies the parasphenoid in a slender posterior process and is bounded by the median ethmoid dorsally and the paired lateral ethmoids dorsolaterally. The lateral ethmoids form the anterior orbital margin and each possesses a circular, centrally located foramen for the passage of the olfactory (I) nerve. The lateral ethmoids contact the frontals posteriorly to form the dorsal margin of the orbit. The median ethmoid separates the lateral ethmoids, and is a spatulate element dorsally overlying the lateral ethmoids and vomer. A pair of flanges extend posteriorly from the median ethmoid to overlie each frontal in the region of the frontal recess, here defined as the anteromedial region of the conjoined frontals that accommodates the premaxillary ascending processes. A thin, median cartilage occupies the anterior margin of the interorbital septum.

The paired frontals are the largest bones of the neurocranium. Each is extremely broad with extensive, gracile lateral flanges. Each frontal overlies its sphenotic laterally and contacts its parietal and the median supraoccipital posteriorly. The frontals enclose the posterior portion of the supraorbital sensory canal; three canal pores are present. The frontals are joined posteromedially in a complex overlapping suture which extends anteriorly into a shallow sulcus approximately halfway between the posterior border of the frontals and the posterior orbital margin. Immediately anterior to the sulcus each frontal is expanded into a narrow median shelf; the paired shelves do not contact in the midline. Anterior to the medial frontal shelves, the frontal recess accommodates the ascending premaxillary processes.

Paired, plate-like parietals are separated from each other by the supraoccipital. A small, posteriorly oriented flange is present on the posterolateral corner of each parietal and serves to brace the lateral extrascapular anterodorsally. Each parietal overlies the supraoccipital medially, contacts the epioccipital posteriorly, and the pterotic laterally. The supraoccipital lacks a mid-sagittal crest, but possesses a marked, transverse crest dorsal to its borders with the paired exoccipitals (here termed the transverse supraoccipital crest, TSC). Another, smaller, posteriorly directed crest (the accessory supraoccipital crest, ASC) is located anterior to the transverse crest and buttresses the median extrascapulars anterodorsally. Paired epioccipitals are bordered medially by the supraoccipital, medioventrally by an exoccipital, dorsally by the parietals of either side, and laterally by the pterotics. Each epioccipital possesses a posterolateral process with which the dorsal limb of the posttemporal articulates.

The paired sphenotics suture anteriorly to the frontals and posteriorly to the pterotics. The sphenotic is irregularly exposed dorsally, as the anterior pterotic process is adjacent to the posterolateral margin of the frontal, exposing the prominent lateral portion of the sphenotic as well as an oblong medial portion connected by a thin exposed isthmus. The pterotic overlies the sphenotic in a gracile anterior process and is overlapped medially by the epioccipital. The pterotic bears the posterior portion of the postorbital canal medially, and possesses a prominent, sculptured posterolateral wing.

On the ventral surface of the neurocranium lies the broadly expanded parasphenoid, which is overlapped anteriorly by the vomer and overlies the basioccipital posteriorly in a bifurcate process. Paired ventral foramina are present near the orbital border for the passage of the internal carotid arteries. The anterolateral wings of the parasphenoid contact the descending wings of the frontals to form the medial portion of the posterior orbital margin. The basisphenoid is a thin, transverse bar uniting the ventral wings of the frontals dorsal to the posterior myodome (not visible in lateral view). The basisphenoid is represented only by the meningost portion (Springer, 1993), and is not firmly ankylosed to the frontal wings. The paired prootics lie dorsolateral to the parasphenoid, and are ovoid elements bounding the trigeminal foramen posteriorly and enclosing the facial foramen near their mid-lateral margins. Each prootic is bound anterodorsally to the sphenotic and frontal, posterolaterally to the pterotic, and posteriorly to the intercalar. An unossified region (apparently occupied by cartilage) is present between the posteromedial margin of the prootics and the basioccipital. The sphenotic articulates anteromedially with the frontal to complete the posterior orbital margin. As noted by Springer (1993; *contra* Dawson, 1982) dactyloscopids lack pterosphenoids.

Ventromedially, the sphenotic bears a hyomandibular fossa for the anterodorsal head of the hyomandibula, with the posterodorsal hyomandibular head articulating with a more

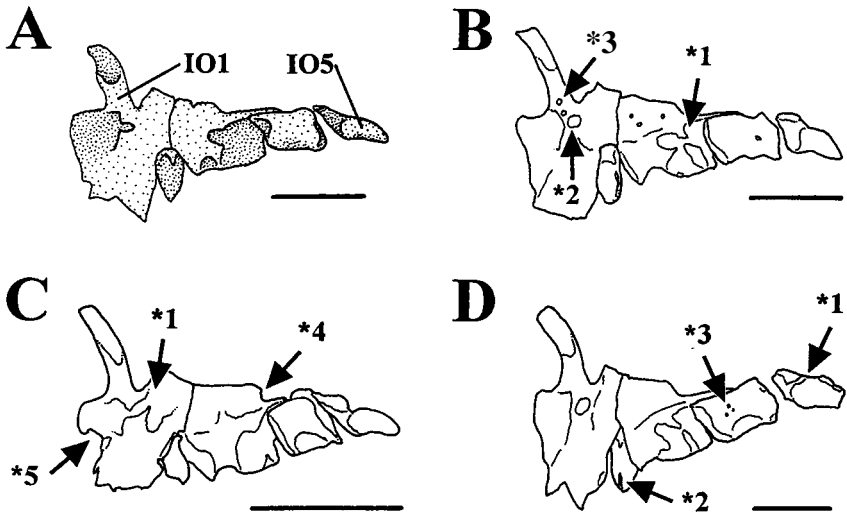


Figure 2. (A) Dorsolateral view of left infraorbital elements of *D. tridigitatus* (ROM 1534CS, SL 45.5 mm), with representative variation: degree of ossification of lateral sensory canal (*1); sensory canal extensions (*2) and pores (*3); IO3 dorsal notch (*4); anterior IO1 margin shape (*5). (B, ROM 1528CS, SL 59.5 mm; C, ROM 1533CS, SL 28.2 mm; D, ROM 1590CS, SL 57.0 mm). Scale bars are 1 mm.

laterally placed fossa on the pterotic. The pterotic is tightly sutured to the prootic by a complex interdigitate articulation, and abuts its sphenotic anteriorly. Medial to each pterotic lies the superficial, ovoid intercalar, which bears a stout posterolateral process to which attaches the ligament binding the ventral arm of the posttemporal to the neurocranium. The paired exoccipitals lie on either side of the foramen magnum and bear posteromedial processes that articulate with anterolateral processes on the first vertebra. Each exoccipital is perforated by a prominent foramen for the passage of the vagus (X) nerve, and articulates laterally with the intercalar, ventrally with the basioccipital, and dorsally with the epioccipital and the supraoccipital. The ventral border of the foramen magnum is completed by the median basioccipital; the exoccipitals are excluded from the dorsal margin of the foramen via a posteroventral supraoccipital process. In well-stained specimens, cartilage may be seen to lie in the region between the exoccipitals. The basioccipital is pentagonally shaped in ventral view, with Baudelot's ligament originating on the posterolateral surface.

Variation.—The neurocranium displays relatively little discrete osteological variation in *D. tridigitatus*. The majority of the differences involve variations in the shapes of bones. Ontogenetic variation was observed in the development of more robust elements in larger specimens; for example, larger specimens exhibited more pronounced, laterally extending parasphenoid wings. This trend was also apparent in the extent of development of the medial frontal flanges, which graded from near absent in specimens <30 mm SL to well developed and closely abutting in larger specimens. Smaller specimens possessed poorly developed transverse supraoccipital crests. A few specimens exhibited a medially notched transverse supraoccipital crest.

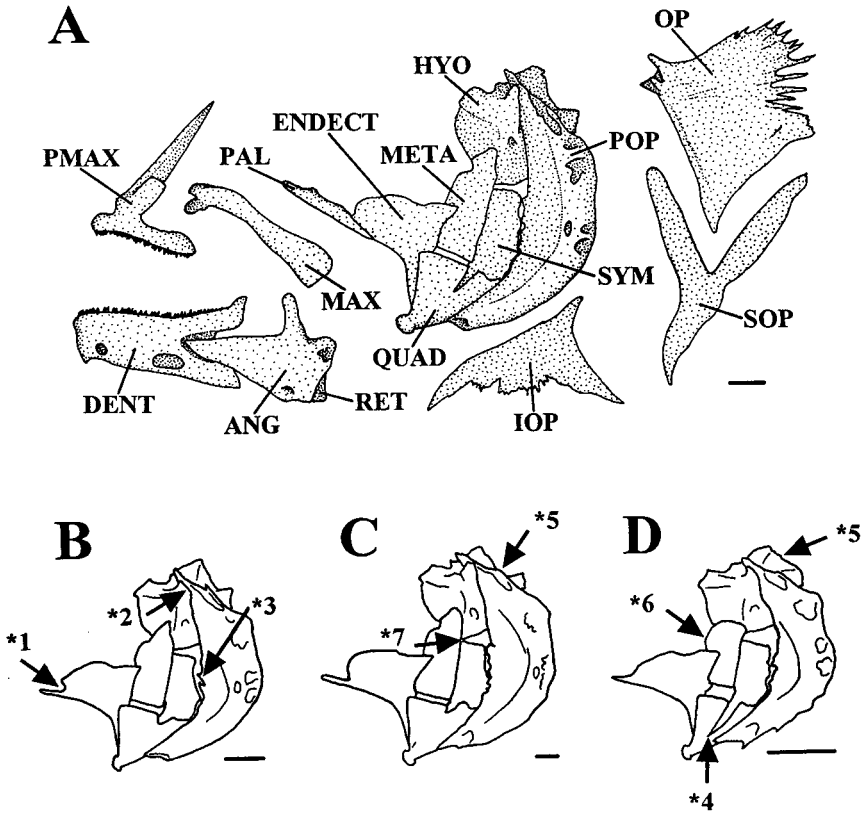


Figure 3. Disarticulated jaws, suspensorium, and opercular series of *D. tridigitatus* (ROM 1590CS, SL 57.0 mm) in left lateral view (A). Representative suspensorial variation (palatine not shown): endo-ectopterygoid shape (*1); hyomandibular spur size (*2); symplectic/preopercular shape (*3); quadrate shape (*4); hyomandibular shape (*5); metapterygoid shape (*6); symplectic/hyomandibular margin (*7). (B, ROM 1534CS, SL 45.5 mm; C, ANSP 142881, SL 63.5 mm; D, ROM 1538CS, SL 28.2 mm). Scale bars are 1 mm.

JAWS, SUSPENSORIUM, AND SUPERFICIAL BONES OF THE HEAD.—*Osteology* (Figs. 2,3).—Five infraorbital bones are present (hereafter referred to as IO1–IO5, with IO1 denoting the dermal lachrymal) with no development of a suborbital shelf. Two axes of the infraorbital canal can be recognized; a cranio-caudal portion perforating IO2 through IO5, and a ventrolateral portion contained entirely in IO1. IO5 is not sutured to IO4 and lies at the anterodorsal juncture of the frontal and sphenotic. With the exception of IO5, the remaining infraorbitals are all tightly bound to the adjacent element(s) in the series. IO4 is suspended tightly under the lateral frontal flange and is a short, closed tube lying on the lateral surface of the inner margin of IO3. A small pore is present on the medial surface of IO4. IO1–IO3 form a complicated pattern of articulation, with IO1 contacting IO3 dorsally and medially, to brace the much smaller, laterally situated IO2. IO3 is an irregularly shaped element, with a closed tube-like anterior portion and an open posterolateral portion. IO3 is bound dorsomedially to IO1, forming a broad dorsal flange. IO2 is a small open element (unclosed bony canal laterally) lateral to IO3 and IO1. The exposed dorso-lateral portion of IO2 forms a prominent hook overhanging the anteriormost portion of

the cranio-caudal infraorbital sensory canal. IO1 is the largest element in the infraorbital series, and is bound to the lateral ethmoid by a prominent notch on the posterodorsal surface of IO1. The dorsal flanges of IO1 and IO3 may form additional support for this articulation. The ventrolateral portion of the infraorbital canal opens dorsolaterally, ventrally, and anterolaterally around the midpoint of IO1. Thus the anterior margin of IO1 forms a prominent anterior flange.

The paired, elongate nasals (not figured) bear the anterior margin of the supraorbital canal. Each nasal articulates ligamentously with the frontal posteriorly and the lateral ethmoid and maxilla laterally. A lateral, triangular process is present midway along the length of the bone. The paired premaxillae are well separated at their symphysis and form the upper jaw margin. The ascending process of each premaxilla is long and slender, and is medial to the plate-like articular process. The postmaxillary process of the premaxilla is indistinct from the alveolar row. Three rows of sharp, slender, and recurved teeth are present, with approximately 20–35 teeth in each row. Each maxilla is broad, with a stout medial premaxillary process and a saddle-shaped dorsal surface into which the anterolateral palatine head inserts. The paired dentaries are tightly opposed at their symphysis. Sharp, recurved teeth of subequal size are borne in two rows (of approximately 20–45 teeth per row). Each dentary articulates with an anguloarticular posteriorly by a prominent sulcus on the lateral surface of the dentary. The anguloarticular possesses a well-developed coronoid process. The dentary and anguloarticular contain the mandibular sensory canal. The small, medial retroarticular is located at the posteroventral margin of the anguloarticular. The large quadrate articulates by a prominent ball-and-socket joint with the anguloarticular.

The quadrate is triangular in shape (with the apex anteroventrally) and is prominently incised midway along the dorsal margin. The palatine is an anteriorly bifurcate, styliform element articulating anteromedially with the lateral ethmoid and anterolaterally with the maxilla. The posterior border interdigitates with the endo-ectopterygoid (a single element formed from the presumed fusion of the endopterygoid and ectopterygoid, see Springer, 1993) through a saddle-shaped articulation, with the palatine extending furthest posteriorly along the medial border of the palatal arch. Two small specimens exhibited cartilage in the region of presumed endo-ectopterygoid fusion, strongly indicating that the two bones are in fact fused (instead of one element being lost). Ventrally, the endo-ectopterygoid extends into an elongate process along the medial margin of the quadrate almost to the articulating head of the latter. Posteriorly the endo-ectopterygoid articulates in a complex fashion with the metapterygoid. A posterodorsally oriented flange on the endo-ectopterygoid joins a notch in the metapterygoid in a tongue-in-groove joint. A portion of the dorsal margin of the endo-ectopterygoid overlaps the metapterygoid laterally. Presumably this articulation pattern serves to strengthen the joint between the two elements. The metapterygoid does not contact the quadrate and lies lateral to the hyomandibula and symplectic.

The symplectic is a broad element articulating with the metapterygoid and quadrate, and posteriorly bordered by the preopercle. The articulation with the quadrate occurs medially along the majority of the cranio-caudal length of that bone. The hyomandibula is robust with a broadly rounded anterior margin. A prominent, lateral hyomandibular “spur” (Pietsch and Zabetian, 1990) overlies and braces the preopercle laterally. The posterior hyomandibular process articulates with the opercle. The preopercle is a robust bone bearing a series of pores in the roofed laterosensory canal. The preopercle articulates with

the hyomandibula dorsomedially, the quadrate anteroventrally, and the interopercle medially.

The opercle is rhomboidally shaped, with the posterodorsal margin extended into numerous filiform processes, corresponding closely in number to the fleshy external opercular fimbriae (distinct bony fimbriae generally number 1 or 2 less than external fleshy fimbriae). A hook-like dilatator process lies lateral to the joint with the hyomandibular. The opercle possesses a well-delineated dorsoventral trough near its anterior margin. The subopercle is bicornate, bound tightly to and overlapped laterally by the opercle. The ventroposterior margin of the preopercle is inconsistently ossified. The interopercle is bound to the medioventral surface of the preopercle and is irregularly shaped with a fimbriate ventral border. The ossified interopercular fimbriae do not correspond to integumentary fimbriae in this region. The interoperculo-retroarticular ligament is exceptionally short, due to the close proximity of these two elements.

Two canal bearing extrascapulars are loosely bound to each half of the dorsal surface of the neurocranium. The lateral extrascapular is a well-ossified, tripartite structure braced medially by the epioccipital. The posterior portion of the postorbital canal enters a limb of this element laterally, with a medial limb present through which passes the lateral portion of the supraoccipital canal. The median extrascapular is a relatively simple, tubular structure that is poorly ossified, especially in smaller specimens.

Variation.—The infraorbital elements are perhaps the most variable osteological complex within *D. tridigitatus* (Figs. 2B–D). Such variation primarily involves the extent of ossification of the lateral portion of the sensory canal (Fig. 2, *1), and the concomitant presence or absence of lateral bony extensions (Fig. 2, *2) and isolated pores (Fig. 2, *3). Several specimens show varying numbers of tiny, discrete pores perforating the dorsal flange of IO3, which also exhibited variation in the development of a dorsal notch (Fig. 2, *4). Shape variation was observed in the anterior margin of IO1 (Fig. 2, *5). IO5 is generally poorly developed in specimens <40 mm SL, the ossified portion being foreshortened anteroposteriorly. The degree of ossification of all elements is correlated with specimen size; however considerable plasticity was observed. For example, a 63.5 mm SL fish had a very poorly ossified lateral portion of IO2.

Minor variation is observed in the jaw elements. The premaxilla is conservative, with the exception of slight shape differences in the postmaxillary margin. The maxilla shows little variation. The distal portion of the coronoid process of the anguloarticular varies in shape from broadly rounded to truncate. The most apparent differences among specimens lie in the number of teeth (20–35 per row in the premaxilla, 20–45 in the dentary), and in the extent of development of distinct tooth rows. The smallest specimen examined (28.2 mm SL) showed only two distinct rows in both jaw elements, while the largest (65.5 mm SL) possessed three well-developed rows in both the premaxilla and dentary. The number of distinct tooth rows appears to be correlated with size; however, only a weak relationship was observed between number of teeth and body length. Generally, three dentary tooth rows develop prior to the three premaxillary rows. No specimens were observed with three distinct rows in the premaxilla and two in the dentary.

The suspensorium is a highly variable region in *D. tridigitatus* (Figs. 3B–D). Differences were observed in: shape of the dorsal margin of the endo-ectopterygoid (Fig. 3, *1); extent of development of the hyomandibular spur (Fig. 3, *2); shape of both the endo-ectopterygoid and metapterygoid at their articulation; shape of both the symplectic and preopercle at their juncture (Fig. 3, *3); extent and shape of the preopercular sensory

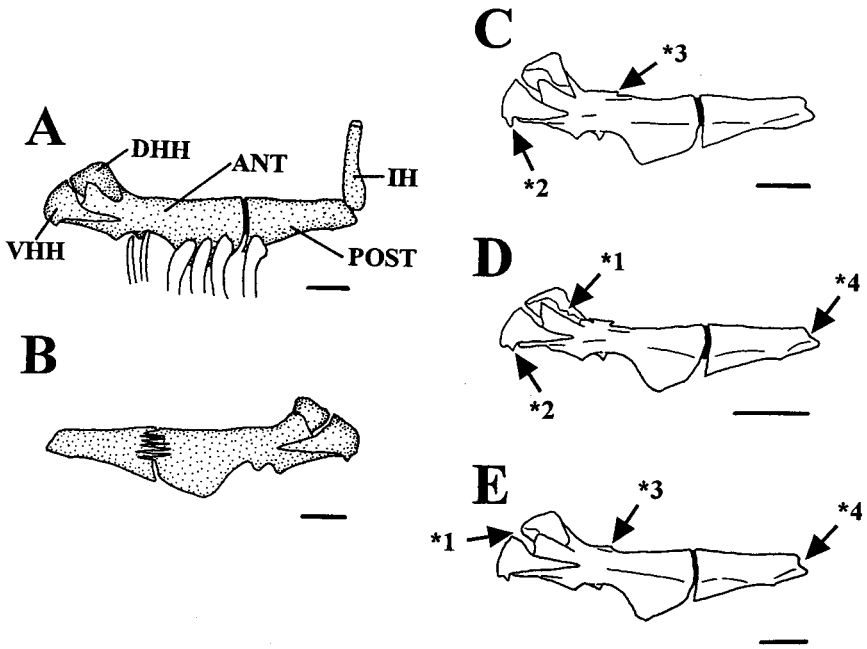


Figure 4. Hyoid arch morphology of *D. tridigitatus* (ROM 1590CS, SL 57.0 mm). (A) lateral view of left hyoid arch with branchiostegal rays; (B) medial view of left hyoid arch, interhyal not shown; (C–E) variation in left lateral hyoid arch morphology (interhyal not shown): dorsal and ventral hypohyal ossification (*1); ventral hypohyal posteroventral hook (*2); anterohyal mid-dorsal flange (*3); posterohyal posterior margin (*4). (C, ROM 1534CS, SL 45.5 mm; D, ROM 1590CS, SL 34.3 mm; E, ROM 1536CS, SL 51.2mm). Scale bars are 1 mm.

canal pores; shape of the posterodorsal margin of the quadrate (Fig. 3, *4); shape of the hyomandibular posterior process (Fig. 3, *5); shape of the anterior margin of the metapterygoid (Fig. 3, *6); and contact margin between the symplectic and hyomandibula (Fig. 3, *7). As might be expected, the degree of ossification and extent of cartilage present varies with SL. The only other character that was observed to be correlated with ontogeny is the degree to which the lateroposterior hyomandibular flange overlaps the preopercle (less overlap in smaller specimens). The opercle and interopercle each exhibit variation in the development of fimbriate margins. Such variation is most prominent in the opercle, and correlates poorly with specimen size. This relationship is consistent with the observations of Dawson (1982), who recorded a weak correlation between specimen length and the number of external opercular fimbriae (slightly greater in number than distinct bony fimbriae). Smaller specimens (SL <35) possessed poorly developed interopercular fimbriae. With the exception of moderate opercle shape variation, no further gross differences were observed among respective elements of the opercular series.

HYOID ARCH.—*Osteology* (Figs. 4,5).—A single, median basihyal articulates ligamentously with the paired dorsal hypohyals anteriorly and with the paired anterohyals posteriorly. Each dorsal hypohyal is tightly sutured to and overlapped medially by the anterohyal, and is largely obscured in lateral view by a prominent dorsoanterior flange of the anterohyal. The paired ventral hypohyals are bifurcate and straddle the anterior sur-

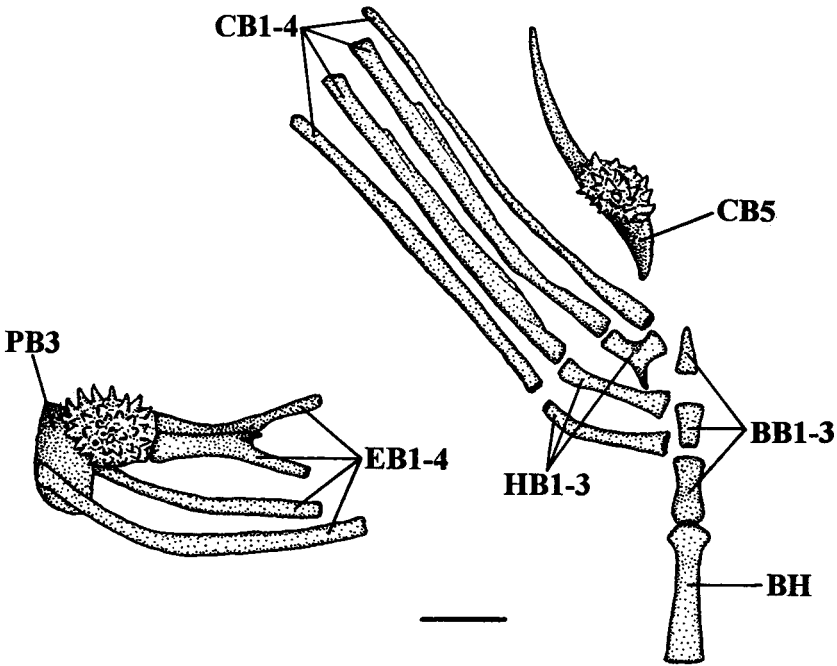


Figure 5. *Dactyloscopus tridigitatus* (ROM 1590CS, SL 57.0 mm) basihyal, basibranchials, and right branchial arches in dorsal view, with right dorsal elements reflected to expose ventral surface. Scale bar is 1 mm.

face of each anterohyal both laterally and medially. A ligament from the ventromedial face of each ventral hypohyal stretches to the lateral face of the urohyal. The anterohyal is a barbell-shaped element bound by a tight interdigitating suture to the smaller posterohyal. A small medial flange is present on the anterohyal between the points of articulation of the first two branchiostegals. The posterohyal articulates posteriorly with the styliiform interhyal, and laterally with the interopercle through a stout ligament. The median urohyal possesses a broad, concave anteroventral surface. The urohyal is moderately stocky, and is closely bound to the ventral surfaces of the anterior portions of each hyoid branch. Six branchiostegals are present, the anterior five articulate with the anterohyal, the most posterior with the anterior margin of the posterohyal. The first two branchiostegals are gracile in comparison to the remaining four, with the first branchiostegal possessing a well developed anteromedial flange midway along the element's length.

Variation.—The hyoid arch displays considerable intraspecific variation (Figs. 4C–E) in all elements except the basihyal, urohyal, and interhyal. In smaller specimens the dorsal and ventral hypohyals are poorly ossified, a characteristic that is almost certainly ontogenetically correlated (Fig. 4, *1). The ventral hypohyal displayed a variously developed posteroventral hook, either rounded or extended into a prominent posterior protuberance (Fig. 4, *2). The anterohyal exhibited a variously developed mid-dorsal flange; either absent as a discrete structure, poorly developed, well-developed with a slight anterior extension, or well-developed and perforated by tiny anterior foramina (Fig. 4, *3). A similar structure is variant within the blennioid genera *Paralticus* and *Praealticus* (Springer and Williams, 1994). As well, the ventral median flange of the anterohyal varied in shape

from bluntly triangular to styliform. The shape of the posterohyal varied along its posterior margin at the articulation point of the interhyal. This border exhibited a range of forms from subround to distinctly notched (Fig. 4, *4). The branchiostegal elements consistently exhibited the relative size relation (first two slender, posterior four broad) discussed previously. However, in several specimens the sixth (last) branchiostegal was massive, nearly twice as wide as the next largest branchiostegal element. Furthermore, a small number of specimens exhibited a small posterior flange midway along the posterior margin of branchiostegal two. The distal margins of the last two branchiostegals (5 and 6) varied considerably in degree and consistency of ossification.

BRANCHIAL ARCHES.—*Osteology* (Fig. 5).—The branchial elements consist of three median basibranchials, three paired hypobranchials, five paired ceratobranchials, four paired epibranchials, and one pair of pharyngobranchials. Basibranchial 1 is tightly bound between the hyoid arches of either side, and articulates posteriorly with the cone-shaped basibranchial 2 (apex anteriorly). Basibranchial 3 is also a small, cone-shaped element, but is more slender and has a posteriorly directed apex. The first two hypobranchials are styliform, but the third is a stout bone with a prominent anteroventral process and a well-developed posterodorsal fossa. Ceratobranchials 1 through 3 are elongate with a variously developed and generally weakly ossified anterior and/or posterior flange. Ceratobranchial 4 is styliform and the most slender of the ceratobranchials. The fifth ceratobranchial is robust, with a slender posterior process and a broad, hook-shaped anterior process. It bears 13–28 sharp, recurved teeth. Epibranchial 1 is a slender, elongate, slightly recurved element articulating with the anteroventral margin of the pharyngobranchial. Epibranchial 2 is a straight, styliform bone slightly smaller than the first epibranchial. Epibranchials 3 and 4 are bound tightly together, with the third element possessing a posterolateral uncinat process which lies in an obliquely oriented sulcus on the ventral surface of epibranchial 4. One pharyngobranchial element is present, presumed to be the third. Springer (1993) noted that, with few exceptions, blennioid fishes lack pharyngobranchials 2 and 4, with the first pharyngobranchial represented primarily by cartilage. No evidence of cartilage representing this element was found in any specimens examined, an observation that is consistent with Dawson's (1982) diagnosis of the family. Approximately 15–30 sharp, recurved teeth constitute the pharyngobranchial dentition.

Variation.—The branchial arches constitute a relatively conservative osteological region within *D. tridigitatus*. The primary exception to this conservatism is in the tooth number on both pharyngobranchial 3 and ceratobranchial 5. Neither of these two variables appears correlated with specimen size, and may only bear a weak relation to each other. Discrete variation is detectable in the shape of basibranchial 2, which possesses states of indistinctly ossified, conical, and dumbbell-shaped. As well, the uncinat process on epibranchial 3 varied from styliform to truncate. Variation in the degree of ossification of the branchial elements (over the size range of the specimens examined) is observed, but is not prominent.

APPENDICULAR SKELETON.—*Osteology* (Fig. 6).—The pectoral girdle is linked to the cranium by a canal-bearing posttemporal, a two-pronged bone which is weakly bound to the epioccipital dorsally and the intercalar ventromedially by a strong ligament. The posttemporal articulates medially and posteriorly with the dumbbell-shaped supracleithrum, which in turn articulates medially with the cleithrum. The latter is a robust bone with a prominent anteroventromedial limb which is firmly sutured to its antimere at the ventral

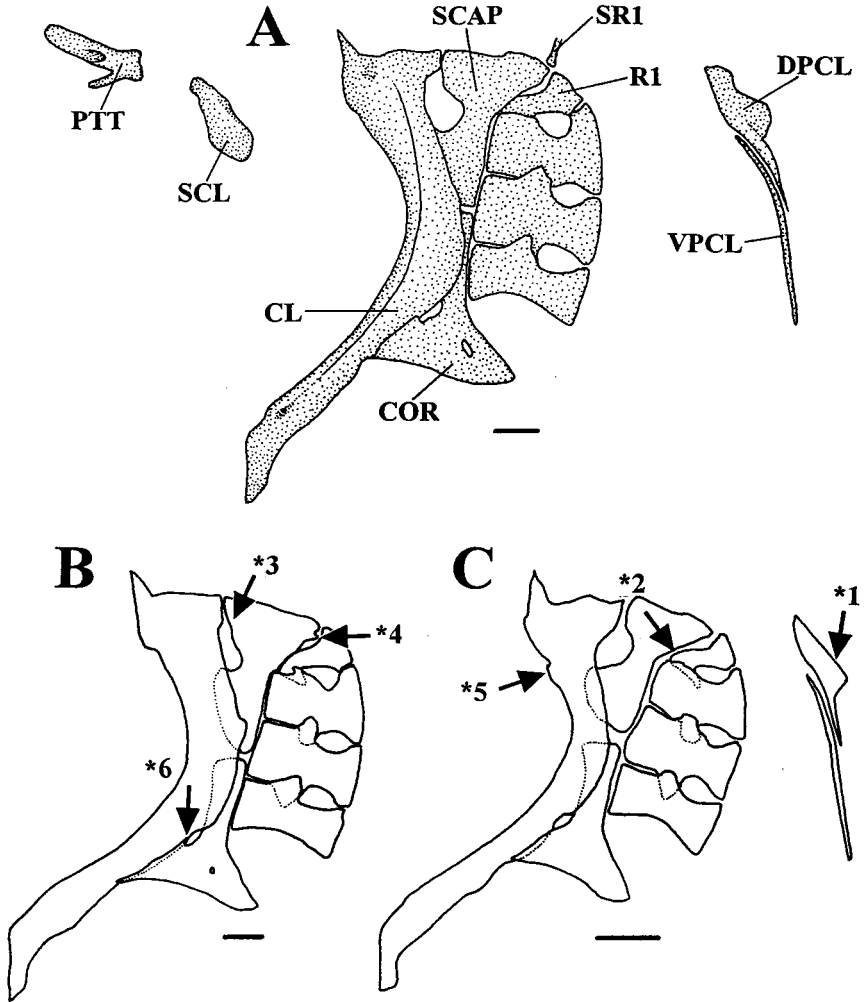


Figure 6. Left pectoral girdle of *D. tridigitatus* (ROM 1590CS, SL 57.0 mm) in lateral view (A), with posttemporal, supracleithrum, and postcleithra dissociated. Representative variation: dorsal postcleithrum posterior flange (*1); articulation point of radial 1 with the scapula (*2); scapular shape (*3, *4); anterodorsal cleithral "hook" (*5); anterior margin of the coracoid (*6). (B, ANSP 142881, SL 63.5 mm; C, ROM 1589CS, SL 49.0 mm). Scale bar is 1 mm.

midline. Sutured medially to the cleithrum is the dorsal, dumbbell-shaped scapula and the ventral, sub-triangular coracoid. Both are of roughly equal size. The coracoid typically possesses an ovoid foramen just posterior to the center of the bone. The ventral margin of the coracoid overlies the cleithrum laterally. Two postcleithra are situated medial to the pectoral girdle. The dorsal-most bone possesses a broadly expanded posterodorsal flange, while the ventral postcleithrum is a very slender, sigmoidally shaped element. Four proximal radials are present, all of which are longer than wide. The ventral-most (fourth) radial overlaps the third laterally, with a similar spatial relationship applying among the more dorsal radials. The ventral three radials are relatively large; the first is smaller. A broad, lateral band of cartilage unites the posterior margins of the radials and

serves as the articulation point for the 13 pectoral rays. The first (dorsal-most) ray articulates with an extension of this cartilage on the posterior margin of the scapula.

Dorsal to the articulation of the cleithra lies the pelvic girdle (not illustrated), the anterior margin of which extends beyond the most anterior border of the pectoral girdle. The pelvic girdle is roughly pod-shaped (open ventrally), and is not tightly bound to the cleithra. Anterior, median pelvic processes are absent. The pelvises abut dorsally for the majority of their length but are not fused. Two small, bilaterally paired foramina (variably incomplete medially) perforate the dorsal margin of each pelvis two-thirds of the distance to the posterior margin. One stout pelvic spine and three unbranched, expanded and recurved rays are present.

Variation.—The pectoral girdle exhibits considerable variation in *D. tridigitatus* (Figs. 6B–C). In contrast to the sigmoidal border between the dorsal and ventral postcleithrum (the common condition), several specimens exhibited nearly straight ventral postcleithrum (with the ventral process of the dorsal postcleithrum straight as well). A few specimens possessed dorsal postcleithra with a truncated or inconsistently ossified posterior flange (Fig. 6, *1). In a few specimens the ventral postcleithrum was extremely foreshortened, with a short posterior extension bracing the ventral margin of the dorsal postcleithrum. Variation in the extent of development of the coracoid foramen is also observed (from large and ovoid to absent). Dawson (1982:17) noted that in dactyloscopids the “upper pectoral-fin ray articulates with the upper radial”. While this condition is the most common one observed in *D. tridigitatus*, several specimens displayed the upper-most fin ray articulating between the first radial and the scapula at the margin of the cartilage ring bordering the radials and posterior scapular process. In one specimen the upper-most fin ray articulates primarily with the scapula. Further variation involves: articulation of dorsal border of radial 2 with scapula (Fig. 6, *2); variation in the shape of the anterior scapular margin (Fig. 6, *3); variation in the shape of the posterior scapular margin (Fig. 6, *4); development of an anterodorsal cleithral “hook” ventral to the region of articulation of the supracleithrum (Fig. 6, *5); and development of a dorsal process at the anterior margin of the coracoid (Fig. 6, *6). Both the supracleithrum and posttemporal are relatively conservative elements, with the exception of one specimen possessing an incompletely fused posttemporal canal.

Variation in the pelvic girdle was rare in the specimens dissected. Some specimens possessed more prominent lateral pelvic shelves, and a few specimens possessed dorsal pelvic foramina of variable shapes.

VERTEBRAL COLUMN, RIBS, AND CAUDAL FIN.—*Osteology* (Fig. 7).—The vertebral column consists of 43–45 vertebrae (11 abdominal and 32–34 caudal, excluding the ural complex). The anteriormost four vertebral centra are shortened, with broad neural arches bearing poorly developed neural spines. The neural arches of the first three abdominal vertebrae are slightly wider than their respective centra, the more posterior vertebrae possess arches with a more typical sub-equal relationship between neural arch and centrum width. Epineurals are present, suspended off all abdominal vertebrae, as well as the first 0 through 3 caudal elements, for a total of 11–14 epineurals (but see variation). Four ribs are present, articulating with the dorsal margin of the respective epineurals on vertebrae 3 through 6. All vertebrae, including the ural centrum, have neural and haemal arches that are very narrow (anteroposteriorly) in relation to the centrum length.

The caudal skeleton is composed of a ural complex, two epurals, and 10 segmented rays. The ural complex is presumed to be formed by the fusion of the ural centrum

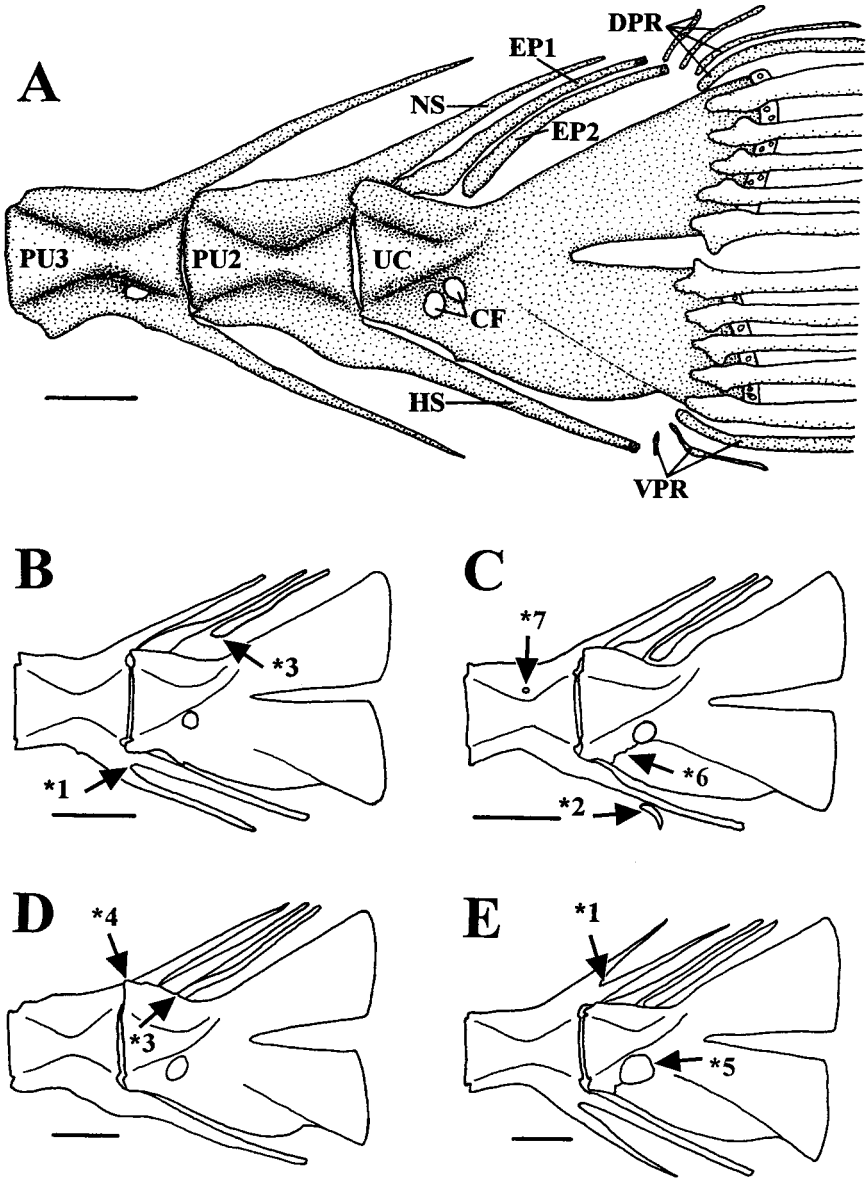


Figure 7. (A) Left lateral view of caudal skeleton of *D. tridigitatus* (ROM 1590CS, SL 57.0 mm). Representative variation: bifid neural and haemal spines on Pu2 (*1); sesamoid ossification (*2); epural 2 (*3); ural centrum anterodorsal zygapophyses (*4); caudal foramen shape (*5); retention of the parhypural sutural trace (*6); Pu2 neural arch foramina (*7). (B, ROM 1589CS, SL 38.1 mm; C, ROM 1528CS, SL 33.9 mm; D, ROM 1589CS, SL 49.0 mm; E, ROM 1591CS, SL 49.5 mm). Specimen (A) possesses aberrant caudal foramen condition bridged by bony isthmus. Scale bars are 0.5 mm.

(PU1+U1+U2) with the dorsal and ventral hypural plates (the latter including the parhypural). Each of these plates probably corresponds to hypurals 1+2 ventrally and 3+4 dorsally; there is no evidence of hypural 5 which might either have been lost or incorporated into the dorsal hypural plate. No uroneurals are distinguishable; presumably these are either lost or incorporated into the lateral margins of the urostylar portion of the ural centrum. The parhypural is not autogenous, and is fused in varying degrees to the ventral hypural plate posteriorly. Four dorsal and three ventral procurrent rays are typically present. The dorsalmost and two ventralmost segmented rays are unbranched, while the medial rays are branched once. A full neural spine is present on PU2.

Variation.—Variation in the vertebral region of the axial skeleton is restricted to small differences in the number of caudal vertebra (32–34), and minor variation in the ossification of the epineural bones. Epineurals are always present, suspended from all thoracic vertebrae; however, marked variation in the development of epineurals in the anterior caudal vertebra is observed. Some specimens possessed up to three caudal epineurals suspended from the vertebra of one side, with none present on the other. Among the specimens examined, most combinations of bilateral caudal epineural number were observed.

The caudal skeleton is one of the most variable osteological complexes within *D. tridigitatus* (Figs. 7B–E). Several specimens of *D. tridigitatus* possessed complete, bifid neural and haemal spines on PU2 (Fig. 7, *1). This condition probably represents the incorporation of the spines of PU2 into the body of PU3 (or vice versa—one specimen displayed partial fusion of these two vertebra); however, the small sample size renders a direct comparison with caudal vertebral number unwarranted. Variants of this condition include PU2 with a bifid haemal arch (but normal neural arch), as well as the reverse variant. Some specimens exhibited a small, hook-like sesamoid ossification anterior to the haemal arch of PU2, possibly representing a remnant haemal arch of an incorporated vertebral body (Fig. 7, *2). Two epurals were present in all specimens examined; however, considerable variation in position and structure of the second epural was observed. Epural 2 was either styliform or with the distal margin bent posteriorly, and was either in contact (or in close proximity) to the ural centrum or well separated from it (Fig. 7, *3). One specimen displayed epurals that appeared to be fused proximally. Considerable differences in relative depth (and occasionally shape) of the caudal vertebral centra is apparent, and does not appear to be well-correlated with specimen size. Distinct procurrent caudal ray ossifications varied from three to five; dorsal procurrent rays were always greater or equal in number to ventral procurrent rays. Additional variation included: varying development of ural centrum anterodorsal zygapophyses (Fig. 7, *4); shape variation in caudal foramen (Fig. 7, *5); development of foramina in Pu2 neural arch (Fig. 7, *6); and retention of the parhypural sutural trace (Fig. 7, *7). Dawson (1982) observed ontogenetic variation in the development of bifurcating caudal rays; no conditions were observed in the specimens examined to contradict these observations. Clark (1979) observed similar levels of variability within several species of the tripterygiids *Helcogramma* and *Enneapterygius*.

DORSAL AND ANAL FINS.—*Osteology.*—The dorsal fin is composed of 11–12 spines, 29–31 rays, and their serially associated pterygiophores. However, the proximal pterygiophore supporting the last spine also supports the first segmented ray, thus there is one fewer pterygiophore than the total number of spines plus rays. This corresponds to the presence of a single supernumerary spine associated with the first dorsal fin

pterygiophore. The pterygiophores are composed of a single element, presumably representing the fused proximal and middle radials. The distal radial of the preceding pterygiophore is most likely absent (see Mooi, 1993; Springer, 1993). Posteriorly, the distal pterygiophore elements become firmly braced on the succeeding proximal/medial pterygiophore.

The anal fin is composed of two spines, 32–34 rays, and associated pterygiophores. The first spine is associated with a very poorly developed first proximal pterygiophore. The second pterygiophore supports the second spiny ray and first segmented ray, thus the first spine is supernumerary. Pterygiophores posterior to the first pterygiophore are composed of fused proximal/medial elements and the paired distal elements with which the hemitrichs articulate. The first four pterygiophores lie anterior to the first haemal arch. In mature males, the anteriormost two segmented rays are enlarged and recurved (Dawson, 1982; Springer, 1993). As is the condition in the dorsal fin, the posterior distal pterygiophore elements become more firmly braced by the next posterior proximal/middle pterygiophore. In the anal fin, however, this condition is structurally more pronounced.

DISCUSSION

A review of the osteology and osteological variation in *Dactyloscopus tridigitatus* has revealed five osteological regions that display the greatest morphological plasticity: the infraorbital bones, suspensorium, hyoid arch, pectoral girdle, and caudal skeleton (see Table 6). In contrast, the neurocranium and pelvic girdle were found to be conservative regions. The identification of variation is essential to the proper delineation of putative phylogenetically informative characters and character states. However, information on the extent and nature of within-species osteological variation is exceedingly scarce. Numerous osteological studies have discussed variation in a passing context, or have focused on meristic variation (e.g., Springer and Gomon, 1975). However, few have concentrated on intraspecific osteological variation (e.g., Arratia, 1983; Bruner, 1976; Schlueter and Thomerson, 1971). This is unfortunate due to the potential import of osteological variability to species or population identification as well as to the defense of hypotheses of character acquisition or conservation.

The type species of *Dactyloscopus* (*D. tridigitatus*) is among the most common dactyloscopid species. Dawson (1982) noted that while several eastern Pacific species of *Dactyloscopus* exhibit considerable geographic external meristic variation, such is not the case with abundant Atlantic forms. This observation suggests that variation in *D. tridigitatus* may be more reasonably attributed to individual phenotypic plasticity than to population differentiation. Due to a limited sample size and lack of detailed ontogenetic data, the cause of the observed variation within *D. tridigitatus* remain speculative. However, among the specimens examined, apparently well-correlated ontogenetic variation in the degree of element ossification is observable. Population level differences cannot reasonably be detected in a study of this size. The presence of aberrant osteological structures (teratologies) would tend to bias character selection towards excluding potentially informative characters (overestimation of variation). In this study, bilaterally paired variation was generally presumed to be real; however, this methodological limitation is unlikely to be satisfactorily resolved in the absence of ontogenetic data. Differences in

staining quality among specimens may contribute to either an overestimate or an underestimate of true variation.

An infrequently emphasized concern in the systematic literature has been the importance of within taxon variation in the initial diagnosis of both the characters and character states to be employed in a phylogenetic analysis (but see Kesner, 1994; Pimentel and Riggins, 1987). Such variation could critically affect implied phylogenies; for example, true polymorphic characters may never be detected if small samples of specimens are examined, or certain states that appear discontinuous when sparingly sampled may have a near continuous (or undefinable) underlying distribution. Unfortunately, for many taxa enough specimens are simply not available to destructively examine large numbers of individuals. It is thus important to examine taxa that are abundant for the purposes of inferentially assessing levels of variation in related taxa.

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