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KANSAS HAMILTON QUARRY (UPPER PENNSYLVANIAN)
ACANTHODES, WITH REMARKS ON THE PREVIOUSLY
REPORTED NORTH AMERICAN OCCURRENCES OF THE GENUS¹

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ABSTRACT

A large collection of *Acanthodes* recovered from an abandoned quarry (Hamilton Quarry) near the town of Hamilton, Kansas, contains individuals ranging in total length from 54 mm to 410 mm, making this the best material assembled to date for the study of the young of the genus. The collection includes two species, *A. bridgei* Zidek, n. sp., and a second species differing from *A. bridgei* in having remarkably large orbits, a shorter pre-pectoral region, and shallower insertions of the fin spines. The second species is represented by only a single specimen, which is among the smallest juveniles found at the locality, and as it might prove impossible to identify it with a conspecific individual of different size it is left unnamed pending the possibility of a future discovery of a sufficiently complete growth series.

Acanthodes bridgei is characterized by the size relation of the anal and dorsal spines (equal length), by the rate and pattern of the squamation development, by the extent of the polygonal dermal plates in the head, by the time of beginning of ossification of the endoskeleton in ontogeny, by the shape and spacing of the caudal radials (straight and widely spaced), and by the morphology of the posteroventral portion of the longitudinal division of the hypochordal lobe (lack of expansion). Some of these features may be found similarly developed in other species, but their combination is unique, indicating a new species. A sample representative of the entire size range available reveals a positive differential growth for the tail, and a negative differential growth for the orbits and the mandibular bones. The length ratios of the fin spines, and probably also the distribution of the fin spines relative to each other, show no allometry. The scales increased in size by the addition of areal zones of growth to the crown throughout ontogeny, and there appears to be a definite correlation between the scale size and the overall specimen size. The scale cover spread forward from the tail in an anteriorly pointed triangle divided by the main lateral sensory line into a smaller dorsal and a larger ventral part. The more rapid development of the ventral part resulted in connecting of the ventral triangle with the scales associated with the ventrolateral sensory line. Most of the squamation

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formed before the fish reached approximately 50 percent of their "full" length. After that the squamation progressed very little, except for the anterodorsal area over which the scales spread into the otic region.

All previously described North American specimens of *Acanthodes* either belong to other genera or are indeterminate as to species, and the European species urgently need revision. *A. bronni*, in fact, is a conglomerate of several species, and, consequently, at the present time the genus lacks a type species. *A. rouvillei* is not distinguishable from *A. "bronni,"* *A. major* in all probability is a large individual of *A. wardi*, and *A. punctatus* is indeterminate as to species. The structure of the pectoral girdle in *A. gracilis* and the large extent of the dermal bones of the head and the more posterior position of the pelvic spines in *A. wardi* are points in favor of validity of these species, but the definite decision will have to await a revision of them and of *A. "bronni."*

INTRODUCTION

During the period of 1973-75, I had the opportunity to study an extensive collection of *Acanthodes* recovered by students and faculty of the Division of Earth Sciences of Emporia Kansas State College, Emporia, Kansas, from an abandoned limestone quarry two miles east of the town of Hamilton, Greenwood County, Kansas (Hamilton Quarry, sec. 8, T. 24 S., R. 12 E) (Fig. 1). Collecting was initiated and supervised by Dr. Thomas E. Bridge, Professor of Geology at Emporia Kansas State College. Mr. Walter Lockard found the first acanthodian and brought it to the geology department for identification in 1969. Since then, he and others have added many vertebrate and invertebrates to the Hamilton Quarry collection. In addition to *Acanthodes*, the Hamilton Quarry collection includes a dissorophid amphibian, a lungfish, palaeoniscoid fishes, a hybodontoid shark, a xenacanthoid shark, eurypterids (see Andersen, 1974), scorpions, arachnids, insects, including unusually large cockroaches (see Hanson, 1973), myriapods, ostracodes. It also contains abundant, though mostly fragmentary, flora (*Walchia*, *Cordaites*, *Alethopteris*, *Annularia*, *Asterophyllites*, *Dichophyllum*, *Neuropteris*, *Pecopteris*, *Samaropsis*, *Walchianthus*) bearing a close resemblance to the flora known from near Garnett, Kansas.

The only work done previously on this locality consists of two unpublished Master of Science theses on some of the invertebrates (Hanson, 1973; Andersen, 1974). Neither of these authors could adequately define the stratigraphic position of the

clastic limestone of the quarry, although Andersen dated it as pre-Atokan on the basis of the eurypterids he examined. He recognized eleven beds, grading from marine at the base to terrestrial at the top, with *Acanthodes* recovered only from his C-6 bed, a one-foot-thick, dark gray to blue limestone ranging from micrite to sparite. The absence of marine fossils in this bed, plus exceptionally good preservation of both flora and fauna indicated to him that deposition had been in quiet, nonmarine waters.

Bridge, who since the time of assembling the collection has been studying the geology of the area, is uncertain at present (written commun., 1975) whether the fossiliferous channel deposit is associated with the post-Topeka erosional surface or is a local channel in the Hartford Limestone Member of the Topeka Limestone Formation (Shawnee Group, Virgilian). The channel cuts through the Hartford Limestone and locally even deeper into the underlying Calhoun Shale Formation. Based on the lithology and fossil content of the deposits, Bridge tentatively interprets the depositional environment as that of a stream channel that formed during the post(?)—Topeka erosional interval.

In the condition of their preservation, the Hamilton Quarry specimens of *Acanthodes* are comparable with the specimens described from the Autunian of France by Heyler (1969), although the two occurrences differ in one important respect; whereas the French specimens are mostly mature, or nearly so, in the Hamilton Quarry the

majority of individuals found are immature, some barely exceeding 50 mm in total length. Based on the articulated state of preservation of even the smallest, delicate specimens, it can be concluded that they underwent little, if any, post-mortem transport. Consequently, and in agreement with Andersen's (1974) findings, the Hamilton Quarry *Acanthodes*-bearing bed can be regarded paleo-environmentally as a low energy part of a stream that was either the site of actual hatching, or close to such a site. The restricted collecting area and geologic time interval give a reason to believe

that a majority of the specimens belonged to a single population.

A few immature specimens of *Acanthodes* are known from the Lower Permian in Lebach near Saarbrücken, West Germany (Watson, 1937). However, the smallest individual described from that locality is over 100 mm in total length (MNB P6192, 76 mm from nose to the dorsal spine; see Watson, 1937, p. 111), and, as is the case in the French material, the majority of the specimens from Lebach appear to be mature or nearly mature individuals. The Hamilton Quarry collection thus provides the best material known so far for study of the young of *Acanthodes*.

The genus ranges from the Mississippian into the Lower Permian (Beyrich, 1848; Roemer, 1857; Troschel, 1857; Egerton, 1866; Kner, 1868; Sauvage, 1883; Fritsch, 1893; Reis, 1896, and earlier works; Watson, 1937; Augusta, 1939; Miles, 1966, 1973b; Heyler, 1969; Simpson, 1973, 1974; Zidek, 1973, 1975a, 1975b). The Lower Permian of Europe has produced many more and better preserved specimens of *Acanthodes* than the Permian deposits of North America, where most finds are exceedingly fragmentary and the number of occurrences is probably even lower than previously thought (Simpson, 1973; Zidek, 1973, 1975a, 1975b). Also the Pennsylvanian record of *Acanthodes* up to now has been based chiefly on European occurrences, but in this case it has been so because some significant North American materials have not been described (e.g., the presently discussed Kansas occurrence, and the Field Museum of Natural History collection from Mecca and Logan quarries, Desmoinesian, of Indiana; see Zangerl & Richardson, 1963), rather than because of any significant discrepancy in number and quality of occurrences. The more recent discoveries of *Acanthodes* in the Upper Pennsylvanian and Lower Permian of North America have been discussed elsewhere (Zidek, 1973, 1975a, 1975b), and certain morphological aspects of those finds are noted in this paper. The North American finds recorded in the older literature are *Acanthodes semistriatus* (Woodward, 1892, p. 3) from the Lower Devonian of New Brunswick, *A. affinis* (Whiteaves, 1889, p. 91) and *A. concinnus* (Whiteaves, 1887, p. 107) from the Upper Devonian of Quebec, *Acanthodes* (?) *pristis* (Clarke, 1885, p. 42) from the Upper Devonian of New York State, and *A. marshi* and *A. beecheri*

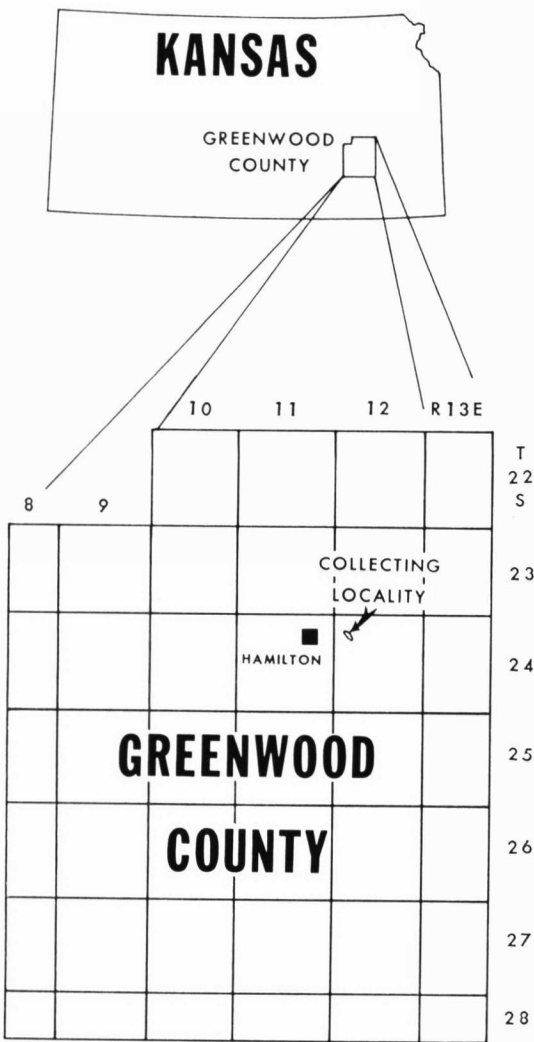


FIG. 1. Study area in Greenwood County, Kansas, showing collecting locality.

(Eastman, 1902; see also Gregory, 1951) from the Pennsylvanian of Mazon Creek, Illinois. The three Canadian species belong in fact to the genera *Mesacanthus*, *Triazeugacanthus*, and *Homalacanthus*, respectively (see Gardiner, 1966, p. 55-57 for further references), and the specimen of Clarke (1885), although indeterminate, cannot have possibly anything to do with the genus *Acanthodes*. The specimens of Eastman (1902) belong to *Acanthodes*, however, and I have used the opportunity of preparing the present paper to re-examine them.

Most of our current knowledge of *Acanthodes* is based on the specimens from Lebach, and, therefore, they are frequently referred to in this paper. However, from Watson's account it is evident that the Lebach material comprises specimens with such wide proportional variations, unaccountable for by growth, that undoubtedly not one (*A. bronni*) but several species are present (Watson, 1937, p. 95-96, fig. 20, pl. 14; see also Dunkle & Mamay, 1956; Zidek, 1975b). Since Agassiz's (1833-44) syntypes of *A. bronni* cannot be identified in that material, and since his description is inadequate for determination as to on which one of the variations recorded by Watson the species had been based, it is impossible to erect a neotype, and, accordingly, *A. bronni* should be regarded as *nomen dubium* or a collective name. To emphasize the matter, I have used the name *bronni* in quotes throughout the text.

Explanation should be given here of the terms "mature or nearly mature" and "juvenile" or "immature" as used above and throughout the text. These terms ought to be used to imply the state of development of the reproductive organs, but this can almost never be determined in fossils. Maturation of the gonads is a physiological process correlative with age, and its rate often is not the same for both sexes (which due to the lack of pelvic or any other secondary sexual dimorphism cannot be recognized in the *Acanthodii*; see Miles, 1967, p. 117; 1970, p. 351). Even if we disregard the possibility of difference in size between the sexes and lower the difference in growth rate by assuming a single population, the fact still remains that growth never occurs at the same rate in all individuals, and, therefore, a larger size does not necessarily indicate a greater ontogenetic age and vice versa (Weatherley, 1972, p. 18; see also the size hierarchy effect in Brown, 1957, p. 372). The extent of the scale cover increases with specimen

size, but as will be shown below it is not possible to decide whether the factor governing the squamation development was size or age (as a matter of fact, such decisions are disputable even for a number of modern fishes). It is known that although most fishes continue to grow after attaining sexual maturity, the subsequent average growth rates are generally lower than those of immature fishes (Brown, 1957). Since in *Acanthodes* appreciable amount of length was attained after the process of squamation development was completed, it can be concluded that the fish became fully scaled fairly early in its ontogeny, but exactly how early, and whether before, simultaneously with, or only after, the reproductive maturity was reached, is impossible to say. The above terms thus should be understood as arbitrary, indicating only the relative specimen size and the "related" extent of the squamation.

Hamilton Quarry is abbreviated HQ throughout the following text. AMNH stands for American Museum of Natural History, EKSC for Emporia Kansas State College, LACM for Los Angeles County Museum of Natural History, MNB for Museum für Naturkunde Berlin, OUSM for Stovall Museum of Science and History of the University of Oklahoma, USNM for the U.S. National Museum, YPM for Peabody Museum of Natural History of Yale University.

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HAMILTON QUARRY ACANTHODES

MATERIAL

The HQ collection of *Acanthodes* contains a large number of specimens ranging from small fragments to nearly complete fish, and there is much duplication in the overall size as well as in the preservation of various skeletal elements. I have, after a preliminary examination of the entire collection, chosen some of the specimens as representative, or reference specimens, the criteria being: 1) preservation with respect to both completeness and detail, and 2) dimensions, with selections made for the widest possible representation of size range.

List of reference specimens:

EKSC 1A1+bl (counterparts), 2a-d (counterparts), 3A1, 4Ab+Bb (counterparts), 5b+6b (counterparts), 8bb, 11A1, 22b, 23B, 28Ab, 30A+B (counterparts), 39C (tail only), 47A+B (counterparts), 52, 56, 61, 108+222 (counterparts), 201 (counterparts), 221+224 (counterparts), 228, 230B, 231, 232, 240, 281b, 315A, 417A, 417B+421 (counterparts), 459, unnumbered lower jaw.

OUSM 00470, 00471, 00472, 00497 (counterparts).

Compared to the size of the entire collection, the number of the specimens selected is admittedly low. Along with the above noted duplication the primary reason for this was the difficulty of finding specimens complete enough, and undistorted enough, for taking measurements. The number of such suitable specimens turned out to be so small that some less completely preserved individuals had to be included in order to obtain an adequate size range series. Among the 34 specimens selected there are some that are of little use,

or even totally useless, for the purposes of biometry; these were included because of fine preservation of certain structural detail.

The abbreviations for morphological features used in the following descriptions and in the illustrations are shown in Table 1.

DESCRIPTION AND DISCUSSION

THE HEAD AND BRANCHIAL SKELETON

These parts are unfortunately not as well preserved as the corresponding parts in the two previously mentioned European occurrences of *Acanthodes*. The neurocranium and the upper jaw are present as small fragments only, most of which cannot be properly identified, and also most of the elements of the branchial arches cannot be made out. However, the labyrinth, the lower jaw, and the exoskeleton, including the gill rakers, are complete enough to warrant a description.

The labyrinth is well preserved in the EKSC 2a-d specimen (Fig. 2,B; Pl. 1,B, C, *lbr*), where it is exposed in lateral view and fully confirms the tentative restoration of Miles (1973b, fig. 6; Fig. 2,A, of this paper). The only other specimen that shows the labyrinth is the EKSC 3A1 (Fig. 2,C; Pl. 5,B, *lbr*); in this specimen, however, it is exposed dorsolaterally, and due to distortion its parts are difficult to identify. The sacculus evidently was the last part of the labyrinth to ossify, and even in a specimen as large as the EKSC 2a-d, which is 268 mm long, it is too indistinct to be described with any degree of confidence. It appears to have been narrower than the utriculus, quite deep, and posteriorly it may have been differentiated into a lagena. An anterodorsal expansion of the sacculus is suggestive of a remnant of the utricular recess. There is no evidence of an endolymphatic duct. Since the 2a-d specimen is

TABLE 1.—Abbreviations Used in Text and Illustrations.

<i>al</i>	axial lobe	<i>mca</i>	anterior ossification of mc
<i>ama</i>	anterior ampulla	<i>mcp</i>	posterior ossification of mc
<i>amp</i>	posterior ampulla	<i>mdl</i>	mandibular sensory line
<i>amx</i>	external ampulla	<i>mdo</i>	mandibular bone
<i>asp</i>	anal spine	<i>mdo. gr</i>	groove in mdo for attachment to mc
<i>aup</i>	autopalatine ossification of pq	<i>mll</i>	main lateral sensory line
<i>a. zyg</i>	"prezygapophysis"	<i>mtp</i>	metapterygoid ossification of pq
<i>bbr</i>	basibranchial	<i>mvl</i>	median ventral sensory line
<i>br. a</i>	fragments of posthyoidean branchial arches, presumably epibranchials	<i>na</i>	neural arch
<i>br. sk</i>	branchial skeleton	<i>ncr</i>	unidentified neurocranial ossification
<i>bsc</i>	scapular blade	<i>n. sh</i>	notochordal sheath
<i>cmo</i>	circumorbital bones	<i>n. sp</i>	neural spine
<i>crh</i>	ceratohyal	<i>oto</i>	otolith
<i>csa</i>	anterior semicircular canal	<i>pjc</i>	profundus sensory line
<i>csp</i>	posterior semicircular canal	<i>pgl</i>	pectoral girdle
<i>csx</i>	external semicircular canal	<i>poc</i>	preopercular sensory line
<i>d. mll</i>	dorsal branches of main lateral sensory line	<i>pq</i>	palatoquadrate
<i>dm. pl</i>	dermal plates of head	<i>pr. art</i>	articular process
<i>dmt</i>	dermotrichia	<i>pr. pregl</i>	preglenoid process
<i>dpl</i>	dorsal basal plate	<i>pr. proco</i>	procoracoid process
<i>dsp</i>	dorsal spine	<i>psp</i>	pectoral spine
<i>end. l</i>	endochondral lining	<i>psp. gr</i>	pectoral spine groove
<i>glr</i>	gill rakers	<i>pv. pl</i>	pelvic basal plate
<i>ha</i>	hemal arch	<i>pv. sp</i>	pelvic spine
<i>hmv</i>	ventral ossification of hyomandibula	<i>qu</i>	quadrate ossification of pq
<i>h. sp</i>	hemal spine	<i>rbr</i>	branchiostegal rays
<i>ifc. ot</i>	otic branch of infraorbital sensory line	<i>rdl</i>	radialia
<i>ifc. pt</i>	postorbital branch of infraorbital sensory line	<i>sac</i>	sacculus
<i>ifc. sb</i>	suborbital branch of infraorbital sensory line	<i>scc</i>	"scapular" sensory line
<i>lag</i>	lagena	<i>sc. oss</i>	semicylindrical laterosensory ossifications
<i>lbr</i>	labyrinth	<i>sml</i>	supramaxillary sensory line
<i>ld</i>	longitudinal division of hypochordal lobe	<i>soc</i>	supraorbital sensory line
<i>mc</i>	meckelian cartilage	<i>stus</i>	superior utricular sinus
		<i>utr</i>	utricle
		<i>vl</i>	ventral division of hypochordal lobe
		<i>vll</i>	ventrolateral sensory line
		Z1 through Z4	scale zones of caudal fin
		I through V	posthyoidean branchial arches

exposed laterally and the duct, if present, would be found at the dorsomesial side of the sacculus, it cannot be said definitely that the endolymphatic duct was absent. Nevertheless, considering that no endolymphatic duct has been so far demonstrated for any acanthodian (Miles, 1973a, p. 128-129, concerning its alleged presence in *Climatius reticulatus*), that there is an otolith, presumably saccular, present in the 3A1 specimen (Fig. 2,C), and that "otoliths seem to develop in those cases where there is a 'closed-circuit' membranous labyrinth, without direct communication with the surrounding sea-water by an open endolymphatic duct" (Ørvig, 1972, p. 147), the chances for an endolymphatic duct being present are extremely low. The utricle is situated above the sacculus

and behind (mesiad of) the external ampulla extends anterodorsad, toward the anterior ampulla. There is a well-developed, superior utricular sinus forming a vertically narrowing cylinder above the utricle. The anterior semicircular canal is substantially shorter than the posterior one. The external canal is the shortest of the three and is also narrower than the two vertical canals.

Except for the absence (although not quite undisputable) of an endolymphatic duct, these conditions are shared by the holocephalians and teleostomians (see Retzius, 1881; Stensiö, 1963; Baird, 1974; and further references cited in those papers). There is, however, no evidence of a prominent utricular recess such as found in holocephalians or dipnoans, but rather a true utricle

incorporated into the base of the canal system (see Baird, 1974, p. 17, 19 for further comments). Should the anterior semicircular canal be longer than the posterior one and the sacculus shallower or antero-posteriorly prolonged, it would be hard to differentiate between the gross morphology of the labyrinth in question and that of a typical teleostomian labyrinth (e.g., Lowenstein, 1957, fig. 7a; Stensiö, 1963, fig. 34G; Baird, 1974, fig. 4A).

From the descriptions and illustrations available (Dean, 1907, fig. 29; Watson, 1937, p. 102; Heyler, 1969, fig. 2, pl. 5, figs. 6, 7, pl. 8, fig. 1; Miles, 1973b, fig. 6, pl. 3A), it is evident that the labyrinth has not previously been recorded in truly small specimens of *Acanthodes*. Watson (1937) described this structure as being the first part of the neurocranium to ossify (perhaps simul-

taneously with the anterior part of the basisphenoid), with the ossification spreading from the vertical semicircular canals to the ampullae, to the external canal, and finally to the utriculus and sacculus. He did not note the size of his DMSW P470 specimen that has only the upper parts of the vertical canals ossified, but since the smallest specimen at his disposal was over 100 mm in total length (MNB P6192), it can be assumed that EKSC 3A1 is substantially smaller than the P470 specimen from Lebach. Yet, in this HQ specimen, which is only 95 mm in total length, the ossification of the labyrinth extended to the utriculus. A situation comparable to that seen in the Lebach *Acanthodes* exists also in the GE18, FB2, and Re1 specimens described from the Autunian of France by Heyler (1969, fig. 2). These specimens can be estimated to have been 130-170 mm

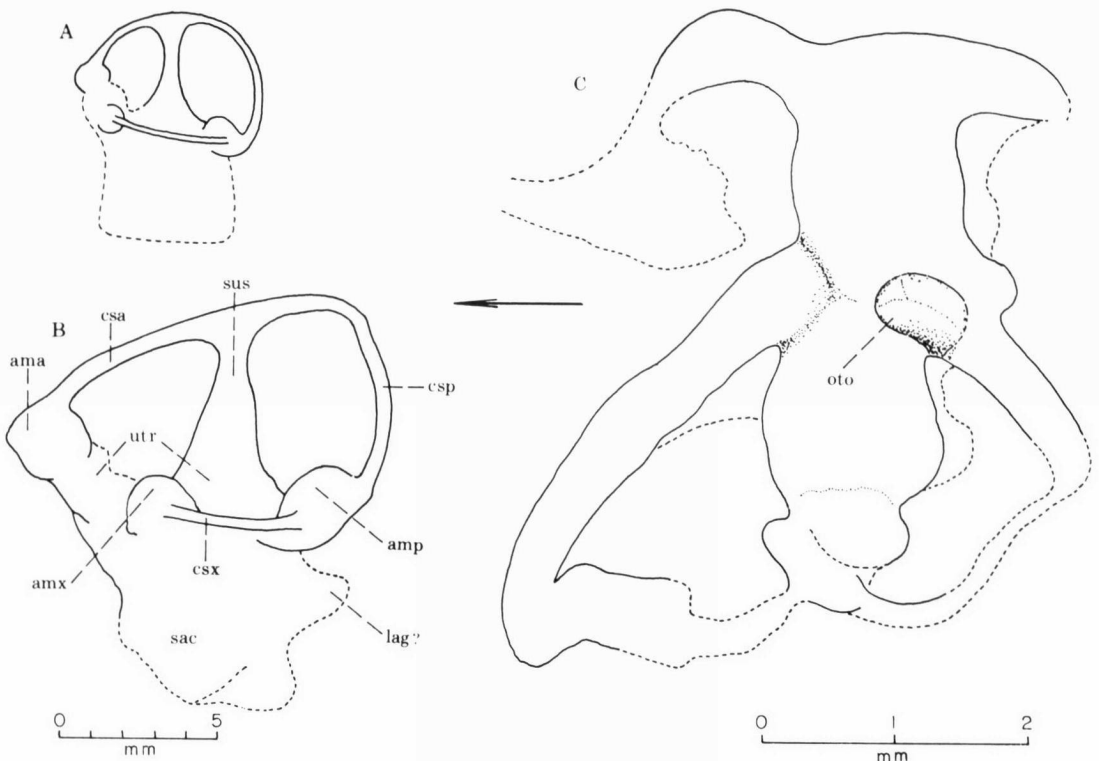


FIG. 2. A. A tentative restoration of the left labyrinth of *Acanthodes "bronni"* in lateral view (from Miles, 1973b, fig. 6).—B. *A. bridgei* Zidek, n. sp., paratype EKSC 2a-d (see Pl. 1,C), the left labyrinth in lateral view.—C. *A. bridgei* Zidek, n. sp., paratype EKSC 3A1 (a juvenile 95 mm in total length; see Pl. 5,B), a distorted labyrinth in dorsolateral view. The parts shown in broken lines are present, but are too indistinct to be accurately outlined. The arrow points toward the nose for all the specimens. [Explanation: *ama*, anterior ampulla; *amp*, posterior ampulla; *amx*, external ampulla; *csa*, anterior semicircular canal; *csp*, posterior semicircular canal; *csx*, external semicircular canal; *lag*, lagena; *oto*, otolith; *sac*, sacculus; *sus*, superior utricular sinus; *utr*, utriculus.]

in total length, yet the external canals of their labyrinths are apparently not ossified. Thus, in the degree of ossification of the labyrinth as related to specimen size, there is a definite difference between the two Lower Permian occurrences in Europe on one side and the Upper Pennsylvanian Kansas occurrence on the other. This difference is more likely due to the time of beginning of the ossification in ontogeny than to the rate of ossification, as is evidenced by the following comparison: According to Watson (1937, p. 102) in the DMSW P470 specimen from Lebach the only neurocranial ossifications present are the upper parts of the vertical semicircular canals and the anterior part of the basisphenoid. In the HQ material, however, even specimens less than half the size of the P470 specimen (EKSC 240 and 28Ab, 56.5 and 67 mm in total length, respectively) exhibit traces of ossification of the neurocranium. Although these ossifications cannot be properly identified, enough is clear to determine that they belong neither to the labyrinth nor to the basisphenoid (see Pl. 5, *A, ncr*).

A specimen figured by Heyler (1969, fig. 2, C, pl. 5, fig. 6) suggests some misinterpretation of the structure (*sac., amp. ext.*), but more importantly, the anterior canals appear to be longer than is the case in the HQ *Acanthodes*. In the light of recent studies on labyrinths of modern teleosts (Baird, 1974, p. 12) this detail may be worth mentioning.

The palatoquadrate is imperfectly preserved in dorsolateral view in the EKSC 1A1+bl specimen (Pl. 2, *pg*; pl. 3A, *aup, mtp, qu*). Only the quadrate ossification is reasonably well preserved,

but its articulation with the meckelian cartilage is broken off.

The lower jaw is partially preserved in several specimens, but its joint can be seen in only one instance (Fig. 3; detached jaw, unnumbered). In this example the jaw is 40 mm long and its morphology is identical with that shown for *Acanthodes "bronni"* by Miles (1973b, fig. 12), except for being about one-third shorter and having its anterior (mentomandibular) and posterior (articular) ossifications not as widely separated. In the Lower Carboniferous *Acanthodes sulcatus* there appears to have been no gap between the two ossifications (Miles, 1966, fig. 5), and the HQ specimen could thus be regarded as intermediate in the trend toward a lesser ossification as found in the Lower Permian *Acanthodes*. However, it is known that in large individuals of *A. "bronni"* the anterior and posterior regions of the lower jaw may be perichondrally co-ossified (Miles, 1968, p. 111, fig. 1C), and the same may have been true of the large HQ specimens (e.g., EKSC 1A1+bl). More material will be needed to determine whether the extent of the ossifications is constant for specimens of similar size.

The mandibular bones (dentohyoids of Reis, 1891, figs. 1, 3, 6; extramandibular spines of Reis, 1895, pl. 1-6, 1896, pl. 6, fig. 1, 5; splenials of Jaekel, 1899, fig. 1; mandibular splints of Watson, 1937; "splenials" of Stensiö, 1947, p. 48, fig. 11D) can be seen in their entirety in the EKSC 3A1, 4Ab+Bb, 8bb, 240, and OUSM 00470 specimens, and are present, but less completely preserved, also in the EKSC 2a-d, 47A+B, and 108+222 specimens. These bones are gently

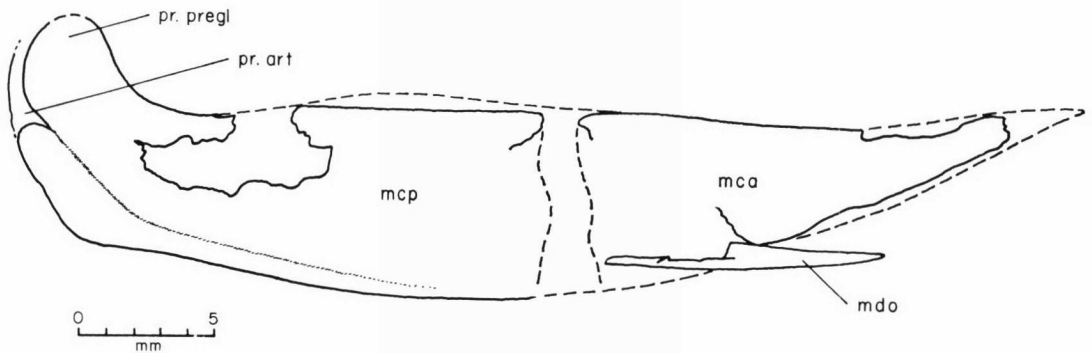


FIG. 3. *Acanthodes* sp. indet. (EKSC unnumbered), a detached lower jaw in mesial view. [Explanation: *mca*, anterior ossification; *mcp*, posterior ossification; *mdo*, mandibular bone; *pr. art*, articular process; *pr. pregl*, preglenoid process.]

curved sinusoidally, their posterior ends are somewhat expanded, and in most of the specimens cited there is a clearly discernible groove for attachment to the ventrolateral margin of the meckelian cartilage (Fig. 4,C, *mdo. gr.*). The mandibular bones extend almost the entire length of the lower jaw, but in proportion to the jaw they are not as long in the HQ *Acanthodes* as in *A. sulcatus* (Miles, 1966, fig. 5). Ornamentation is entirely lacking in these bones. In *A. sulcatus*, however, a well-developed ornamentation is present in the posterior halves of the mandibular bones, which confirms their dermal origin (Miles, 1966, fig. 5, and p. 154). The mandibular bones together with the circumorbital bones, the gill-cover (branchiostegal rays), gill rakers, the skeleton of the neuromast system, and the caudal squamation, are present in even the smallest specimens (EKSC 8bb, 240; see Pl. 4,B and 5,B, respectively), in which no ossification of the jaws, and only a very limited ossification of the neurocranium (see above) can be detected.

The circumorbital ring (*cmo* in Pl. 1-5) consists of five equally broad, thin, transversely convex bones, of which the dorsal is the longest and the antero- and posteroventral the shortest. The entire surface of all the bones in the ring is ornamented with fine striae interrupted by pits. The pattern of the ornamentation is decidedly radial, with an imaginary common point in the center of the orbit.

The allometry of both the circumorbital and the mandibular bones is dealt with in the section "Fin Spines, Body Proportions, Growth."

Except for the elements already discussed, the exoskeleton of the head consists of only a localized mosaic of minute polygonal plates and elements surrounding the lateral-line sensory canals. A mass of delicate plates is found above the orbit in the EKSC 1Al+bl specimen (Fig. 5, Pl. 3A, *dm. pl.*). They are only 0.25-0.50 mm in diameter, lack ornamentation, and their margins are exceedingly thin and translucent in some instances. Watson (1937, p. 107-108) found mosaics of such dermal plates in what he termed "a rarer type" of *Acanthodes* from Lebach, in which "the squamation extends forward on to the head, passing into a continuous shield of very thin polygonal bones just as it does in the earlier acanthodians, *Climatius*, *Mesacanthus* and *Diplacanthus*. This region lies entirely dorsal to the main lateral line and orbit and does not continue over the snout.

. . . Reis, 1896, fig. 2 is a good example of this type." Reis (1896) shows the plates extending well behind the orbit. As far as can be judged from the much distorted and crushed head of the 1Al+bl specimen (Pl. 3,A), the plates do not extend behind the orbit, and from their position relative to the profundus sensory line (*pf*) it seems clear that they were situated above as well as below that line. The posterior extent of the plates appears to be similar to that in the specimens of *Acanthodes* from the Upper Pennsylvanian of New Mexico, in which, however, the squamation reaches into the otic region and passes into a shield of polygonal plates above the posterior margin of the circumorbital ring (Zidek, 1975b, fig. 2E, pl. 1A, *dpl*). In contrast, in the much larger EKSC 1Al+bl specimen the dorsal squamation reaches only the level of the pelvic spine (see Fig. 13), and consequently there is an extensive gap between the most anterior dorsal scales and the plates of the head.

The sensory lines of the head can be seen in the EKSC 1Al+bl, 2a-d, 3Al, 4Ab+Bb, 8bb, 221+224, 240, and OUSM 00470 specimens. Although in all these specimens the neuromast system is fragmentarily preserved, it nevertheless allows a comparison with, and a few comments on, the previous observations of Troschel (1857), Woodward (1891), Reis (1896), Dean (1907), Watson (1937), Stensiö (1947), Miles (1966), Heyler (1969), and Ørvig (1972). In those specimens that are not exposed laterally (all except 2a-d and 240) the sensory lines, namely the post-orbital branch of the infraorbital line, the profundus line, the supraorbital line, and the supramaxillary line, are a useful (and often the only) means of determining the orientation of the head and consequently also of the poorly preserved branchial skeleton.

The main lateral line (see also the section "Squamation and Its Development") can be traced without difficulty in all the specimens cited, but it is seen best in the laterally exposed 2a-d specimen (Pl. 1, *ml*), in which the line of both sides and its dorsal branches are preserved in a fashion similar to the Lebach specimens figured by Troschel (1857, pl. 1) and Dean (1907, figs. 28, 29). On the flank the laterosensory component (Ørvig, 1972) of the main lateral line cannot be recognized, but above the pectoral girdle and anteriorly of it the line is enveloped in a chain of semi-cylindrical ossicles ("*pièces hémicylindriques*" of

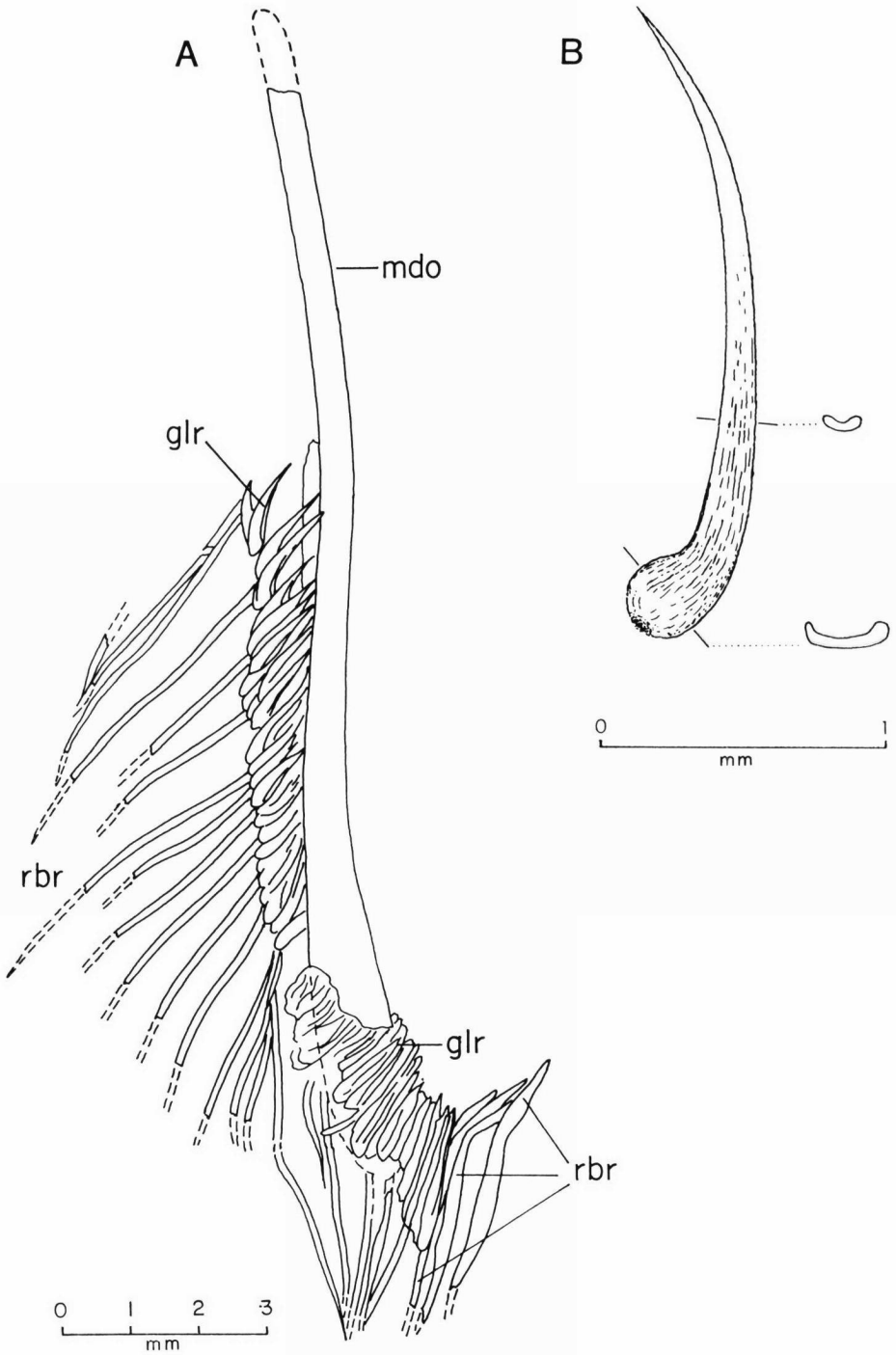


FIG. 4. (See explanation on page 12.)

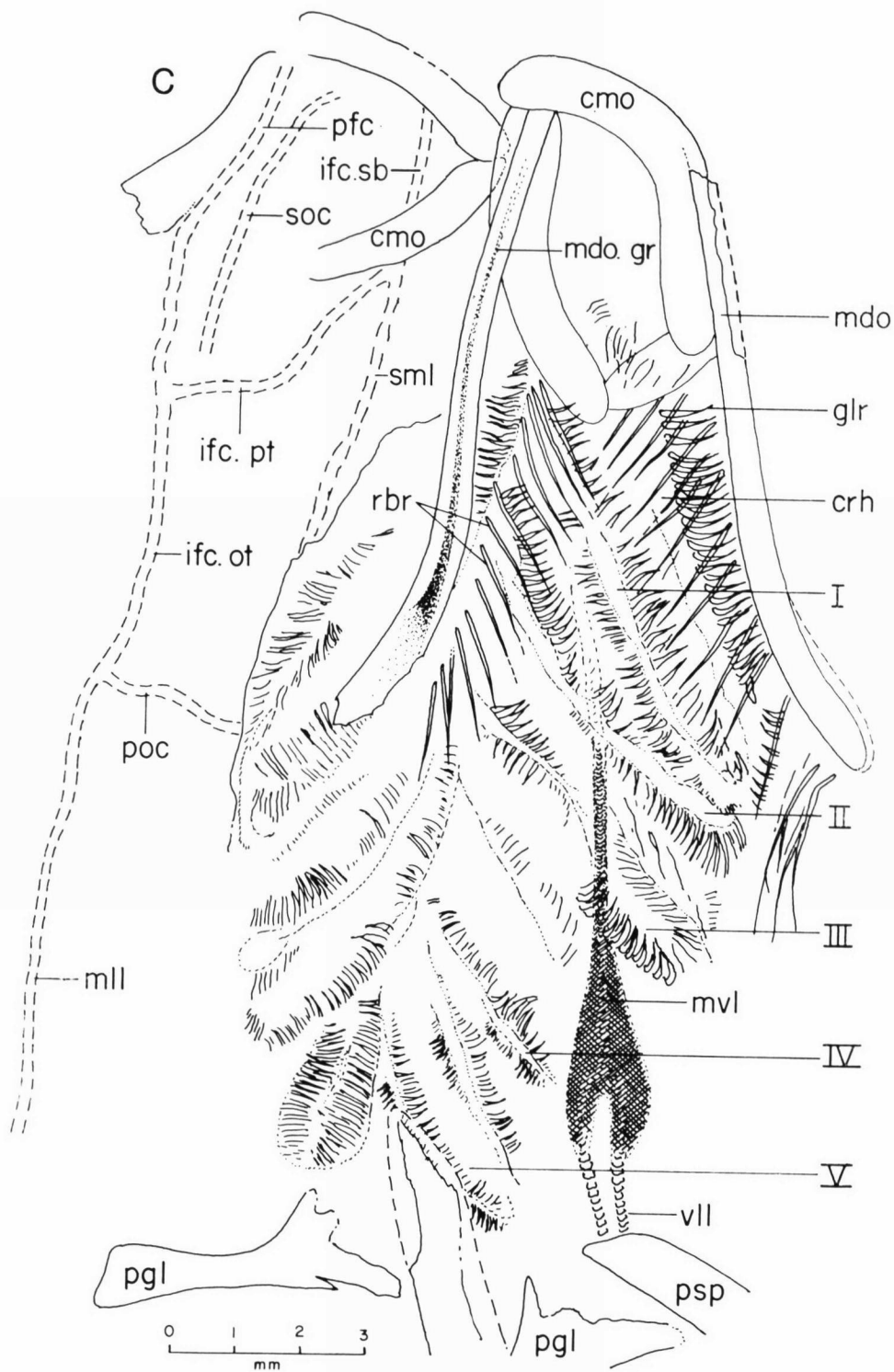


FIG. 4 (continued). (See explanation on page 12.)

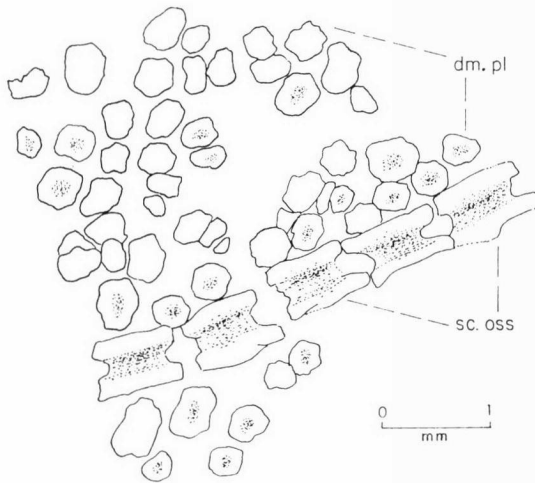


FIG. 5. Dermal plates (*dm. pl*) and semicylindrical ossicles of the profundus sensory line (*sc. oss*) in *A. bridgei* Zidek, n. sp. (EKSC 1A1+bl, holotype). See also Plate 3, A.

Heyler, 1969) that are characteristic of the majority of sensory lines of the head (see Fig. 5, *sc. oss*). Five dorsal branches (*d. mll*) issue from the main lateral line posterior to the pectoral region, one directly above the pectoral girdle, and three anterior to the girdle. The connection of the preopercular line (*poc*) with the main lateral line is not preserved, and it is thus not quite clear whether the most anterior dorsal branch issues from the main lateral line or from the otic branch of the infraorbital line (*ifc. ot*). Should this branch prove to belong to the main lateral line, then it would be in a position corresponding to the transverse occipital (supratemporal) canal supplied by the ramus supratemporalis of the vagus nerve (Goodrich, 1930, fig. 717, 720; also Lowenstein, 1957, fig. 2); if it were shown to issue from the otic branch of the infraorbital line, however, then the anterior dorsal branch would be supplied either by the posterior branches of the superior

ophthalmic stem of the facial nerve or by the dorsal branch of the glossopharyngeal and would thus have to be identified as either the middle or the posterior line of pit organs on the head (Stensiö, 1947, fig. 20D, *mp*). Unfortunately, the branch in question is not preserved extensively and clearly enough to show whether it was a continuous canal (a commissure) crossing the back and connecting the lateral line of both sides; also, it is not clear whether it actually issued from the lateral line or whether it instead crossed the lateral line and was present also ventrad of it. The preservation of the 2a-d specimen thus does not warrant a definite decision on the matter, although a comparison of this specimen with an illustration of *A. "bronni"* by Reis (1896, fig. 2 on p. 195) makes the identification of the branch in question as the transverse occipital the more plausible choice.

In discussing the branches of the main lateral line, Watson (1937, p. 108) stated that they "pass dorsally toward the mid-dorsal line," although he did not support that statement by reference to any particular specimen. Apparently, Watson had in mind not the dorsal line of pit organs on the trunk, but a truly sagittal line of considerable length. There is no such line in all the variously oriented HQ specimens, however, and to my knowledge no such line has ever been described and/or illustrated from any other material. Considering the limited extent and inconsistency of the mid-dorsal line in fishes in general (Lowenstein, 1957, p. 157), the presence of Watson's mid-dorsal line must be regarded as conjectural and most unlikely.

Reis (1896, p. 195-196, fig. 2) was the first to give a good account of the profundus and the supraorbital sensory lines in *Acanthodes*. In the HQ specimens these two lines, and also the suborbital branch of the infraorbital line, are only fragmentarily preserved (EKSC 1A1+bl, 4Ab+

FIG. 4. *A. Acanthodes* sp. (U.S. Natl. Museum 187147) from the Upper Pennsylvanian of the Manzanita Mountains, New Mexico; detail of a mandibular bone and branchiostegal rays.—B. A ceratohyal gill raker from the EKSC 2a-d specimen (*A. bridgei* Zidek, n. sp., paratype).—C. *A. bridgei* Zidek, n. sp., paratype EKSC 4Ab+Bb (see Pl. 5, C), detail of the sensory lines of the head, branchiostegal rays, and branchial skeleton. [Explanation on facing page.] [Explanation: *cmo*, circumorbital bones; *crh*, ceratohyal; *glr*, gill rakers; *ifc. sb*, suborbital branch of infraorbital sensory line; *ifc. ot*, otic branch of infraorbital sensory line; *ifc. pt*, postorbital branch of infraorbital sensory line; *mdo*, mandibular bone; *mdo. gr*, mandibular bone groove; *mll*, main lateral sensory line; *mvl*, median ventral sensory line; *pfc*, profundus sensory line; *pgl*, pectoral girdle; *poc*, preopercular sensory line; *psp*, pectoral spine; *rbr*, branchiostegal rays; *sml*, supramaxillary sensory line; *soc*, supraorbital sensory line; *vll*, ventrolateral sensory line; I through V, post-hyoidean branchial arches.]

Bb, 8bb, 221+224, OUSM 00470; Fig. 4,C; see Fig. 15; Pl. 3,A). The profundus line (*pf*) extends over the orbit and presumably ends in the area in front of the dorsal half of the circumorbital ring. Anteromesiad of the profundus line is the supraorbital line (*soc*) that ends posteriorly above the junction of the postorbital and otic branches of the infraorbital line with the profundus line. The frontal part of this line is poorly preserved, but in the EKSC 8bb, 221+224, and OUSM 00470 specimens there is a clearly apparent double rostral commissure (Pl. 4,B, *r. comm*; "transverse sensory line commissure in snout" of Miles, 1966, figs. 4, 14; "*commissure ethmoïdienne*" of Heyler, 1969, fig. 2C, pl. 4, fig. 1, pl. 5, fig. 6, 7, pl. 8, fig. 1, 3-6) the upper member of which connects the frontal ends of the supraorbital line of both sides, whereas the lower member apparently belongs to the infraorbital line and connects its suborbital branches (*ifc. sb*) of both sides (see Fig. 15). This lower rostral commissure probably is the one compared by Reis (1896, p. 196) with the rostro-median canal in *Chimaera*, and termed "*commissure ethmoïdienne*" by Heyler (1969).

The postorbital branch of the infraorbital line (*ifc. pt*) is essentially vertical, with the upper end bending posteriorly before joining the frontal continuation of the main lateral line, and with the lower end bending anteriorly at a point transitional with the suborbital branch of the same line. Jaekel (1925, fig. 6), Watson (1937, fig. 20), and Miles (1966, fig. 14) illustrated the junction of the postorbital and suborbital branches of the infraorbital line with the supramaxillary line in *A. "bronni"* as T- or Y-shaped. In the HQ specimens (EKSC 4Ab+Bb, 8bb, 221+224, OUSM 00470), however, it appears rather that the supramaxillary line more or less maintains its horizontal course anteriorly and connects with the posterior end of the suborbital branch of the infraorbital line behind the ventral half of the circumorbital ring (Fig. 4,C, *ifc. pt*, *ifc. sb*, *sml*).

A sensory line of an obliquely vertical course descends from the main lateral line over the hindmost part of the gill-cover. As has been noted by Stensiö (1947, p. 48), "because of its position far caudally and its connection with the main lateral line the line in question (*scc*) must be assumed to have been supplied by lateralis branches of the n. vagus," and consequently it cannot be an opercular line as Watson (1937, fig. 20, p. 110) main-

tained. The EKSC 2a-d specimen shows this line of both sides (Pl. 1,B, *scc*) joining with either the foremost part of the ventrolateral line (*vll*), or possibly but less likely with the hindmost part of the median ventral line (*mvl*). This point of juncture corresponds to a point in front of the pectoral girdle at which the *mvl* branches into the paired *vll* (Fig. 4,C, and further comments in the section "Squamation and Its Development"). Due to the lateral exposure of the 2a-d specimen the *mvl-vll* transition cannot be seen, although the closeness of the mandibular line (*mdl*) to the ventral line is indicative of the *vll* rather than of the *mvl*. It appears from this that Stensiö (1947) was essentially correct in assuming that the line in question represents the anterior descending part of the ventrolateral line comparable to the "scapular" line of the Rajiformes, and I have followed Stensiö in labeling it as such.

The skeletal support of the integumental gill cover consists of a series of slender, well-spaced dermal bones, the branchiostegal rays (Jarvik, 1963, p. 7, 27, fig. 12C; Miles, 1965, p. 242, 1966, fig. 4, 1973b, p. 99, pl. 6; McAllister, 1968, p. 3, footnote). In the HQ material only the lower part of the series, below the basibranchial and the ceratohyal, is preserved in the EKSC 4Ab+Bb (Fig. 4,C, *rbr*), 108+222, 221+224, and OUSM 00470 specimens. In this lower part there are 14 to 16 straight or only slightly sinusoidally curved virgaform rays (see McAllister, 1968, fig. 1 for terminology of branchiostegal form), but below the posterior end of the mandibular bone, where the series starts turning upward to continue behind the lower jaw and the quadrate, the rays are broader, virgaform to acinaciform, and angularly bent. The change of shape from virgaform to acinaciform is even more pronounced in the USNM 187147 specimen from the Upper Pennsylvanian of the Manzanita Mountains, New Mexico (Fig. 4,A), in which the branchiostegals are proportionally larger in relation to the mandibular bones (see Fig. 4,A, vs. 4,C) than in the HQ specimens; the illustrations of Reis (1891, fig. 6; 1895, pl. 1, fig. 3, 4; 1896, pl. 6, fig. 1), Watson (1937, fig. 18B, 19, 20A, C), and Miles (1966, fig. 4; 1973b, pl. 6) do not show this change of shape in the Lower Permian *Acanthodes* from Lebach. Because of the usually fragmentary preservation of the material, however, this detail is evident probably too infrequently to be used taxonomically.

In a specimen figured by Miles (1966, fig. 4) the pectoral girdle does not appear to have been displaced anteriorly to any significant degree, and antithetic to Miles' statement (1973b, p. 99), it seems to me that the dorsal branchiostegals do reach across a substantial portion of the gill chamber. If the position of the "scapular" line (see above and Pl. 1, *B*, *sc*) is taken as corresponding approximately to the posterior margin of the operculum, the dorsal branchiostegals appear to have extended posteriorly quite close to that margin.

The branchial arches are ossified only in the largest HQ specimen, EKSC 1A1+bl, but due to distortion of the entire pre-pectoral region only the ventral ossification of hyomandibula and some of the postthyoidean arch elements, presumably epibranchials, can be recognized in this specimen (Pl. 3, *A*, *hmv*, *br. a*). An incomplete hyomandibular and a ceratohyal show that the hyoidean arch was ossified also in two intermediate size specimens, EKSC 2a-d (Pl. 1, *C*, *hmv*) and EKSC 108+222 (Pl. 4, *A*, *crh*); in these, however, the postthyoidean arches were apparently still cartilaginous and their elements are therefore not distinguishable. In specimens smaller than the two just noted, EKSC 4Ab+Bb, 28Ab, 221+224, 228, OUSM 00470 and 00471 (see Fig. 13 for total size estimates), all the arches including the hyoidean are unossified and can be recognized only from their dermal component, the gill rakers, that are present in even the smallest juveniles (EKSC 228, 54 mm in total length). It is clear, therefore, that the ossification of the branchial arches was differential in that it progressed from the prootic arches backward (see also Watson, 1937, p. 107, remarks on the third and fourth branchial arches).

Reis (1891, fig. 5; 1896, pl. 6, fig. 3) indicated the presence of five postthyoidean arches and his observation was confirmed by Dean (1907, fig. 12), Watson (1937, p. 107), and Nelson (1968, p. 131 and fig. 3A; 1969, fig. 16A; see also Miles, 1971, p. 69, and 1973b, figs. 17, 18). In the HQ material the fifth postthyoidean arch is preserved in the EKSC 2a-d (Pl. 1, *C*), 4Ab+Bb (Fig. 4, *C*), and OUSM 00470 specimens, and in all of them it has well-developed gill rakers. The latter two specimens are less than 100 mm in total length, and the opinion held by Watson (1937, p. 107) that the gill rakers of the fifth arch developed only

in extreme old age has to be attributed to incomplete preservation of his specimens.

The morphology of the gill rakers was described by Reis (1896 and earlier works), Watson (1937), and Miles (1968; see also 1973b, pl. 6) for *A. "bronni,"* and, as far as I can determine, at least for the postthyoidean gill rakers, there is no noticeable difference in their appearance in the HQ and the Lebach material. The ceratohyal gill rakers are longer than the hyomandibular and the postthyoidean ones and differ also in having less expanded (although still clearly bulbous) bases (Fig. 4, *B*). The hyoidean arch definitely bears only anterior gill rakers in all the specimens examined. As regards the postthyoidean arches, EKSC 4Ab+Bb (91 mm in total length) shows both anterior and posterior gill rakers on all the arches (Fig. 4, *C*), EKSC 108+222 (200 mm long) on the second through fifth arch, and EKSC 2a-d (268 mm long) on the fourth and fifth arch only. The preservation prevents a definite statement, but it seems likely that in the latter two specimens the posterior rows of gill rakers are restricted to the epibranchials, indicating that there was a tendency in ontogeny toward the loss of posterior rows of gill rakers. Miles (1968, p. 114) found a similar situation in *Acanthodes* from Lebach, in which "two rows of gill rakers are present on the first four postthyoidean branchial arches (as shown by Reis) in *juvenile individuals only*," and it can be said, without requiring much extrapolation, that this tendency existed, with minor modifications, in the entire genus.

VERTEBRAL COLUMN

The vertebral column can be seen only in the largest HQ specimen, EKSC 1A1+bl (Fig. 6; Pl. 2; 3, *B*; 6, *A*), in which it comprises 17 vertebrae reaching from the pectoral region approximately halfway back to the tail, and the caudal skeleton. The total number of trunk vertebrae can be estimated at between 35 and 40, slightly less than in the *A. sulcatus* specimen illustrated by Miles (1970, fig. 1) in which there are about 35 vertebrae between the pectoral region and the dorsal fin.

The vertebrae consist of separate neural and hemal elements; they lack centra, and the notochord thus is persistent and uncontracted. There are no separate intercalaries. In the specimen of

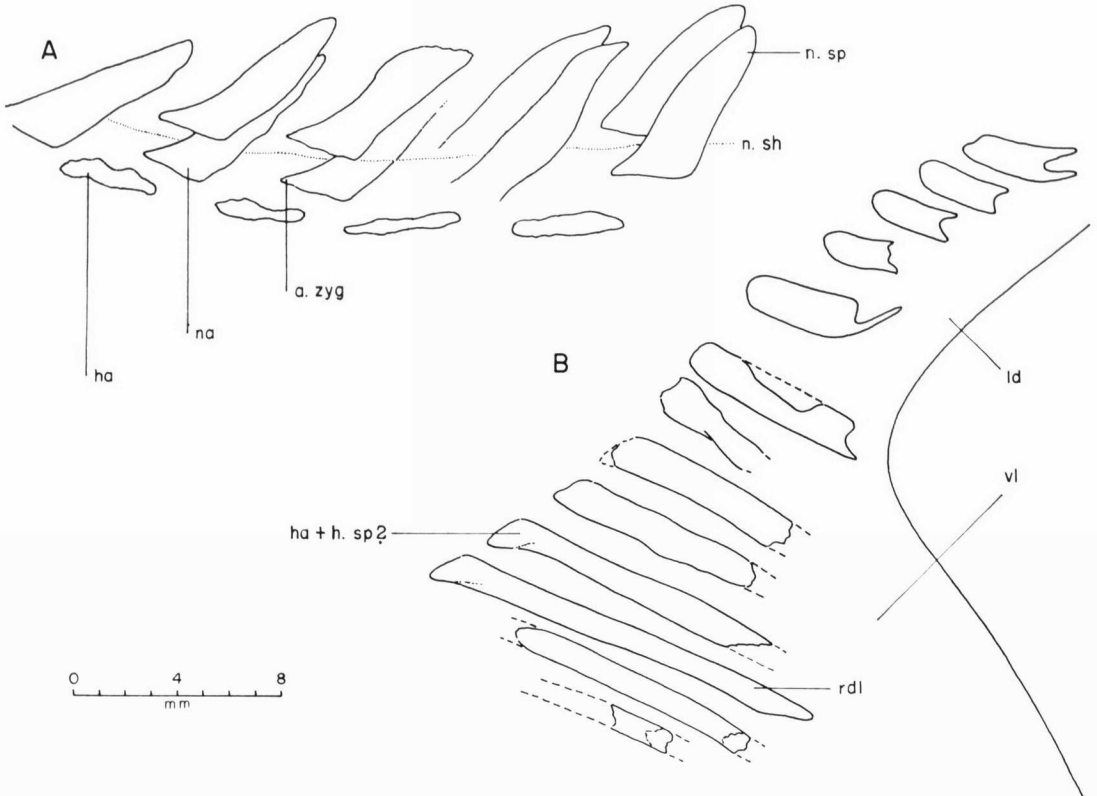


FIG. 6. The first post-pectoral vertebrae (A), and the hypochordal skeleton in the tail (B) of *A. bridgei* Zidek, n. sp. (EKSC 1A1-bl, holotype). Composite, drawn from both the counterparts. Scale pertains to both figures. See also Plates 2, 3,B and 6,A. [Explanation: *a. zyg*, "prezygapophysis"; *ha*, hemal arch; *h. sp*, hemal spine; *ld*, longitudinal division of hypochordal lobe; *na*, neural arch; *n. sh*, notochordal sheath; *n. sp*, neural spine; *rdl*, radialia; *vl*, ventral division of hypochordal lobe.]

Miles mentioned above both members of a pair are seen only in the hemal series; in contradistinction to that, in the HQ specimen it is the neural arches in which both members of a pair can be seen. Both the neural and hemal arches conform to the description given by Miles (1970) in most respects. As in *A. sulcatus*, the neural arches extend anterobasally into pointed beaks (anterior "zygapophyses" of Miles) that, however, do not come in touch with the preceding arch. The neural spines are not as prolonged and pointed as in the Miles specimen. It is unlikely that there was any more extensive cartilaginous base developed in the neural arches. This is evidenced by a dark line, apparently the notochordal sheath, that runs between the preserved, bony bases of the arches and outlines the extent of the notochord in relation to them (Fig. 6,A, *n. sh*). The hemal arches are quite flat, platelike, and although they appear to gain in thickness pos-

teriorly, there is no evidence of hemal spines in the abdominal region. In *A. sulcatus* the hemal spines first appear only a short distance in front of the anal fin, as is evidently true also in the HQ *Acanthodes*.

The caudal skeleton is partially obscured by the squamation and, in the longitudinal division of the hypochordal lobe, is preserved only as much flattened, vaguely outlined impressions. No neural elements can be seen, and due to the obscuration by scales, no divisions of the hypochordal parts of the segments can be distinguished. Although only eight segments are preserved in the ventral division of the hypochordal lobe, altogether there may have been as many as 12. In the longitudinal division of the hypochordal lobe there are five segments preserved, but the total number may have been around 10. From EKSC 1A1 (Pl. 6,A) it appears as that short hemal spines were separate from the radialia, although

when the counterpart *lbl* is superimposed (Fig. 6, *B*) no such divisions are recognizable. In the light of Davis' (1894) statement that in *Acanthodes wardi* the proximal ends of the radials are expanded, it may be that the parts here tentatively identified as the hemal arches and spines (Fig. 6, *B*, *ha+h.sp?*) actually belong to the radials.

In contrast with *A. "bronni"* (Reis, 1891, fig. 8a-c, 1896, pl. 6, fig. 14; Dean, 1907, fig. 25; Miles, 1970, fig. 2) and *A. gracilis* (Kner, 1868, pl. 2, fig. 1; pl. 5, fig. 2), the radials in EKSC 1A1+bl are straight instead of arched, and the segments do not lie as close together. In these two respects, the specimen in question thus appears to be closer to *A. wardi* (see Davis, 1894, pl. 27, fig. 2) than to the other two European species.

GIRDLES AND PAIRED FINS

The pectoral girdle is preserved in a majority of the specimens studied. In no instance, however, are the suprascapular or the procoracoid ossifications preserved, nor is the pectoral spine ever quite in place, and the scapulocoracoid shows some of its structure in only one specimen. In the juvenile specimens, especially, both the terminations of the scapulocoracoid are often either crushed or altogether missing. It is evident, nevertheless, from the few specimens in which they are preserved that there was no appreciable proportional or morphological difference between the scapulocoracoids of mature and immature individuals (Fig. 7). As a rule, the surface of the scapulocoracoid is fairly smooth in *Acanthodes*, and this is the case in all the HQ material. The HQ girdles differ in this respect from those found in the Lower Permian of Oklahoma (Zidek, 1975a), in which the scapulocoracoid is covered with short longitudinal rugae and pits.

The scapular blade is circular in cross section and gradually narrows ventrally before expanding again into the scapulocoracoid plate. The dorsal termination of the scapular blade is somewhat higher posteriorly and lacks perichondral cover (Fig. 7, *B*, *end. l*), suggesting that it was connected to the suprascapular by cartilage. Miles

(1973a, p. 156, fig. 21A) remarked that the swollen top of the scapulocoracoid in one of Davis' (1894) specimens of *A. wardi* is indicative of co-ossification of the suprascapula with the scapular blade. In this connection it should be noted that also in both the HQ *Acanthodes* and in the Oklahoma specimens, the dorsal end of the scapular blade is swollen so that it is thicker than the middle portion of the blade. The termination proper, however, is either flat or slightly concave, with endochondral lining only, leaving no doubt that the suprascapula ossified separately. It is the character of the termination itself, therefore, rather than the dorsal widening that is indicative of either co-ossification or separate ossification of the scapulocoracoid and the suprascapula. As an example, although in the pectoral girdles of *A. gracilis* figured by Fritsch (1893, fig. 261, 263, 270, pl. 107, fig. 11) the upper part gradually narrows proximally and terminates in a blunt point, it is apparent from the proportions and from the character of the termination that the more dorsal part actually is the suprascapula co-ossified with the scapular blade.

The scapulocoracoid plate is discernible only in outline except in the EKSC 1A1+bl specimen (Fig. 7, *C*; pl. 2; 3, *A*; *pgl*), where it is exposed anterolaterally and exhibits the procoracoid process and the pectoral spine groove. In this specimen there is evidence also of what appears to be an additional, smaller process situated immediately posterolaterad of the procoracoid process. A similar structure can be recognized in the Oklahoma girdles, in which, however, only its upper margin is preserved. In these girdles, I have interpreted this feature as a somewhat laterally extended surface of the scapulocoracoid capping the pectoral spine (i.e., as a part of the pectoral spine groove) (Zidek, 1975a, fig. 5, *psp. gr*). From the evidence afforded by the 1A1+bl specimen it now appears, however, that the structure in question is a real process that can be explained functionally only as participating in the dorsal articulation of the procoracoid. If so, this articulation must have been either extended transversely or a double one,

FIG. 7. *A*. EKSC 240, a juvenile of an unnamed species, scapulocoracoids and incomplete pectoral spines of both sides (see Pl. 5, *A*).—*B*. *Acanthodes* sp. cf. *A. bridgei* (OUSM 00497), right scapulocoracoid and associated fin elements. The radials are preserved only as vague impressions and their number and shape cannot be established with certainty.—*C*. *A. bridgei* Zidek, n. sp., holotype EKSC 1bl, the left scapulocoracoid in lateral and somewhat anterior view (Pl. 2). The scapular blade has been restored from counterpart 1A1. [Explanation: *bsc*, scapular blade; *dmt*, dermatrichia; *end. l*, endochondral lining; *pr. proco*, procoracoid process; *psp*, pectoral spine; *psp. gr*, pectoral spine groove; *rdl*, radialia.]

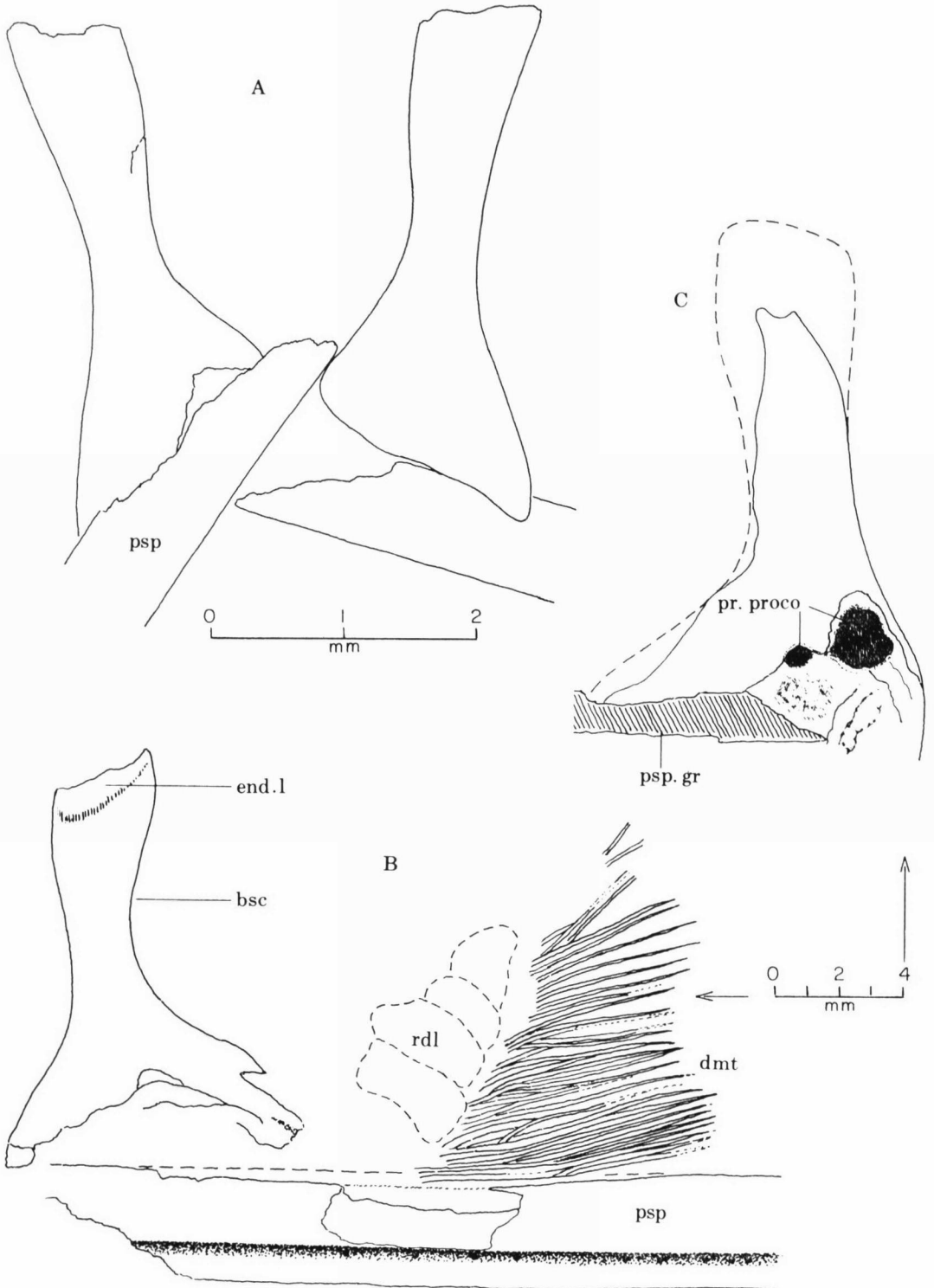


FIG. 7. (Explanation on facing page.)

and the posterodorsal surface of the procoracoid can thus be expected to differ from those previously described.

The “infraclavicula” figured in *A. gracilis* by Fritsch (1893) and referred to by Miles (1973a, p. 156) as “a possible procoracoid” is, in the case of Fritsch’s figures 261 and 263, clearly an error resulting from misorientation of the girdle. Figure 270 (*A. gracilis*) of Fritsch, also referred to by Miles (1973a), is a restoration of a disarticulated specimen (Fritsch, 1893, pl. 107, fig. 10, 11), the “infraclavicula” of which appears more like a pelvic basal plate present in the EKSC 1A1+bl specimen (Fig. 8B, pl. 2, *pv. pl*). In all the

matrix. However, enough can be recognized to show that it has a perichondral cover, that it is spoon-shaped, with probably a crestlike thickening along its long (anteroposterior) axis, and that the crest extends anteriorly into a process. Due to the “on edge” exposure any closer comparison with the above “infraclavicula” of Fritsch (Fig. 8A) could be made only if having his “*Fauna der Gaskohle*” specimen at hand. Nevertheless, the two may easily be visualized as being of similar morphology.

The pectoral fin skeleton is known to consist of three perichondrally ossified radials that articulate proximally against the margo radialis on the posterolateral surface of the scapulocoracoid and are overlain distally by the proximal ends of the fin rays (Reis, 1895, pl. 1, fig. 2, 7; pl. 2, fig. 4; pl. 3, fig. 3, 6, 7; pl. 6, fig. 5; 1896, pl. 6, fig. 11; Jaekel, 1899, fig. 2; Watson, 1937, p. 114; Miles, 1973a, p. 153, fig. 20). In the HQ material the pectoral radialis are preserved only as vague impressions in the OUSM 00497 specimen (Fig. 7B, *rdl*), where not three but four elements appear to be present, although neither the number nor the shape of these radials can be established with certainty.

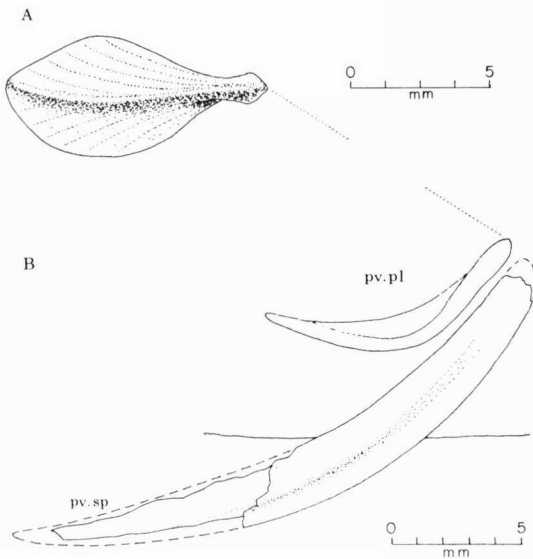


FIG. 8. A. A probable pelvic basal plate (“infraclavicula” of Fritsch) of *Acanthodes gracilis*, Lower Permian of the Boskovic trough, Moravia, Czechoslovakia (after Fritsch, 1893, fig. 270, pl. 107, fig. 10).—B. *A. bridgei* Zidek, n. sp., holotype EKSC 1A1+bl, pelvic spine (*pv. sp*) and “on edge” view of a pelvic basal plate (*pv. pl*) suggestive of morphology similar to that seen in figure A.

Acanthodii the pelvic girdle has been recorded previously only in one specimen of *Ischnacanthus gracilis* (Watson, 1937, p. 81; see also Miles, 1970, p. 350-351, regarding the alleged pelvic girdle described by Dean [1907] for *Diplacanthus striatus*), in which it was described by Watson as “some evidence of a calcified, cartilaginous girdle, associated with the base of the pelvic fin spine, but no details can be given.” The 1A1+bl girdle does not show much detail either, for it is exposed in an “on edge” view and cannot be freed from the

MEDIAN FINS AND THEIR SUPPORT

Remnants of the dorsal and anal fins are preserved in the EKSC 2a-d, 5b, 47A+B, and OUSM 00472 specimens as rows of caudad inclined profundal dermal fin rays that appear to be restricted to the very bases of the fins. The squamation is partially preserved only in the anal fins of the 2a-d and 5b specimens (Fig. 9), in which the transition between the flank and the fin is marked by a change in orientation of the scale rows from diagonal on the flank to roughly vertical (i.e., inclined toward the fin spine) on the fin web. The diminishing in size of the fin scales appears to be more rapid caudad than distad. Only the more anterior and proximal scales are preserved, and it is possible that posteriorly the scale rows of the fin become a straight-line continuation of those on the flank. In another paper I have described the squamation of both the anal and dorsal fins in *Acanthodes* from the Upper Pennsylvanian of New Mexico (Zidek, 1975b, Fig. 3, A, G) that, although incomplete, show the more proximal parts of the scale rows inclined toward the fin spines, while distad they bend to



FIG. 9. *A. bridgei* Zidek, n. sp. (EKSC 5b), detail showing fractured spine (*asp*), squamation, and dermatrichia (*dmt*) of partially preserved anal fin.

and become parallel with the spines. The inference thus can be made that the pattern of the squamation is similar in the two fins.

In the 2a-d the caudal extent of the rays cannot be established in either fin. In 47A+B, which is 250-270 mm in total length, the anal fin rays extend 30 mm behind the spine and their caudal inclination increases posteriorly so that the last rays are in a nearly horizontal position. The extent of the dorsal fin rays cannot be determined in this specimen. In 5b, which is 230-250 mm in total length, the dorsal fin rays extend 15 mm behind the spine, and, as in the anal, their inclination increases posteriorly. The anal fin is incomplete. In a great majority of the rays only their ossified proximal parts are preserved. Nevertheless, it is evident from the few more complete ones that their distal extent was rather limited and that they could not have reached anywhere near the fin margin. Although it is not possible to compare the posterior extent of the dorsal and anal fin rays in an individual, assuming the extent to be similar relative to the length of the fins, the

anal fin should be longer than the dorsal. This is in accord with the observation that the anal fin was quite long in advanced acanthodiforms (Miles, 1970, p. 350, fig. 5). In the 47A+B specimen there is a 30 mm gap between the last anal fin rays and the base of the tail. *A. sulcatus* (Traquair, 1890, fig. 1; Miles, 1970, fig. 5, 1971, fig. 4.4) and at least one specimen of *A. wardi* (Davis, 1894, pl. 27, fig. 1) demonstrate that the anal fin reached the immediate vicinity of the tail base. Davis (1894, p. 256) stated that: "The anal fin extends to the extremity of the spine, and for the most part is triangular in outline; but before its posterior margin reaches the body it sweeps away, forming a long narrow fin, extending toward the base of the caudal, gradually diminishing in depth until it disappears. . . . Under the scales are small ridges, indicating the fin-rays. The anal fin of the smaller specimen (Pl. XXVII., fig. 3, a.) is proportionately larger than the one described; but while the triangular portion is larger, the elongated portion, extending toward the tail, is shorter. . . . So far as can be ascertained from

the specimens examined, there is no evidence of an extension of the (dorsal) fin along the dorsal surface in the manner the anal extends along the ventral, and it is smaller than the latter." Davis does not specify whether the anal fin rays extend throughout the length of the fin or are present only anteriorly, at the base of its triangular-shaped portion. However, from his description of the smaller specimen it appears that the length of the anal fin increased gradually during ontogeny by addition of marginal scales, perhaps in a manner comparable to the process seen in the caudal fin and described below. With regard to the smaller size of the 47A+B specimen it is likely that the anal fin did not extend into the immediate vicinity of the tail base.

There is no evidence of basal support for the anal fin. The OUSM 00472 specimen (Fig. 10) is

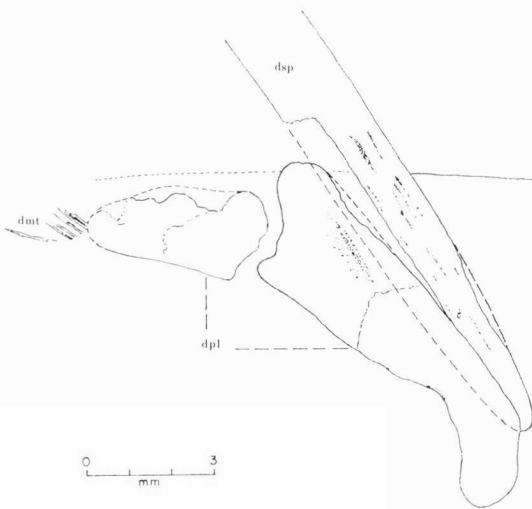


FIG. 10. *Acanthodes* sp. cf. *A. bridgei* (OUSM 00472), remnants of the dorsal fin. [Explanation: *dmt*, dermatrichia; *dpl*, dorsal basal plates; *dsp*, dorsal spine.]

misleading. It consists of a small section of the flank which exhibits a fractured spine, and the basal support, and from the convex curvature of the body margin the fragment might be interpreted as being the area around the anal fin. However, similar curvature may be seen in the area of the dorsal fin of the 2a-d, 5b+6b, and 47A+B specimens, and the associated squamation makes it clear that the 00472 specimen exhibits remnants of not the anal, but of the dorsal fin. Judged from the size of the spine and from

the scale count (2.5 sc/mm), the specimen may have been 250-270 mm in total length. The spine is supported by a basal plate the height of which corresponds roughly to the length of the embedded portion of the spine, and, consequently, also to the extent of the posterior cavity of the spine, in which the anterior margin of the plate is inserted. Since the cavity shallows gradually toward the body surface, the anterior margin of the plate is inclined caudad somewhat more than the spine. The plate is narrow at its lower end and expands in the posterodorsal direction. Its posterior surface is concave. Contrary to Watson's (1937, p. 113) finding of a single basal plate supporting the dorsal fin in the Lebach *Acanthodes*, it can be demonstrated from the 00472 specimen that there is another, smaller basal element situated behind the posterodorsal end of the large supporting plate. This posterior basal element appears to be irregularly oval-shaped, with its long axis horizontal, but its outline is poorly defined and a more accurate definition is therefore impossible.

The caudal fin is preserved in four mature or nearly-mature specimens (EKSC 1A1+bl, 5b+6b, 39C, 47A+B) and in eight of the juveniles (EKSC 3A1, 4Ab+Bb, 8bb, 22b, 228, 232, 240, OUSM 00471). The caudal skeleton has been discussed in the section on the vertebral column, and the following account concentrates mainly on the squamation.

The most recent work on the caudal fin is that of Miles (1970), who studied a sufficiently wide range of genera to be able to establish that the differentiation of the caudal squamation in *Acanthodes* is typical for the class Acanthodii as a whole (see also Miles, 1973a, p. 120-121, fig. 3). In the same paper (1970) he discussed the concept of tail development in fishes founded by Graham-Smith (1936) on an acanthodian model, and introduced the terms "ventral division of hypochordal lobe," "longitudinal division of hypochordal lobe," and "axial lobe." The numbering of the scale zones used by Miles follows Heyler (1969, p. 38, fig. A; also 1958, 1962) and is used also in this paper.

Both Graham-Smith (1936) and Miles (1970) mentioned the caudal extent of the main lateral sensory line, but neither could establish it conclusively. The HQ 5b+6b and 39C specimens (Pl. 6,B and 7,B of this paper) show clearly this line reaches beyond the point of juncture of Z1,

Z3, and Z4 scales and onto the posterior margin of Z4, where its bordering scales are larger than the surrounding scales.

In describing the longitudinal division of the hypochordal lobe, Miles (1970, p. 355) noted that "In *Acanthodes* and a few other genera (e.g., *Carycinacanthus*) the longitudinal division is expanded posteriorly as it passes into an axial lobe (*al*), but no further scale differentiation of Zone 4 is associated with this lobe." The tip of the tail is labeled accordingly in this paper (*al*, Fig. 11, *A₁*), although I have not found the expansion indicated by Miles in any of the HQ specimens, and it certainly should not be regarded as characterizing the genus as a whole. (In Pl. 7, *B* the expansion is clearly an artifact caused by a missing portion of Z4).

Although little can be added to the descriptions of the individual scale zones as presented by Heyler (1969) and Miles (1970), it should be pointed out that the actual boundary lines between the zones are difficult to recognize and that certain sections of them can only be approximated. In about the anterior two thirds of the tail in mature or nearly mature individuals the Z1 scales of the caudal prolongation of the trunk are clearly distinguishable from the epichordally positioned Z2 and Z2' scales. The boundaries can be followed accurately here because of a difference in orientation of the scale rows in these zones, which are diagonal in Z1 and Z2' and vertical or nearly so in Z2 (Fig. 11, *A₂*). In the posterior third of the tail, however, the Z2 scales finger out (Fig. 11, *A₁*, *C*), so that Z2' merges with Z1.

The situation is different in immature individuals. In the 8bb and 228 specimens, for example, each of which is only 54 mm in total length, there is no trace of Z2 scales (Fig. 11, *D*). In the 240 (Fig. 11, *C*) and 00471 specimens, 56.5 mm and 60 mm long, respectively, Z2 has been acquired, but it contains only 3 scales in a row. 4Ab+Bb (Fig. 11, *B*) and 3Al (Pl. 5, *B*), which are 91 mm and 95 mm long, respectively, have 4 scales in a row in Z2, but there is no trace of Z2' as yet. However, in 22b, which is only slightly longer (103 mm), the Z2' has already been acquired, although it is still quite narrow with only two to three scales in a row. In the 5b+6b specimen, which is 230-250 mm in total length, and in the other larger specimens, Z2 contains four or five scales in a row, and Z2' is fully developed, with 10 or more scales in a row.

Z1 is delimited from Z3 of the ventral division of the hypochordal lobe and from Z4 in the anterior portion of the longitudinal division of the hypochordal lobe by an abrupt shift in orientation of the scale rows (Fig. 11, *A₁*, *B₁*, *D*). There is no such abrupt change apparent between Z3 and Z4 in the ventral division nor between Z1 and Z4 in the more posterior portion of the longitudinal division. Instead, the transition is very gradual both in orientation of the scale rows and in decrease in scale size, and the Z1/Z3, Z4 boundary line cannot be drawn accurately throughout.

Besides lacking the posterior expansion of the longitudinal division, the caudal fins of the HQ specimens differ somewhat from those illustrated by Heyler (1969) and Miles (1970) also in showing a more profound bending of the Z1/Z3, Z4 boundary line in the area transitional between Z1/Z3 and Z1/Z4. I have used the point of intersection of the main lateral sensory line with the Z1/Z3, Z4 boundary line arbitrarily as a means of distinguishing between the Z3 and Z4 scales in the ventral division of the hypochordal lobe (Fig. 11, *A₁*).

As in *A. "bronni"* from Lebach (Miles, 1970, fig. 2), four or five rows of the Z3 scales overlie each radial in the ventral division of the hypochordal lobe. The radials of the longitudinal division of the hypochordal lobe are overlain mainly by the Z4 scales, and it is thus not surprising to find the Z4 scales developed in even the smallest specimens (see EKSC 228, Fig. 11, *D*). Because of this arrangement in the longitudinal division, the number of scales per radial increases toward the distal end of each radial element, where the Z4 scale rows branch and intercalate.

The proximo-distal lengthening of the Z3 and Z4 scales noted in the ventral division of the hypochordal lobe of *A. wardi* (= *A. major*) by Miles (1970, p. 355, fig. 3), as well as the branching and intercalating of their rows, are clearly apparent in all the HQ mature individuals but are absent in the juveniles.

REMARKS ON THE DERMAL FIN RAYS

The dermal rays (dermotrichia) of the pectoral, pelvic, anal, and dorsal fins are scale-covered (profundal, deeply-seated), straight, unjointed, proximally ossified rods arranged in layers, and they are invariably narrower than the scale rows

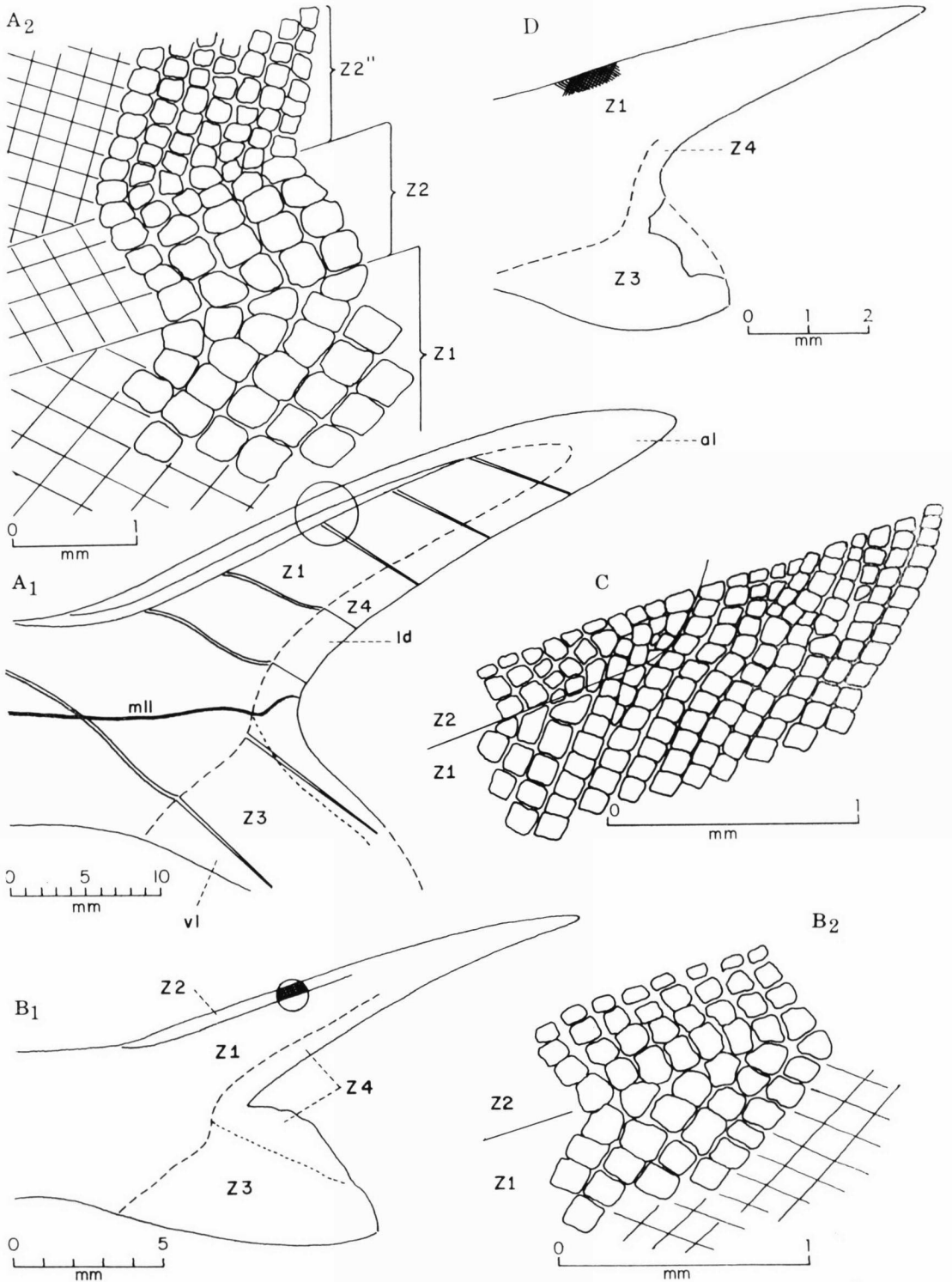


FIG. 11. Development of scale zones (Z1 through Z4) of the caudal fin. (Continued on facing page.)

covering them (see Zidek, 1975b, concerning the seemingly different pelvic fin rays in *Pseudacanthodes pinnatus*). The arrangement of the rays is apparent in the first dorsal fin of *Diplacanthus striatus*, in the pelvic fins of *Climatius reticulatus* and *Cheiracanthus latus*, in the pectoral fins of *Ischnacanthus gracilis*, *Cheiracanthus murchisoni*, and *Diplacanthus striatus* (Watson, 1937, p. 60, 78, 90, 95, fig. 10, 15; Miles, 1970, p. 358 and fig. 8; 1973a, p. 155, 158, pl. 20, fig. 2). In *Acanthodes* it can be seen in all the fins except the caudal (Fig. 7, 9, and Pl. 5,C; see also Zidek, 1975b, fig. 2,C, D. The pectoral dermatrichia have been illustrated numerous times in the works of Davis, Reis, Jaekel, Watson, Jarvik, Heyler, and Miles cited herein).

In the caudal fin the profundal rays have not been found in the *Acanthodii* (Reis, 1895, pl. 3, fig. 4 and 1896, pl. 6, fig. 14 shows a series of short dermatrichia in the tail, but the figures are none too clear and are suggestive of displaced dermatrichia of the anal fin). Instead, in the distal portion of the ventral division of the hypochordal lobe (Z3 scales) there is the tendency toward proximo-distal lengthening of the scales in a row that has been compared by Jarvik (1959) and Miles (1965, 1970) to the theoretical primitive structure of the osteichthyan lepidotrichia. If the profundal fin rays are regarded as early generations (ontogenetically) of scale rows sunk into the dermis (Goodrich, 1903, 1909; Jarvik, 1959; Miles, 1965, 1970), then their absence in the tail may perhaps be linked with the radials, the distal extent of which is great enough to make the development of dermal support unnecessary in a juvenile, whereas later in life, due to the aplesodic condition of the caudal fin (Jarvik, 1959, p. 14), the need for additional support of the distal part of the ventral division of the hypochordal lobe is expressed in the tendency toward formation of the lepidotrichia. This is in accord with the structure

of the juvenile caudal fin in *Acanthodes* (see above), in which such dermal support is absent.

As acanthodians are not known to possess epichordal radials, the epichordal lobe is said to be absent in them. Graham-Smith (1936, p. 597) claimed the existence of a true epichordal lobe in *Mesacanthus mitchelli*, but according to Miles (1970, p. 357) that species, and also *Rhadinacanthus longispinus*, simply have the Z2 of the tail well developed. Heyler (1958, 1969) compared the epichordally situated Z2 scales with the epichordal fulcral scales of palaeoniscoids, and Blot (1966, p. 48-49, 76) questioned whether there is any fundamental difference between fulcra and lepidotrichia, especially since in palaeoniscoids the unsegmented fulcra may be replaced posteriorly by segmented lepidotrichia (see also Miles, 1970). As shown above, the Z2 and Z2' scales were acquired only later in life, and their development may be related to strengthening of the superior margin of the tail as well as to its upward expansion. Thus, from the functional viewpoint it seems that the epichordal lobe was in a sense present, either as a rudiment or as a secondary formation. Since the differentiation of the caudal squamation in *Acanthodes* is typical for the *Acanthodii* as a whole (Miles, 1970, p. 354), this may be true of most, if not all, acanthodians and perhaps of the palaeoniscoids as well.

In the pelvic, anal, and dorsal fins the profundal rays are restricted to the fin bases (except in the dorsal fin of *Diplacanthus*; see Watson, 1937, fig. 15), but no evidence of lepidotrichia-like formations has been found in any of these fins. An explanation of this deficiency is perhaps provided by the fin spines, the supporting function of which may have eliminated the tendency toward formation of the lepidotrichia. The radial arrangement of the scale rows in the acanthodian pectoral fin (e.g., *Euthacanthus*; see Miles, 1973a, p. 185, and pl. 15, fig. 1) is suggestive of the

A. EKSC 1A1+bl, 5b+6b, 39C, and 47A+B, mature or nearly-mature individuals; A₁, composite, in part after Heyler's (1969) scheme. The caudal extent of the main lateral sensory line is apparent in the 5b+6b and 39C specimens (see Pl. 6,B and 7,B, respectively); A₂, EKSC 39C, detail of Z1, Z2, and Z2' scales from the area circled in A₁.

B. EKSC 4Ab+Bb, a juvenile 91 mm in total length (Pl. 5,C); B₁, overall view of the tail; B₂, detail of Z1 and Z2 scales from the area circled in B₁. This specimen contains no scales attributable to Z2'.

C. EKSC 240, a juvenile 56.5 mm in total length (see Pl. 5,A). Detail of Z1 and Z2 scales, with apparent caudal reduction of Z2. The Z2' is not developed.

D. EKSC 228, a juvenile 54 mm in total length. This specimen contains no scales attributable to Z2. (EKSC 1A1+bl, 4Ab+Bb, 5b+6b, 47A+B, 228=A. *bridgei* Zidek, n. sp.; EKSC 39C=*Acanthodes* cf. *A. bridgei*; EKSC 240=an unnamed species different from *A. bridgei*.) [Explanation: *al*, axial lobe; *ld*, longitudinal division of hypochordal lobe; *vl*, ventral division of hypochordal lobe (Miles, 1970, fig. 7).]

theoretical primitive lepidotrichia. I know of no example, however, that would demonstrate any proximo-distal lengthening of the scales in a row. As regards the profundal rays of the pectoral fin in *Acanthodes*, Watson (1937, p. 114) found that, in addition to the proximal series (Fig. 7,B), there is in some specimens from Lebach also a distal series of more slender and less closely spaced rays, the non-ossified ends of which may have reached the fin margin. To my knowledge, the distal series has not been found in specimens from any other locality, although one can think of a number of localities where the depositional conditions were as favorable for preservation of the non-ossified parts as in Lebach. An interesting parallel may be seen in the xenacanth sharks of which *Xenacanthus decheni* from the Lower to Middle Permian lacustrine deposits of the Inner-Sudeten depression, Bohemia, has the margin of the pectoral fin stiffened with abundant ceratotrichia. *X. oelbergensis* from the same deposits, on the other hand, as well as the rest of the species of this genus, and of *Orthacanthus* as well, show no evidence of ceratotrichia in spite of the often favorable conditions for their preservation (Fritsch, 1889, 1890; Zidek, 1966). Consequently, it appears unlikely to me that the lack of the distal series of rays in the pectoral fin of *Acanthodes* could be due solely to faulty preservation, or for obvious reasons even more unlikely that it could indicate sexual dimorphism. It is more likely that this absence has taxonomic significance, although due to the infrequent preservation it could hardly ever be used as a basis for classification.

Watson (1937, p. 112, 114, and fig. 21) noted that in *Acanthodes* the dermotrichia of the pectoral fin ossify very early in life and that both the pelvic and pectoral fins remain scaleless in even quite large specimens (P. 490 and P. 496 from Lebach, both at least 270 mm in total length). In the HQ specimens the pectoral dermotrichia can first be observed in EKSC 4Ab+Bb (91 mm in total length; see Pl. 5,C), in which they are a maximum of 0.06 mm broad. In the larger specimens the breadth of the rays increases to 0.08 mm in EKSC 221+224 (± 140 mm in total length), 0.2 mm in EKSC 2a-d (268 mm in total length), and 0.3 mm in EKSC 1A1+bl (410 mm in total length). Thus, the profundal rays were present before any squamation was acquired on the fin and grew by apposition of con-

centric layers throughout ontogeny. In the light of Jarvik's (1959) work on the dermal fin rays and Holmgren's principle of delamination, the early appearance of the rays, preceding the formation of the fin scales, can be readily understood and does not require further comments here, but a remark is in order concerning the number of generations of exoskeletal formations in acanthodian fins. Watson (1937, p. 78, 114) and Miles (1970, p. 358 and 173a, p. 155, 158) described the profundal rays of the pectoral fin in *Ischnacanthus*, *Cheiracanthus*, and *Acanthodes* as being arranged in two layers, dorsal and ventral, and such arrangement can now be confirmed also for the dorsal, anal, and pelvic fins (HQ specimens EKSC 2a-d, 5b, 47A+B, and Manzanita Mountains, New Mexico, specimens OUSM 00447A and 00449; Fig. 9; and Zidek, 1975b, fig. 2A, D, G). Consequently, only a single generation of the profundal rays was present in the dorsal, anal, and in the paired fins, and none at all are found in the tail. Since all the fins ultimately become scaled, and since there are lepidotrichia-like formations present in the tail, the Acanthodii may be said to possess three superimposed generations of the fin exoskeleton; however, the formation of the lepidotrichia is suppressed except in the tail.

FIN SPINES, BODY PROPORTIONS, GROWTH

Spines similar in appearance to those in the HQ specimens have been described previously on many occasions from *Acanthodes*. Unfortunately, with rare exceptions (e.g., Fritsch, 1893; Reis, 1891, 1896) the descriptions lack detail, and the question as to whether the spine morphology alone is diagnostic of the genus cannot be settled as yet. From the material I have examined it appears that detached fin spines from stratigraphic levels as far removed from each other as Lower Mississippian and Lower Permian contain nothing in their morphology which would prevent their assignment to the genus *Acanthodes* (Zidek, 1976), or even, should their provenance be unknown, to a single species of that genus. In the other two genera assignable to the family Acanthodidae, *Traquairichthys* and *Pseudacanthodes* (*Traquairia* and *Protacanthodes* of Fritsch; see Whitley, 1933, and White & Moy-Thomas, 1941, respectively, for changes of the names), the spines are of somewhat different morphology (Fritsch,

1893), but this does not mean that the detached spines of the *Acanthodes* morphology, namely the Mississippian ones, may justly be termed *Acanthodes* sp. They may have belonged to a genus not yet known, and the more general term "acanthodid spines" would thus be more in accord with the present state of our knowledge.

The morphology of the spines of *Acanthodes* has been dealt with elsewhere (Zidek, 1975a, 1975b), and since there is nothing unusual about their morphology in the HQ specimens, the discussion is here restricted to the spine distribution and size relation. In *Acanthodes* the single dorsal and the anal spines are situated far back, close to the tail, the anal being either equal in length to the dorsal (in HQ *Acanthodes* and *A. beecheri* only), or slightly longer, and somewhat in front of it. The pectoral spines are the largest, whereas the pelvic spines are the smallest and are placed

close behind the pectorals. This distribution and size relation are comparable to those in *Pseudacanthodes*, in which, however, the pelvic spines are placed farther back and are substantially smaller than in *Acanthodes*. In *Traquairichthys*, the pectoral, anal, and dorsal spines appear to be of identical size in all measurable specimens. Although a large number of specimens of *Traquairichthys* has been examined, no pelvic spine has ever been found in this genus (Fritsch, 1893, fig. 246 and p. 49; Zidek, 1973).

Since the insertions of the fin spines are the only available (although not completely reliable) points for calculating the overall body proportions, the two are here treated together. Ratios of a sample representative of the entire size range present in the HQ collection of *Acanthodes* (see Fig. 12 for graphical presentation) are shown in Table 2.

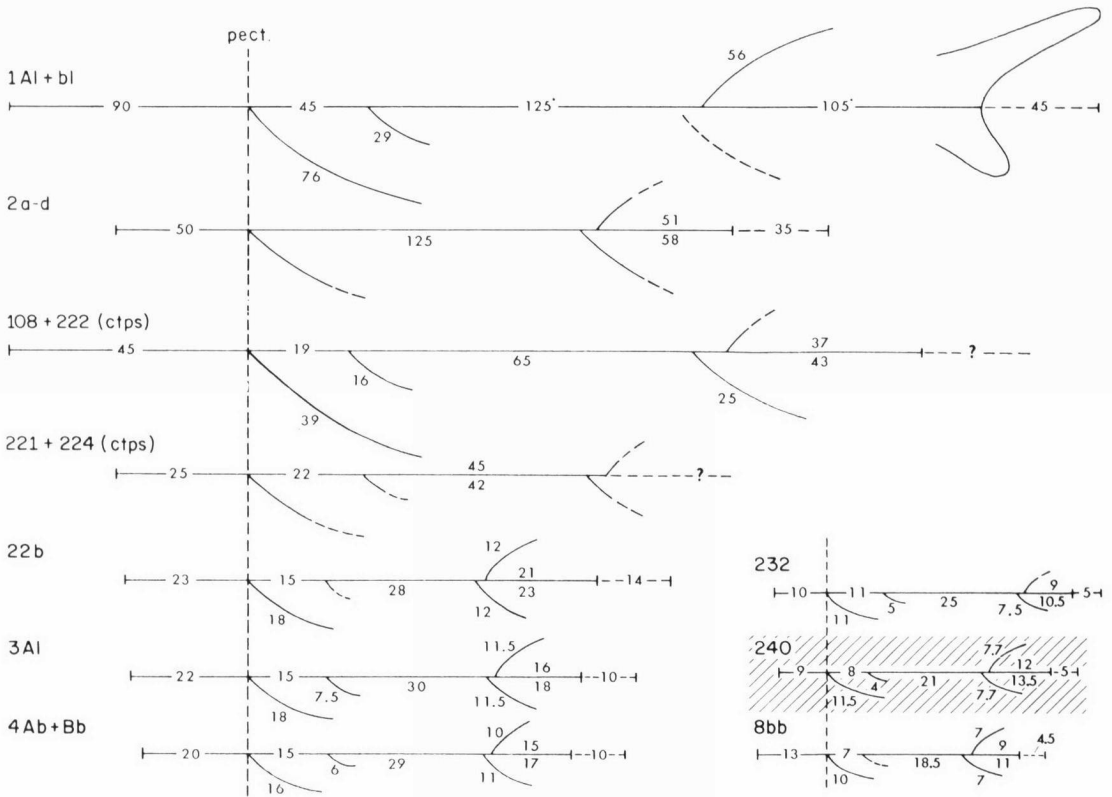


FIG. 12. A sample representative of the size range present in the Hamilton Quarry collection of *Acanthodes bridgei* Zidek, n. sp. (except for EKSC 240 that belongs to another, unnamed species). 1Al+bl and 2a-d are reduced by one half as compared to the other specimens. In 2a-d the length of the longitudinal division of the hypochordal lobe (+axial lobe) has been restored from 47A+B which appears to be of similar size. All measurements are in mm. Doubtful measurements signified by *; instead of 125 and 105 mm may be rather 150 and 80 mm, respectively.

TABLE 2.—A Sample Representative of the Size Range Present in the Hamilton Quarry Collection of *Acanthodes bridgei* Zidek, *n. sp.*

EKSC HQ SPECIMEN NO. AND TOTAL LENGTH	MEASUREMENTS ¹											
	A	B	C	D	E	F	G	H	I	J	K	L
1Al+bl, 410 mm	0.74	0.38	0.19	0.14	0.07	0.39*	0.28	0.22	0.26*	0.11	0.20(18)
2a-d, 268 mm	0.47	0.19	0.19	0.13	0.26(13)(28)
108+222 (<i>ctps</i>), ±200 mm	0.64	0.41	0.20	0.13	0.08	0.42	0.32	0.22	0.18
221+224 (<i>ctps</i>), ±140 mm	0.46	0.30	0.18	0.28(7)
22b, 103 mm	0.67	0.17	0.12	0.42	0.27	0.22	0.20	0.13
3Al, 95 mm	0.64	0.42	0.19	0.12	0.08	0.47	0.31	0.23	0.17	0.10	0.28(6.2)	0.53(9.5)
4Ab+Bb, 91 mm	0.66	0.37	0.18	0.12	0.07	0.48	0.32	0.22	0.16	0.11	0.62(10)
232,61.5 mm	0.68	0.45	0.18	0.12	0.08	0.58	0.41	0.16	0.15	0.08
240,56.5 mm	0.67	0.35	0.20	0.14	0.07	0.51	0.37	0.16	0.21	0.09	0.44(4)	0.74(8.5)
8bb, 54 mm	0.70	0.19	0.13	0.47	0.34	0.24	0.17	0.08	0.35(4.5)	0.75(7.5)

¹ [Explanation of ratios: *A*, anal or dorsal spine length : pectoral spine length; *B*, pelvic spine length : pectoral spine length; *C*, pectoral spine length : total length; *D*, anal or dorsal spine length : total length; *E*, pelvic spine length : total length; *F*, distance between pectoral and anal spines : total length; *G*, distance between pelvic and anal spines : total length; *H*, pre-pectoral length : total length; *I*, distance from dorsal spine to caudal cleft : total length; *J*, length of longitudinal division of hypochordal lobe plus axial lobe : total length; *K*, outer diameter of circumorbital ring : pre-pectoral length; *L*, mandibular bone length : pectoral spine length; *ctps*, counter-parts; * doubtful, may be rather 0.45 for *F* and 0.19 for *I*. The circumorbital ring diameter and the mandibular bone length could not be included in Fig. 12 for lack of space, and the measurements (mm) are therefore listed in parentheses in the columns *K* and *L*.]

The measurements that appear in Figure 12 and in columns *K* and *L* (Table 2) should not be regarded as error-free. Although the value of the spine insertions for calculating the overall body proportions is obvious, it is in fact exceedingly difficult to establish the exact points of the insertions, and in the small specimens a one-millimeter error may result in substantially different ratio. An error may possibly be present even in the largest specimen, EKSC 1Al+bl (Pl. 2), which is preserved longitudinally twisted in such a way that the dorsal and anal spines may have been confused. The more completely preserved spine that appears to be situated dorsally has been interpreted as such in Figure 12. Should this interpretation be faulty (i.e., should the other, more fragmentary spine, be the dorsal), the distance between it and the tail cleft would be not 105 but only 80 mm, and the pelvic-dorsal distance would increase accordingly. The *F* and *I* ratios would thus change from 0.39 and 0.26 to 0.45 and 0.19, respectively, putting them well within the range of all but one (EKSC 232) of the specimens. A wider margin for error should be left for the pre-pectoral length (*H*), for *I* may have erred in estimating the pre-orbital length, which is poorly indicated in the HQ specimens (since the snout is exceedingly short, the error could hardly be significant, however), and, more importantly, because the branchial region appears to have been somewhat stretched in some specimens and some-

what compressed in others, and it is impossible to restore its original length.

In spite of the reservations just noted, however, the above ratios, in my opinion, indicate at least the following:

- The length ratios of the fin spines relative to each other (*A,B*), as well as the ratios of fin spine length to total specimen length (*C-E*), show neither positive nor negative allometry for the sample, and their proportions can be summarized as follows: the length of the pectorals amounts to 0.16-0.2, the pelvics to 0.07-0.08, and the anal and dorsal spines to 0.12-0.14 of the total specimen length. The length of the pelvic spines amounts to more than 0.3 and less than 0.5 of the length of the pectorals. The length of the anal and dorsal spines is the same and amounts to about 0.7 of the length of the pectorals.
- The distances between the pelvic and anal spines (*G*), and perhaps also between the pectoral and anal spines (*F*), appear to be slightly longer proportionally in the smallest specimens. However, considering the chance for error in recognizing the exact points of insertions in the 240 and 8bb specimens, the evidence has to be regarded as inconclusive.
- The sample demonstrates a positive differential growth in length of the tail as compared to the total length increase (*J*). Furthermore, with reference to the above section on the caudal

fin it may be concluded that the increase in the surface area has been in part accomplished by adding the Z2 and Z2' scales above and by increase in width of the Z4 below, the caudal prolongation of the trunk. No conclusion can be made as to whether the development of these scale zones corresponds only to maintaining the surface area : length ratio, or whether it represents a relative increase of the surface area over the length of the tail.

- d) The negative differential growth of the orbits is apparent from the relative decrease in diameter of the circumorbital rings, which in relation to the total specimen length amount to about 4 percent (from 8% in the smallest specimen down to only 4% in the largest), or, in relation to the pre-pectoral length (*K*) to as much as 15 percent (from 35% in the smallest specimen down to only 20% in the largest). In the latter respect the EKSC 240 specimen differs substantially from the rest of the sample, for instead of the expected 35 percent or less the circumorbital ring comprises close to one half of the pre-pectoral length. Although no figures can be given, it appears that the length : width ratio of the circumorbital bones decreases with growth (i.e., the bones are relatively broader in large individuals; see Pl. 1, *B*, *C*, 3, *A* in contrast to Pl. 5, *A*, *C*).
- e) The mandibular bones can be measured in only five of the specimens sampled (*L*), but in spite of that their negative allometry in relation to the other categories can be readily seen. These bones comprise about 14 percent of the total specimen length in the smallest specimens and about 10 percent in the largest, and the negative differential growth of 4 percent is thus comparable to that seen in (d). Compared with the pectoral spines, however, the negative differential growth of the mandibular bones amounts to 25 percent or more for the sample [in the case of the EKSC 2a-d specimen the length of the pectoral spine has been approximated according to (a)]. This condition is further verified by the EKSC 47A+B and 315A specimens, although they are too fragmentary to be included in the sample.
- f) In categories *B*, *F*, and *G*, EKSC 232 differs from the rest of the sample; EKSC 240 differs in category *K*. Furthermore, EKSC 240 has

all its spines inserted shallowly, apparently not a condition resulting from its mode of preservation (Pl. 5, *A*). These shallow spine insertions are quite atypical of *Acanthodes*, and in fact of the entire families of Acanthodidae and Cheiracanthidae in the Acanthodiformes (Miles, 1966, p. 166-172). The shallow insertions of spines, together with the large size of the circumorbital ring (d), makes the EKSC 240 specimen a more likely candidate for a species distinction than EKSC 232, notwithstanding its having fewer inconsistent ratios.

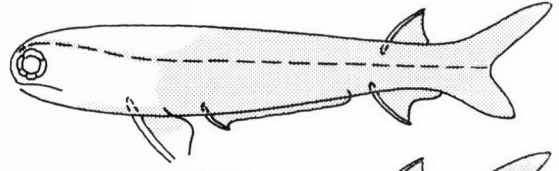
Unfortunately, of all the specimens examined only 2a-d (Pl. 1) and 240 (Pl. 5, *A*) are exposed laterally. They both appear to have attained the maximum height in the pectoral girdle region or immediately behind it, and, in spite of the great difference in overall size, the height in both is approximately 0.16 of the total length. Due to the features just noted in the 240 specimen (f), however, this cannot be regarded as suggestive of stability of the length : height ratio during growth in either intraspecific or interspecific terms.

SQUAMATION AND ITS DEVELOPMENT

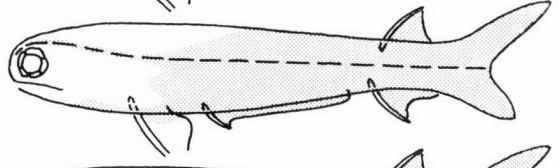
The squamation consists of nonimbricating, minute scales with transversely rhombic, flat to convex, unornamented crowns. Although the crowns overlap the scale bases, namely posteriorly, the overlap is negligible and in no way affects the scale counts (below and Fig. 13). A few specimens are split in the sagittal plane so that both the counterparts show most of the squamation in the internal view (i.e., with only the scale bases exposed, see Zidek, 1975b, pl. 2C, for detail of *Acanthodes* squamation so preserved). However trivial it may seem, there is in fact a good reason for mentioning this kind of preservation of the scale cover, as in several instances the scale bases have been mistaken for the crowns and used as such taxonomically.

The scales bordering the main lateral sensory line on the flank do not differ in size and orientation from the rest of the flank scales. Nevertheless, the line can be traced because its bordering scales are farther apart and appear not to lie in exactly the same plane as the scales surrounding them ("ridge-like displacement of two series" of Woodward, 1891, p. 5). This observation is in accord with the findings of other authors, possibly with the exception of Dean (1907, p. 219, fig. 35), who

1A1+bl, 410mm, 1.5 sc/mm in a row

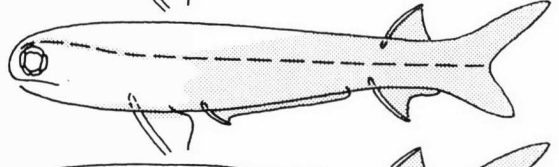


2a-d, 263mm, 2 sc/mm

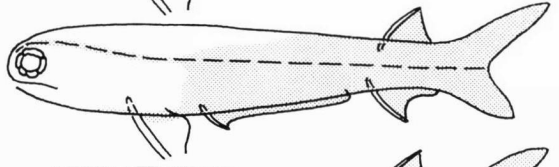


[47A+B, 250-270 mm, 2.5 sc/mm
5b + 6b (ctps), 230-250mm, 3 sc/mm
39C, tail only, 3 sc/mm]

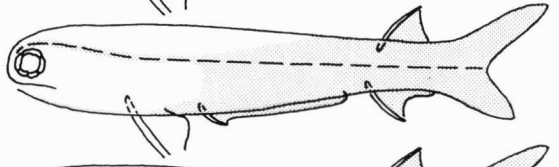
108+222 (ctps), ± 200 mm, 3sc/mm



221 + 224 (ctps), ± 140 mm, 4 sc/mm

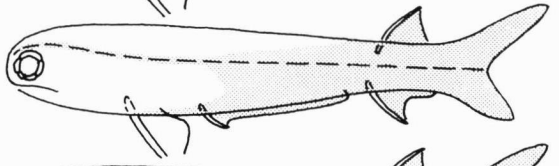


22b, 103 mm, 7 sc/mm

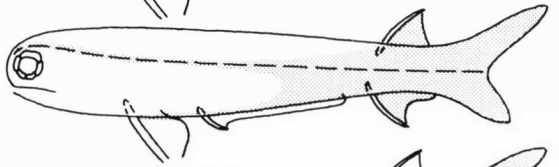


[23B, ?, 7 sc/mm]

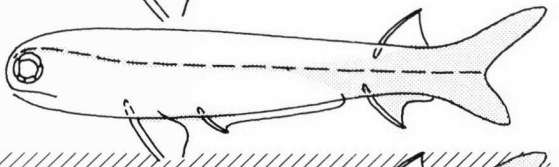
3A1, 95 mm, 7 sc/mm



4Ab + Bb, 91 mm, 8 sc/mm

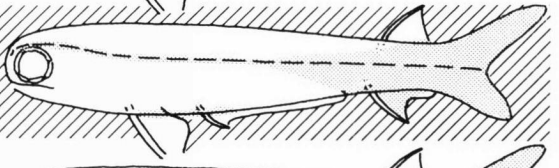


[28Ab, 67mm, 9 sc/mm]
232, 61.5 mm, 10(11?) sc/mm



[OUSM HQ00471, 60 mm, 9sc/mm]

240, 56.5 mm, 9 sc/mm



8bb, 54 mm, 10 sc/mm in a row

[228, 54 mm, 10 sc/mm]

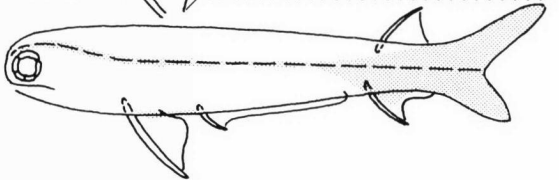


FIG. 13. (Explanation on facing page.)

described the scales bordering the lateral line in *A. "bronni"* as enlarged and prosalient. Through the kindness of Dr. H. Remy, Geologisch-paläontologisches Institut of the Friedrich Wilhelms Universität, Bonn, I have been able to examine specimens of *A. "bronni"* from Lebach and found the scales of the main lateral sensory line to be no different from those in *Acanthodes* from New Mexico (Zidek, 1975b) and Kansas (HQ). Only in the pectoral region and forward of it the line becomes more distinct because its bordering scales decrease in size less rapidly than the rest of the anterior scales. In contrast to the ventrolateral line (see below), however, the scales bordering the main lateral line maintain their rhombic shape. Taking this into account, it therefore appears that the figure 35 of Dean (1907) does not pertain to the main, but to the ventrolateral sensory line.

The ventrolateral sensory line is much more distinct than the main lateral line because throughout its course (from the pectoral region almost to the anal fin; see Pl. I, A) the bordering scales are significantly larger than the scales surrounding them. From a New Mexico specimen with only the bases of the bordering scales exposed (Zidek, 1975b, pl. 1C) I have inferred that the scales imbricate, which makes them seemingly broader than long. In the EKSC 1A1+bl and 2a-d specimens the ventrolateral line is preserved in both the external and internal views (Fig. 14, A, B). Although the preservation does not allow a truly accurate description, it is good enough to show that the scales of this line do not imbricate but are in fact prolonged perpendicularly to the line's course and are therefore different from the rhombic flank scales. Also, the smaller scales surrounding the bordering ones both above and below the line differ from the flank scales in that their crowns are irregularly polygonal rather than rhombic. The shape of the bordering scales cannot be established precisely, for it is not clear whether it is the scale crowns or a separate ossification (the laterosensory component, see Ørvgil, 1972), or both that form the thin, semitranslucent

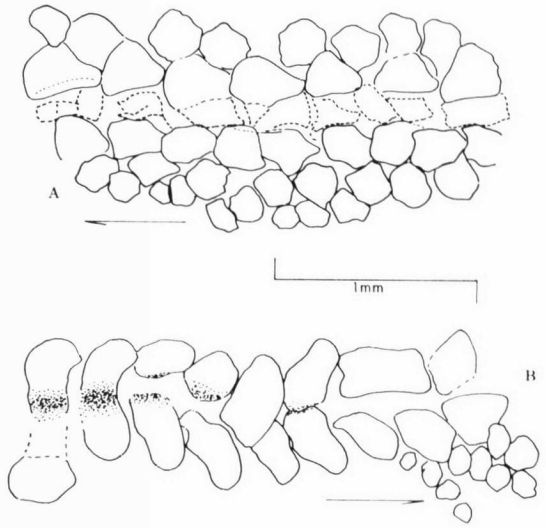


FIG. 14. *A. bridgei* Zidek, n. sp., the ventrolateral sensory line in external (A, EKSC 2a-d, paratype) and internal (B, EKSC 1A1+bl, holotype) views. The thin, semitranslucent roofing of the canal is shown in figure A by broken line. The arrows point in the cranial direction.

roofing of the canal (Fig. 14, A). So much is clear, however, that the ventrolateral sensory line was an enclosed canal that opened on the surface only interruptedly.

Regardless of specimen size, the largest body scales are always situated around the main lateral sensory line in the postdorsal-precaudal region, and only a slight forward shift in their location, from the tail closer to the dorsal spine but never quite reaching the spine level, occurs during growth. The size of the body scales diminishes toward the head, as well as both upward and downward from the main lateral line. The vertical decrease in scale size is more profound in the ventral direction, which may be accounted for by the larger area below the main lateral line that runs somewhat above the center of the body.

Based on specimens in various stages of growth, Watson (1937) described the development of the squamation in *Acanthodes* and concluded

FIG. 13. Development of the squamation shown on the same sample of specimens as used in Figure 12 (*Acanthodes bridgei* Zidek, n. sp., and EKSC 240 that belongs to another, unnamed species), and with additional specimens (in brackets) further demonstrating the correlation between the total specimen length and the scale size. The specimen numbers are followed by the total specimen length and by the number of scales per millimeter in a row. The scale counts are from the proximity of the main lateral sensory line in the postdorsal-precaudal region, where the scales are largest and their rows are the least disturbed. The shapes and sizes of the fins are based on a restoration of *Acanthodes sulcatus* (Miles, 1970, fig. 5; 1971, fig. 4.4), and for the pectorals and pelvises the chronology of the scale cover is purely conjectural.

that its mode accounts for the "remarkable fact that the scales of large specimens of *Acanthodes* may be no larger than those of small individuals" (p. 112), and consequently that "the scales seem to reach their maximum size early in life of the fish and growth takes place by the addition of new scales" (p. 117). Doubts have been expressed concerning this mode of spreading of the scale cover (Miles, 1966, p. 160; Zidek, 1975b), and it can now be shown on the HQ suite of specimens that the scales increased in size by the addition of areal zones of growth to the crown throughout ontogeny. Due to the small size of *Acanthodes* scales, it has been found convenient (and in case of the smallest specimens necessary) to count the number of scales per millimeter in a row in the region of the largest scales (noted above), in which also the scale rows are usually the least disturbed. The counts (Fig. 13) indicate an increase in size of these largest body scales from 10 scales/mm in a row in the smallest specimens (EKSC 8bb and 228, both 54 mm in total length) to only 1.5 scales/mm in a row in the largest specimen (EKSC 1A1+bl, 410 mm in total length). All but one specimen in the suite examined conform in their scale size as related to the overall specimen size. The one specimen that does not quite conform with the rest of the suite is EKSC 232, a specimen that has been recognized in the previous section as being different on several counts. In this connection, it is interesting to note that the specimens of *Acanthodes* from the Upper Pennsylvanian of the Manzanita Mountains, New Mexico (Zidek, 1975b), conform to a remarkable degree with the HQ specimens of comparable size as far as the scale counts are concerned (although the two are not conspecific). It thus appears that within certain ranges the scale counts can be used to estimate the total specimen size in *Acanthodes*, but are useless in species determinations (since I have not had the opportunity to examine a sufficient number of European specimens, the above statement is meant to pertain only to the North American material of *Acanthodes*). In the light of what has just been said, the meaning of the deviation found in the EKSC 232 specimen is not at all clear and therefore cannot be used taxonomically.

The smallest HQ specimens (EKSC 8bb, 228; Fig. 13; Pl. 4,B) are 54 mm long and have the area posterior to the dorsal and anal spines fully scaled. Making the allowance of ± 10 mm, it

can be approximated that the first scales appeared on the tail when the fish were 30 to 40 mm long. The development of the squamation (Fig. 13) can be followed quite confidently in the three smallest and the two largest specimens (EKSC 8bb, 240, 232, 2a-d, 1A1+bl). In the intermediate specimens, the anterior extent of the squamation can be easily recognized by following the main lateral line, but since all these specimens are longitudinally twisted, the transgression of the scale cover above and below the main lateral line can only be approximated. Because of the different scale morphology (see above), there is no difficulty in distinguishing between the main and the ventrolateral sensory lines in even highly distorted specimens. In the HQ material the fins are only rarely and incompletely preserved, and there is no evidence whatever of the pelvic fins. However, it is most likely that long pelvic fins were present in all species of *Acanthodes* and that due to their narrowness and the obscuration of their minute dermatichia by scales, in a great majority of specimens they simply cannot be identified. Based on this assumption, the pelvic fins have been included in the restoration (Fig. 13, Fig. 15). The shapes and sizes of all fins are based on the restoration of *A. sulcatus* (Miles, 1970, fig. 5; 1971, fig. 4.4), and instead of showing the posterior lengthening of the anal fin during growth, the fin is drawn as fully developed in all the specimens.

Watson's (1937, p. 111, 112) description of development of the squamation in *Acanthodes* was based on four specimens from Lebach, of which the smallest (P. 6192) was slightly over 100 mm and the largest (40049) around 500 mm in total length. Comparing the P. 6192 with an HQ specimen of similar size (EKSC 22b, Fig. 13), it is evident that the two differ in the rate as well as in the pattern of squamation development. The scale cover of the Lebach specimen is comparable in extent with that seen in the smallest HQ specimens (EKSC 8bb, 240) that are only about one-half of its size, but the dorsal and ventral margins of the Lebach specimen appear to be scaleless. According to Watson (1937), no traces of the main lateral line are visible in the anterior part of the trunk or on the head of the P. 6192 specimen. The main lateral line is fully developed from tail to head in even the smallest HQ specimens and it is obvious that the absence of this line in the P. 6192 specimen is due to faulty preservation rather than to a truly different condition. In 22B the

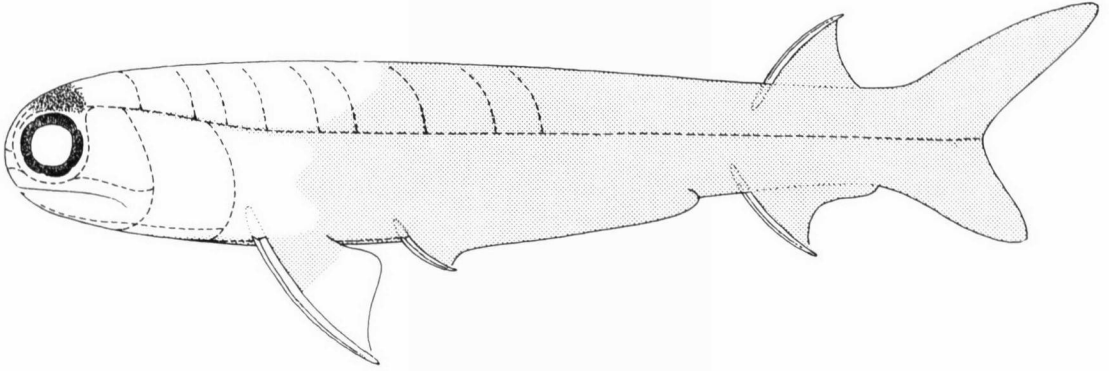


FIG. 15. *Acanthodes bridgei* Zidek, n. sp., restoration with the scale cover after the largest Hamilton Quarry specimen (EKSC 1A1+bl, holotype). The shapes and sizes of the fins are based on a restoration of *A. sulcatus* (Miles, 1970, fig. 5; 1971, fig. 4.4), and for the pectorals and pelvics the scale cover extent is purely conjectural.

squamation between the main and the ventrolateral sensory lines reaches the level of the pelvic spine, whereas dorsad of the main lateral line its development lags behind substantially, leaving most of the back in front of the dorsal spine barren of scales. This dorsal deficiency in the scale cover is apparent throughout the sample, although it decreases in the largest specimens. In the smallest three specimens, EKSC 8bb, 240, and 232, the squamation forms an anteriorly pointing triangle, the ventral side of which ends in front of the anal spine and the dorsal side behind the dorsal spine. The part of the triangle above the main lateral line is thus less extensive than the part below it. In these specimens the ventrolateral line is developing in the caudad direction and can be traced only a short distance behind the pelvic spine (since the line is so developed in at least five specimens, it is unlikely that its incompleteness could be due to partial preservation). In the fourth smallest specimen, EKSC 4Ab+Bb, the unevenness between development of the dorsal and ventral scale cover is even more profound, for here the scales ventrad of the main lateral line connect with the ventrolateral line, and, presumably, squamation develops also between the posterior parts of the ventrolateral lines of both the sides. Consequently, the scale cover below the main lateral line no longer progresses in a straight, ventrocaudad inclined line but becomes an anteriorly concave loop that in the larger specimens gradually shallows (EKSC 3A1, 22b) and doubles up by bulging in its center (EKSC 221+224, 2a-d, 1A1+bl). Apart from

this bulging, however, little scale transgression occurred below the main lateral line in the latter four specimens. Instead, at this point it was the squamation above the main lateral line that progressed forward in a straight or gently undulating line that gradually steepened with growth. Consequently, in the largest specimens the unevenness between development of the ventral and dorsal scale cover has been reduced. In the four largest specimens both the ventrolateral and the median ventral sensory lines are surrounded by strips of minute scales, and at the point of transition between the two lines, in the pectoral girdle region, the strip broadens to form a bulge around the posterior end of the median ventral line (Fig. 4,C, *mv1*). The strip of surrounding scales makes the median ventral line prominent enough to be traceable.

In the largest Lebach specimen (40049, ± 500 mm) the dorsal scales extend into the otic region and the scale cover thus is more extensive above the main lateral line (and its frontal extension, the otic branch of the infraorbital sensory line) than below it. In contrast, in the largest HQ specimen (EKSC 1A1+bl, 410 mm) the dorsal squamation reaches only to the level of the pelvic spine; consequently, there is a large gap between the most anterior dorsal scales and the dermal plates of the head, and the scale cover is more extensive below the main lateral line than above it. However, there are strong reasons to believe that the "contrast" is due only to the unfinished development of the squamation in the HQ specimen. It has been noted already by Watson (1937)

that in the Acanthodiformes the squamation was undergoing a regressive development (see also Miles, 1965, p. 247). Although generally this may not be noticeable below the family level and within such a short interval as Upper Pennsylvanian to Lower Permian, the above comparison of the Lebach P. 6192 and HQ EKSC 22b specimens nevertheless demonstrates clearly the ontogenetically earlier development of the scale cover in the HQ *Acanthodes* (there is no substantial difference in size between the largest specimens from HQ and Lebach, and there is no reason to assume any significantly different growth rates for them). This does not necessarily mean that the scale cover was more extensive in Upper Pennsylvanian than in Lower Permian *Acanthodes*, but it nonetheless makes it unlikely that the EKSC 1A1+bl specimen would be exhibiting the ultimate extent of its squamation. This argument is further supported by the above noted *Acanthodes* from the Manzanita Mountains of New Mexico, which is roughly contemporary with the HQ material and in which the squamation extends into the otic region, as it does in the 40049 specimen from Lebach. The New Mexico *Acanthodes* is of interest also in another respect: The squamation is present in the otic region in specimens that are only 230 and 180 mm in total length (OUSM 00447 and 00448, respectively; Zidek, 1975b, pl. 1A, *sq*). Yet another specimen (OUSM 00449; Zidek, 1975b, pl. 2B), although fragmentary, shows that at the Manzanita Mountains locality the size attainable did not differ substantially from that of the largest HQ and Lebach specimens. Consequently, the extensive scale cover of the New Mexico specimens cannot be explained away by assuming a significantly smaller "full" (governed by life span and environmental conditions) size for them. It appears rather that they acquired squamation more rapidly, and that over 50 percent of the growth occurred only after the fish were fully scaled.

To summarize, in the Lebach specimens studied by Watson (1937) the pattern of squamation development remained relatively unchanged during growth, with the squamation proceeding forward in a triangle divided by the main lateral line into two equal halves, dorsal and ventral, and with the scales around the ventrolateral sensory line remaining isolated from the squamation of the ventral half of the triangle. In the HQ specimens, on the other hand, the pattern gradually

changed, the change being due to the fusion of the more rapidly acquired squamation in the larger, ventral part of the triangle with the scales associated with the ventrolateral sensory line. Either most (HQ, Lebach) or all (Manzanita Mountains) of the squamation formed before the fish reached roughly 50 percent (over 200 mm) of their "full" length. After that the squamation progressed very little, except for the anterodorsal area over which the scales spread into the otic region.

The opportunity to study the ontogenetic development of the squamation in fossil fish is extremely limited, and observations are thus difficult to interpret with any degree of confidence unless inference can be made from study of the living fish (the fact that the Acanthodii is an entirely extinct group of obscure relationships should not be a serious setback as far as the squamation is concerned). Unfortunately, the process of squamation development is not among the best known aspects of ichthyology, being presently known for relatively few genera, namely of the Polypteridae, Lepisosteidae, Anguillidae, Clupeidae, Salmonidae, Cyclopteridae, Centrarchidae, Sciaenidae, and Cyprinidae (see van Oosten, 1957; Jollie, 1962; Ørving, 1972; and Armstrong, 1973, for further references). Even in modern fish it is not always clear whether the scale appearance is correlated to specimen length or to its age (see van Oosten, 1957, p. 227; Armstrong, 1973, for comments), and it appears that the determining factor may be both, either size or age, in a single family. In the study of modern fish a simple way of determining the governing factor would be the detection of the time of appearance of the very first scales. Thus, for instance, in the cyprinid *Brachydanio rerio* (zebra fish) Armstrong (1973) found that "all fish, regardless of age, showed evidence of scale development only when they reached a mean length of 1.15 cm (± 0.03)," leaving no doubt that in the zebra fish the scale development is correlated to specimen size rather than to age. In the HQ *Acanthodes* the extent of the scale cover appears to be correlated to the specimen size, although there are no specimens small enough to demonstrate the appearance of the very first scales. Needless to say, a number of very small and extraordinarily well-preserved specimens would be needed to determine the governing factor. Furthermore, the sample represents only a highly discontinuous sequence in

which the gaps are certainly large enough to obscure any variation in growth rate between individuals and which almost certainly includes more than one generation and cannot thus be regarded as truly ontogenetic. Under these circumstances it is best concluded that the material presently available does not provide a conclusive answer to the question of the determining factor.

In the light of Ørvig's (1972, p. 147-148) discussion of the structure and growth of the acanthodian scales as compared to the ganoid scales and to the zonally growing scales of Paleozoic elasmobranchs such as *Protacrodus* and *Holmesella*, the overall similarity between *Acanthodes* and various teleostomians in the pattern of squamation development looks less impressive and, as Ørvig (1972) concludes, "presumably not particularly significant from the point of view of phylogeny." Nevertheless, the numerous patterns of squamation development known to exist in modern teleostomians even below the family level at least allow the inference that the two *Acanthodes* patterns outlined above do not differ from one another substantially and should not be regarded as more than an additional evidence for differentiating between the HQ and Lebach *Acanthodes*. In the Manzanita Mountains *Acanthodes* the pattern of squamation development is not known, but nevertheless these specimens may be separated from the HQ and Lebach ones based on the significantly different rate of squamation development.

TAXONOMY

GENERAL REMARKS

All the previously reported North American occurrences of *Acanthodes* either belong to other genera or are indeterminate as to species (see Introduction and the section on Mazon Creek *Acanthodes*), and the European species need revision urgently. The situation may be summarized as follows: Although since the publication of Watson's (1937) paper a considerable amount of work has been done on the anatomy of *Acanthodes* by Miles, Nelson, and Heyler (see references cited), most of this work has been aimed at solving the question of relationships of the Acanthodii, with the genus *Acanthodes* chosen simply because it exhibits the most structure, and the taxonomical situation within the genus has not been dealt with. From Watson's work, which

remains the most recent work of value in the taxonomy of *Acanthodes*, it is clear that *A. bronni* Agassiz is in fact a conglomerate of several species (see also Introduction, p. 4), and consequently that at the present time the genus lacks a type species. Of the other Upper Carboniferous (Pennsylvanian) and Lower Permian European species, *A. rouvillei* Sauvage shows no characters to permit its distinction from *A. bronni* (Heyler, 1969, p. 40, footnote); *A. major* Davis in all probability is a large individual of *A. wardi* (Miles, 1970, fig. 3 and p. 348, 354 labeled the tail of *A. major* as *A. wardi*; however, no reason was given for the change of name and the specimen may have been simply mislabeled); and *A. punctatus* Fritsch is clearly indeterminate as to species. According to Kner (1868), *A. gracilis* (Beyrich) Roemer differs from *A. bronni* in its more slender proportions, relatively larger scales, and more anteriorly situated pelvic fin. However, Kner referred also the Lebach specimens to *A. gracilis*, and his opinion concerning the difference between the two species was contested by Woodward (1891), who placed *A. gracilis* in synonymy of *A. bronni*. Finally, *A. wardi* Egerton was described as being less bulky than *A. bronni*, but not as slender as *A. gracilis* (Egerton, 1866; Davis, 1894). The data available in the literature obviously are too vague for making conclusions concerning the status of these two species. The structure of the pectoral girdle in *A. gracilis* (see Fritsch, 1893; Miles, 1973a, p. 156), and the large extent of the dermal bones of the head and the more posterior position of the pelvic spine reported by Davis (1894) in *A. wardi*, are points in favor of validity of both the species, but the definite decision of the matter will have to await a revision of these species and of *A. "bronni."*

The specimen length : height ratio is unlikely to be of taxonomic value, for the body height can almost always be only roughly estimated, and the ratio appears to have been approximately 5.5 to 6.5 in most, if not all, species so far described. Two notable exceptions are the restorations of *A. beecheri* by Eastman (1902, fig. 14) and of an *Acanthodes* sp. specimen from Lebach by Watson (1937, fig. 21), in which the ratios are 9 and 8, respectively. Although the existing two specimens named *A. beecheri* are juveniles in which the length : height ratio may be expected to have been somewhat higher than in the mature individuals, their examination reveals that Eastman

has underestimated the body height, and consequently that the ratio is only 6 or 7. A similar explanation is to be expected also for the restoration of the Lebach *Acanthodes* by Watson.

The spine-length ratios and probably also the distribution of the fin spines relative to each other appear to have been stable throughout ontogeny and would thus make the most convenient taxonomic criteria, allowing identification regardless of specimen size. However, it will require re-examination of all the existing materials to determine which of these ratios are usable only on the generic level and which can be used also on the species level. In case of the species erected below the situation is simplified by the anal and dorsal spines being of equal length.

In regard to scale size compared to overall specimen size, the existing accounts are scarce, too general, and contradictory. The scale counts obtained from the HQ and New Mexico *Acanthodes* indicate that the scale size cannot be used in species determinations, but far more data will be needed before this question can be answered conclusively.

The mandibular bone length and the circum-orbital ring diameter should prove to be good criteria, although for both accurate measurements are difficult to obtain, and their negative differential growth has to be taken into consideration. Unfortunately, the lack of data eliminates the two elements from taxonomic considerations at the present time.

The dermal plates of the head (size, morphology, extent), the branchiostegal rays (number, form, size in relation to the adjacent mandibular bones), the pectoral girdle (namely the co-ossification vs. separate ossification of the scapular blade and the suprascapula), the tail (namely its endoskeletal support), the squamation development (rate and pattern), and the ossification of the endoskeleton (its beginning in ontogeny and rate) may be important criteria, although some of them probably are not useful below the sub-generic level. Furthermore, in most instances their application is likely to be hindered by inadequate preservation, and, in case of the latter two, because of unavailability of adequate growth series.

It is apparent from the above account that it will require a thorough revision of the genus to establish exactly what the criteria for differentiat-

ing between species should be and which of the previously described species are valid. In the absence of such a revision the grounds for comparison of the HQ specimens with the other collections of *Acanthodes* are severely limited and arbitrary. These limitations notwithstanding, it is nevertheless possible to recognize the existence of two species of *Acanthodes* in the HQ, *A. bridgei*, Zidek, n. sp., and a second species which is so far known from only a single specimen, the EKSC 240, and for reasons given below is left unnamed here.

The HQ specimens EKSC 39C (Fig. 11, *A*; Pl. 7, *B*), EKSC 56, OUSM 00472 (Fig. 10), and OUSM 00497 (Fig. 7, *B*) are too fragmentary to be referred to the new species with certainty, and they are here therefore labeled as *Acanthodes* sp. cf. *A. bridgei*. EKSC 52, 230B, 315A, and the EKSC unnumbered lower jaw (Fig. 3) do not provide any criteria for species identification and can be labeled only as *Acanthodes* sp. indet.

SYSTEMATIC DESCRIPTIONS

Genus ACANTHODES Agassiz, 1833

Type species.—*A. bronni* Agassiz, 1833, p. 20.

ACANTHODES BRIDGEI Zidek, new species

Figures 2, *B,C*; 4, *B,C*; 6, *B*; 7, *A,C*; 8, *B*; 9; 11, *A,B,D*; 12; 13; 14, *A*; 15; Plates 1; 2; 3; 4, *A,B*; 5, *B,C*; 6, *A,B*; 7, *A*

Etymology.—The species is named in honor of Dr. Thomas E. Bridge of Emporia Kansas State College, who initiated and supervised collecting in the Hamilton Quarry and personally collected many of the specimens discussed in this paper.

Holotype.—EKSC 1A1+bl, an almost complete fish 410 mm in total length, in counterparts (see Pl. 2 for preservation; also Fig. 5; 6; 7, *C*; 8, *B*; 11, *A*; 14, *B*; Pl. 3; 6, *A*).

Paratypes.—EKSC 2a-d (Fig. 2, *B*; 4, *B*; 14, *A*; Pl. 1), 3A1 (Fig. 2, *C*; Pl. 5, *B*), 4Ab+Bb (Fig. 4, *C*; 11, *B*; Pl. 5, *C*), 8bb (Pl. 4, *B*), 22b, 108+222 (Pl. 4, *A*), 221+224. (See Fig. 12 and 13 for measurements and squamation development in the type series specimens, and Fig. 15 for a restoration).

Discussion.—Although, except for the neurocranium, the new species is known in considerable detail, due to the situation outlined in the above remarks it is not possible at the present time to provide a rigorous diagnosis for it. Nevertheless,

its erection is justifiable on the grounds apparent from the following comparisons.

The anal and dorsal spines are of equal length, as is the case also in the HQ unnamed species and in *Acanthodes* "beecheri" from Mazon Creek, Illinois, but these species differ from *A. bridgei* in several respects. The HQ unnamed species has substantially larger orbits, a shorter pre-pectoral (namely branchial) region, shallower spine insertions, and spines that are somewhat longer in proportion to the total body length. *A. "beecheri"* is different in having the scapular blade co-ossified with the suprascapula, in the spines being substantially shorter in proportion to the total body length, and in that the jaws ossified remarkably early in ontogeny.

A. bridgei differs from the Lebach *Acanthodes* in a faster rate of squamation development and also in its pattern. For the other materials of *Acanthodes* the squamation development is not known, but some New Mexico specimens that are roughly contemporary with *A. bridgei* offer evidence that the scale cover developed significantly more rapidly in them than in *A. bridgei*.

The extent of the polygonal dermal plates in the head differs from that described for the Lebach *Acanthodes* in that in *A. bridgei* they appear to be absent behind the orbits and reach below the profundus sensory line. The other dermal elements are present in even the smallest HQ juveniles, in which no ossification of the jaws and only a very limited ossification of the neurocranium can be detected. Thus, the development of the exoskeleton preceded the ossification of the endoskeleton in ontogeny, and it is therefore interesting that in spite of favorable preservation of the HQ juveniles the polygonal dermal plates are found only in the mature or nearly mature specimens. This may be caused by deficient preservation, but considering the number of specimens examined, and the contrast in this respect between them and a New Mexico juvenile in which the polygonal dermal plates are clearly apparent (Zidek, 1975b, fig. 2E), the matter is worth mentioning.

A. bridgei does not differ markedly from the other Pennsylvanian and Lower Permian *Acanthodes* in the ultimate extent of ossification of the endoskeleton, but particularly with respect to the neurocranium and the jaws differs definitely in the time of beginning of the ossification in

ontogeny. As noted above, the jaws are well ossified in a 65 to 70 mm-long juvenile from Mazon Creek (*A. "beecheri"*, Desmoinesian), whereas in the Lower Permian *Acanthodes* from Lebach the endoskeleton of the head remains unossified even in specimens over 100 mm long (MNB P6192; see Watson, 1937, p. 103). In *A. bridgei* the labyrinth ossified earlier in ontogeny than it did in the Lebach *Acanthodes* (the specimens described by Heyler, 1969, from the Lower Permian of France are in this respect comparable to those from Lebach), but in the juvenile individuals of *A. bridgei* that are in the size range of the Mazon Creek specimen there is no evidence of ossification of the jaws and only small traces of ossification of the neurocranium. Consequently, in correspondence with its Virgilian age, *A. bridgei* may be said to be intermediate between the Desmoinesian and Autunian (Lower Permian) materials in regard to the time in ontogeny when the ossification of the endoskeleton began. An *Acanthodes* sp. specimen from the Virgilian of New Mexico (USNM 187147; see Zidek, 1975b, pl. 1E) that may be estimated to have been ± 150 mm in total length shows no ossification of the endoskeleton in the head, but in this case it is not clear whether this is the true condition or whether it is rather the result of deficient preservation. From the few available juveniles it is thus not clear whether the difference just outlined could be used in differentiating between species, namely between the contemporary ones; nevertheless, at the present state of our knowledge it seems practical to use it at least provisionally as a basis for separating the species under discussion from other species described to date.

The caudal radials are straight and are more widely spaced than are the arched radials in *A. "bronni"* and *A. gracilis*. In this respect the tail of *A. bridgei* is similar to that of *A. wardi*, but in contrast to that species the longitudinal division of the hypochordal lobe in *A. bridgei* is not expanded posteriorly as it passes into the axial lobe.

Although this account is limited by the paucity of features that can be compared at present, it is nevertheless adequate to show that the combination of characters found in the HQ specimens under discussion is unique, indicating a new species.

Referred specimens.—EKSC 5b+6b (Fig. 9; 11, A; Pl. 6, B), 11A1, 23B, 28Ab, 30A+B, 47A+B

(Fig. 11, *A*; Pl. 7, *A*), 61, 201, 228 (Fig. 11*D*), 231, 232, 281*b*, 417*A*, 417*B*+421, 459, OUSM 00470, 00471.

Occurrence.—All specimens are from an Upper Pennsylvanian clastic limestone in the Hamilton Quarry, Greenwood County, Kansas (see Introduction).

UNNAMED SPECIES FROM HAMILTON QUARRY

Plate 5, *A*

The specimen studied (EKSC 240) is a juvenile 56.5 mm in total length, in which no ossification of the jaws, and only a very limited ossification of the neurocranium can be detected. The anal and dorsal spines are of equal length as in *Acanthodes bridgei*, but the specimen differs in the remarkably large diameter of the circumorbital ring and in the shallow insertions of the fin spines (see the section "Fin Spines, Body Proportions, Growth," paragraphs d and f). Also, the spines are somewhat longer in proportion to the total size of the fish, whereas the pre-pectoral region is shorter than in *A. bridgei* (see Fig. 12). From the mode of preservation it is apparent that the shallow spine insertions are not the result of post-mortem loosening of the spines, a point which might come under question, but the large size of the circumorbital ring cannot be disputed. In

relation to the pre-pectoral length the diameter of the circumorbital ring comprises 44 percent of that length, as compared to only 35 percent or less in the other HQ specimens of comparable size. This discrepancy is remarkably high and it thus seems clear that the EKSC 240 specimen belongs to a species other than *A. bridgei*. Unfortunately, only this one specimen has been found so far, and it is among the smallest of the juveniles known from the locality. In absence of a sufficiently complete growth series it might prove impossible to identify this juvenile with a conspecific individual of different size. For that reason the species is left unnamed, pending the possibility of future discoveries in HQ.

The shallow spine insertions and the relatively short pre-pectoral (namely branchial) region are atypical of *Acanthodes*, and the recovery of additional specimens may show that the species is not assignable to this genus. However, the EKSC 240 alone certainly does not warrant the erection of a new genus, and therefore the specimen is here assigned to *Acanthodes*, although with some doubt.

Referred specimen.—EKSC 240 (Pl. 5, *A*).

Occurrence.—Upper Pennsylvanian clastic limestone, Hamilton Quarry, Greenwood County, Kansas.

MAZON CREEK ACANTHODES

The acanthodian specimens from the Pennsylvanian of Mazon Creek, Illinois, were described under the names of *Acanthodes marshi* and *A. beecheri* by Eastman (1902). These two species, and also *Cercariomorphus parvisquamis* Cope from Linton, Ohio (regarded as an amphibian by Cope, 1885, and Moodie, 1916, and as a xenacanth shark by Romer, 1930), were later commented upon by Gregory (1951), who concluded that the scaleless *A. beecheri* specimens are immature and possibly represent the young of *A. marshi*, and that the squamation of *C. parvisquamis* (as illustrated by Moodie, 1916, pl. 24, fig. 2) reveals strong resemblance to acanthodian scales such as those in *A. marshi*. My re-examination of the type specimen of *Cercariomorphus* (AMNH 2560) has shown, however, that it is an aistopod amphibian.

The holotype of *Acanthodes marshi* consists of a small section of the squamation (YPM 2803;

Eastman, 1902, pl. 7, figs. 1, 2), the individual scales of which were characterized by Eastman (1902, p. 93) as "averaging about one square millimeter in size, smooth and polished externally, gently convex or rounded on both the outer and attached surfaces. . . . Attached surface of some scales crossed by a shallow diagonal groove." The other specimens assigned by Eastman to this species are the remnant of a large pectoral fin consisting of the spine, dermatrichia, and vaguely preserved radial elements (YPM 2804; Eastman, 1902, pl. 6, fig. 3; cf. also Jarvik, 1959, fig. 5*D*), a smaller fin, possibly the dorsal, showing an almost complete spine and a large portion of the fin squamation (YPM 2805; Eastman, 1902, pl. 5, fig. 3), and several detached spines. Also, a patch of scales associated with a spine and a lower jaw (LACM 1353) from the Mazon Creek area was identified as *A. marshi* by Gregory

(1951, pl. 11, 12), and Romer (1952, p. 49) referred certain spines from the Pennsylvanian and Permian of southwestern Pennsylvania to *Acanthodes* sp. cf. *A. marshi* (see also Lund, 1970, p. 238). In the specimen of Gregory the scales are only slightly smaller than in YPM 2803, and the jaw has a distinct gap between the anterior and posterior ossifications.

Gregory (1951) noted similarities between LACM 1353 and YPM 2803 in the large size of both and in the strong convexity of the scale crowns. It should be stressed, however, that the relief of the crowns is subject to variation in an individual, generally increasing both dorsad and ventrad from the main lateral line. Since the scales increased in size by the addition of areal zones of growth to the crown throughout ontogeny, their size simply reflects the overall size of an individual. Thus, both the scale relief and the scale size are totally valueless as criteria for species assignments. In the case of the fin spines, the only thing that distinguishes them from some other, although not all, *Acanthodes* fin spines is their large size (Zidek, 1975a, fig. 4, 6A for equally large spines of identical morphology from the Lower Permian of Oklahoma). As far as is known, there is no morphological feature present in the spines of *Acanthodes* that would allow a basis for distinction between species, and as in case of the scales, their size alone is taxonomically worthless. It is thus quite obvious that all the specimens listed in the previous paragraph are identifiable only generically, and therefore that the species *A. marshi* is not valid.

A. beecheri is based on two specimens, YPM 114 and YPM 630, the latter of which was designated as the lectotype by Gregory (1951). Eastman (1902, p. 94-95, fig. 14, composite) characterized the species as follows: "A very small species, attaining an extreme length of about 5.5 cm. Body elongated and slender, the maximum depth being contained about nine times in the total length. Pectoral spines not much stouter or longer than the others; pelvic fins small, slightly nearer the pectorals than the anal; anal fin slightly larger than the dorsal, which is placed immediately behind. Length of dorsal and anal spines greater than maximum depth of the trunk. Caudal lobe remarkably elongate. Scales very minute."

Both the specimens are incomplete, lacking

the tails and with the heads only partially preserved as vague impressions. YPM 114 probably did not exceed 55 mm but YPM 630 may be estimated to have been 65 to 70 mm in total length. YPM 630 is exposed laterally and shows that the flank was 7 mm high in the area between the dorsal and anal spines. In the pectoral girdle region the body height thus had to be 9 to 10 mm, showing the maximum body height to be 0.14 to 0.16 of the total length. Eastman (1902) considered the most marked characteristic of *A. beecheri* to be the small size of the pectoral spines. However, in YPM 630 the pectoral spines are completely missing, and in YPM 114 there is only a fragment too small to allow estimating the spine size. The 114 specimen shows long scapular blades that apparently co-ossified with the suprascapulae (Fritsch, 1893, figs. 261, 263, 270, and pl. 107, fig. 11, all of *A. gracilis*, for pectoral girdles of similar morphology), and it is possible that Eastman confused them with the spines. In the 114 specimen the pelvic spine is 2 mm long and lies 6 mm behind the pectoral girdle; the anal spine is 4.5 mm long and lies 13 mm behind the pelvic; the dorsal spine is not preserved. The 630 specimen exhibits only the dorsal and anal spines, both 8 mm long, with the dorsal spine slightly caudad of the anal. The evidence of the dorsal and anal fin webs consists only of a few scattered scales. Also, the scales on the flank are extremely poorly preserved and scarce, making it impossible to determine either the extent of the scale cover or the number of scales per millimeter in a row. The 630 specimen exhibits a complete lower jaw with the mandibular bone, and a part of the palatoquadrate (the quadrate ossification). The lower jaw is 7 mm long, with an extensive gap between the anterior and posterior ossifications.

From comparison with the HQ *Acanthodes* (see Fig. 12) it is apparent that the distribution and the mutual size relation of the fin spines are the same, but also that the spine length : total specimen ratios are significantly higher (i.e., that the spines in the YPM specimens are remarkably short for fish 55 or 65-70 mm long). Furthermore, YPM 114 differs from all the HQ specimens in having the scapular blade co-ossified with the suprascapula and the YPM 630 in the remarkably early ossification of the jaws. It is probable, but not certain, that the two specimens belong to the same species. However, as they are only poorly

preserved juveniles, they should not receive species names, although future discoveries of additional *Acanthodes* material in the Mazon Creek area

may make it possible to give them a species assignation.

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EXPLANATIONS OF THE PLATES

PLATE 1

A. bridgei Zidek, n. sp., overall view of the somewhat more complete counterpart (*A*), and enlargement of the head and pectoral region of both the counterparts (*B*, *C*), of the paratype EKSC 2a-d ($A=2b+d$, $B=2b$, $C=2a$). The main lateral and the ventrolateral sensory lines of both sides of the flank are traced in ink. Three more dorsal branches of the main lateral line are preserved on the trunk of the 2a+c counterpart (Fig. 15). See Figure 2, *B*, for detail of the labyrinth. [Explanation: *asp*, anal spine; *cmo*, circumorbital bones; *d. mill*, dorsal branches of main lateral sensory line; *dsp*, dorsal spine; *hmv*, ventral ossification of hyomandibula; *ifc. ot*, otic branch of infraorbital sensory line; *lbr*, labyrinth; *mca*, anterior ossification of meckelian cartilage; *mdl*, mandibular sensory line; *mdo*, mandibular bone; *mill*, main lateral sensory line (of both sides); *pgl*, pectoral girdle; *poc*, preopercular sensory line; *pq*, palatoquadrate; *psp*, pectoral spine; *sc*, "scapular" sensory line (of both sides); *soc*, supraorbital sensory line; *vll*, ventrolateral sensory line (of both sides); *I-V*, posthyoidean branchial arches.]

PLATE 2

A. bridgei Zidek, n. sp., overall view of the largest specimen (EKSC 1A1+bl, holotype, the bl counterpart). See Plate 3, *A*, for detail of the head, Figure 6, *A*, and Plate 3, *B*, for the vertebral column, Figure 7, *C*, for the pectoral girdle, Figure 6, *B*, and Plate 6, *A*, for the caudal skeleton, and Figure 8, *B*, for the pelvic fin support. [Explanation: *asp*, anal spine; *cmo*, circumorbital bones; *dsp*, dorsal spine; *ld*, longitudinal division of hypochordal lobe; *mc*, meckelian cartilage; *mill*, main lateral sensory

line (of both sides); *pgl*, pectoral girdle; *pq*, palatoquadrate; *psp*, pectoral spine; *pv. pl*, pelvic basal plate; *pv. sp*, pelvic spine; *vert. col*, vertebral column; *vl*, ventral division of hypochordal lobe; *vll*, anterior part of ventrolateral sensory line.]

PLATE 3

A. bridgei Zidek, n. sp., holotype EKSC 1A1+bl, detail of the head and pectoral region (*A*, bl counterpart), and of the vertebral column (*B*, A1 counterpart). See Figure 5 for the semicylindrical laterosensory ossifications and the dermal plates of the head, Figure 6, *A*, for a schematic presentation of the vertebral column, and Figure 7, *C*, for the pectoral girdle. [Explanation: *aup*, autopalatine ossification; *br. a*, fragments of posthyoidean branchial arches, presumably epibranchials; *cmo*, circumorbital bones; *d. mill*, dorsal branches of main lateral sensory line; *dm. pl*, dermal plates of the head; *dmt*, dermatrichia of pectoral fin; *ha*, hemal arches; *hmv*, ventral ossification of hyomandibula; *mca*, anterior ossification of meckelian cartilage; *mcp*, posterior ossification of meckelian cartilage; *mill*, main lateral sensory line; *mtp*, metapterygoid ossification; *mvl*, posterior end of median ventral sensory line; *na. + n. sp.*, neural arches and spines (both members of a pair); *pfc*, profundus sensory line; *pgl*, pectoral girdle; *psp*, pectoral spine; *qu*, quadrate ossification; *soc*, supraorbital sensory line; *vll*, anterior part of ventrolateral sensory line.]

PLATE 4

A. bridgei Zidek, n. sp., an intermediate size paratype EKSC 108+222 (*A*; the 222 counterpart), and the small-

est juvenile, paratype EKSC 8bb (B). [Explanation: *asp*, anal spine; *bbr*, basibranchial; *br. sk*, branchial skeleton; *cmo*, circumorbital bones; *crh*, ceratohyal; *dsp*, dorsal spine; *mdo*, mandibular bones; *mll*, main lateral sensory line; *pgl*, pectoral girdle; *psp*, pectoral spine; *r. comm*, rostral commissure; *vll*, ventrolateral sensory line.]

PLATE 5

A juvenile of an unnamed species (EKSC 240, *A*), and two juveniles (paratypes) of *A. bridgei* Zidek, n. sp. (EKSC 3A1, *B*, and EKSC 4Bb, *C*). Note the diameter of the circumorbital ring and the shallow spine insertions in the 240 specimen. See Figure 2, *C*, for detail of the labyrinth (EKSC 3A1), Figure 4, *C*, for the mandibular bones, sensory lines, and branchial skeleton (EKSC 4Ab+Bb), and Figure 7, *A*, for the pectoral girdle (EKSC 240). [Explanation: *asp*, anal spine; *br. sk*, branchial skeleton; *cmo*, circumorbital bones; *dmt*, dermatrichia; *dsp*, dorsal spine; *lbr*, labyrinth; *mdo*, mandibular bones; *mll*, main

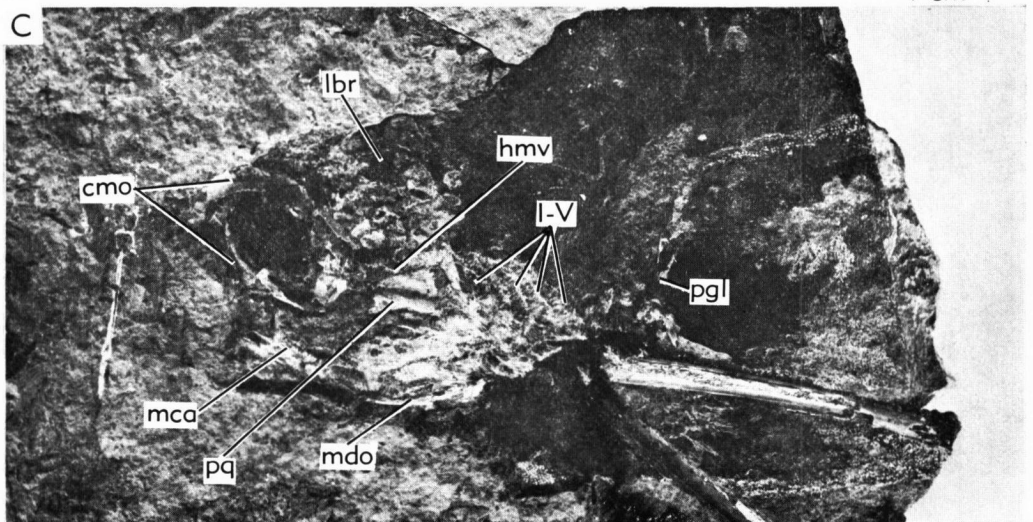
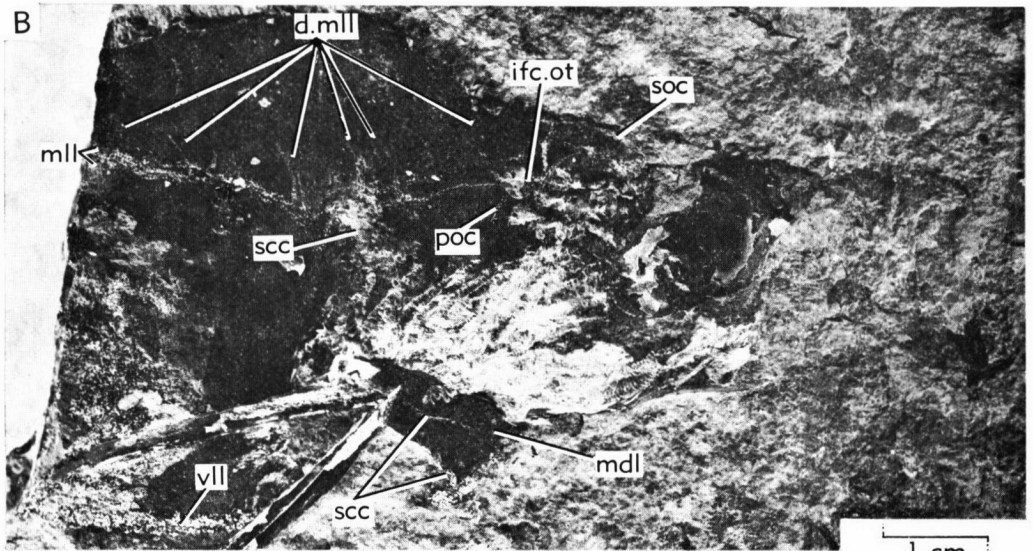
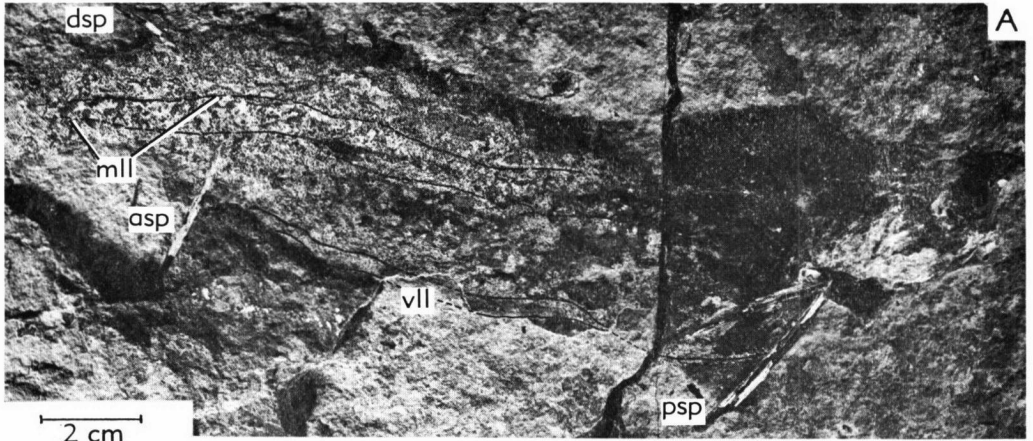
lateral sensory line (of both sides); *mvl*, median ventral sensory line; *ncr*, unidentified neurocranial ossification; *pgl*, pectoral girdle; *psp*, pectoral spine; *pv. sp*, pelvic spine; *vll*, ventrolateral sensory line.]

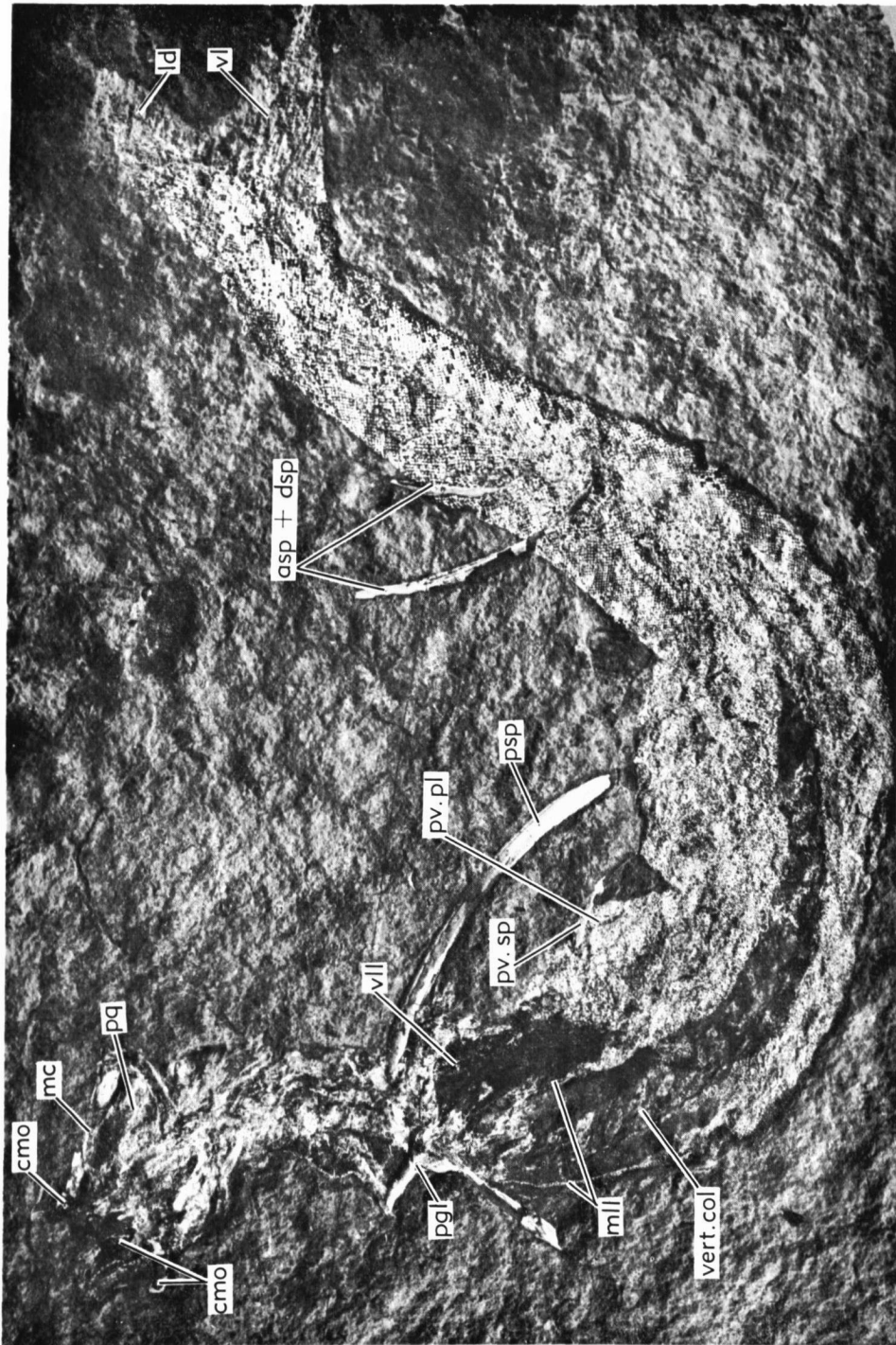
PLATE 6

A. bridgei Zidek, n. sp., skeleton and squamation of the caudal fin in the holotype EKSC 1A1 (*A*) and in the 5b specimen (*B*). The main lateral sensory line is traced in ink. See Figure 11, *A*, for a composite illustration and explanation of the squamation, and Figure 6, *B*, for the skeleton.

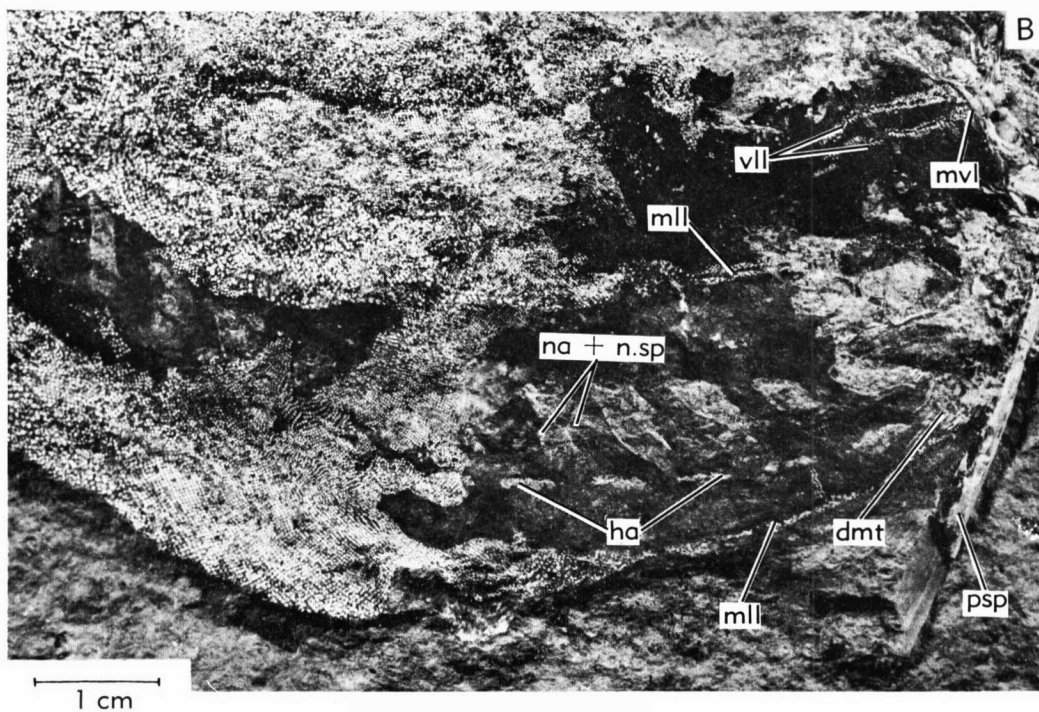
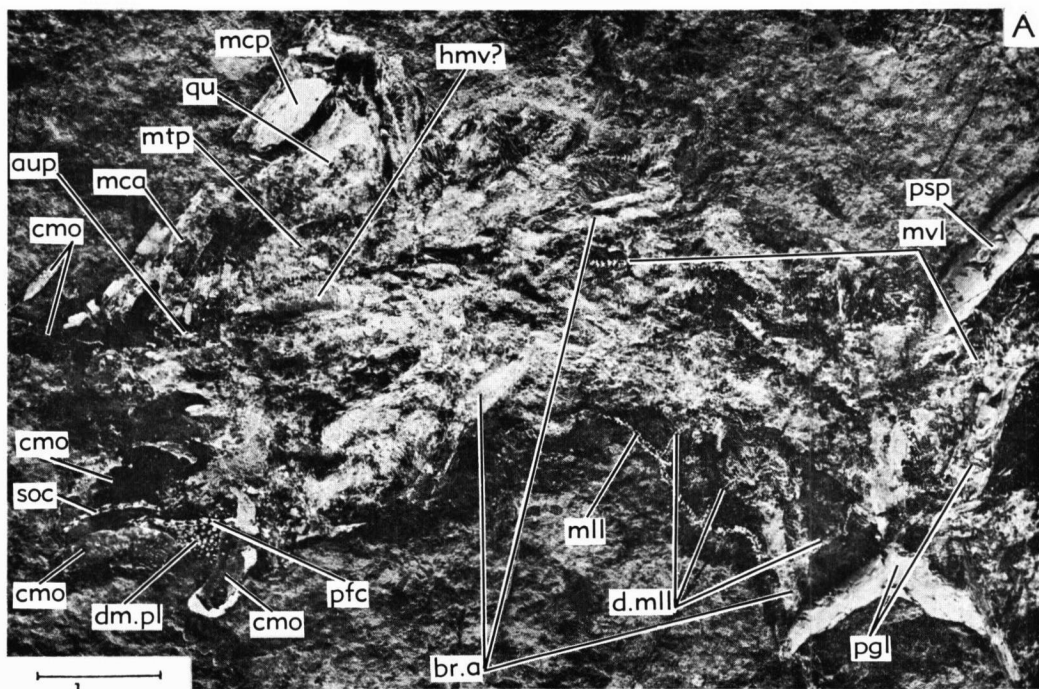
PLATE 7

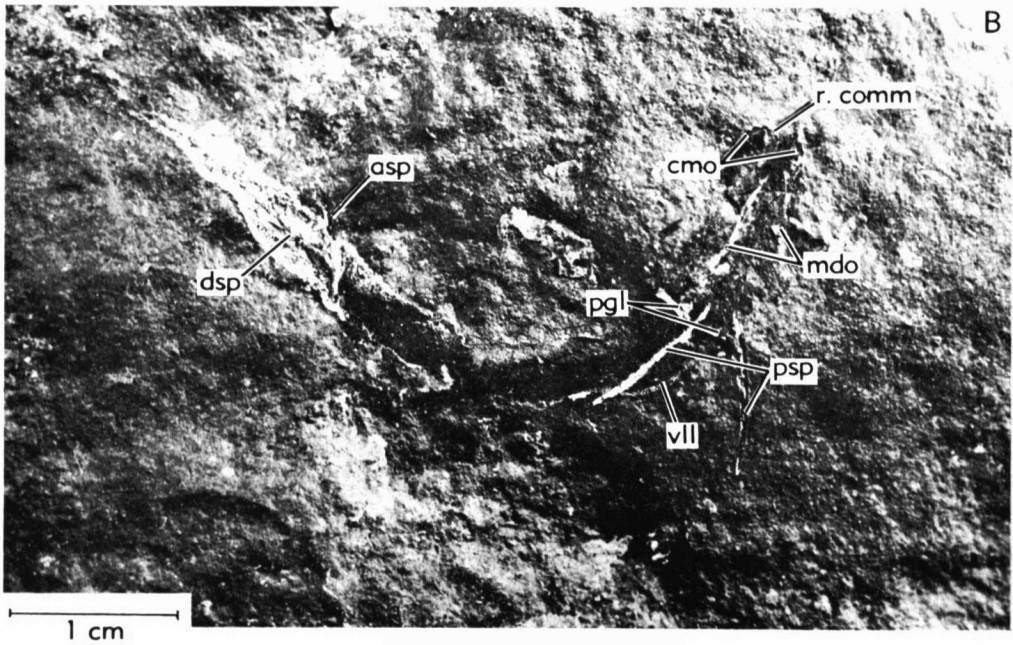
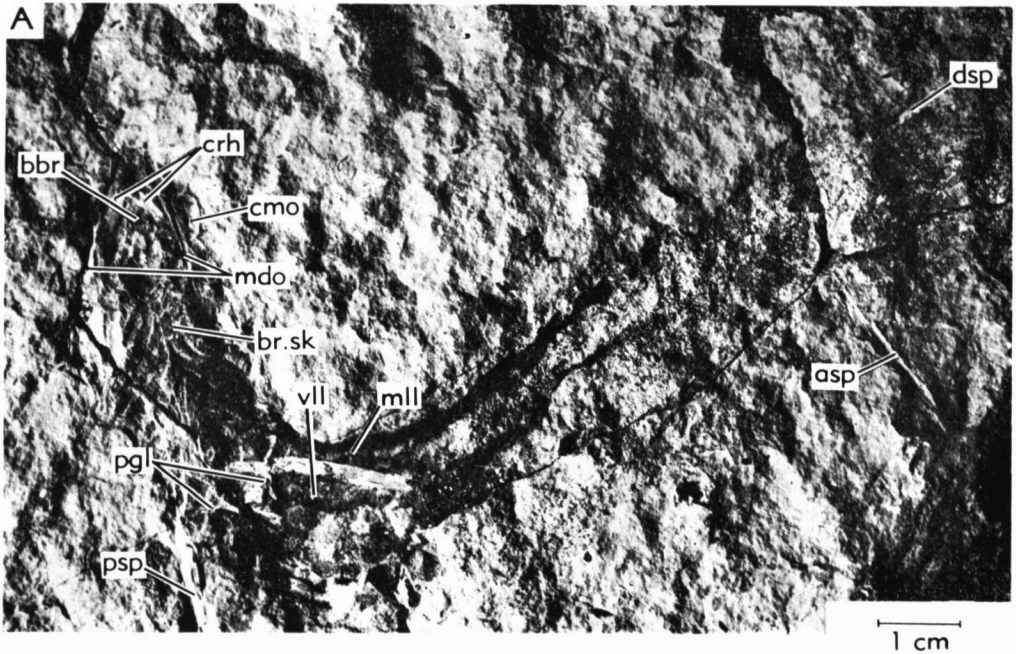
A. bridgei Zidek, n. sp., squamation of the caudal fin in the EKSC 47A (*A*) and 39C (cf. *A. bridgei*, *B*) specimens. The main lateral sensory line is traced in ink. See Figure 11, *A*, for a composite illustration and explanation of the squamation.

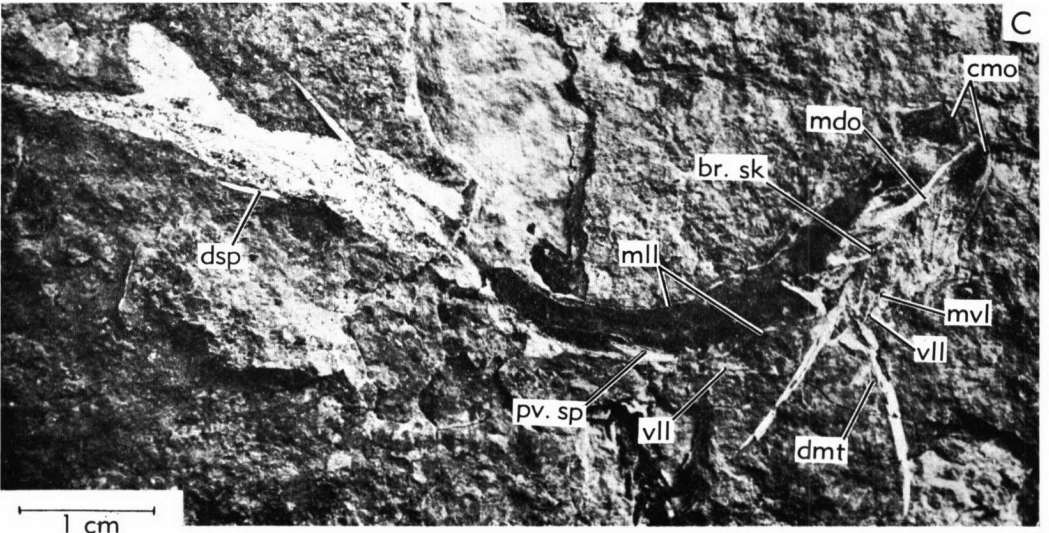
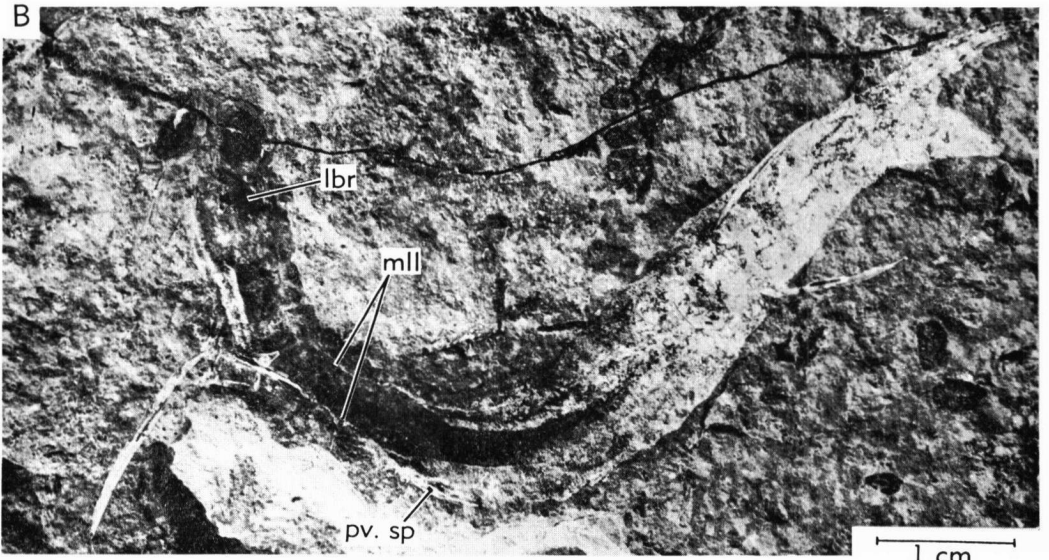
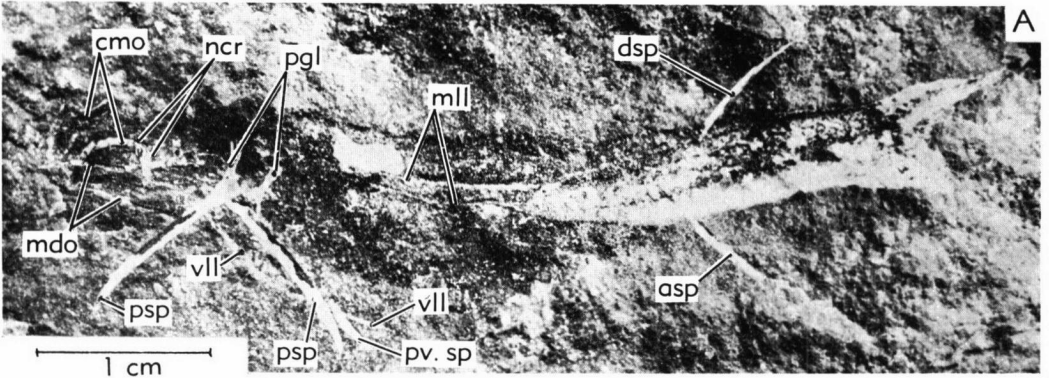


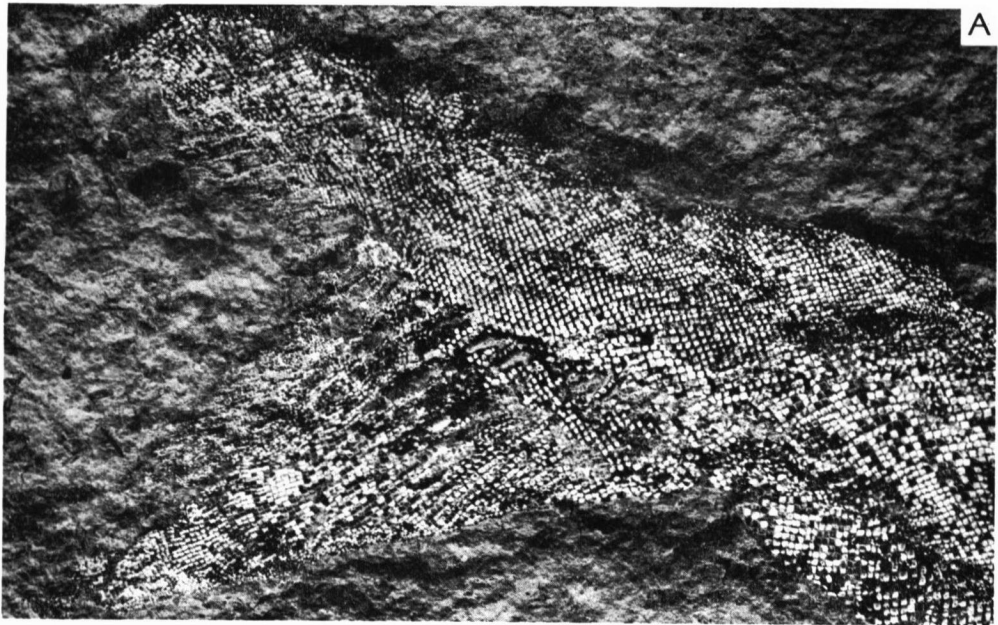


5 cm









A

1 cm



B

1 cm

