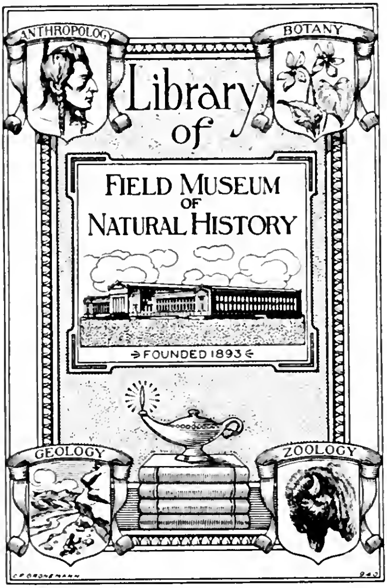
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PART III. ARTHRODIRA

ROBERT H. DENISON

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Curator of Fossil Fishes

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INTRODUCTION

The Osteostraci and Heterostraci of the Water Canyon Formation of northern Utah have been described in previous papers of this series (Denison, 1952, 1953). In the first of these a general account of the occurrence of the vertebrate remains was presented, together with detailed information on the collecting localities. For easy reference a list of the localities is repeated here. They are all in the Water Canyon Formation of Cache County, Utah, and all except Locality I are in the Bear River Range.

A. Blacksmith Fork, east side of Left Fork.

B. Blacksmith Fork, immediately south of forks.

C. Blacksmith Fork, immediately northwest of forks.

D. Blacksmith Fork, Left Fork, in the two side canyons downstream from Charlie's Hollow.

E. Green Canyon.

F. Water Canyon.

G. Cottonwood Canyon.

H. Crest of ridge, south-southeast of Naomi Peak.

I. Northwest of Dry Lake, on the eastern edge of the Wellsville Range.

Arthrodires have been found at all of these localities, but those from Locality H near Naomi Peak will not be included in this paper. The small and mostly rather poorly preserved collection from these beds represents a distinct fauna and almost certainly comes from a higher stratigraphic level, though probably below the beds referred to the Jefferson Formation.

The only previous account of arthrodires of the Water Canyon Formation was published by Branson and Mehl (1931). The form that they described as an arthrodire and named *Camptaspis utahensis* is really *Cephalaspis,* as was shown previously (Denison, 1952, p. 272). The fragments that they described and figured (pp. 516–517, pl. 1, figs. 4–6) as *Aspidichthys* sp. indet. probably belong to *Aethaspis major,* a new species to be described below. The median dorsal plate of *Dinichthys* (?)*jeffersonensis* and the jaws of *Ptyctodus* described by Branson and Mehl probably came from the lower part of the overlying Jefferson Formation, as later defined by Williams (1948, pp. 1139-40); they are Late or perhaps Middle Devonian in age.

As in my studies of the Osteostraci and Heterostraci from Utah, close comparisons have been made with the fauna from Beartooth Butte, Wyoming. In those two groups the same genera, and in some cases the same species were present in the two regions, but the common arthrodires from Utah are quite distinct genera. No specimens of the Beartooth Butte *Anarthraspis*, and only a single fragment of *Bryantolepis* have been found in the Water Canyon Formation.

The names employed for the plates of the dermal armor are those in common usage. I have avoided as far as possible the use of plate names that imply homologies with elements in Osteichthyes. New plates not previously named or described include the following: (1) paired antero-ventrals, bounded by the anterior ventro-laterals, intero-laterals, and anterior medio-ventrals, and confused with the latter by Stensiö (1944, fig. 17, B) and others; (2) posterior dorsals, median plates lying behind the median dorsal in certain early arthrodires, including those from the Beartooth Butte and Water Canyon Formations; similar plates were described as body scales in *Phlyctaenaspis acadica* by Heintz (1933, p. 142, pl. 3, fig. 4).

The specimen numbers given in the text refer to Chicago Natural History Museum specimens, unless otherwise noted. The drawings in this paper have been made, many from my original sketches, by Miss Maidi Wiebe, Staff Artist, Chicago Natural History Museum.

CLASSIFICATION OF PLACODERMS

In view of the current instability of placoderm classification, the following remarks are necessary to define and justify the usage of the higher categories employed here. Placodermi M'Coy 1848 is retained as a name for the class. Aphetohyoidea Watson 1937 is rejected, since the presence of a full hyoidean gill slit has not been clearly demonstrated in either the Acanthodii or Placodermi. Moreover, even if both groups should possess this feature, it would be improper to unite them in Aphetohyoidea since they are not closely related, as shown by many other features. Placodermi was originally proposed (M'Coy, 1848, p. 6) to exclude the ostracoderms now called Osteostraci and to include those forms now known as *Coccosteus*, *Bothriolepis*, *Pterichthyodes*, *Asterolepis*, *Chelyophorus*, and *Dipterus*. The *Dipterus* was a cranial roof described as *Polyphractus* and was not then recognized as a dipnoan. With this exception, the original use of Placodermi was to include the groups now called Euarthrodira, Antiarcha, and Ptyctodontida. It may well be extended to include the more recently discovered related groups, Phyllolepida, Petalichthyida, Radotinida, Acanthothoraci, Rhenanida, and very doubtfully the Stegoselachii. There is little justification for the procedure of Stensiö (1944, p. 75; 1948, p. 222) and White (1952, p. 298) of expanding the Arthrodira to include all the Placodermi, since the latter name has priority and long usage in this sense.

Arthrodira was proposed by Woodward (1891, p. xxi) as an order to include *Coccosteus, Brachydirus, Phlyctaenaspis, Chelyophorus, Dinichthys, Titanichthys, Macropetalichthys, Homosteus, Heterosteus, Asterosteus, Phyllolepis, Holonema,* and *Mylostoma.* The Antiarcha were specifically excluded. The genus *Asterosteus,* which could not be properly interpreted in 1891, is now known to be a representative of the highly specialized, ray-like Rhenanida. This group is probably best excluded from the Arthrodira, although Westoll (1945, p. 394) believes that they had a common origin with the Petalichthyida, and White (1952, p. 297) considers them to be related to the Brachythoraci on the slender evidence of a slight similarity in the shape of the nuchal plate. With this exception, we may follow Woodward by including in the Arthrodira the Euarthrodira, Petalichthyida, Phyllolepida, and Ptyctodontida, and may add as well the recently described Acanthothoraci and Radotinida. There can be no question of the close relationship of all of these groups.

The order Euarthrodira was introduced by Gross (1932, pp. 9, 54) to distinguish certain arthrodires from the Petalichthyida and Ptyctodontida. This name has found general acceptance. Gross subdivided the Euarthrodira into two groups: the suborder Acanthaspida of Heintz (1929, p. 24) with long trunk shields, and the Brachythoraci, a new suborder, with reduced trunk shields. Heintz (1937, p. 14) replaced Acanthaspida by Arctolepida, since *Acanthaspis,* the type genus, was found to be a petalichthyid. Stensiö (1944, p. 2) later introduced a new name, Dolichothoraci, for this group, but Heintz's earlier name is to be preferred. I consider the use of the groups Arctolepida and Brachythoraci to be unsatisfactory in that they represent a more or less arbitrary, horizontal classification without regard to phyletic considerations. In spite of the assumptions of Stensiö (1944) and White (1952), there is little doubt that the ancestors of the Brachythoraci are to be found among the Arctolepida. But until such time as euarthrodiran evolution is more clearly understood, these two groups are retained provisionally as representing a primitive (Arctolepida) and a more specialized (Brachythoraci) complex.

The classification adopted in this paper is essentially that of Gross (1937, p. 50):

- Class Placodermi M'Coy 1848
  - Superorder Antiarcha Cope 1885
  - Superorder Arthrodira Woodward 1891
    - Order Euarthrodira Gross 1932
      - Suborder Arctolepida Heintz 1937
      - Suborder Brachythoraci Gross 1932
    - Order Phyllolepida Stensiö 1934
    - Order Petalichthyida Gross 1932
    - Order Ptyctodontida Gross 1932
    - Order Radotinida Gross 1950
    - Order Acanthothoraci Stensiö 1944
  - Superorder Rhenanida Broili 1930
  - ?Superorder Stegoselachii Woodward 1924

The relationships and classification of the various genera of Arctolepida are poorly understood today. Perhaps this is not surprising when one considers that only three genera were known previous to 1929. Today, including two new genera to be described in this paper, there are 21 valid or probably valid genera, although some of them are inadequately known. For example, *Murmur* is known only from a single plate of the trunk shield that reveals little about its affinities. One genus (*Heterogaspis*) is based upon trunk shields, and another (*Svalbardaspis*) upon cranial roofs, many of which belong to other genera. *Lataspis* has been referred to *Actinolepis* by Føyn and Heintz (1943, p. 19) but is probably better retained as a distinct genus at present. *Taunaspis* is of uncertain affinities and may not belong to the Arctolepida.

For these arctolepid genera there are available four family names, not including those based upon synonyms. Two of these families, Actinolepidae Gross (1940) and Williamsaspidae White (1952), have been used to include only the type genus. The family Arctolepidae Heintz 1937 (=Monaspidae Heintz 1929; Jaekelaspidae Heintz 1932; Heterogaspidae Strand 1933) was proposed to include the Spitsbergen Arctolepida characterized by the fusion of the plates of the shield, a feature of doubtful significance. The fourth family, Phlyctaenaspidae (=Mediaspidae Heintz 1929), was apparently first used by Jaekel (1907, p. 176, "Phlyctaenaspiden") to separate *Phlyctaenaspis* from the Coccosteidae. Heintz (1932a, p. 210) employed it to include genera without completely fused plates (*Phlyctaenaspis, Mediaspis,* and *Huginaspis*), and in the 1932 edition of Zittel it included all of the Arctolepida.

In my opinion, the known Arctolepida, with one or two exceptions, are best retained for the present in a single family, for which the name Phlyctaenaspidae is selected. The exceptions are the Middle Devonian *Williamsaspis*, for which White's familial name Williamsaspidae is available, and possibly the Late Devonian *Gronlandaspis*, which, when better known, may well reveal sufficient specializations to warrant the erection of a distinct family to include it. *Taunaspis* and *Murmur* must be considered at present of uncertain affinities, but the remaining 17 genera form a relatively compact group in which subdivision into different families, particularly monotypic ones, would serve no useful purpose in our present state of knowledge. Of course, the 17 genera represent various phyletic lines, but the distinction of these lines as families (e.g. Actinolepidae) would tend to overemphasize the differences and to mask the interrelationships of the Arctolepida as a whole. However, a subdivision of the Phlyctaenaspidae into two subfamilies is made here. Definitions are given below, but a discussion of the significance of this classification is deferred until later.

Suborder **ARCTOLEPIDA** Heintz 1937

These Euarthrodira have unreduced lateral trunk shields, long contacts between the lateral and ventral trunk shields, and small to medium-sized pectoral fenestrae between the anterior laterals and anterior ventro-laterals, indicating the presence of stenobasal pectoral fins. Spinals are always present and are usually large. The median dorsal lacks an internal keel. On the cranial roof, the preorbitals are generally relatively small, the rostral and pineal are fused in adults, and the nuchal characteristically is pointed anteriorly and has the sides subparallel or converging posteriorly. The orbits are generally far anterior, small, and notch the cranial roof only slightly. The suborbital has a short suborbital process. The endocranium is platybasic, with a large suborbital shelf and a short occipital region. The ventral shield is relatively short and broad. Most Arctolepida lived in the Early Devonian, though a few survived into the Middle and Late Devonian.

Family PHLYCTAENASPIDAE Jaekel 1907

The ventral shield is nearly flat, and the spinal plates are at the lower edges of the lateral faces of the trunk shield. The spinal plates are moderately short to very long and always project posterior to their sutures with the anterior laterals and anterior ventro-laterals.

The pectoral fenestrae are small or possibly medium-sized in some genera.

Subfamily ACTINOLEPINAE, new rank

The median dorsal is short and broad. Paired antero-ventrals are present. The spinal plate is medium-sized to rather short. There is no differentiated exoskeletal articulation between the anterior dorso-laterals and the paranuchals. The following genera are included: *Actinolepis* Agassiz 1844; *Aethaspis* gen. nov.; *Anarthraspis* Bryant 1934; *Bryantolepis* Camp, Welles, and Green 1949 (=*Euryaspis* Bryant 1932); *Kujdanowiaspis* Stensiö 1942; *Lataspis* Strand 1932 (=*Plataspis* Heintz 1929); *?Mediaspis* Heintz 1929; *Simblaspis* gen. nov.; *Svalbardaspis* Heintz 1929 (in part).

Subfamily PHLYCTAENASPINAE Hay 1929

The median dorsal is long and narrow. The paired antero-ventrals are lost or indistinguishably fused with adjacent plates. The spinal plates are long. The anterior dorso-laterals have well-developed trochleae for articulation with the glenoid fossae on the paranuchals. The following genera are included: *Arctaspis* Heintz 1929; *Arctolepis* Eastman 1908 (=*Jaekelaspis* Heintz 1929); *Diadsomaspis* Gross 1937; *Elegantaspis* Heintz 1929; *?Gronlandaspis* Heintz 1932b; *Heterogaspis* Strand 1932 (=*Monaspis* Heintz 1929); *Huginaspis* Heintz 1929; *Phlyctaenaspis* Traquair 1890; *Prosphymaspis* Gross 1937; *Svalbardaspis* Heintz 1929 (in part).

"Phlyctaenaspis" heintzi Gross (1933b) resembles the Phlyctaenaspinae in most respects, but the median dorsal referred here on the evidence of its ornamentation is short and broad, as in the Actinolepinae; if the median dorsal really does belong to *"P." heintzi*, this species must be intermediate between the two subfamilies. *"Coccosteus" angustus* Traquair 1903 was referred to *Phlyctaenaspis* by Gross (1933a, p. 28) but appears to represent a new genus intermediate between the Phlyctaenaspinae and Coccosteidae. The posterior ventro-laterals and cranial roof resemble *Coccosteus*, the median dorsal is close in shape to that of *Phlyctaenaspis*, and the anterior ventro-laterals, spinals, and suborbitals are comparable both with those of *Coccosteus minor* and certain Arctolepida.

Family WILLIAMSASPIDAE White 1952

The ventral shield is convex and the spinal plates are placed rather high on the sides of the trunk shield. The spinal plates are reduced so that they do not project posteriorly to their sutures with the anterior laterals and anterior ventro-laterals. The pectoral fenestrae are rather large. One genus is included: *Williamsaspis* White 1952.

INCERTAE SEDIS

Murmur Whitley 1951 (=*Ptychaspis* Bryant 1935; *Euptychaspis* White and Moy Thomas 1941); *Taunaspis* Schmidt 1933.

ARCTOLEPIDA FROM UTAH

Arthrodires of the Water Canyon Formation occur as isolated plates, except when the plates are fused together as is often the case in cranial roofs, occasionally with the median dorsal and anterior and posterior dorso-laterals, and usually with the anterior ventro-laterals, antero-ventrals, intero-laterals, and spinals. For this reason the determination of which plates belong to the same genus and species is beset with many difficulties. Most helpful has been the type of ornamentation, which appears to be characteristic of a species. But this must be used with caution, since the ornament changes with the growth of an individual, owing to the formation of larger tubercles on the younger parts of a plate and the overgrowth by secondary tubercles on the older parts. An isolated plate of a young individual may be neither generically nor specifically identifiable, since its shape, proportions, and ornamentation may differ from that of the adult. For this reason there are many plates in the collection from Utah that must be considered as indeterminable.

Simblaspis,[1] new genus

Type species.—*S. cachensis,*[2] new species.

Diagnosis.—*Simblaspis* includes Actinolepinae with rather short, broad cranial roofs. The rostral and pineal plates are not fused to the rest of the cranial roof. The preorbital plates are relatively long, with their centers of ossification in front of the centers of the plates and with their anterior borders moderately concave for the reception of the pineal plate. The nuchal plate is very short and relatively broad. The orbital notches are shallow to moderately distinct. The endocranium is not ossified. The median dorsal plate is short and broad, with a prominent, rounded, postero-median lobe. The anterior lateral

[1] From σιμβλος, a beehive, for Utah, the beehive state, and ασπις, shield.

[2] *cachensis*, from Cache County, Utah.

plate is low, has a rather flat external face lacking ridges, a well-developed inner wing, a moderately long edge for the spinal plate, and an expanded postero-dorsal portion.

Simblaspis cachensis, new species

Type.—CNHM–PF 504, a small but well-preserved and little crushed cranial roof, lacking only the rostral and pineal plates (fig. 86, A).

Referred specimens.—An incomplete cranial roof, PF 499 (fig. 86, B); fragments of cranial roofs, PF 306, 308, 316, 500, 923 (part); left marginal, PF 521; median dorsal (fig. 88, A) and incomplete anterior or posterior medio-ventral, PF 301; incomplete median dorsal, anterior and posterior dorso-laterals, fused together, PF 965; left anterior lateral, PF 562 (fig. 88, B).

Horizon.—Early Devonian, near base of Water Canyon Formation.

Locality.—The type is from Locality D, Blacksmith Fork, NE. ¼, sec. 26, T. 11 N., R. 2 E. The referred specimens are from Localities A, B, and D in Blacksmith Fork, and Locality G in Cottonwood Canyon. All localities are in Cache County, Utah.

Diagnosis.—A species attaining a rather large size for an arctolepid; the length of the cranial roof, excluding the rostral and pineal, is 91 mm. in the largest individual. The ornament consists of small, crowded tubercles, lacking any distinctive pattern and overgrown in certain areas by large, crowded, secondary tubercles.

Description and discussion.—The considerable difference in size and the lesser differences in the shape of the cranial roofs of the smallest and largest individuals referred here suggest at first that two species are represented. The type, PF 504 (fig. 86, A), has a cranial roof, excluding the rostral and pineal, that is 47 mm. long; in PF 499 (fig. 86, B) the corresponding measurement is 91 mm. The small individual has a prominent postorbital process that forms a distinct orbital notch, and also has a deep notch between the postorbital process and the prominent postero-lateral corner formed by the marginal and postmarginal. In large individuals, the postorbital process and the orbital notch are less distinct, and the lateral margin of the cranial roof is less irregular. In both large and small individuals, with one exception, the plates of the cranial roof are completely fused together and the sutures indistinct. The fusion of the plates is indicative of cessation of growth, but it is not possible to assume at present that this was necessarily permanent. It is possible that at certain

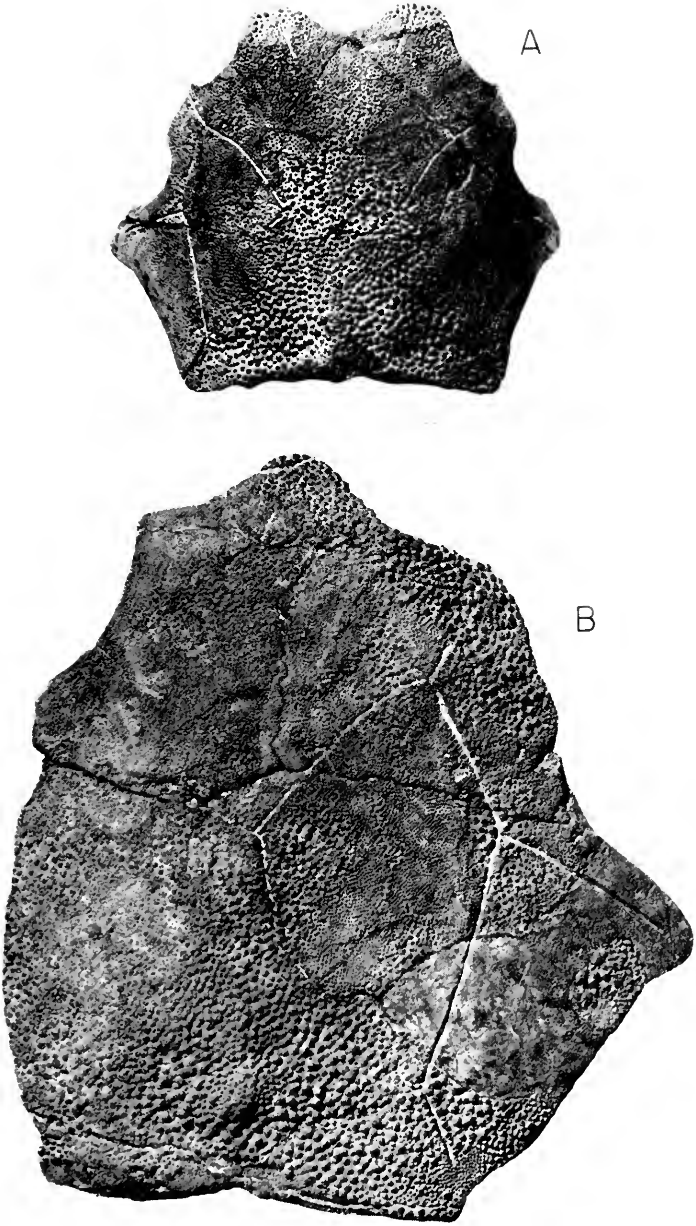

FIG. 86. *Simblaspis cachensis,* cranial roofs (× 1). A, type, PF 504; B, PF 499, incomplete on left side.

periods there was resorption at the sutures, followed by another period of growth. It is also possible that there was a high degree of variation in the time at which the sutures closed and growth ceased. A fragment of a cranial roof on PF 923 has the sutures open and the plates free in spite of the fact that this is a moderately large individual. PF 306, 308, and 316 are fragments of cranial roofs of intermediate size, and PF 308, at least, is also intermediate in the configuration of the lateral margin. These intermediate specimens, as well as the similar type of ornamentation found in all specimens, indicate that they represent a single species.

The ornament of *Simblaspis* is distinctive. The primary tubercles are small and crowded and lack any noticeable arrangement. These are overgrown by large, crowded tubercles, also lacking any pattern. The distribution of these large tubercles, however, appears to be characteristic. On the cranial roof (figs. 86, 87) they develop in a postero-median triangle covering the nuchal and the medial parts of the paranuchals and centrals. They appear on the anterior tips of the preorbitals and in large individuals develop on the rims of the orbital notches, as well as at the center of the marginals. The remainder of the cranial roof apparently retains the minute primary tubercles. In an old individual such as PF 499 (fig. 86, B) the secondary tubercles attain a much larger size than in a young individual such as PF 504 (fig. 86, A); they may well represent a third or even fourth generation of tubercles. The median dorsal (fig. 88, A) represents an old individual and is completely covered with large tubercles. On this specimen it is possible to see large tubercles, possibly representing a third generation, overgrowing medium-sized tubercles, probably of the second generation; no small, primary tubercles are visible. On the anterior lateral (fig. 88, B) the large tubercles are limited to a dorsal triangular area, while the small, primary tubercles remain on the anterior and ventral parts of the plate.

Simblaspis has a relatively unspecialized cranial roof (figs. 86, 87, 105, D). From *Kujdanowiaspis* (fig. 105, F) it is distinguished mainly by two features: one is the elongation of the preorbitals, which has taken place mostly posterior to the centers of ossification; the other is the shortness of the nuchal, which is a result of the reduction of the posterior part of the cranial roof that has affected the paranuchals as well. The posterior part of the cranial roof is similar to that of *Bryantolepis* (fig. 105, C), but *Simblaspis* does not have the firmly attached rostral and pineal, the greatly enlarged postnasals, and the short, very wide preorbitals that characterize *Bryantolepis*.

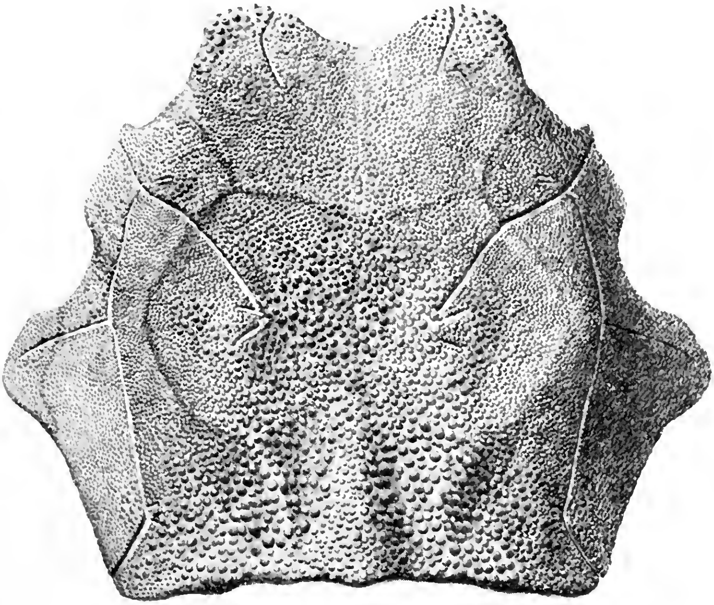

FIG. 87. *Simblaspis cachensis*, cranial roof, slightly restored from type, PF 504 (× 3/2).

The lateral line canals of the cranial roof are arranged in general as in other Arctolepida, but certain canals or pit lines rarely seen in this group are indicated in the type of *S. cachensis* (fig. 86, A). The profundus canal(= premarginal canal of Bryant, 1934, p. 137), which is prominent in *Bryantolepis* (fig. 105, C, *pfc*) and sometimes encountered in *Kujdanowiaspis* (Stensiö, 1945, p. 50), is indicated in *S. cachensis* (fig. 105, D, *pfc*) by a short groove and pits on the postorbital immediately anterior to the infraorbital canal, as well as by scattered pits postero-lateral to the end of the supraorbital canal on the preorbital. The middle and posterior pit lines (fig. 105, D, *mp, pp*) are indicated by short grooves posterior to the termination of the central canal in the middle of the central; these lines are seen also in *Aethaspis, Kujdanowiaspis,* and *Actinolepis*. On the paranuchal a short, transverse groove anterior to the opening of the endolymphatic duct indicates the posterior end of the posterior pit line (fig. 105, D, *pp*), while a similar groove posterior to the endolymphatic duct represents part of the supratemporal commissure (fig. 105, D, *stc*);

the only other arctolepid showing these canals is *Actinolepis* (fig. 105, H).

The median dorsal of *Simblaspis* (figs. 88, A; 107, G) is relatively short and broad, as is typical of the Actinolepinae. It is very similar to that of *Kujdanowiaspis* (fig. 107, I) and *Bryantolepis* (fig. 107, H), though having a more prominent postero-median lobe than the former, and possessing an antero-median convexity not found in the latter. On either side of this antero-median convexity is a smooth, non-tuberculated area (fig. 107, G, *x*), a feature found also in *Aethaspis* and *Actinolepis,* as well as in a median dorsal referred to "*Phlyctaenaspis*" *heintzi* by Gross (1933b, p. 60, fig. 9:1). This may signify that the median dorsal was actually overridden slightly by the cranial roof when the head was elevated.

The anterior lateral (figs. 88, B; 110, C) resembles that of *Bryantolepis* (fig. 110, E) and differs from *Aethaspis* (fig. 110, D) and *Anarthraspis* (fig. 110, F) in being relatively low. Anteriorly it has a large and sharply marked inner wing (fig. 110, C, *iw*), covered, even in the large PF 562, with very small tubercles. The dorsal part of the plate is relatively long and has coarse tuberculation. The ventral part of the plate is somewhat shortened, suggesting that the spinal may have been reduced to some extent. The shape of the posterior, concave edge indicates that the pectoral sinus was relatively narrow, especially when compared to *Aethaspis.*

The only anterior and posterior dorso-laterals referred here with certainty (PF 965) are incomplete and so closely fused to each other and to the median dorsal that little can be said of their form. Another specimen (fig. 88, C), representing a smaller individual with firmly fused median dorsal and anterior and posterior dorso-laterals (PF 963, from Locality A), cannot be referred to *S. cachensis* because of its different type of ornament, consisting of moderately small, widely spaced tubercles. One small indication of relationship to *Simblaspis* is the peculiar dorsal twist to the lateral line at its anterior end on the anterior dorso-lateral, a feature also present in PF 965. The bone radiation can be made out in part and indicates a relatively long and shallow anterior dorso-lateral, similar to those of *Kujdanowiaspis* (fig. 108, I) and *Bryantolepis* (fig. 108, H) in shape, but with the overlap area for the anterior lateral not as deep, especially anteriorly. The posterior dorso-lateral also shows resemblances to those of *Kujdanowiaspis* (fig. 109, I) and *Bryantolepis* (fig. 109, H), having an exposed area that is of moderate depth anteriorly, constricted at the middle, and deepened greatly posteriorly.

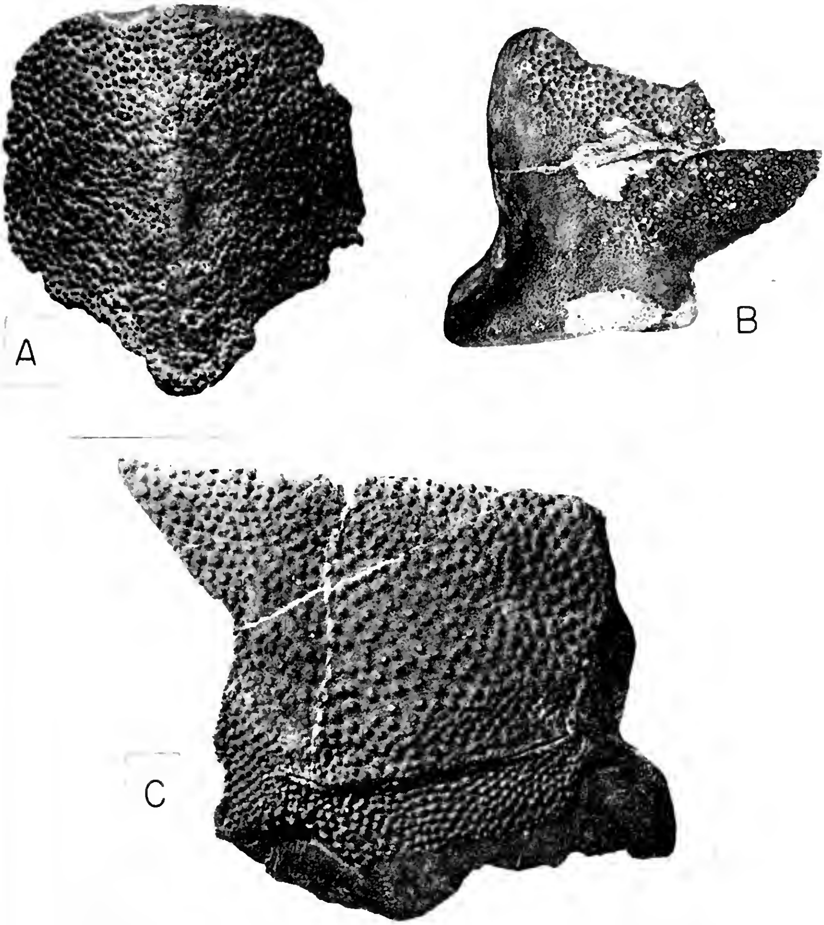

FIG. 88. A, B, *Simblaspis cachensis* (× 3/4): A, median dorsal, PF 301; B, anterior lateral, PF 562. C, *?Simblaspis* sp., anterior and posterior dorso-laterals and half of median dorsal, PF 963 (× 3/2).

In conclusion, *Simblaspis* may be said to be a moderately primitive arctolepid, most closely comparable to *Kujdanowiaspis* and *Bryantolepis*. It differs from the former especially in the elongated preorbitals and shortened nuchal and paranuchals, as well as in the shape of the anterior laterals. From *Bryantolepis* it is distinguished particularly by the fact that the rostral and pineal are not fused to the rest of the cranial roof, as well as by the elongate preorbitals and presumably small postnasals.

Aethaspis,[1] new genus

Type species.—*A. major*, new species.

Diagnosis.—*Aethaspis* includes Actinolepinae with the cranial roof broad posteriorly and tapering to a narrow anterior end. The rostral and pineal plates are fused to the preorbitals in large individuals. The postnasal plates are small and sometimes fused to the preorbitals. The preorbital plates are lengthened, especially posterior to the centers of ossification. The nuchal plate is greatly elongate and extends anteriorly between the centrals to meet the preorbitals; it is notched laterally in its posterior half by the paranuchals. The orbital notches are small. The endocranium is ossified perichondrally. The median dorsal plate is short and broad and is crested externally in its posterior half. The anterior and posterior dorso-laterals are relatively high. The anterior lateral is relatively short and high, with a well-developed inner wing, and an edge for the spinal plate of moderate length. The spinal is rather short and stout. The posterior ventro-laterals are relatively short and broad.

Aethaspis major, new species

Type.—CNHM–PF 503, a nearly complete cranial roof (fig. 89, A).

Referred specimens.—Nearly complete cranial roofs, PF 311, 1404 (fig. 89, B); fragments of cranial roofs, PF 300, 302, 313, 506, 507, 514–518, 915–919 (fig. 89, C), 1635, 1636; median dorsals, PF 563 (fig. 92, B), 905–907 (fig. 92, A), 910 (fig. 92, C), 911; posterior dorsals, type 1, PF 558 (fig. 93, A), and type 2, PF 314, 559 (fig. 93, B), 967; anterior dorso-laterals, PF 305, 532 (fig. 95, A), 922 (fig. 95, B), 971; posterior dorso-lateral, PF 303 (fig. 95, C); anterior laterals, PF 560 (fig. 97, A), 561 (fig. 97, B), 925; posterior lateral, PF 924 (fig. 98, A); intero-lateral, PF 994; anterior ventro-laterals, some with attached intero-laterals, spinals, and antero-ventrals, PF 307, 939 (fig. 98, B), 940 (fig. 98, D), 983, 988, 989 (fig. 98, C), 990, 991; ?posterior medio-ventral, PF 315 (fig. 98, F); posterior ventro-laterals, PF 913 (fig. 98, E), 968.

Horizon.—Early Devonian, near base of Water Canyon Formation.

[1] From αηθης, curious, unusual; and ασπις, shield.

Locality.—The type is from Locality B, Blacksmith Fork, S. ½, sec. 3, T. 10 N., R. 2 E. The referred specimens are from Localities A, B, C, and D in Blacksmith Fork, Locality F in Water Canyon, and Locality G in Cottonwood Canyon. All are from Cache County, Utah.

Diagnosis.—A large species attaining the following dimensions: total length of cranial roof approximately 136 mm.; length of median dorsal approximately 95 mm. The adult ornamentation is characteristic, though differing in various parts of an individual. Much of the surface is covered with large tubercles that locally in older individuals tend to coalesce to form a ridge-like ornament. Parts of certain plates have a sharply contrasting ornament of fine, crowded tubercles; this occurs on the anterior and lateral margins of the cranial roof and on the anterior face of the anterior laterals.

Aethaspis utahensis, new species

Type.—CNHM–PF 1405, a nearly complete cranial roof (fig. 90).

Referred specimens.—Suborbital, PF 1403 (fig. 94, C); incomplete median dorsal, PF 964 (fig. 94, A); posterior dorsals, type 2, PF 975, 976 (fig. 94, B), 978, 1639; anterior ventro-lateral with attached intero-lateral, spinal, and antero-ventral, PF 321 (fig. 94, E, F); and posterior ventro-lateral, PF 322 (fig. 94, D).

Horizon.—Early Devonian, near base of Water Canyon Formation.

Locality.—All of the specimens are from Locality A in a thin, limy sandstone exposed in a gully about 200 yards southwest of the northeast corner of sec. 3, T. 10 N., R. 2 E., Cache County, Utah.

Diagnosis.—A moderate-sized species; the total length of the cranial roof is approximately 68 mm. as estimated from the type, and the length of the median dorsal is 50 mm. in PF 964 (probably neither of these specimens is fully adult). The ornamentation consists of very small, moderately spaced, primary tubercles, commonly with a distinctly linear arrangement. These are overgrown by medium-sized, secondary tubercles in the centers of the plates, and primary tubercles of medium size often occur in the younger parts of plates near their periphery.

Description and discussion of Aethaspis.—The two species of *Aethaspis* are distinguished by their size and ornamentation. Since both of these features change during growth, there must be additional evidence that *A. utahensis* does not represent merely young individuals of *A. major.* The evidence from the present collection is not as satisfactory as one could wish. Although *A. major* is the most

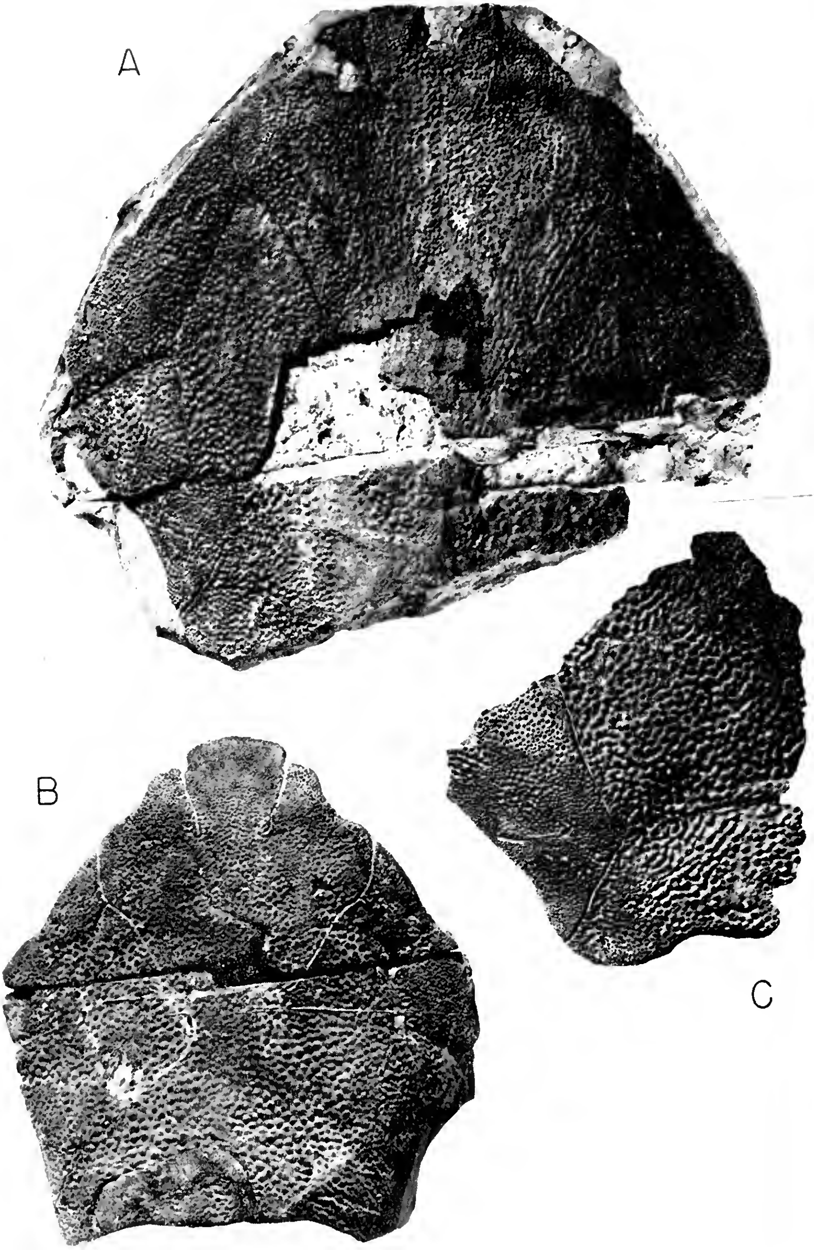

FIG. 89. *Aethaspis major*, cranial roofs (× 2/3). A, type, PF 503; B, PF 1404; C, left postero-lateral part of cranial roof, PF 919, showing main lateral line and opercular pit line on paranuchal.

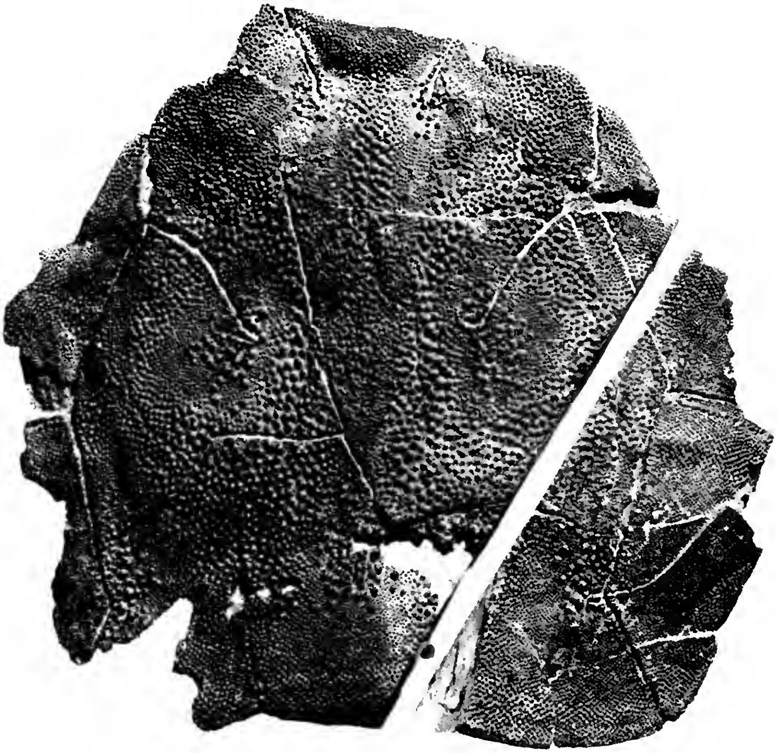

FIG. 90. *Aethaspis utahensis*, cranial roof, type, PF 1405 (× 3/2).

common arthrodire in the Water Canyon Formation and shows a certain amount of variation in size, there is only a single specimen that can be determined with certainty as belonging to a juvenile individual. This is an incomplete median dorsal (PF 563, fig. 92, B), whose total length is estimated to be 36 mm. Its median region is missing, but its outer parts are ornamented with moderate-sized tubercles showing a tendency, anteriorly at least, to unite at their bases into ridges. This ornament is distinctly of the *A. major* type. Among the known specimens of *A. utahensis* there is not one that can be proved to belong to a fully adult individual, and it is probable that the cranial roof of the type specimen is not fully grown, since its sutures are quite distinct. However, the median dorsal referred here (PF 964, fig. 94, A) is considerably larger than that of the juvenile

A. major, yet it retains the characteristic type of ornament of *A. utahensis*. Additional evidence of the distinctness of these species is provided by the posterior dorsals, type 2. PF 314, 559 (fig. 93, B), and 967 have in their posterior halves relatively large tubercles with an indication of concentric arrangement and a tendency to unite at their bases into ridges; their anterior halves are ornamented with tubercles of a sharply contrasting small size. This ornament agrees with that of *A. major*. On the other hand, PF 975 and 976 (fig. 94, B), though of similar size and shape, have the very different ornament of *A. utahensis*. These posterior dorsals also differ in their convexity. In *A. major* they are strongly vaulted and sharply crested in the posterior halves, while in *A. utahensis* the crest is lacking and the posterior half is only slightly more convex than the anterior.

With the exception of size and ornament, the two species of *Aethaspis* are very similar. There are a few other differences whose systematic importance is not certain. In *A. major* (fig. 105, B) the nuchal is relatively narrower and longer; posterior to its presumed center of ossification, it is deeply notched on both sides. In *A. utahensis* (fig. 105, A) the nuchal is relatively shorter and broader and has smaller notches in its posterior half. Another difference involves the relations of the central and marginal; in *A. major* these plates have broad contacts, while in *A. utahensis* they are separated by slender processes of the postorbital and paranuchal. In *A. utahensis* the middle and posterior pit lines are indicated on the central by short, shallow grooves (fig. 105, A, *mp, pp*), and the external opening of the endolymphatic duct is apparent on the paranuchal. None of these are seen in *A. major*, but this species sometimes shows a groove or series of grooves laterad to the main lateral line canal on the paranuchal (figs. 89, C; 105, B, *opc*). If, as seems probable, these represent a pit line of the sensory canal system, they have no known homologue in other arthrodires. However, they may be homologous to the lines in *Acanthodes* that cross the posterior part of the gill covers and which were identified as opercular lines by Watson (1937, p. 121, fig. 20) and as scapular lines by Stensiö (1947, pp. 48–49, fig. 11, D).

The most distinctive feature of *Aethaspis* is its greatly elongate nuchal (fig. 105, A, B) that meets the preorbitals and completely separates the centrals from each other. Nothing approaching this condition is found in any other euarthrodiran. The elongate preorbitals with the centers of ossification in the anterior halves are also characteristic. Long preorbitals also occur in *Actinolepis* (fig. 105, H), but there the centers of ossification are far posterior and near or at the midline. The anterior end of the cranial roof is narrow, with a small rostral and pineal, probably derived from separate ossification centers but fused in all known specimens. The postnasals were apparently extremely small. In PF 507 and 1404 (fig. 89, B) the anterior end of the preorbital is cut off in a concave fashion just laterad to the supraorbital sensory line; presumably the postnasals are absent here. In PF 311 and 313 the preorbitals are continuous with an anterior lobe that continues the convex rostral contour; probably the anterior parts of the lobes represent the postnasals, completely fused to the preorbitals.

A number of cheek plates and jaws occur in the Water Canyon Formation collection, but with one exception they are undetermin-

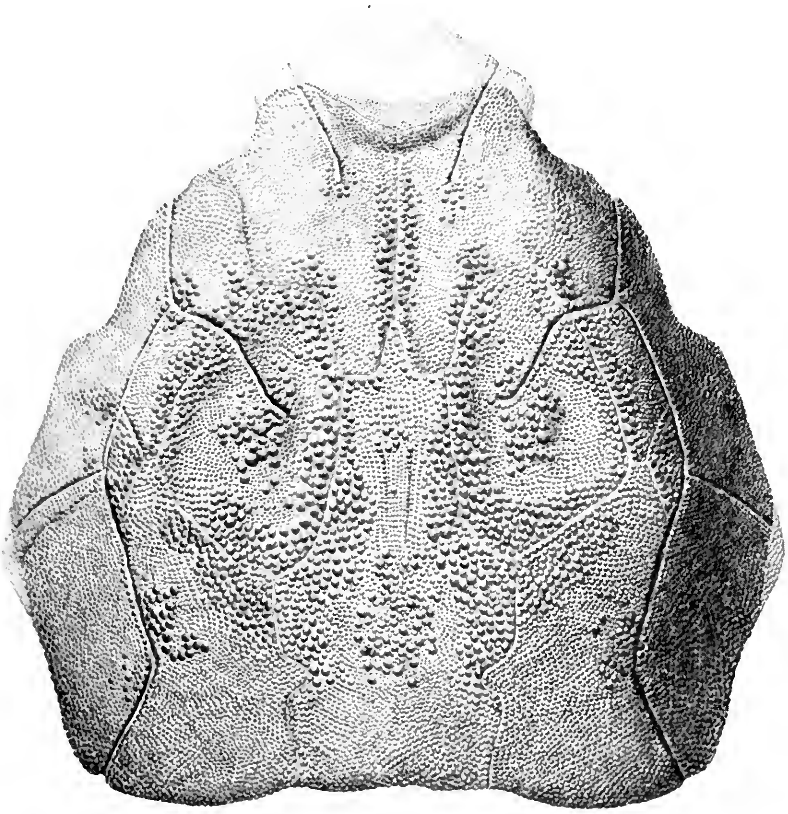

FIG. 91. *Aethaspis utahensis*, restoration of cranial roof based largely on PF 1405 (× 3/2); lightly shaded anterior and lateral parts restored from *A. major*.

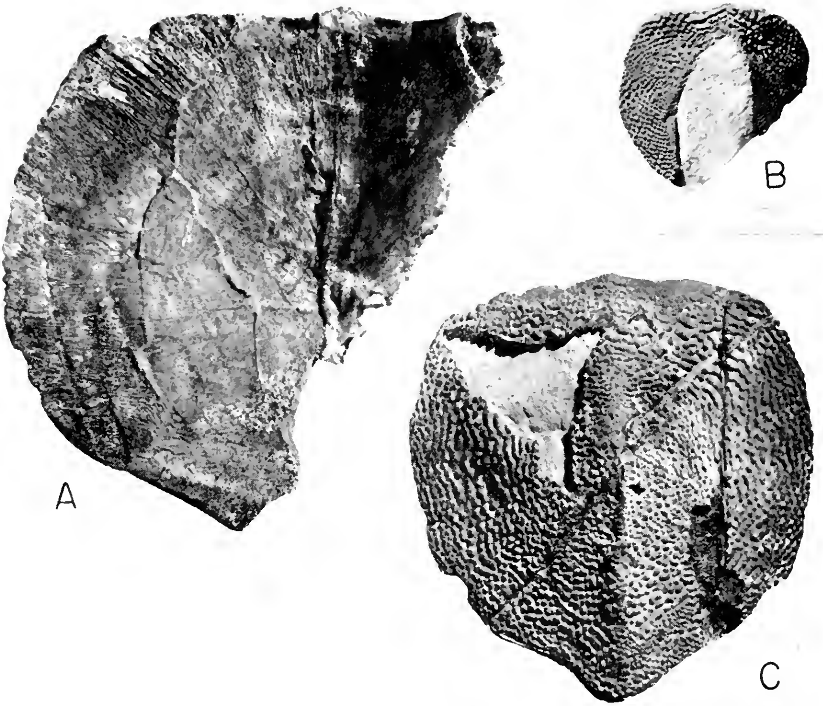

FIG. 92. *Aethaspis major*, median dorsals (× 3/4). A, inner side, PF 907; B, outer side of juvenile, PF 563; C, outer side, PF 910.

able specifically and generically. They will be described separately below, although presumably some of them belong to *Aethaspis*. A suborbital plate (PF 1403, figs. 94, C; 106, F) resembles *A. utahensis* in ornament and is referred to that species. It is of particular interest since this plate has been described adequately only in *Phlyctaenaspis* among the Arctolepida (Heintz, 1933, pp. 128–129, figs. 1, 2). The suborbital of *Aethaspis* is nearly flat and lacks the medially curved lower edge of *Phlyctaenaspis*. The anterior, suborbital process is relatively deeper, and the posterior "blade" is not as deep as in *Phlyctaenaspis* and has nearly straight, sub-parallel, dorsal and ventral edges. The dorsal margin of the "blade" has a narrow, unornamented external surface for articulation with the inner side of the postorbital. The posterior edge is thick and must have had a harmonic suture

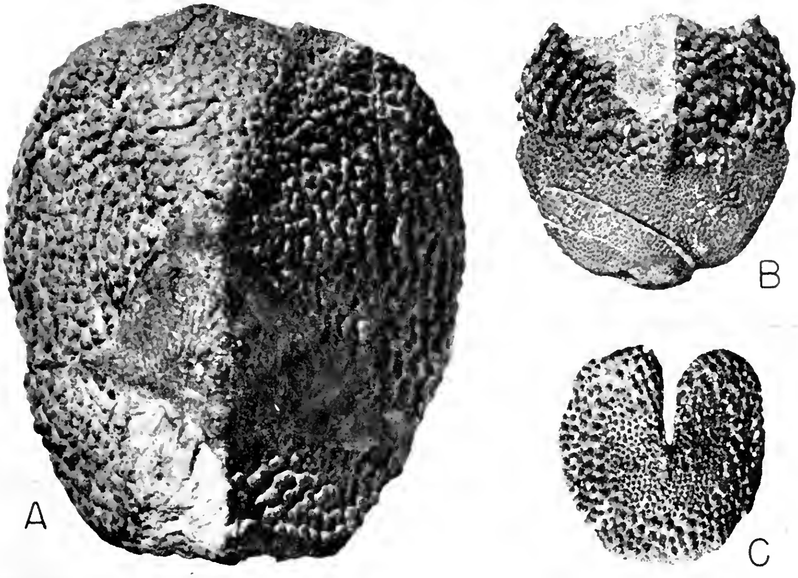

FIG. 93. *Aethaspis*, posterior dorsals. A, *A. major*, type 1, PF 558 (× 4/3); B, *A. major*, type 2, PF 559 (× 4/3); C, *A.* sp., type 2, juvenile, PF 557 (× 2).

with the postsuborbital, rather than overlapping it as in *Coccosteus* and *Dinichthys*.

The median dorsal of *Aethaspis* is a short, broad plate (figs. 92; 94, A; 107, E), having the characteristic proportions of the Actinolepinae. It is considerably arched, has a median crest in its posterior half, and a nearly central center of ossification. Internally it has a small, median ridge (fig. 92, A) in the central part of the plate, but lacks, as do other Arctolepida, a prominent keel. In shape and proportions it agrees very closely with the median dorsal of *Actinolepis* (fig. 107, D) and *Kujdanowiaspis* (fig. 107, I). Anteriorly it has a median convexity, and on either side of this there is a small unornamented area resembling a sutural overlap (fig. 107, E, x). Similar areas are found in *Actinolepis* and *Simblaspis* (fig. 107, G, x) and perhaps indicate overlap by the cranial roof. There is a distinct postero-median lobe, but it is less prominent than in *Simblaspis* and *Bryantolepis* (fig. 107, H). Several median dorsals, ranging in estimated length from 36 to 95 mm., are referable to *A. major* on the evidence of their ornament. The tendency to a ridged ornament is quite pronounced in the anterior and lateral parts of some of the plates. Only one median dorsal is referable to *A. utahensis* (fig. 94, A); it is incomplete at the sides, but its contours may be restored with some confidence by reference to the concentric arrangement of the tubercles.

There is evidence in *Aethaspis* that there were additional median plates lying behind the median dorsal. One of these, here called the posterior dorsal, type 1, is represented by PF 558 (fig. 93, A). This is a highly arched, oval plate, with a median crest extending for two-thirds of its length. Since it is symmetrical, it is certainly median, and its great convexity is a strong indication that it is dorsal. Its ornament shows that it belongs to *A. major*, but it is smaller and of a very different shape than the median dorsal of this species. It resembles the median dorsal of no other arthrodire, except for the problematical *Taunaspis* (Gross, 1937, fig. 13, D). It is assumed that this plate lay behind the median dorsal in the midline. A second type (type 2) of posterior dorsal of *Aethaspis* is represented by PF 314, 559 (fig. 93, B), 967, 975, and 976 (fig. 94, B). The first three, as already mentioned above, have the ornament of *A. major*, and the last two of *A. utahensis*. These plates are also symmetrical, slightly broader than long, rounded in what is believed to be the anterior end and indented in the opposite end. In *A. utahensis* (fig. 94, B) they are gently arched anteriorly and moderately arched posteriorly. In *A. major* (fig. 93, B) the anterior end is gently arched, while posteriorly they are strongly vaulted and provided with a median crest. It is assumed that these plates occupied a position behind the larger posterior dorsal, type 1. PF 557 (fig. 93, C) is a small plate that may represent a juvenile example of the posterior dorsal, type 2, of *Aethaspis*. It is remarkable particularly for the slot in the midline in its posterior half, a feature that is suggested by the tubercle pattern of the larger posterior dorsal, PF 976 (fig. 94, B). Apparently other Arctolepida possessed posterior dorsal plates, although they have never been found in position. Heintz (1933, pp. 141–143, pl. 3, figs. 3–6) has described a number of small plates and scales in *Phlyctaenaspis acadica;* some of these are relatively large, sharply arched, and incut behind, and resemble the second type of *Aethaspis*. *Bryantolepis* has some small, slightly arched, oval plates that may represent the same elements (Bryant, 1935, pl. 6, fig. 2). These cannot represent the median dorsal of a juvenile individual,

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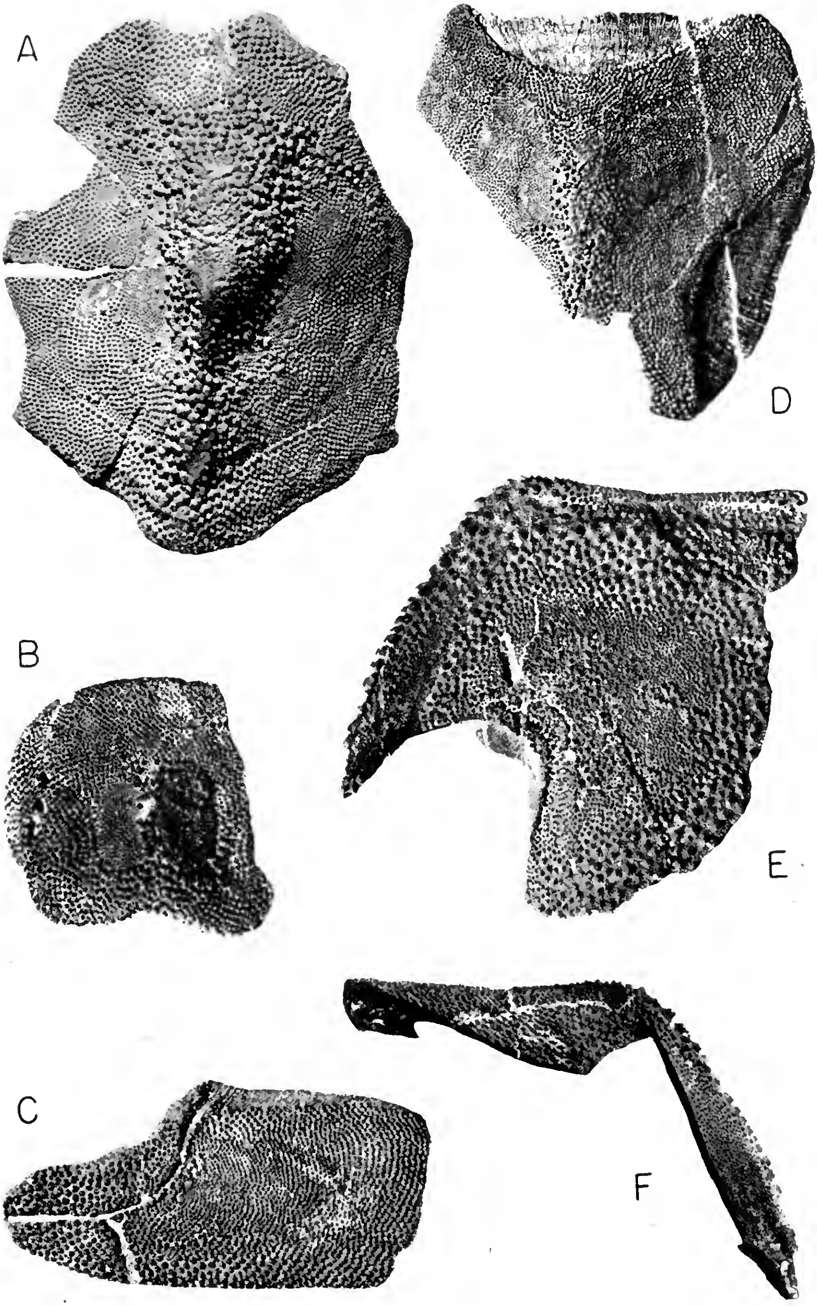
FIG. 94. *Aethaspis utahensis*. A, median dorsal, PF 964 (× 3/2); B, posterior dorsal, type 2, PF 976 (× 3/2); C, left suborbital, PF 1403 (× 9/4); D, right posterior ventro-lateral, PF 322 (× 3/2); E, right anterior ventro-lateral, antero-ventral, intero-lateral, and spinal, ventral view, PF 321 (× 3/2); F, right intero-lateral and spinal, dorsal view, PF 321 (× 3/2).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since such are known possessing the same shape as in the adult. Similar oval plates are known in *Anarthraspis* (PF 1536–7; 1539–40) and in *Kujdanowiaspis*. As far as is known, posterior dorsal plates do not occur in the Brachythoraci.

The anterior dorso-lateral plate of *Aethaspis major* (figs. 95, A, B; 108, F) is relatively high both in the exposed face and in the overlap areas for the median dorsal and anterior lateral. In general shape and proportions it is most similar to *Anarthraspis* (fig. 108, G), and differs considerably from *Bryantolepis* (fig. 108, H) and *Kujdanowiaspis* (fig. 108, I), in which the exposed face is very shallow. As in all Actinolepinae, the anterior edge lacks a trochlea for articulation with the cranial roof, but in the dorsal half there is a wide, unornamented area that was overlapped presumably by the paranuchal. Between this unornamented area and the overlap area for the median dorsal is a narrow, coarsely ornamented process of the exposed surface that extended toward the midline in front of the median dorsal. On the ventral part of the anterior margin there is a smaller, finely tuberculated process of the exposed face that extended in front of the anterior lateral. The posterior part of the plate has internally a long overlap area for the posterior dorso-lateral (fig. 108, F, *s. PDL*). Dorsal to the lateral line canal, there is a posteriorly projecting lobe of the anterior dorso-lateral, as is commonly the case in Actinolepinae; in *Aethaspis major* this is distinctive in shape in that it usually involves only the lower half of the exposed face above the lateral line. The anterior dorso-lateral is not known with certainty in *A. utahensis*, but one specimen doubtfully referred here (PF 1638, fig. 96) shows fused left anterior and posterior dorso-laterals and half of the median dorsal. As far as can be determined, this anterior dorso-lateral agrees in all respects except size and ornamentation with that of *A. major*.

The posterior dorso-lateral of *A. major* (figs. 95, C; 109, F) is also a relatively high plate, with wide external overlap areas for all the adjacent plates. The exposed face is of nearly uniform depth throughout, although its ventral edge is slightly concave to accommodate the posterior lateral. In this respect it is perhaps most closely comparable to *Anarthraspis* (fig. 109, E). The posterior dorso-laterals of *Kujdanowiaspis* (fig. 109, I) and *Bryantolepis* (fig. 109, H) differ in having the exposed faces shallow anteriorly, high posteriorly, and incut between deeply by the posterior lateral and shallowly by the median dorsal. In *Aethaspis major* the overlap area for the anterior dorso-lateral (fig. 109, F, *s. ADL*) is widened dorsally to accommodate the posterior lobe of that plate. The lateral line canal can be traced only a short distance on the posterior dorso-lateral, as is commonly

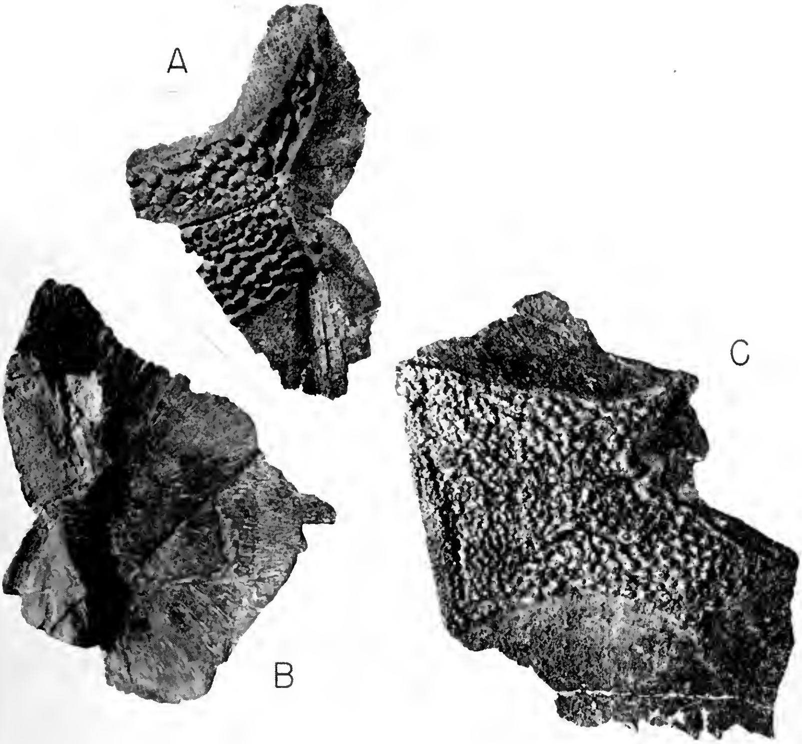

FIG. 95. *Aethaspis major* (× 1). A, right anterior dorso-lateral, outer side, PF 532; B, right anterior dorso-lateral, inner side, PF 922; C, right posterior dorso-lateral, outer side, PF 303.

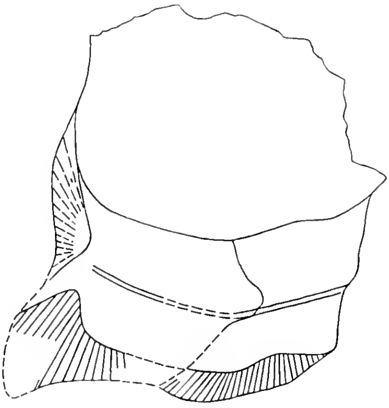

FIG. 96. *Aethaspis* cf. *utahensis*, PF 1638, fused left anterior and posterior dorso-laterals and incomplete median dorsal (× 2).

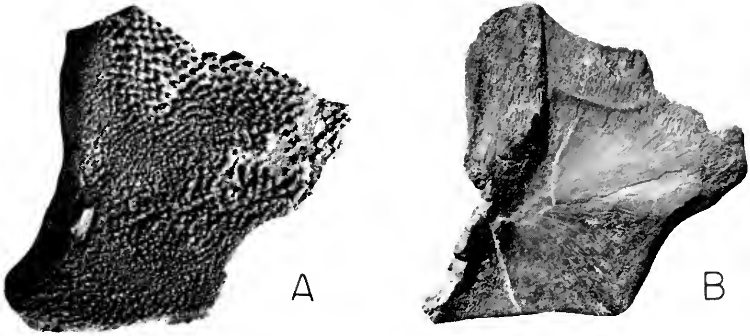

FIG. 97. *Aethaspis major*, anterior laterals (× 2/3). A, left side, outer face, PF 560; B, right side, inner face, PF 561.

the case in Actinolepinae. In PF 1638 (fig. 96), doubtfully referred to *A. utahensis*, the posterior dorso-lateral agrees in general shape and proportions with that of *A. major*.

The anterior lateral plate is known only in *A. major* (figs. 97; 110, D), where it has quite distinctive features. The center of ossification is placed anteriorly and low, and in front of it the plate is bent sharply mediad to form a clearly demarked and finely tuberculated inner wing (fig. 110, D, *iw*). The dorsal part of the plate is unreduced and on the inner side shows wide areas for overlap of the anterior and posterior dorso-laterals (fig. 110, D, *s. ADL*, *s. PDL*). Behind the posterior dorso-lateral overlap there is probably a very small overlap area for the posterior lateral (fig. 110, D, *s. PL*), although this is not clear on the one specimen showing the inner side (PF 561). Lateral and ventral to the posterior lateral overlap area, the posterior edge of the anterior lateral is concave; in its dorso-median part it is thickened, indicating the probable position of the pectoral fenestra and fin; in its ventro-lateral part it is thinner where presumably it came in contact with the anterior ventro-lateral. The ventral edge of the plate is somewhat shortened, a feature that is indicative of a reduced attachment for the spinal. The plate is relatively higher than in *Simblaspis* (fig. 110, C) and *Bryantolepis* (fig. 110, E). It differs from *Anarthraspis* (fig. 110, F), in which the dorsal part of the plate is greatly shortened antero-posteriorly, resulting in a relatively short, high anterior lateral.

The posterior lateral plate has been recognized in very few Arctolepida, probably because it is small and with no very striking shape. In the Water Canyon Formation collection, PF 924 (figs. 98, A; 111, C) is identified as a posterior lateral of a large individual of *Aethaspis major*. It differs from the posterior lateral of *Phlyctaenaspis* (fig. 111, A, B) in two important respects. First, it is relatively short and deep. Second, the area overlapped by the anterior lateral (fig. 111, C, *s. AL*) is very small and is widely separated from the posterior ventro-lateral overlap area (fig. 111, C, *s. PVL*). In *Phlyctaenaspis* and also in *Anarthraspis* (fig. 111, D) these two overlap areas meet anteriorly, indicating that the posterior ventro-lateral came into contact with the anterior lateral. In *Aethaspis* and also in *Bryantolepis* (fig. 111, E) the overlap areas indicate that the posterior ventro-lateral and anterior lateral were separated and that the posterior lateral must have bounded the pectoral fenestra posteriorly. It is interesting that in a restoration of *Phlyctaenaspis sherwoodi* (Denison, 1950, pl. 3, fig. 2) this situation was inferred, although the posterior lateral itself was not preserved.

The spinal plate of *Aethaspis major* (PF 939, figs. 98, B; 112, D) is relatively short and blunt-tipped and is characterized by the presence of large, irregularly arranged, round tubercles on its outer edge, and smaller tubercles on the medial edge. In *A. utahensis* (PF 321, figs. 94, E, F; 112, F) the spinal is relatively slightly longer; laterally it has a distinctive double row of large tubercles arranged in pairs, as well as a cluster of large tubercles near the tip on the medial side. In addition to these two specimens, there are a number of other spinals in the Utah collection, some of which are doubtfully referable to *Aethaspis* and others are at present undeterminable. These specimens are of medium or small size, and reveal the interesting fact that the spinal is relatively longer in small individuals and shorter in large individuals.

	Length ant. vent.-lat.	Length spinal	Length, spinal / Length, ant. vent.-lat.
Aethaspis major, PF 939	69 mm.	55 mm.	0.80
Aethaspis utahensis, PF 321	36	32	0.89
Aethaspis sp., PF 536	35	35	1.00
Aethaspis sp., PF 547	35	39	1.11
indet., PF 923	20	27	1.35
indet., PF 553	11	16	1.45

This correlation raises the interesting question as to whether the small individuals may not represent young of *A. major* and *A. utahen-*

sis, and suggests that during growth the spinal did not keep pace, at least in length, with the anterior ventro-lateral. However, both of the very small forms, PF 923 (fig. 112, E) and 553, differ from *Aethaspis* in possessing several prominent, forwardly curved barbs on the inner side of the spinal, and unless this is a juvenile character they are probably distinct from *Aethaspis*.

The intero-lateral is a long, slender, transversely oriented plate that extends from the midline to the anterior end of the spinal. It is sharply folded at its anterior edge so as to form a ventral lamina and a dorsal or inner lamina. In *Aethaspis* (figs. 94, E, F; 98, C, D; 112, D, F) the inner lamina is not present in the median part of the plate but begins in front of the antero-ventral and widens laterally to its widest point, where it meets the inner wing of the anterior lateral. Together with the latter it forms a constriction in the neck region extending from the upper half of the anterior lateral nearly to the midline. The suture of the intero-lateral with the anterior lateral is not overlapping. The ornamentation of the inner lamina is distinctive and would hardly be recognized as belonging to *Aethaspis* if found separately. In *A. utahensis* it consists of linear groups of three, four, or five, pointed tubercles, with the central one largest, and all leaning anteriorly. Probably a similar ornament occurs in *A. major*, and in PF 560 it is continued for a short distance onto the inner wing of the anterior lateral. The ventral lamina of the intero-lateral bounds anteriorly the anterior medio-ventral, antero-ventral, anterior ventro-lateral, and spinal. It overlaps the anterior medio-ventral externally but appears to be overlapped by the antero-ventral and apparently abuts against the anterior ventro-lateral and spinal in non-overlapping sutures. In both species of *Aethaspis* the antero-ventral edge of the intero-lateral forms a distinct ridge which is undercut in such a way that it actually overhangs ventrally the posterior part of the ventral lamina. Internally, between the dorsal and ventral laminae, lay the bracing cartilage of the shoulder region; this is indicated by perichondral ossification extending from the anterior medio-ventral suture in a lateral direction. The ossification was called the pre-spinal

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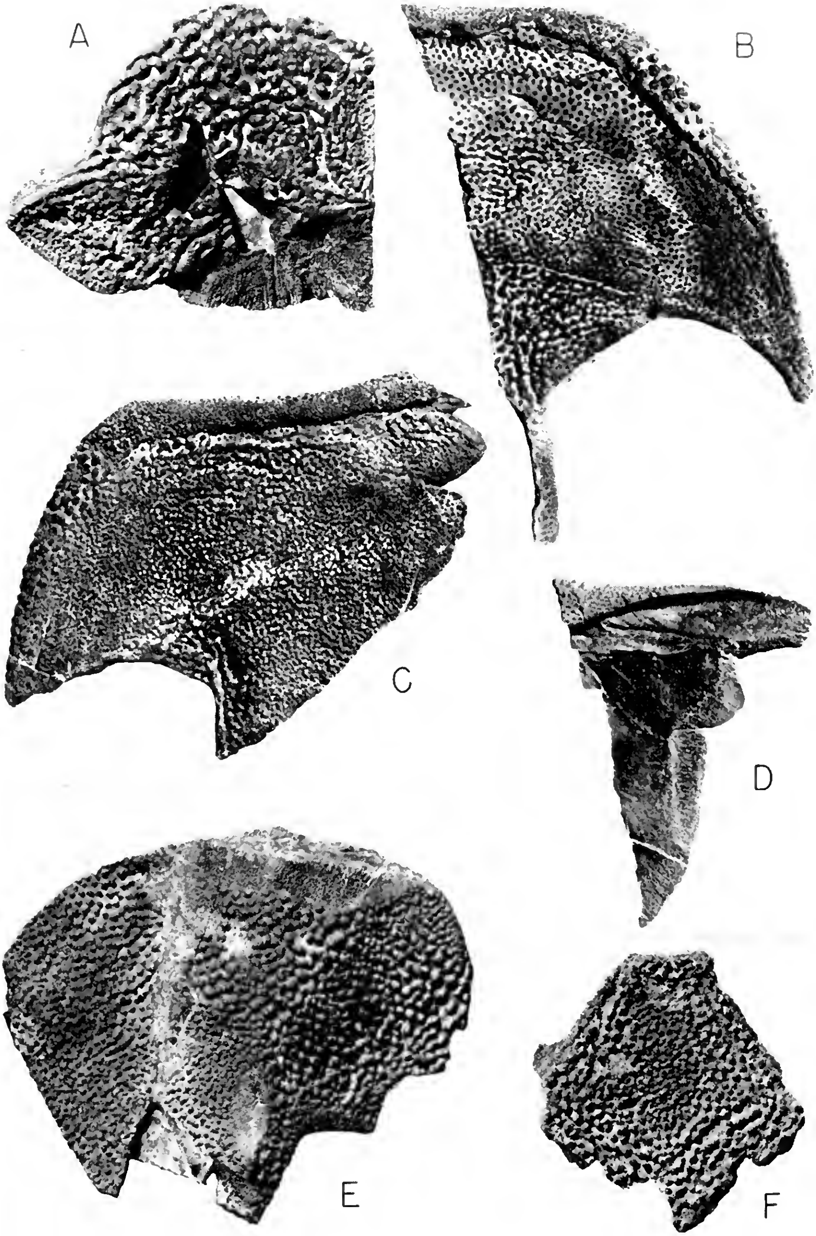
FIG. 98. *Aethaspis major* (× 1). A, left posterior lateral, PF 924; B, left spinal with incomplete anterior ventro-lateral and intero-lateral, PF 939; C, right anterior ventro-lateral, antero-ventral, intero-lateral, and spinal, PF 989; D, left antero-ventral with parts of intero-lateral and anterior ventro-lateral, inner side, PF 940; E, left posterior ventro-lateral, PF 913; F, presumed posterior medio-ventral, PF 315.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lamella by Heintz (1929, p. 41), and this part of the cartilage was homologized with the coracoid process by Stensiö (1944, p. 56).

The anterior ventro-lateral plate shows no particularly remarkable features in *Aethaspis* (figs. 94, E; 98, B–D; 112, D, F). It overlaps the adjacent antero-ventral, anterior and posterior medio-ventrals, and posterior ventro-lateral, but its sutures with the intero-lateral and spinal are harmonic or only slightly overlapping. There is no suggestion of any contact with or overlap of the posterior lateral, such as occurs in *Bryantolepis* (p. 528). The edge for the spinal is of moderate length, not as long relatively as in *Kujdanowiaspis* (fig. 112, H) and many Phlyctaenaspinae (fig. 112, I) and not shortened as much as in *Anarthraspis* (fig. 112, C) and *Actinolepis* (fig. 112, B); this feature is apparently correlated with the moderate length of the spinal. The posterior edge of the anterior ventro-lateral is rather deeply concave between the posterior ventro-lateral and spinal contacts. In the anterior and antero-median parts of this concavity some specimens show a thick lamina of unornamented bone lying internal to the ornamented external face of the anterior ventro-lateral (fig. 112, D, F, *pf*). This lamina represents an ossification of endoskeletal cartilage that forms the base of attachment of the pectoral fin. It is the most posterior part of the "scapulo-coracoid" of Stensiö (1944) and White (1952). It occupies the pectoral fenestra and presumably bridges the gap of this fenestra between the anterior ventro-lateral and the anterior lateral. It indicates the presence of a stenobasal pectoral fin that has an attachment relatively no wider than in *Kujdanowiaspis*. Lateral to the pectoral fenestra the anterior ventro-lateral probably meets the anterior lateral. The medial edge of the fenestra is presumably bounded by the posterior lateral in *Aethaspis*.

Stensiö (1944, fig. 17) has indicated the presence of paired "anterior median ventral" plates in *Kujdanowiaspis*. The evidence in *Aethaspis* and other Actinolepinae clearly shows that a median anterior medio-ventral was also present in this subfamily, so the paired plates are here called antero-ventrals to distinguish them. In *Aethaspis* (figs. 94, E; 98, C, D; 99; 112, D, F) they are small, triangular plates with their centers of ossification lateral to the centers of the plates. They are overlapped by the anterior ventro-laterals posteriorly and in *A. utahensis* they appear to overlap the intero-laterals, at least medially. PF 940 and 988, fragments of *A. major*, demonstrate the presence of a wide internal overlap area on the medial side (figs. 98, D; 99, B, *s. AMV*). This could only represent a suture for the anterior medio-ventral, and could not possibly have contacted the opposite antero-ventral because of its position and the absence of an external overlap area on the medial side of any antero-ventral. This is one of the many indications that the antero-ventrals are distinct from the anterior medio-ventral.

Of the median ventral plates, there is only one incomplete specimen (PF 315) that can be referred to *Aethaspis* (fig. 98, F). Its size indicates that it belongs to *A. major*, although there is no very strong tendency toward union of tubercles into ridges. It is a relatively short, broad, five-sided plate, agreeing closely in shape with the posterior medio-ventral of *Anarthraspis* (fig. 113, D). It is considered to be the posterior medio-ventral of *A. major*.

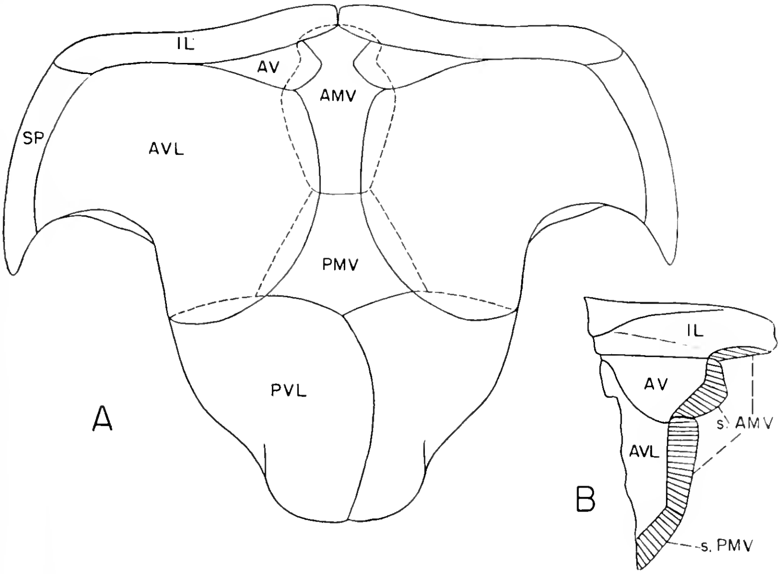


FIG. 99. *Aethaspis major.* A, restoration of ventral shield (× 1/2); B, inner side of antero-ventral and medial parts of intero-lateral and anterior ventro-lateral, showing sutural overlap areas for anterior medio-ventral (*s. AMV*) and posterior medio-ventral (*s. PMV*), PF 940 (× 3/4).

AMV, anterior medio-ventral; *AV*, antero-ventral; *AVL*, anterior ventro-lateral; *IL*, intero-lateral; *PMV*, posterior medio-ventral; *PVL*, posterior ventro-lateral; *SP*, spinal.

The posterior ventro-lateral plates are poorly known in *Aethaspis* (figs. 94, D; 98, E; 114, C, E). From incompletely preserved specimens it is evident that the sutural overlaps are conventional, with the left posterior ventro-lateral overlying the right in the median line. The ventral lamina is relatively short and broad, even more so than in

Kujdanowiaspis (fig. 114, F), and is strongly contrasted with the long, narrow ventral lamina of *Anarthraspis* (fig. 114, B), *Bryantolepis* (fig. 114, D), and *Actinolepis* (fig. 114, H); posteriorly it is probably bluntly rounded. The lateral lamina is short and relatively high, rising to overlap the posterior lateral; it is distinctly set off by a sharp curvature from the ventral lamina.

In conclusion it may be said that *Aethaspis*, though in every respect a typical member of the Arctolepida, differs in so many features from previously described genera of this suborder that it cannot be considered as closely related to any of them. The outstanding specializations of the cranial roof are not even suggested in any other arctolepid; these include the lengthening of the preorbitals posterior to the centers of ossification, and the elongation of the nuchal to separate the centrals and to meet the preorbitals. Some of the lateral plates of the trunk shield resemble those of *Anarthraspis*, but this may be only an indication of a relatively high trunk shield in both genera. The shortening of the spinal and of the spinal edge of the anterior ventro-lateral reflects only a common evolutionary trend within the Arctolepida. Thus *Aethaspis* must be considered as representing a distinct phyletic line within the suborder.

Bryantolepis Camp, Welles, and Green

PF 329, from Green Canyon (Locality E), is the only specimen from the Water Canyon Formation that is referable to one of the genera of Beartooth Butte Arctolepida. It is a small fragment of a cranial roof consisting of the rostral, pineal, and postnasal, and parts of the preorbital and postorbital (fig. 100). The large, five-sided pineal and the very large, wide postnasal leave no doubt that this is *Bryantolepis*. As in the latter, these anterior plates are fused to the preorbital, and there is an indication that the endocranium was perichondrally ossified. The fragment cannot be identified with any of the Beartooth Butte species. *B. brachycephalus* (Bryant), the common species at Beartooth Butte, is smaller. *B. obscurus* (Bryant) is doubtfully distinct from *B. brachycephalus*. *B. cristatus* (Bryant) was based on the median dorsal, and its cranial roof is not known with certainty. *B. major* (Bryant, 1935, p. 126) was based on a specimen that was considered to be a cranial roof but is probably an imperfectly preserved median dorsal of *Anarthraspis*.

Undetermined Arctolepida

Because of the lack of association of plates in the Water Canyon Formation, there are a number of specimens that cannot be referred with certainty either to *Aethaspis* or to *Simblaspis*. Among the most interesting of these are dermal bones of the cheek, lower jaw, and perhaps upper jaw. Hitherto the only jaw elements known in Arctolepida were described in *Phlyctaenaspis acadica* (Heintz, 1933, pp. 132–133, pl. 2, figs. 2–4), but their preservation is not good. There are five rather well-preserved infragnathals in the collection from the Water Canyon Formation (PF 509–512, 984).

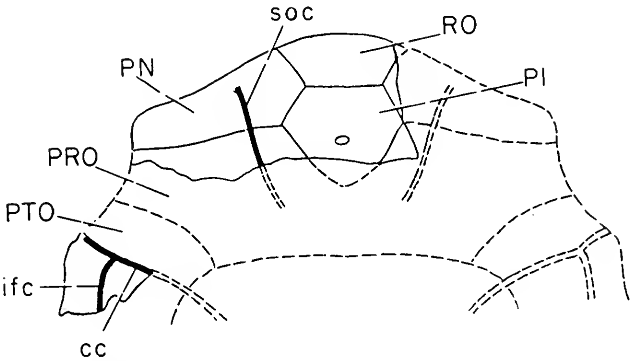


FIG. 100. *Bryantolepis* sp. indet., restoration of anterior part of cranial roof based on PF 329 (× 3/2). *PI*, pineal; *PN*, postnasal; *PRO*, preorbital; *PTO*, postorbital; *RO*, rostral; *cc*, central canal; *ifc*, infraorbital canal; *soc*, supraorbital canal.

The infragnathal is well known in many Brachythoraci. In *Coccosteus*, which may be used as a typical form for comparison (Heintz, 1931, fig. 4; Watson, 1934, figs. 1, D, E; 2, D), it consists of a posterior blade and an anterior tooth-bearing part. In the Utah Arctolepida no blade is present, and the smooth, thin, posterior edge of the tooth-bearing part in PF 510 and 511 (fig. 101, B–D) shows that this is not caused by breakage. The probable implication of this is that the infragnathal of Brachythoraci is a compound bone with a separate center of ossification posteriorly. In Arctolepida the posterior dermal ossification may not have formed or may not have been discovered or recognized as a distinct element.

The anterior, tooth-bearing part of the infragnathal of the Utah Arctolepida is similar in its general structure to that of *Coccosteus*. PF 509–511 (fig. 101, A–D), all of which may belong to the same species, illustrate the character of this bone well, especially PF 511, which has been prepared free of the rock. The bone is solid only along the dorsal, biting edge. Below this it consists of two nearly parallel, thin laminae, a deep lateral one and a shallow medial one. Between these laminae is a deep groove that must have been occupied in life by Meckel's cartilage. The groove extends to the anterior end of the jaw, where it is closed by the union of the two laminae in the symphysial region. As one progresses forward, at midlength the infragnathal curves slightly mediad, and near the anterior end it is bent sharply toward the midline; the bends are stronger ventrally than dorsally, resulting in a twisting of the ventral edge inward.

The dorsal edge of PF 509 (fig. 101, A) is set with teeth in much the same way as in *Coccosteus*. The teeth occur in the anterior part of the posterior half of the bone and include seven rather large, distinct elements posteriorly; in front of these are four smaller and increasingly indistinct elements, grading anteriorly into a worn ridge in which separate tooth elements are not distinguishable. In PF 511 (fig. 101, C) the tooth-bearing edge is partly broken away. In PF 510 (fig. 101, B), the largest infragnathal, the separate teeth are relatively small, probably because of wear; twelve are distinguishable along the dorsal edge and four occur just below them on the lateral face, where they are definitely attached and not displaced. The anterior part of the dorsal edge shows no distinct teeth in any of these specimens, but is a relatively smooth, worn surface. In distinction to *Coccosteus* and *Dinichthys* there is little indication of shearing wear on the outer side, but only a blunting wear on the dorsal edge itself. The only sign of the prominent prongs that occur anteriorly in *Coccosteus* and *Dinichthys* are slight convexities of the dorsal edge. In PF 509 (fig. 101, A) these convexities form the tops of two oblique ridges on the lateral face, extending postero-ventrally to the ventral edge. They may mark the position of two relatively large teeth that are completely surrounded by bone. The convexity at the top of the anterior ridge forms the most anterior part of the dorsal edge and is the region from which the bone radiation spreads. Below this convexity is the antero-median edge of the infragnathal, which is set with three teeth comparable to the 3–6 "symphysial teeth" of *Coccosteus*. In PF 511 (fig. 101, C) the uppermost of these teeth is worn on top, its wear surface being continuous with that of the dorsal edge of the bone behind. In PF 509 (fig. 101, A) the dorsal wear surface is not worn down to the upper symphysial tooth, but there is wear on the uppermost part of the antero-lateral face, and this has involved slight wear of the side of the upper tooth. This approaches the condition found in a specimen of *Coccosteus decipiens* (PF 1335) where the antero-lateral faces of the upper four of the six symphysial teeth are worn, as well as the antero-lateral face of the infragnathal itself. This anterior wear is, no doubt, the result of occlusion with the "symphysial teeth" of the anterior supragnathal.

PF 512 (fig. 101, E) is a very small infragnathal, incomplete posteriorly, and may represent a young individual of the same type as is represented by the lower jaws described above. On its dorsal edge fourteen small teeth are distinguishable; they decrease in size anteriorly and blend into the smooth, worn, anterior biting edge. The lateral face shows the two ridges described above, the posterior one extend-

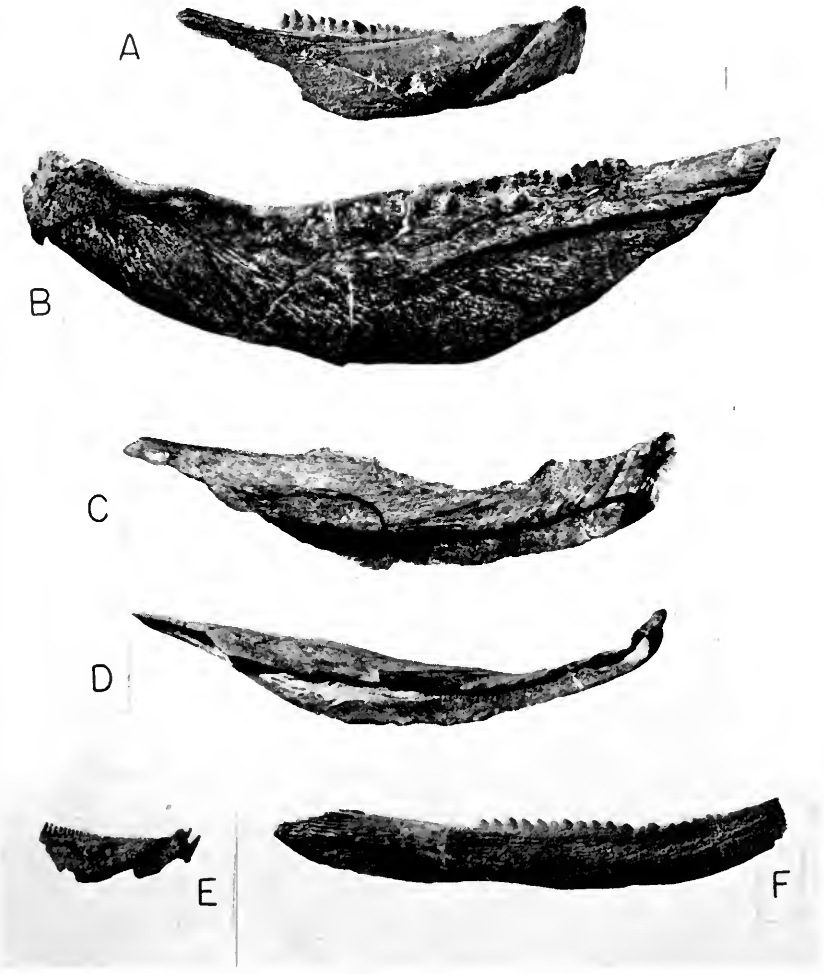


FIG. 101. Arctolepida indet., infragnathals (× 3/2, except E). A, PF 509, lateral view; B, PF 510, lateral view; C, D, PF 511, medial and ventral views; E, PF 512, lateral view (× 3); F, PF 984, lateral view.

ing postero-ventrally and lacking any convexity on the biting edge, the anterior one nearly vertical and terminating dorsally in a high, tooth-like projection on the biting edge. There are two prominent symphysial teeth.

PF 984 (fig. 101, F) is quite a different type of infragnathal and may represent an acanthodian rather than an arctolepid. It is incomplete anteriorly and is missing a section in its posterior half, though there is a contact on the underlying rock that gives its length. The antero-posterior convexity indicates that it is the lateral face that is exposed. This infragnathal is relatively long and shallow compared to those described above. Ventrally it is grooved for Meckel's cartilage. The medial lamina bordering the groove is deep posteriorly and shallow anteriorly, while in the lateral lamina the reverse is true; as a result the groove is open laterally in its posterior part. The middle section of the preserved part is set with small teeth on its biting edge, twenty of them being distinguishable. Posteriorly they are larger, closely spaced, and inclined somewhat backward; anteriorly they decrease in size, perhaps because of wear, until they blend anteriorly into the smooth anterior part of the biting edge. The symphysial region is not preserved.

The collection of the Water Canyon Formation contains several specimens that may be dermal bones of the upper jaw, but I am unable to identify them definitely with any of the anterior or posterior supragnathals described in the Brachythoraci or in *Phlyctaenaspis*. One type is represented by PF 981 and 1645. The face illustrated in figure 102, A, lacks a smooth bone surface and consists of honeycomb-like reticular bone; this may have attached to the palatoquadrate. Adjacent to it is a narrow face (fig. 102, A, B) that is quite flat and smooth except for an isolated tubercle or tooth at one end. Opposite the latter is a narrow, convex face (fig. 102, C) that is nearly smooth except for several tubercles at one end. The face opposite that for the palatoquadrate (fig. 102, C) is broad, lacks any ornament, and may have occluded with the infragnathal.

Another type of bone (PF 526, 979) is built on a similar plan, but is smaller, of different shape, and without any tubercles or teeth. The broadest face (fig. 102, D) has exposed reticular bone, similar to that of PF 1645, and may have attached to the palatoquadrate. The opposite face (fig. 102, E) is relatively narrow and deeply grooved and may have been occlusal.

Finally, there are three rather flat, externally tuberculated, dermal bones that probably belong to the cheek. PF 540 (fig. 103, A, B) is a five-sided plate with two long, subparallel sides (*a-b*, *d-e*), with one end pointed (*b-c*, *c-d*) and the other slightly convex (*a-e*). There are no external overlap areas, and while internal ones are possible on sides *a-b*, *b-c*, and *d-e*, they are not certain. At all of the margins except *a-e*, the bone tapers to a thin edge. Margin *a-e* is thick and bluntly cut off and probably abutted against another plate. It is possible that PF 540 is a postsuborbital and that it joined the suborbital at this edge. In *Dinichthys* and *Coccosteus* the suborbital externally overlaps the postsuborbital, and the latter is a relatively small, triangular plate, but the suborbital of *Aethaspis utahensis* (PF 1403) has a bluntly

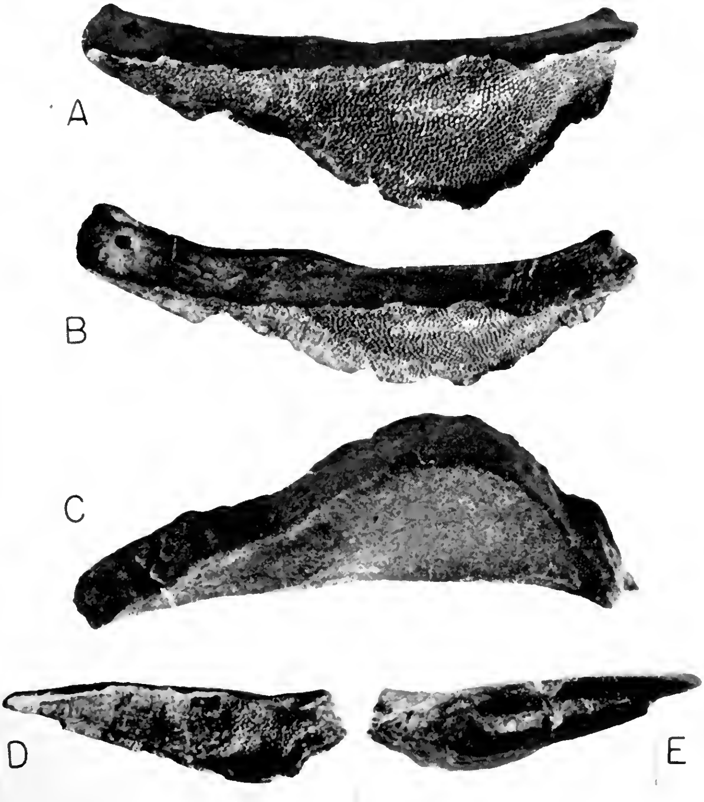


FIG. 102. Arctolepida indet., possible supragnathals (× 3). A–C, PF 1645; D, E, PF 526.

truncated posterior end and must have had a harmonic rather than an overlapping suture here. The internal face of PF 540 (fig. 103, B) has a sinuous ridge extending from the pointed end (*c*) toward the middle of the opposite edge (*a-e*). This ridge is of solid bone and so is almost certainly not the quadrate; since its surface is relatively smooth it is not at all certain that the quadrate attached here. For this reason a definite identification of this bone as a postsuborbital is not possible.

PF 530 (fig. 103, C, D) is an elongate bone with one long edge (*a-b*) somewhat concave and the opposite one (*c-d*) strongly convex, and with short, blunt ends (*b-c*, *a-d*). At the margins it tapers to a thin edge all around, so that it could not form a harmonic suture with the posterior edge of the suborbital. The external face (fig. 103, C) is tuberculated except for an area extending from near corner *c* to the middle of edge *a-b;* this smooth area presumably was overlapped by an adjacent bone. The inner surface (fig. 103, D) is rather featureless except for an area underlying the external overlap area; here there is an elongate depression marked off by a ridge extending from corner *c* toward the center of the bone, and then curving toward the middle of edge *a-b*. The appearance of this depression indicates that cartilage may have attached here, and this, of course, suggests that it may be a postsuborbital, but other characters of the bone do not support this theory. It may be the internal bone, lying between the suborbital and postsuborbital and the cranial roof, but it is not closely comparable to the internal bone where it is known in Brachythoraci and *Phlyctaenaspis*.

PF 1641 (fig. 103, E, F) may represent the same element as PF 530, although its shape is more complex. The edge *a-g-f-e* may correspond to edge *c-d* of PF 530 but differs in having the notch *e-f-g*. The edge *a-b-c-d* may correspond to edge *a-b* of PF 530, but it differs in having a sharply marked projection *b-c-d*. However, the external face has a smooth, external overlap area exactly corresponding to that of PF 530, and beneath it on the inner surface (fig. 103, F) is a groove corresponding again to that on the inner surface of PF 530. It is possible that this also is an internal bone, and if this is so, the external, smooth area was probably overlapped by the postsuborbital.

GEOLOGIC RANGE AND HABITAT OF ARCTOLEPIDA

The earliest known arctolepid, and the first of the Order Euarthrodira to appear (fig. 104), is *Kujdanowiaspis,* one of the Actinolepinae. It is found in the Middle Dittonian of Great Britain and in the Old

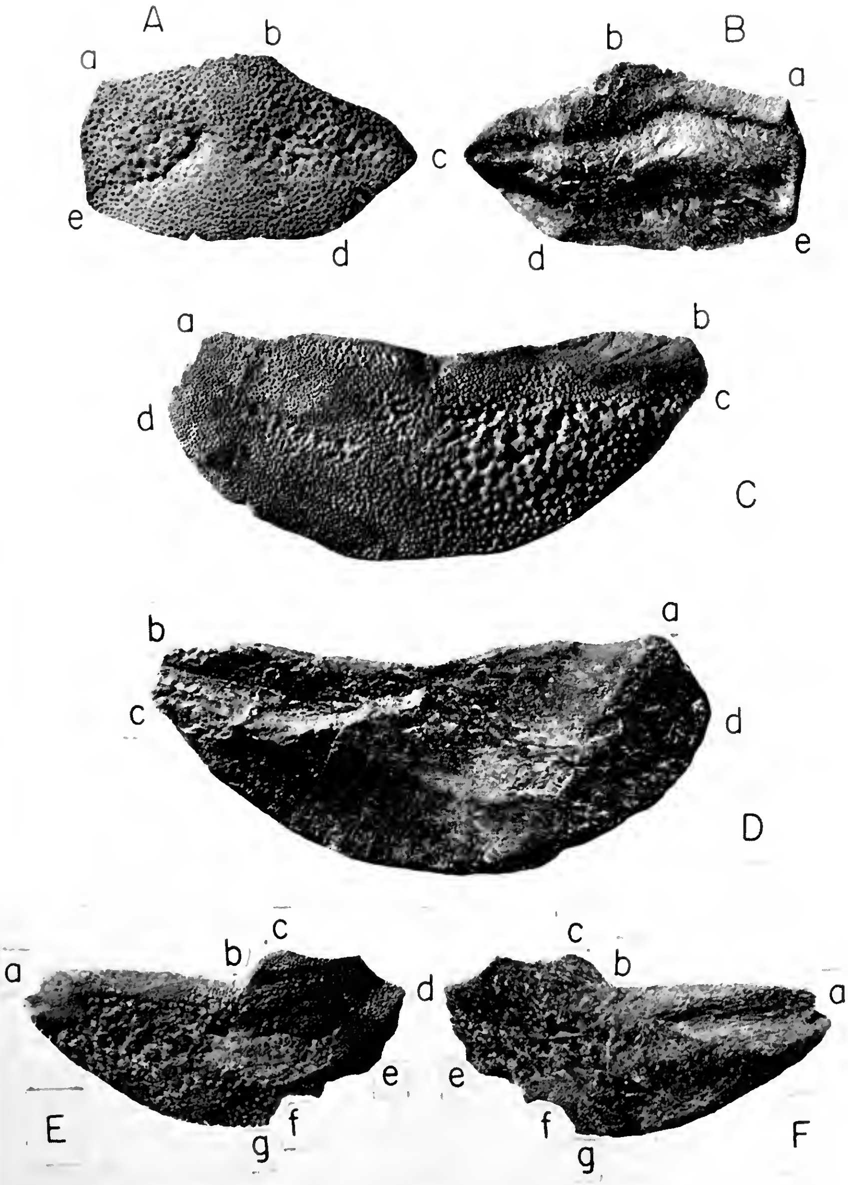


FIG. 103. Arctolepida indet., cheek plates, outer and inner views (× 3/2). A, B, PF 540; C, D, PF 530; E, F, PF 1641.

Red, Stage I, of Podolia, both probably Upper Gedinnian in age (Denison, 1956, pp. 404, 406; White, 1956, p. 2). Other orders of Arthrodira appear slightly earlier: the Acanthothoraci (*Palaeacanthaspis*) occur in the Czortków Stage of Podolia, probably of Middle Gedinnian age, and the Radotinida (*Radotina*) are found in the Lochkov Limestone of Bohemia, generally considered to be Late Silurian but possibly Downtonian in age (Denison, 1956, p. 398). *Kujdanowiaspis* is also found in the Upper Dittonian of Great Britain, and in Stages II and III of the Podolian Old Red, thus probably persisting into the Lower Siegenian. This genus is not reported elsewhere, but there are forms from the lower or Kapp Kjeldsen Division of the Wood Bay Series in Spitsbergen that resemble it, at least in the pattern of the dermal bones of the cranial roof. One of these is "*Svalbardaspis*" *angulatus* (Heintz, 1929, p. 58), and others are yet to be described. These are also Lower Siegenian in age.

No later Actinolepinae are reported from Great Britain, and none at all are known with certainty from France, Belgium, or Germany. In Spitsbergen *Lataspis* is found in the middle or Lykta Division of the Wood Bay Series, whose age is perhaps Emsian. It has been referred by Føyn and Heintz (1943, p. 19) to *Actinolepis* but is best retained as a distinct genus at present. Relatives of *Actinolepis* from the Lykta Division include "*Svalbardaspis*" *rotundus*, "*S.*" *polaris*, and certain undescribed forms. A large member of the Actinolepinae from Stage III of the Podolian Old Red has been referred to *Lataspis* by Brotzen (1934, p. 119), but it is not generically determinable at present. The only other Spitsbergen genus that may belong to the Actinolepinae is the inadequately known *Mediaspis* from the Grey Hoek Series at Gråhuken. Its age is uncertain, but it may be Emsian and thus older than the Grey Hoek Series elsewhere. The typical *Actinolepis* occurs in the Baltic Middle Devonian, specifically in the Pernau, Narowa, and Luga Stages of Givetian age. It is the latest surviving representative of the Actinolepinae.

In North America, Actinolepinae occur in the Beartooth Butte Formation at Beartooth Butte, Wyoming (*Anarthraspis* and *Bryantolepis*), and in the Water Canyon Formation of Utah (*Aethaspis*, *Bryantolepis*, and *Simblaspis*). A provisional correlation, based largely on pteraspids, assigns these formations to the Lower or Middle Siegenian, approximately equivalent to the Upper Dittonian or Lower Breconian of Great Britain.

The Phlyctaenaspinae do not appear as early as the Actinolepinae, the first recorded being Lower Siegenian in age. They occur in the lower or Kapp Kjeldsen Division of the Wood Bay Series of Spitsbergen. Here the typical form is *Arctaspis,* a genus that approaches the Actinolepinae in some respects. The same beds contain *Elegantaspis* and some "*Svalbardaspis*" that may belong to this subfamily ("*S.*" *stensioi* and perhaps "*S.*" *typicus*). Upper Siegenian Phlyctaenaspinae occur in the Wahnbachschichten of Germany; these are *Prosphymaspis* and forms referred, though perhaps not correctly, to *Phlyctaenaspis.* In the Upper Siegenian Hunsrückschiefer is another "*Phlyctaenaspis,*" as well as "*Coccosteus*" *angustus,* a form that is intermediate between the Phlyctaenaspinae and Coccosteidae.

In the upper part of the Early Devonian, probably Emsian, the typical *Phlyctaenaspis* occurs in New Brunswick and possibly in Quebec also. This genus is reported from the German Emsian, but the identification is not certain. In the latter there is also *Prosphymaspis* and *Diadsomaspis.* In probably equivalent beds in Spitsbergen, the Lykta Division of the Wood Bay Series, *Arctolepis* is the characteristic form. "*Svalbardaspis*" *stensioi,* which appears to be related, possibly persists into the Lykta Division. In the upper or Stjørdalen Division of the Wood Bay Series there occurs *Heterogaspis,* a poorly defined genus, some or all of which may belong to the Phlyctaenaspinae. This division may belong, at least in part, to the Middle Devonian, and this is certainly true of the Grey Hoek Series, which also contains *Heterogaspis* and another of the Phlyctaenaspinae, *Huginaspis.*

One species of *Phlyctaenaspis, P. sherwoodi,* is reported from the base of the Late Devonian in New York state (Denison, 1950). This is the last of undoubted Phlyctaenaspinae, although *Gronlandaspis* from the Arthrodire Sandstone of eastern Greenland may also belong here; its age is very late Devonian or possibly even early Carboniferous.

Williamsaspis, from the Middle Devonian of Australia, is a specialized arctolepid that is placed in a family of its own.

Arctolepida occur in fresh-water, marginal-marine, and marine sediments. However, the earliest Actinolepinae (*Kujdanowiaspis*) and Phlyctaenaspinae (*Arctaspis, Elegantaspis,* and "*Svalbardaspis*" *stensioi*) are restricted to fresh-water deposits. This and other considerations suggest that it was in rivers that Euarthrodira had their origin (Denison, 1956, pp. 426–427). Certain later genera in both subfamilies remained in this environment; these include *Lataspis* and *Actinolepis* among the Actinolepinae, and the typical *Phlyctaenaspis, Arctolepis,* some *Heterogaspis,* and *Gronlandaspis* among the Phlyc-

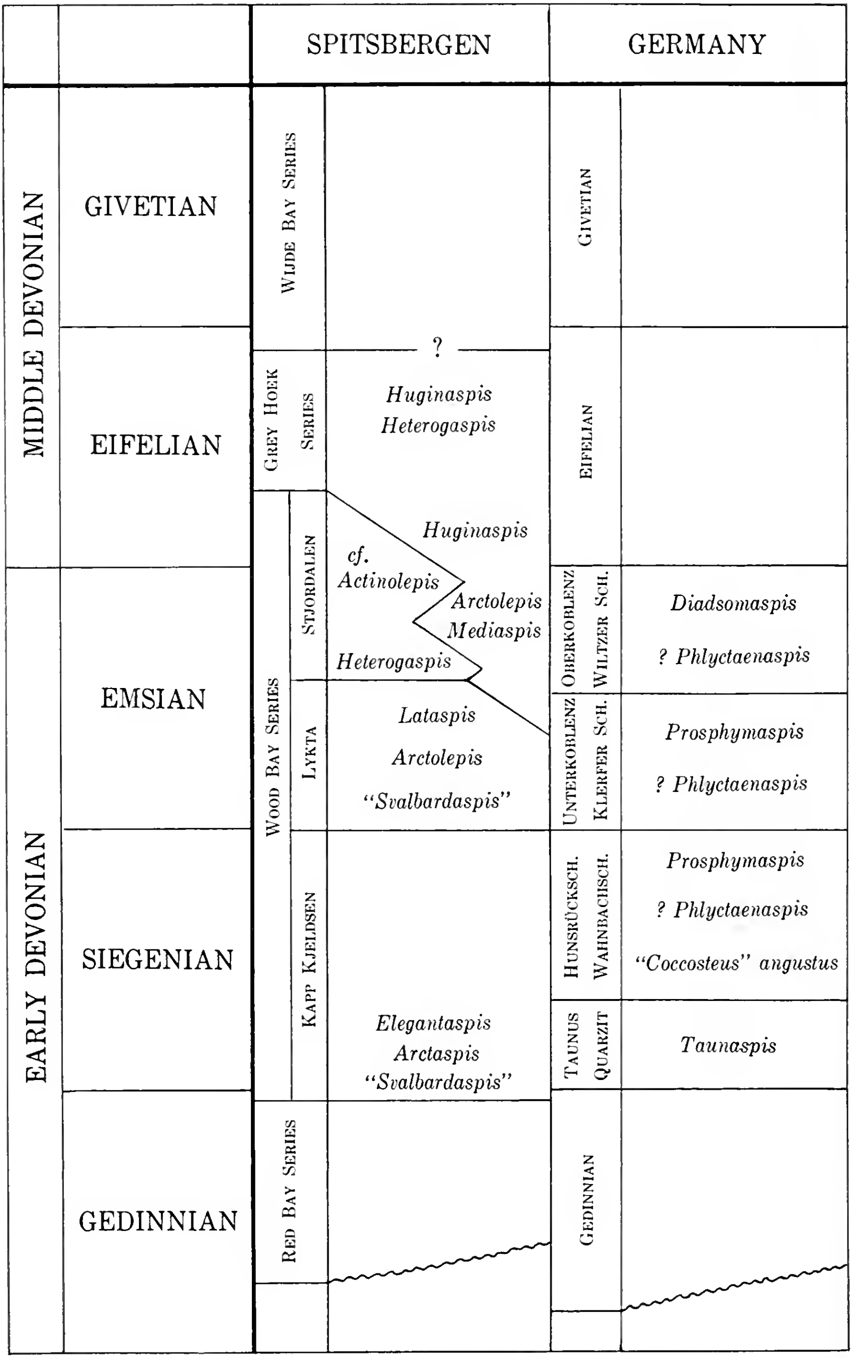


FIG. 104. Correlation chart showing the occurrence of Arctolepida in the Early and Middle Devonian.

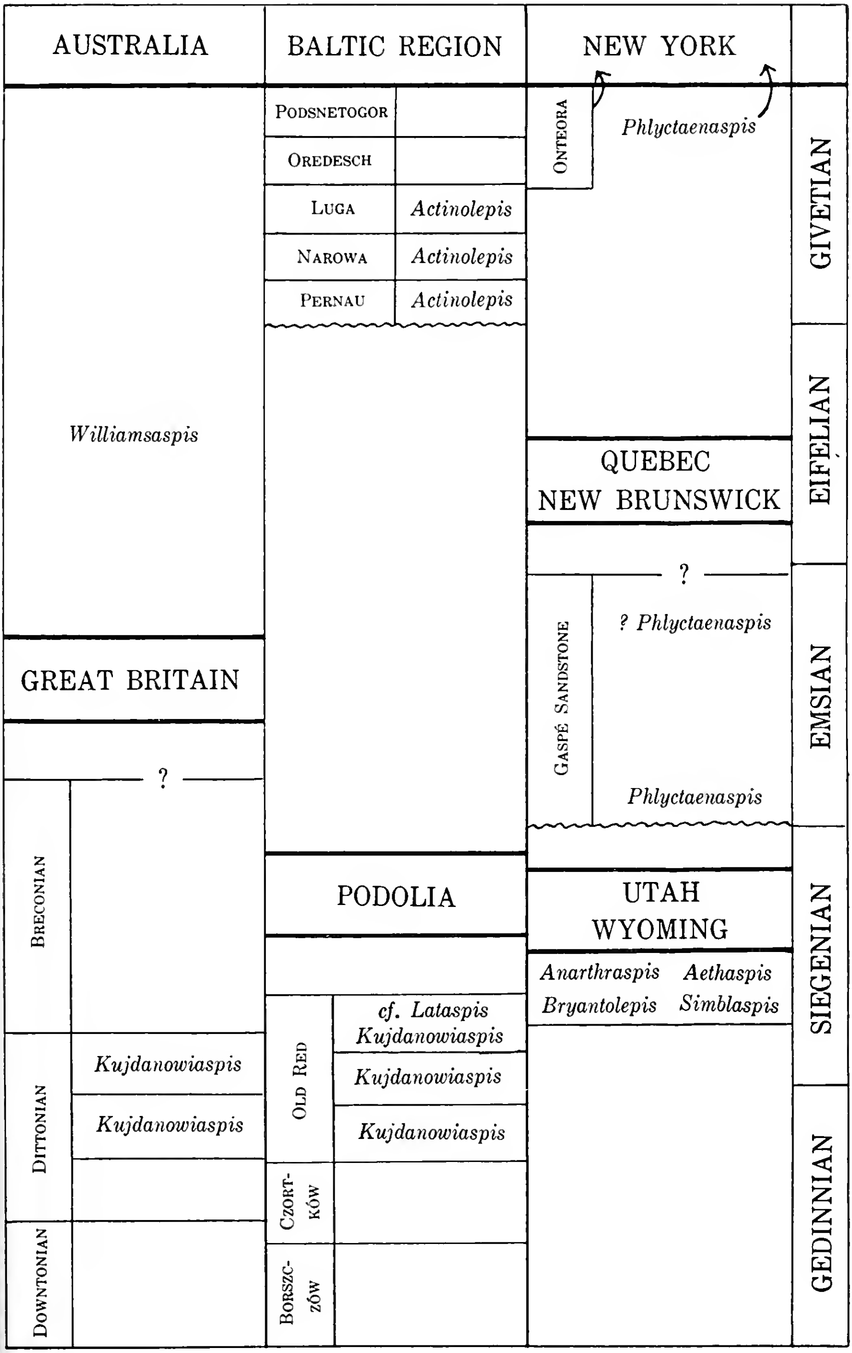


FIG. 104 (*continued*). Correlation chart showing the occurrence of Arctolepida in the Early and Middle Devonian.

taenaspinae. Others moved into habitats along the sea margin; these include *Aethaspis*, *Simblaspis*, possibly *Anarthraspis* and *Bryantolepis*, as well as some of the German forms referred to *Phlyctaenaspis*. Still others were more definitely inhabitants of the sea. In Spitsbergen these include *Mediaspis*, *Huginaspis*, and some *Heterogaspis*. In Germany the marine genera are *Prosphymaspis*, *Diadsomaspis*, some "*Phlyctaenaspis*," and "*Coccosteus*" *angustus*. The Australian *Williamsaspis* of the family Williamsaspidae is a marine form.

MORPHOLOGY OF THE ARCTOLEPIDA

Before considering the phylogenetic interrelationships of the various genera of Arctolepida, it is necessary to have some conception of what is primitive and what is specialized within the suborder. This problem is confused by a difference of opinion regarding the evolution of the pectoral fins. Stensiö (1944) and White (1952) have assumed that a eurybasal fin, such as occurs in some Brachythoraci, is primitive, although they may concede that Arctolepida are primitive in other respects. There is no evidence to support this theory, and the geological occurrence is strongly opposed to it. Heintz (1932a, 1933, 1938) and Westoll (1945), on the other hand, have considered *Arctolepis* to represent a primitive member of the Euarthrodira and have seen the general evolutionary trends within the order to be exemplified by the series: *Arctolepis–Phlyctaenaspis–Coccosteus–Dinichthys*. Evidence of the evolution of the group may be derived from their geological occurrence, and according to this, *Kujdanowiaspis* should be a primitive euarthrodire, as it is the earliest known representative. However, since the occurrence may in some cases be misleading because of the persistence of primitive forms or the precocious development of advanced forms, the comparative morphology of the Arctolepida will be discussed in some detail to see what light it throws on the problem.

Cranial Roof

The *nuchal plate* (fig. 105, *NU*) is commonly relatively long and narrow, pointed in front, tapering slightly posteriorly, and with its center of ossification near the center of the plate (*Kujdanowiaspis*, *Arctaspis*, some "*Svalbardaspis*," and *Actinolepis*). The anterior pointed part projects between the posterior parts of the centrals, and in one specimen of *Kujdanowiaspis* this has been interpreted as a separate ossification and named the median central plate (Stensiö, 1945, pp. 42, 44, fig. 10, A). Stensiö considers this median central as a relic, usually fused to the nuchal, of a once distinct series of median plates. To interpret this as a distinct plate is open to question, since the evidence is only bone radiation; but even if it exists, the plate could more logically be interpreted as a new variant in view of the fact that it has not been observed in other euarthrodires. In *Arctolepis* (fig. 105, I) and *Anarthraspis* (fig. 105, E) the nuchal differs only in having the center of ossification posteriorly placed, while in *Phlyctaenaspis* (fig. 105, G), *Bryantolepis* (fig. 105, C), and *Simblaspis* (fig. 105, D) the nuchal is relatively short and broad with the center of growth far back, particularly in the first two genera. The posterior reduction of the nuchal approaches the condition of the Brachythoraci, but the posterior widening of the nuchal that characterizes the latter group is not known among the Arctolepida. At the other extreme, the most striking condition of the nuchal is found in *Aethaspis* (fig. 105, A, B), where it is so greatly elongated anteriorly that it meets the preorbitals and completely separates the centrals; this condition is not found in other Euarthrodira. This greatly elongate nuchal, as well as the short, broad nuchal of other genera, could best be derived from the common intermediate condition that occurs in *Kujdanowiaspis* (fig. 105, F), *Arctaspis* (fig. 105, L), and others. For this reason a relatively long, narrow nuchal with central growth center is considered to be primitive within the Arctolepida.

The paired *paranuchal plates* (fig. 105, *PAN*) are typically large plates at the postero-lateral corners of the cranial roof. Their contacts with the adjacent plates show considerable variation in restorations, but their precise position may not be correct where the sutures are not visible and the boundaries have been determined from bone radiation. One peculiarity occurs in *Aethaspis* (fig. 105, A, B) where the paranuchals project into notches in the lateral edges of the nuchal. Very commonly each paranuchal has an anterior projection extending between the central and marginal to meet the postorbital; this is known in *Kujdanowiaspis, Arctaspis,* some *"Svalbardaspis," Anarthraspis, Bryantolepis, Simblaspis,* one species of *Aethaspis,* and a relative of *Actinolepis* from Spitsbergen. There may be variation in this character, even in a single individual, so it is not necessarily of great systematic importance. In the Phlyctaenaspinae there are glenoids developed on the posterior edges of the paranuchals for articulation with the anterior dorso-laterals; their significance will be considered below. Each paranuchal is traversed by the main lateral line canal (fig. 105, *lc*), which makes a distinct bend on the plate; at this bend are given off the posterior pit line and the supratemporal commissure (fig. 105, *pp, stc*) where these canals have been observed in the Arctolepida. Where the bone radiation is visible, the center of ossification occurs at the bend in the lateral line canal, and its position here has been inferred in other cases. The center of ossification is placed centrally in the plate in *Kujdanowiaspis, Arctaspis,* some "*Svalbardaspis,*" *Anarthraspis,* and a Spitsbergen form related to *Actinolepis.* It is slightly anterior in *Actinolepis* and somewhat posterior in *Aethaspis, Simblaspis, Bryantolepis,* and *Arctolepis.* In *Phlyctaenaspis* (fig. 105, G) it is near the posterior edge of the plate, a condition resembling that in the Brachythoraci and involving a shortening of the posterior part of the cranial roof. The various modifications of the paranuchals in the Arctolepida are best derived from the condition in *Kujdanowiaspis, Arctaspis,* and *Anarthraspis,* where the plates are large with central growth centers, and this is considered to be primitive within the suborder.

The *central plates* (fig. 105, *CE*) show little variation within the Arctolepida. Commonly they are six-sided, each side corresponding to a contact with an adjacent plate; one of the lateral sides may not be present in those forms where the paranuchal meets the postorbital. The postero-medial borders accommodate the pointed anterior end of the nuchal except in *Aethaspis,* where the nuchal and preorbitals completely separate the centrals. The anterior borders form more or less transverse sutures with the preorbitals except in *Aethaspis,* where the preorbitals extend backward between the centrals, in *Actinolepis* and related forms, where the preorbitals form a pointed projection between the centrals, and in *Arctolepis,* where the pineal projects between the anterior ends of the centrals. The center of ossification is near the center of each plate except in *Anarthraspis,* where it is posterior in position, and in *Actinolepis,* where it approaches close to the midline. The central sensory canal (fig. 105, *cc*) and, where they are indicated, the middle and posterior pit lines (fig. 105, *mp, pp*) radiate laterally from the center of ossification. In only one arctolepid, *Arctolepis,* does the supraorbital line (fig. 105, I, *soc*) extend posteriorly onto the central, a condition that is typical in the Brachythoraci. All the various features of the genera mentioned above could be derived from the usual condition found in the remaining genera, that is, a five- or six-sided central with a central ossification center, separated posteriorly by the pointed anterior end of the nuchal, and with a transverse suture with the preorbital. This condition is considered primitive within the Arctolepida.

The *preorbital plates* (fig. 105, *PRO*) show the most varied development of any of the dermal bones of the arctolepid cranial roof, with the possible exception of the rostral, pineal, and postnasals. This may be taken as an indication of the relative plasticity of the anterior part of the skull. In *Kujdanowiaspis, Arctaspis, "Svalbardaspis" angulatus,* and *Anarthraspis* they are somewhat wider than long and are five-sided, with the sides bounding respectively the opposite preorbital, the pineal and postnasal, the orbit, the postorbital, and the central. Anteriorly the preorbitals are notched shallowly for the pineal. The center of ossification is near the center of each plate, and from this point the supraorbital line (fig. 105, *soc*) extends antero-laterally. A very slight modification of this pattern is found in *Phlyctaenaspis* (fig. 105, G) where the posterior sutures with the centrals are directed obliquely postero-medially, instead of being transverse. In *Simblaspis* (fig. 105, D) the preorbitals are relatively much larger, especially their posterior parts, with the result that the centers of ossification are somewhat in front of the centers of the plates. In *Bryantolepis* (fig. 105, C) these plates are also large but are widened laterally in such a fashion that the centers of ossification lie mediad to the centers of the plates. The preorbitals of this genus are distinctly six-sided as a result of the deep notching anteriorly by the pineal and the enlargement of the postnasals. More striking differences in the form of the preorbitals are found in other genera. In *Arctolepis* (fig. 105, I), and to a lesser extent in *"Svalbardaspis" stensioi* (fig. 105, K), the pineal and rostral have pushed their way backward between the preorbitals and the orbits have notched the cranial roof deeply, even more than in *Bryantolepis,* resulting in relatively narrow preorbitals that are completely separated from each other in *Arctolepis.* This condition approaches that of the Brachythoraci, where the preorbitals are characteristically separated by the pineal and part of the rostral. In *Aethaspis* (fig. 105, A, B) the preorbitals are greatly elongate posterior to the centers of ossification, and their posterior edges have S-shaped sutures with the nuchal and centrals; anteriorly they are notched quite deeply by the pineal and rostral. The most remarkable modification of the preorbitals occurs in *Actinolepis* (fig. 105, H) and related forms from Spitsbergen (fig. 105, J). In these the centers of ossification are far posterior and near or at the midline, resulting in the fusion of the two plates. The growth is almost entirely anterior to the centers of ossification, and the anterior end of the combined preorbitals is deeply notched by the rostral and pineal. A close approach to the *Actinolepis* condition is seen in

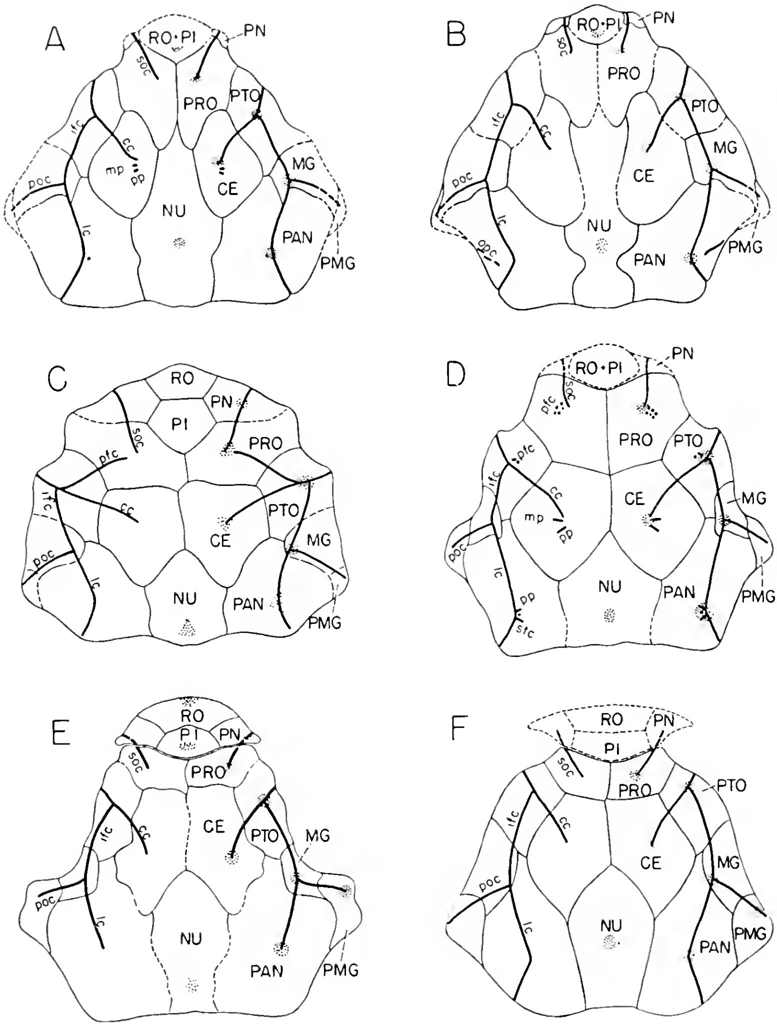


FIG. 105. Restorations of cranial roofs of Arctolepida, all reduced to the same area; centers of ossification stippled. A, *Aethaspis utahensis*, from PF 1405 (× 0.6); B, *A. major*, from PF 503, 917–919 (× 0.3); C, *Bryantolepis brachycephalus*, from PF 158, 1542, 1544 (× 1.3); D, *Simblaspis cachensis*, from PF 504 (× 0.7); E, *Anarthraspis* sp., from PF 1533 and Princeton 13659 (× 0.3); F, *Kujdanowiaspis* sp., based largely on specimen from Old Red, II, Podolia (× 1.2).

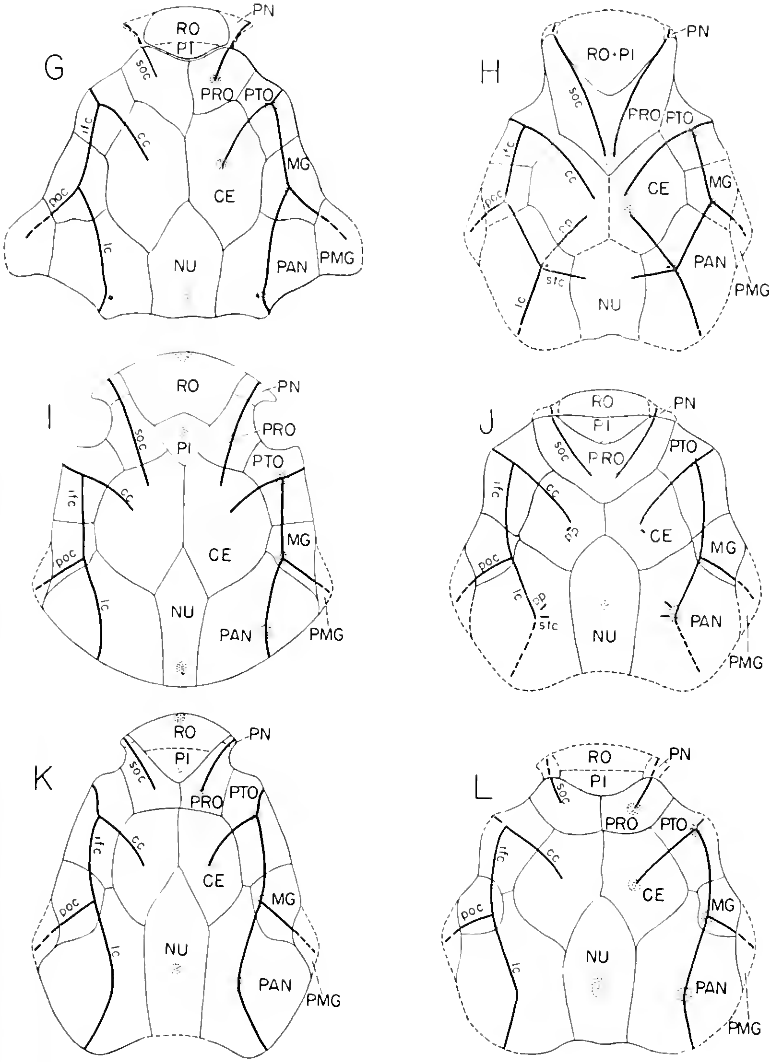


FIG. 105 (*continued*). G, *Phlyctaenaspis acadica*, from British Museum (Natural History), P 5972 (× 0.5); H, *Actinolepis tuberculata*, from specimen figured by Gross, 1940 (× 0.5); I, *Arctolepis solnordali*, modified from Heintz, 1929 (× 0.8); J, Spitsbergen genus related to *Actinolepis*, from specimen in Stockholm (× 0.4); K, "*Svalbardaspis*" *stensioi*, from specimen figured by Heintz, 1929 (× 0.4); L, *?Arctaspis* sp., based on specimen from lower part of Wood Bay Series, Spitsbergen (× 0.5).

CE, central; *MG*, marginal; *NU*, nuchal; *PAN*, paranuchal; *PI*, pineal; *PMG*, postmarginal; *PN*, postnasal; *PRO*, preorbital; *PTO*, postorbital; *RO*, rostral; *cc*, central canal; *ifc*, infraorbital canal; *lc*, main lateral line; *mp*, middle pit line; *opc*, "opercular" canal; *pfc*, profundus canal; *poc*, preopercular canal; *pp*, posterior pit line; *soc*, supraorbital canal; *stc*, supratemporal commissure.

"Svalbardaspis" rotundus and *"S." polaris* (Heintz, 1929, figs. 23–24). All of the modifications of the preorbitals that occur in the Arctolepida can be derived most easily from the condition of *Kujdanowiaspis, Arctaspis,* and *Anarthraspis* simply by changes in the position of the center of ossification and of the relative amount of growth in different directions, and by the posterior movement of the rostral and pineal in the midline. For this reason the type of preorbital exhibited by these genera is considered to be primitive within the suborder.

The *postorbital plates* (fig. 105, *PTO*) show only minor variations within the Arctolepida. Each plate is traversed by the central sensory canal (fig. 105, *cc*), the infraorbital canal (fig. 105, *ifc*), and, in *Bryantolepis,* by the profundus line (fig. 105, C, *pfc*). The center of ossification is at the point where these lines meet. It is nearly central in the plate in *Arctolepis, Actinolepis, Aethaspis, Simblaspis,* and some *"Svalbardaspis,"* slightly lateral to the center in *Arctaspis* and *Bryantolepis,* and antero-lateral in position in *Kujdanowiaspis, Anarthraspis, Phlyctaenaspis,* and *"Svalbardaspis" stensioi.* The only important modification of the preorbital is a deep notching of the lateral edge by the orbit; this is pronounced only in *Arctolepis* (fig. 105, I), although it is foreshadowed in *"Svalbardaspis" stensioi* (fig. 105, K). It is an approach to the condition of the Brachythoraci, where the orbits are characteristically large and form deep notches in the cranial roof. In view of their rare occurrence, the deep orbital notches must be considered as a specialization within the Arctolepida.

The *marginal plates* (fig. 105, *MG*) are relatively small elements traversed by the main lateral line canal (fig. 105, *lc*), the otic branch of the infraorbital line (fig. 105, *ifc*), and the preopercular line (fig. 105, *poc*). The center of ossification is at the point where these canals meet, and generally it lies in the median or postero-median part of the plate. In other words, there is very little growth posterior to the preopercular canal and median to the main lateral line and infraorbital canal. In *Phlyctaenaspis* (fig. 105, G) and *Actinolepis* (fig. 105, H) the ossification center is more centrally placed, and this is related to the fact that the paranuchal and postorbital do not grow medial to the marginal, at least in the individuals upon which the restorations are based. There is little form variety upon which to base any opinion on what is primitive within the Arctolepida.

The *postmarginal plates* (fig. 105, *PMG*) are small elements forming the lateral corners of the cranial roof. Since they are sometimes detached, or incompletely known for other reasons, little can be said about their development within the Arctolepida. Only two genera show any outstanding differences: in *Phlyctaenaspis* (fig. 105, G) they are relatively large, and in *Aethaspis* (fig. 105, A, B) they are very small and crescentic in shape. Both of these developments may be considered as specializations within the suborder.

The *rostral* (fig. 105, *RO*), *pineal* (fig. 105, *PI*), and paired *postnasal* (fig. 105, *PN*) *plates* are almost invariably fused together in known specimens and are distinguishable only by their radiation from distinct centers of ossification. One specimen figured by Bryant (1934, pl. 24, fig. 3) represents a separate rostral, presumably of *Anarthraspis*. In *Aethaspis* the postnasals may or may not be fused to adjacent bones. The rostral, pineal, and postnasals form the roof over separate endocranial elements, which are often ossified perichondrally as paired circumcapsular bones (Stensiö, 1945, p. 8). This may account for the fact that these dermal roofing bones are frequently not fused to the rest of the cranial roof and are absent in many specimens. They are known to be fused in *Aethaspis, Bryantolepis, Arctolepis*, and *"Svalbardaspis" stensioi*, they are sometimes fused in *Kujdanowiaspis, Actinolepis* and related forms from Spitsbergen and possibly in *Arctaspis* and *Phlyctaenaspis*, while they appear to be detached always in *Anarthraspis, Simblaspis*, and the other species of *"Svalbardaspis."* In *Kujdanowiaspis* (fig. 105, F) the rostral and pineal are rather short, wide plates; the pineal usually has a slightly convex posterior edge that fits into the concave anterior edges of the paired preorbitals; and the postnasals are moderately large plates with strong lateral projections that form the anterior edges of the orbits. The situation is essentially the same in *Phlyctaenaspis* (fig. 105, G), while *Anarthraspis* (fig. 105, E) differs only in having relatively longer, narrower rostrals, and pineals and postnasals that do not project so far laterally in front of the orbits. Other genera show more considerable differences. In *Bryantolepis* (fig. 105, C) the pineal is enlarged and deeply notches the anterior borders of the preorbitals; the postnasals are strikingly large, although they do not appear to enter into the anterior borders of the orbits. In *Aethaspis* (fig. 105, A, B) all of these anterior plates are greatly reduced; the rostral and pineal form a small plate occupying a notch in the anterior ends of the preorbitals, while the postnasals are mere vestiges that are sometimes missing and at other times form a small projection at the anterior ends of the preorbitals. In *Actinolepis* (fig. 105, H) the postnasals are probably much reduced, while the rostral and pineal are enlarged antero-posteriorly and lie almost entirely between the expanded anterior ends of the preorbitals. This situation is foreshadowed in related forms from Spitsbergen (fig. 105, J). In *Arctolepis* (fig. 105, I) the pineal and the greatly enlarged rostral completely separate the preorbitals, the pineal even notching the anterior ends of the centrals; it approaches in this respect typical Brachythoraci. *"Svalbardaspis" stensioi* (fig. 105, K) has a condition intermediate between *Arctolepis* and *Kujdanowiaspis*. These anterior cranial plates are surely specialized in *Arctolepis, Actinolepis,* and *Aethaspis,* and probably in *Bryantolepis.* Since they could all be derived from the condition in *Kujdanowiaspis* and *Phlyctaenaspis,* and since intermediates are known in some cases, the latter genera are considered to be primitive in this respect.

Cheek Plates

The *suborbital plate* (fig. 106) is known in a few Arctolepida, while other plates of the cheek region are known with certainty only in *Phlyctaenaspis acadica,* where they have been described by Heintz (1933). The type of *Anarthraspis montanus,* described by Bryant (1932, p. 249, pl. 10, fig. 1) as a rostral and pineal, is actually a suborbital, as is shown by its asymmetrical radiation, and there are other suborbitals known in this genus (fig. 106, E). Bryant has figured (1932, pl. 7, fig. 1) a poorly preserved suborbital of *Bryantolepis,* and another suborbital of this genus (PF 1597) is restored in figure 106, C. Finally, there is a well-preserved suborbital of *Aethaspis utahensis* (figs. 94, C; 106, F) described above. The most striking feature of the suborbital of *Aethaspis* and *Anarthraspis* is the short and relatively deep anterior or suborbital process. This process bounds the orbit below and meets the postnasal in front, so that its shortness in these genera is a clear indication of the smallness of the orbits. This character is also suggested by the small orbital notches on the cranial roof, and is rather characteristic of the Arctolepida. Somewhat larger orbital notches occur in *Phlyctaenaspis, Actinolepis, Simblaspis,* and *Bryantolepis,* and correlated with this the suborbitals of *Phlyctaenaspis* and *Bryantolepis* are seen to have relatively longer suborbital processes. Because of their common occurrence, small eyes and accompanying features are assumed to be primitive within the Arctolepida. In Brachythoraci the eyes are usually large and may be huge in some of the Wildungen genera, and in correlation with this character the suborbitals may be greatly modified. The orbits of *Arctolepis,* although they notch the cranial roof deeply because of their more dorsal position, were not much enlarged; the suborbital is not known in this genus.

The blade or posterior part of the suborbital is relatively large in *Aethaspis, Phlyctaenaspis,* and *Anarthraspis*. In *Anarthraspis* it has a posterior projection that is not known in other euarthrodires. In *Aethaspis utahensis* the blade has an unornamented dorsal border which must have formed a movable joint with the postorbital; the blade is very long and squarely truncate behind. *Phlyctaenaspis* has an angulate posterior border divided into a postero-dorsal edge presumably for the internal plate and a postero-ventral border for the postsuborbital. In *Bryantolepis* the blade is relatively small.

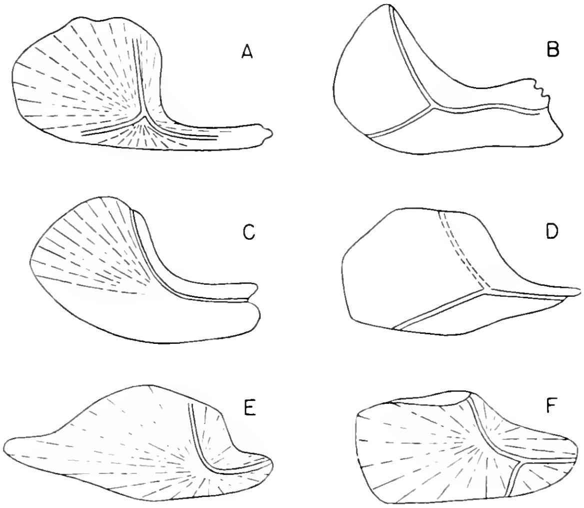


FIG. 106. Right suborbital plate of Arctolepida and Coccosteidae, all reduced to the same area. A, *Coccosteus decipiens*, after Heintz, 1931 (× 0.8); B, *C. minor*, PF 1101 (× 4.4); C, *Bryantolepis brachycephalus*, PF 1597 (× 2.8); D, *Phlyctaenaspis acadica*, British Museum (Natural History), P 6555 (× 1.0); E, *Anarthraspis* sp., restored from PF 1538, 1535 (× 0.9); F, *Aethaspis utahensis*, PF 1403 (× 1.2).

The infraorbital sensory canal always passes ventrally down the blade, then anteriorly along the suborbital process. From this the supramaxillary canal extends postero-ventrally, but this canal has not been seen in *Anarthraspis* and *Bryantolepis*. In *Coccosteus decipiens* (fig. 106, A) the center of ossification is at the junction of these canals, but in *Aethaspis* it is on the infraorbital canal some distance postero-dorsal to this junction.

Two other euarthrodires have suborbitals that resemble those of the Arctolepida. One is *"Coccosteus" angustus* (Traquair, 1903, pl. 6, fig. 1), in which the suborbital appears to be closely comparable to that of *Phlyctaenaspis.* The other is *Coccosteus minor* (fig. 106, B), whose suborbital resembles that of *Bryantolepis* very closely.

Of the other plates of the cheek region very little is known in the Arctolepida. Heintz (1933, pp. 131–132) has described what may be an internal plate in *Phlyctaenaspis acadica.* Some plates that have been described above (pp. 496–498) may represent the postsuborbital and internal of *Aethaspis.* A full understanding of this region must await discovery of better material.

Endocranium

Since the endocranium of *Aethaspis* has not been fully studied and is not described in the present paper, this structure will be considered only briefly here. This discussion is based largely on the work of Stensiö in several publications (1934, 1944, 1945, 1948), and also on his manuscripts and figures, which have very generously been made available to me. Additional information on the arthrodire endocranium has been published by Gross (1937, *?Phlyctaenaspis;* 1940, *Actinolepis*) and White (1952, *Buchanosteus*).

The endocranium was largely cartilaginous but sometimes was provided with perichondral ossification. Among the Water Canyon Formation Arctolepida, perichondral bone is invariably present in *Aethaspis* but no sign of it has been seen in *Simblaspis.* In the Beartooth Butte forms, it is present in *Bryantolepis* but appears to be absent in *Anarthraspis.* It is present in *Kujdanowiaspis* and in some Brachythoraci, but in many others there was apparently no ossification. When present in the Arctolepida, the ossification may consist of a single element or the nasal capsules (circumcapsular bones) may be separate. Separate circumcapsular bones occur in some *Kujdanowiaspis* and in an undetermined form from the lower Wood Bay Series of Spitsbergen. They are fused to the postethmoid ossification in other *Kujdanowiaspis* and in *Bryantolepis.* In the Brachythoraci they are fused where known, with the exception of *Buchanosteus.* It is probable that separate circumcapsular bones are associated with rostral, pineal, and postnasals that are not fused to the rest of the cranial roof. If this is so it would indicate separately ossified nasal capsules in *Anarthraspis, Simblaspis, Phlyctaenaspis,* and some *Svalbardaspis,* besides those mentioned above. In certain Brachythoraci (*Pholidosteus* and *Leiosteus*) the endocranium is divided into several ossifications and may develop large dorsal fontanelles. This would appear to be the result of a secondary reduction in ossification, but the separately ossified nasal capsules may be primitive.

The endocranium of Arctolepida is low and broad (platybasic), with thick lateral walls. The orbits are small and anteriorly placed, with wide suborbital shelves and well-developed supraorbital processes. There are prominent paired lateral processes (posterior postorbital processes of Stensiö) behind the postorbital processes, and the occipital region is short. In the Brachythoraci the endocranium is usually relatively higher and narrower, and in the several genera with large eyes it may be tropibasic, with the orbital cavities very large and with the suborbital shelves and supraorbital processes reduced. The postorbital processes are placed farther back, the posterior postorbital processes are absent, and the occipital region is relatively long.

The platybasic endocranium with a short occipital region and small orbits is probably primitive among placoderms, since it occurs not only in Arctolepida but also in certain Brachythoraci, probably in the Acanthothoraci, and in a modified form in the Antiarcha. The endocranium of many Brachythoraci is surely specialized in its narrowness and height, in the large orbits, and in the lengthened occipital region. *Buchanosteus* and perhaps *Coccosteus* are intermediate between the Arctolepida and Brachythoraci in possessing the primitive arctolepid type of endocranium in conjunction with the typical dermal cranial roof of the Brachythoraci.

Trunk Shield

The *median dorsal plate* takes two very different forms in the Arctolepida. In the Actinolepinae (fig. 107, D–I) it is short and broad and has a nearly central ossification center. In the Phlyctaenaspinae (fig. 107, A–C) it is long and narrow and has the center of ossification placed well behind the center. Strictly intermediate forms are not certainly known in Arctolepida; however, "*Coccosteus*" *angustus* has a relatively short median dorsal compared to that of the Phlyctaenaspinae, and the typical *Coccosteus* median dorsal is intermediate in shape if one forgets the posterior spine. Determination of which condition is primitive within the Arctolepida is not possible on purely morphological grounds, though the central ossification center of most Actinolepinae has the appearance of a simple and unmodified condition, while the posterior ossification center of the Phlyctaenaspinae may be a modification involving an anterior elongation. Stensiö (1944, pp. 25–26; 1948, p. 209) is of the opinion that the single median dorsal of the Euarthrodira is a complex plate formed by the fusion of homologues of the anterior and posterior median dorsal plates of the Antiarcha. If this were true, the long median dorsal of the Phlyctaenaspinae might be primitive, and the laterally notched median dorsal of *Prosphymaspis* (fig. 107, A) might be taken to indicate an incomplete fusion of the two elements. Unfortunately for this theory there is no indication of two centers of ossification in any euarthrodiran median dorsal and, as Parrington has pointed out (1956, p. 410), assumptions of bone fusions without direct evidence is unjustified. A single median dorsal growing from a single ossification center is certainly primitive within the Arctolepida, although the possibility cannot be ruled out that the euarthrodiran ancestor possessed two median dorsals, one of which has been lost. All Arctolepida lack the median keel on the inner side—a feature that is characteristic of the Brachythoraci. Some Arctolepida do possess a low, median, inner ridge from which the keel could have been derived.

The median dorsals of the Actinolepinae (fig. 107, D–I) show little variation in shape. All have a well-developed postero-median projection, and usually there is a slight convexity of the anterior margin in the median line, although this is absent in *Bryantolepis* and *Anarthraspis*. *Simblaspis*, *Aethaspis*, *Actinolepis* (fig. 107, D, E, G, *x*), and *"Phlyctaenaspis" heintzi* have a smooth, untuberculated area on either side of this anterior convexity. Since the trunk shield and cranial roof are very close in Arctolepida, these areas may actually have been overridden by the cranial roof when the head was elevated. Typically the median dorsal of the Actinolepinae has a dorsal crest in the posterior half of the plate.

Among the Phlyctaenaspinae, the shape of the median dorsal is not adequately known in most Spitsbergen forms because of the complete fusion of the bones of the trunk shield, but it is certainly long and relatively narrow in all. The most elongate median dorsal occurs in the Late Devonian *Phlyctaenaspis sherwoodi* (Denison, 1950, fig. 1, B), while *P. acadica* (fig. 107, B) has a more moderately proportioned median dorsal. The latter also has a very distinct postero-median process, which foreshadows the posterior spine of *Coccosteus*. *"Phlyctaenaspis" heintzi* resembles other members of this subfamily in most respects but differs in having a short, wide median dorsal like that of the Actinolepinae; if this median dorsal has been correctly assigned to this species, this form may represent an intermediate between the two subfamilies. The most remarkable median dorsals occur in *Huginaspis* (Heintz, 1929, pl. 20, fig. 2), where the

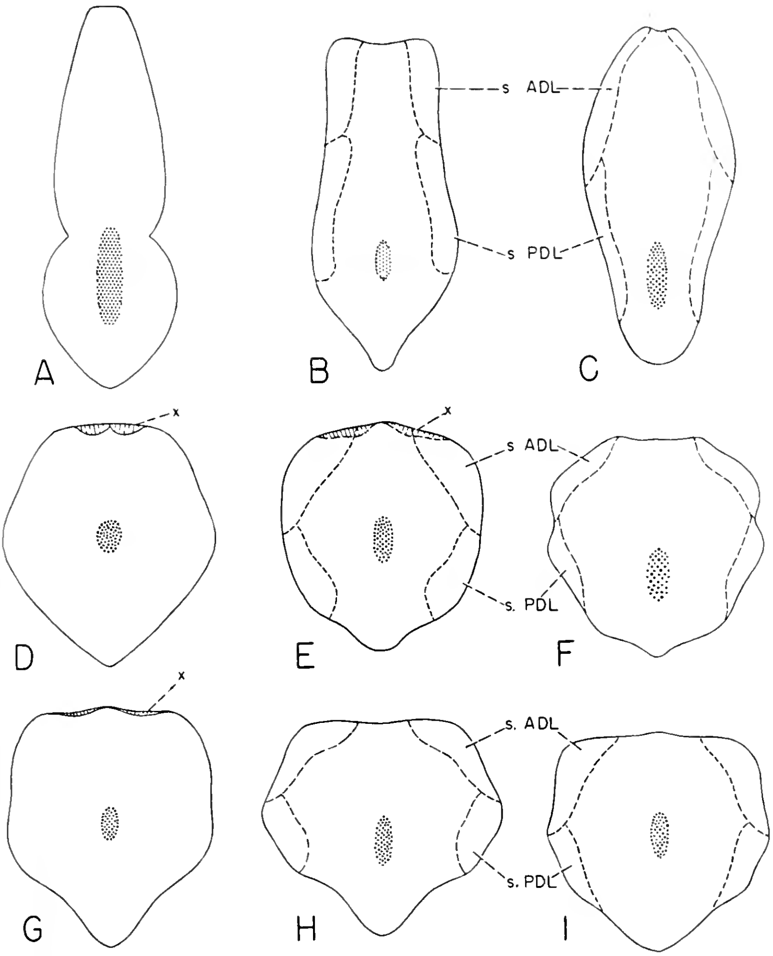


FIG. 107. Median dorsal plates of Arctolepida, all reduced to the same area; centers of ossification stippled. A, *Prosphymaspis constricta*, after Gross, 1933a (× 2.0); B, *Phlyctaenaspis acadica*, modified from Heintz, 1933 (× 0.5); C, *Arctolepis decipiens*, restored from Heintz, 1929 (× 0.9); D, *Actinolepis tuberculata*, after Gross, 1940 (× 3.8); E, *Aethaspis major*, restored from PF 907, 910 (× 0.4); F, *Anarthraspis* sp., restored from PF 1531 (× 0.4); G, *Simblaspis cachensis*, restored from PF 301 (× 0.4); H, *Bryantolepis brachycephalus*, restored from PF 162–164 (× 1.2); I, *Kujdanowiaspis* sp., based on cast of Podolian specimen, PF 1178 (× 0.8).

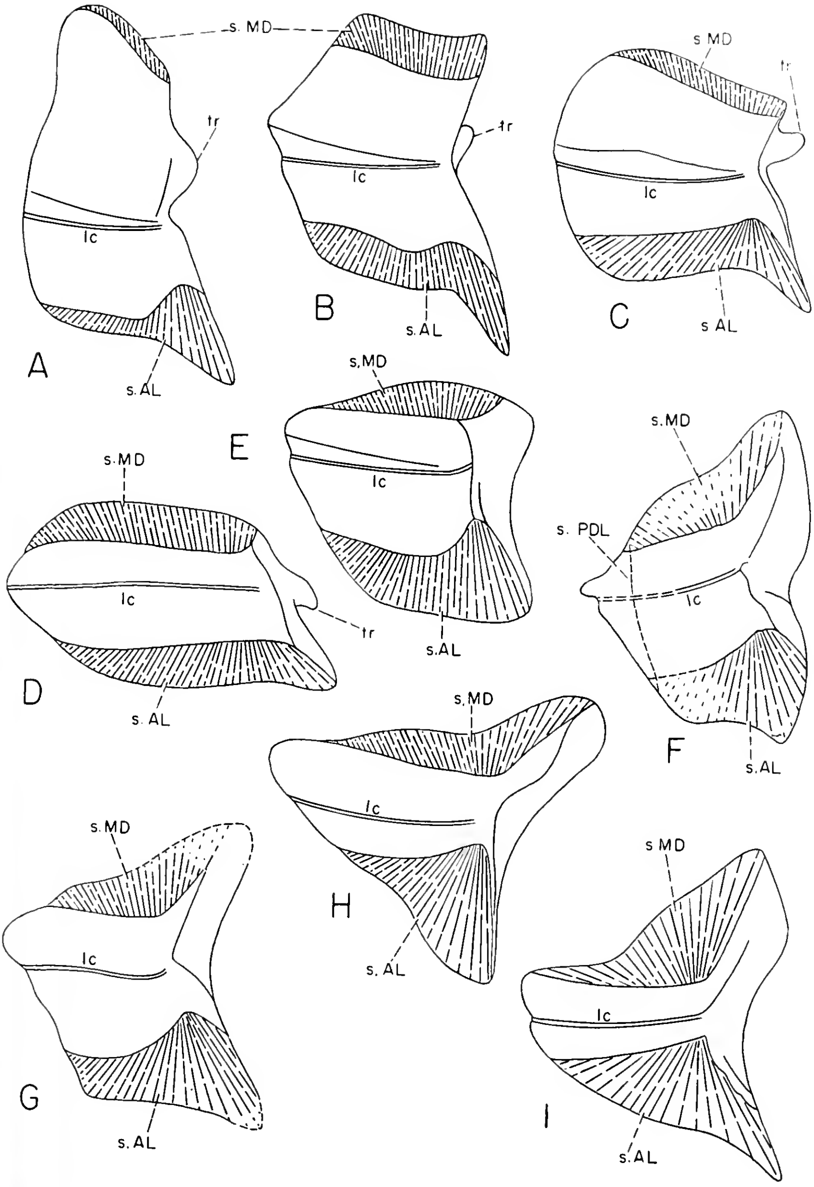
s. ADL, *s. PDL*, extent of inner overlap areas for anterior and posterior dorso-laterals; *x*, external unornamented area.

plate has a very high median dorsal crest, in *Prosphymaspis* (fig. 107, A), where it is deeply notched laterally by the posterior dorso-laterals, and in *Diadsomaspis* (Gross, 1937, fig. 12, N), where it is narrow anteriorly between the anterior dorso-laterals and widens posteriorly between the posterior dorso-laterals. All of these conditions are considered to be specializations because of their unique occurrences.

Posterior dorsal plates have been described above (p. 482) in *Aethaspis*, where they have been compared with similar plates of *Bryantolepis*, *Anarthraspis*, and *Kujdanowiaspis*. Their bilateral symmetry and their highly arched form in *Aethaspis* (figs. 93, 94, B) leave little doubt that they lay in the dorsal midline behind the median dorsal. It is possible that they were generally present in Arctolepida but have not yet been recognized in many genera. Thus the plate described by Gross (1937, fig. 12, B) as the median dorsal of *Phlyctaenaspis pusilla* could be a posterior dorsal, and the same is true of the so-called median dorsal of *Taunaspis eurystethes* (op. cit., fig. 13, D) and of *Murmur arctatus* (Bryant, 1935, pl. 10, fig. 2). All of these differ from typical median dorsals in their shape. The known posterior dorsals of Actinolepinae are relatively large plates. Those of *Phlyctaenaspis acadica*, on the other hand, are quite small. These plates are not known in any Brachythoraci, and it is probable that they were absent in this suborder. But it is possible that comparable elements were present in the Petalichthyida; *Lunaspis* has the posterior part of the body covered with scales, and at least two of these in the median line behind the median dorsal are enlarged to resemble small posterior dorsals. The posterior median dorsal of the Antiarcha may be a homologue of the arctolepid posterior dorsal which has become incorporated into the lengthened trunk shield. The occurrence of these plates in two or three distinct orders of Arthrodira suggests that they were present in the common ancestor;

FIG. 108. Right anterior dorso-lateral plates of Arctolepida, all reduced to the same area. A, *Prosphymaspis subtilis*, modified from Gross, 1933b (× 1.8); B, *Phlyctaenaspis acadica*, after Heintz, 1933 (× 0.8); C, "*Phlyctaenaspis*" *heintzi*, modified from Gross, 1933b (× 1.0); D, *Diadsomaspis elongata*, after Gross, 1933a (× 1.1); E, relative of *Actinolepis* from Spitsbergen, from cast, PF 1183 (× 0.9); F, *Aethaspis major*, restored from PF 532, 922, 971 (× 0.7); G, *Anarthraspis* sp., PF 263 (× 0.9); H, *Bryantolepis brachycephalus*, restored from PF 438, 1600 (× 2.7); I, *Kujdanowiaspis* sp., based on cast of Podolian specimen, PF 1180 (× 1.5).

lc, main lateral line; *s. AL*, *s. MD*, external overlap areas for anterior lateral and median dorsal; *s. PDL*, extent of internal overlap area for posterior dorso-lateral; *tr*, trochlea for articulation with paranuchal.


s. MD
tr
lc
s. AL
A
B
C
D
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F
G
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s. PDL

in this case their loss in the Brachythoraci and other groups would be secondary.

The paired *anterior dorso-lateral plates* differ in the Actinolepinae (fig. 108, E–I) and Phlyctaenaspinae (fig. 108, A–D) in one important respect: in the latter there is a well-developed trochlea which was received in a glenoid fossa on the paranuchal to form an exoskeletal articulation between the head and trunk; in the Actinolepinae there is no trochlea or glenoid, but on the external face there is a smooth, antero-dorsal, untuberculated area which was overlapped by the posterior edge of the paranuchal. The Phlyctaenaspinae resemble the Brachythoraci in which the trochlea-glenoid articulation is almost always well developed. The absence of the differentiated articular surfaces in the Actinolepinae does not mean that no movement was possible between the head and trunk but does suggest that this movement was very limited. An endoskeletal articulation was, of course, also present (Stensiö, 1945, p. 7). Because of its highly differentiated nature, the articulation of the Phlyctaenaspinae and Brachythoraci must be considered as a specialization, while the simple overlap of the anterior dorso-laterals by the paranuchals is presumed to be primitive in euarthrodires. No clearly intermediate forms showing how the articulation developed have been described. It is interesting that in the Antiarcha the articulation is reversed, with the trochlea on the cranial roof and the glenoid fossa on the anterior dorso-lateral; this situation may signify that the differentiated articulation was independently acquired in the Antiarcha and Euarthrodira. Among the latter, the Actinolepinae surely represent an early stage in the development of the exoskeletal articulation. Limited movement between the head and trunk is indicated not only by the simple overlapping of the anterior dorso-laterals by the paranuchals but also by the small space dorsally between the head and trunk shields. In many Phlyctaenaspinae there is also very little space between the cranial roof and the trunk shield; in these forms (*Arctaspis, Arctolepis, Elegantaspis, Gronlandaspis*) the articular trochleae are placed very close to each other in the most antero-dorso-median part of the anterior dorso-laterals. Movement of the head on the trunk must have been very small here also and probably was more definitely limited to a vertical direction than in the Actinolepinae. In *Phlyctaenaspis acadica* (fig. 108, B) the trochleae are better developed and more widely spaced, so probably a greater degree of movement was possible (Heintz, 1933, fig. 5, A). In the Brachythoraci the trochleae are typically well developed and placed far laterally; usually there is such a wide gap between the posterior edge of the cranial roof and the median dorsal that considerable movement may have been possible, although in at least one form, *Coccosteus minor*, the gap was partially filled by paired plates.

The shape and proportions of the anterior dorso-laterals show considerable differences among the Arctolepida. In *Kujdanowiaspis*, *Bryantolepis*, and *Diadsomaspis* the exposed face is long and low, suggesting a relatively low trunk shield; in *Aethaspis*, *Anarthraspis*, *Phlyctaenaspis* and a relative of *Actinolepis* from Spitsbergen it is relatively high, indicating that the trunk shield was high. The extremely short, high anterior dorso-lateral of *Prosphymaspis* (fig. 108, A), with its angulate cross section, is surely a specialized form. The Actinolepinae are characterized by a projection of the posterior margin dorsal to the lateral line; this feature is absent or little developed in the Phlyctaenaspinae. The Actinolepinae also have ornamented processes of the exposed face, one extending dorsally in front of the median dorsal and the other extending ventrally in front of the anterior lateral; the dorsal process and sometimes the ventral process are reduced in the Phlyctaenaspinae.

The *posterior dorso-lateral plates* of various Actinolepinae differ in their proportions. In *Kujdanowiaspis* (fig. 109, I) and *Bryantolepis* (fig. 109, H) the exposed face of the posterior dorso-lateral is rather shallow anteriorly, deep posteriorly, and constricted in between; the anterior shallowness agrees with the assumed low trunk shields of these genera. In *Aethaspis* (fig. 109, F) and *Anarthraspis* (fig. 109, E) the posterior dorso-lateral is deep throughout, indicating a higher trunk shield. The same is true of *Phlyctaenaspis* (fig. 109, A), although the ventral edge is deeply notched for the posterior lateral plate in *"P." heintzi* (fig. 109, D). The most striking modifications of the posterior dorso-lateral occur in *Prosphymaspis* (fig. 109, B) and *Gronlandaspis* (fig. 109, C), both of which have a very short, high posterior dorso-lateral with a deep ventral notch for the posterior lateral plate; *Prosphymaspis* is also distinctive in having the dorsal edge strongly convex where it projects into the notched median dorsal. In the Brachythoraci the relatively high trunk shield has resulted in a high posterior dorso-lateral; in addition this plate is reduced posteriorly, especially postero-ventrally, in connection with the reduction of the lateral wall of the trunk shield.

The *anterior laterals* are among the most interesting plates of the trunk shield, although the modifications in Arctolepida (fig. 110) are relatively slight compared to those that appear in Brachythoraci. Certain genera have relatively flat plates, only slightly convex in

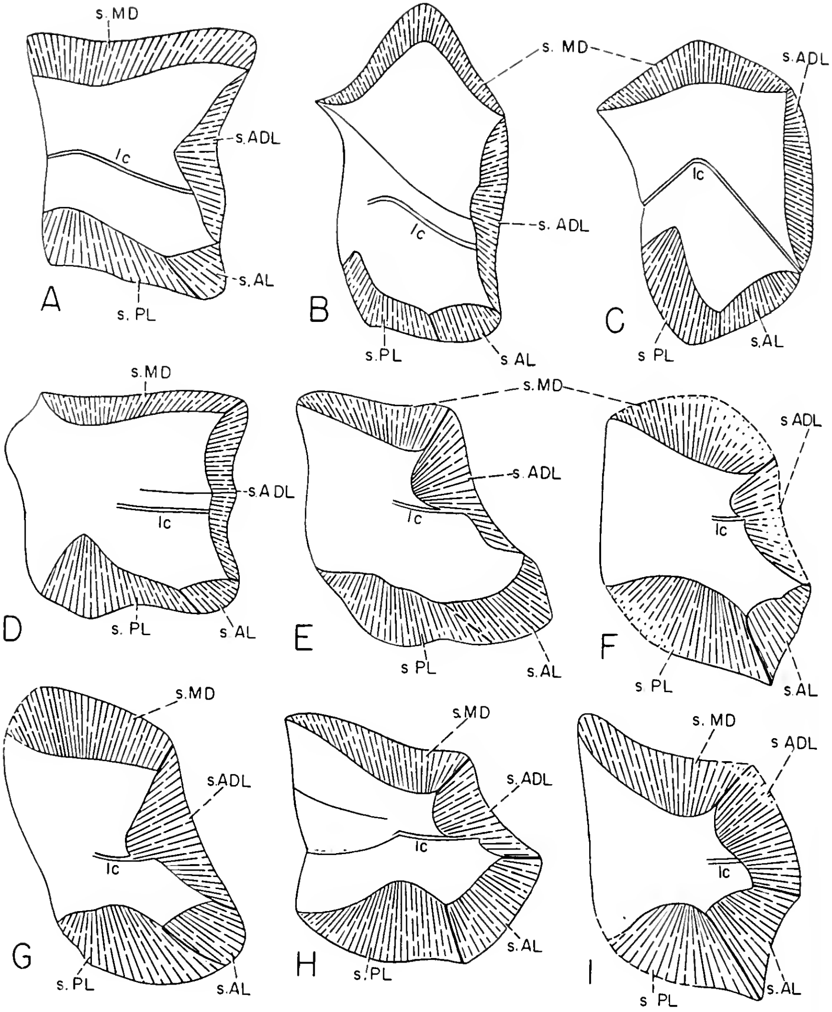


FIG. 109. Right posterior dorso-lateral plates of Arctolepida, all reduced to the same area. A, *Phlyctaenaspis acadica*, after Heintz, 1933 (× 0.8); B, *Prosphymaspis subtilis*, after Gross, 1933b (× 1.2); C, *Gronlandaspis mirabilis*, after Stensiö, 1939 (× 0.5); D, "*Phlyctaenaspis*" *heintzi*, after Gross, 1937 (× 1.0); E, *Anarthraspis* sp., restored from PF 1527, 261 (× 0.8); F, *Aethaspis major*, PF 303 (× 0.6); G, undetermined arctolepid from Utah, PF 534 (× 2.8); H, *Bryantolepis brachycephalus*, PF 180 (× 2.6); I, *Kujdanowiaspis* sp., from cast of Podolian specimen, PF 1173 (× 1.6).

lc, main lateral line; *s. ADL*, *s. AL*, *s. MD*, *s. PL*, external overlap areas for anterior dorso-lateral, anterior lateral, median dorsal, posterior lateral.

the center, with a central ossification center and with ridges of varying strength radiating to the four corners, dividing the plate into quadrants. This is true in *Kujdanowiaspis* (fig. 110, H), *Arctaspis, Elegantaspis,* and *"Phlyctaenaspis" heintzi.* The central ossification center is of course a feature of an early ontogenetic stage and may be correlated to some extent with size. It could be expected in juvenile individuals, and is, in fact, found in an extremely small individual assigned by Gross (1937, p. 20) to *"Phlyctaenaspis" pusilla* (fig. 110, G). It could be argued that this is a primitive character when it occurs in adults in that there has been no major modification due to differential growth. In other Arctolepida there are various departures from this simple scheme. For one thing, the ossification center comes to occupy a more anterior and ventral position as a result especially of a reduction in size of the anterior quadrant. At the same time the anterior quadrant becomes turned inward (fig. 110, *iw*) and is then called the "inner wing" by Heintz (1932a, p. 168), the "medial lamina" by Stensiö (1944, p. 26), and the "apron" by White (1952, p. 292). *Arctolepis* (fig. 110, A) shows this condition to a slight extent; it is marked in *Aethaspis* (fig. 110, D), *Anarthraspis* (fig. 110, F), *Bryantolepis* (fig. 110, E), and *Simblaspis* (fig. 110, C), while a more extreme development is found in *Williamsaspis* and most Brachythoraci (and of course the ptyctodonts). Though projecting inward, the inner wing is ornamented and was formed in the dermis, thus indicating an infolding of the skin in the post-cranial, pre-shoulder region. The infolding is continued ventrally by the intero-lateral, which is joined to the ventral part of the inner wing of the anterior lateral. The significance of this infolding has been discussed recently by White (loc. cit.), who has come tentatively to the conclusion that it does not represent a post-branchial wall but is the result of a neck constriction. Its development is perhaps correlated with an increased mobility of the articulation between the anterior dorso-laterals and paranuchals; where the inner wing is absent, motion of the head on the trunk must have been very slight; where it reaches its maximum development, in the Brachythoraci and Ptyctodontida, a greater amount of movement was possible.

The lower quadrant of the anterior lateral forms at its ventrolateral edge a suture for the spinal (fig. 110, *s. SP*). This is a non-overlapping, harmonic suture in *Aethaspis, Bryantolepis, Simblaspis,* and perhaps in other euarthrodires. The spinal edge is relatively long in *Arctaspis, Arctolepis, Elegantaspis, Huginaspis, Kujdanowiaspis, "Phlyctaenaspis" heintzi* and *P. sherwoodi,* in all of which a long spinal occurs; it is relatively short in *Aethaspis* and *Anarthraspis,* in which the spinal is short, and is intermediate in *Bryantolepis, Phlyctaenaspis acadica,* and *Simblaspis.* The reduction of the spinal edge and of the whole ventral triangle of the anterior lateral is extreme in the Brachythoraci, in which the spinal may be reduced to a vestige or be absent. There can be little question that the well-developed ventral triangle with a long spinal edge is primitive in the Euarthrodira and that this part of the anterior lateral has suffered great reduction in certain Arctolepida and almost all Brachythoraci. *Williamsaspis* is unique among the Arctolepida in possessing a rather long spinal edge in connection with a short, non-projecting spinal; it is reasonable to conclude that this is a specialized condition.

The upper triangle of the anterior lateral, which overlaps the anterior dorso-lateral and part of the posterior dorso-lateral, shows little modification within the Arctolepida. It is relatively high in *Aethaspis, Anarthraspis,* and *Phlyctaenaspis acadica* and helps to form the rather high trunk shield in these forms. In certain high-shielded Brachythoraci in which the lateral walls of the trunk shield are reduced, the anterior lateral is greatly lengthened dorso-ventrally and shortened antero-posteriorly, a condition not approached by any arctolepid.

The posterior edge of the anterior lateral typically overlaps the anterior or antero-dorsal edge of the posterior lateral. More ventro-laterally it does not form a suture with the underlying anterior ventro-lateral, and its exact relationships have been somewhat obscure. Heintz (1933, p. 141) considered that the anterior ventro-lateral and anterior lateral were in contact along this edge in *Phlyctaenaspis acadica.* However, a specimen of *Kujdanowiaspis* figured by Stensiö (1944, fig. 16) clearly demonstrates that the anterior lateral and anterior ventro-lateral are separated to form a fenestra filled internally by perichondral bone that formed the attachment of the pectoral fin. The same situation occurs in a specimen of *Williamsaspis* described by White (1952). A reconstruction of *Phlyctaenaspis sherwoodi* (Denison, 1950, pl. 2) indicated the presence of a pectoral fenestra in this species, and one is definitely present in *Arctolepis* (fig. 115), though Westoll (1945, p. 384) and others have believed it to be absent in this and related Spitsbergen genera. These are a few of the many reasons for believing that the pectoral fenestra was present in all Arctolepida. This fenestra may completely separate the anterior lateral and anterior ventro-lateral, as in *Williamsaspis,* or, on the other hand, the anterior lateral and anterior ventro-lateral

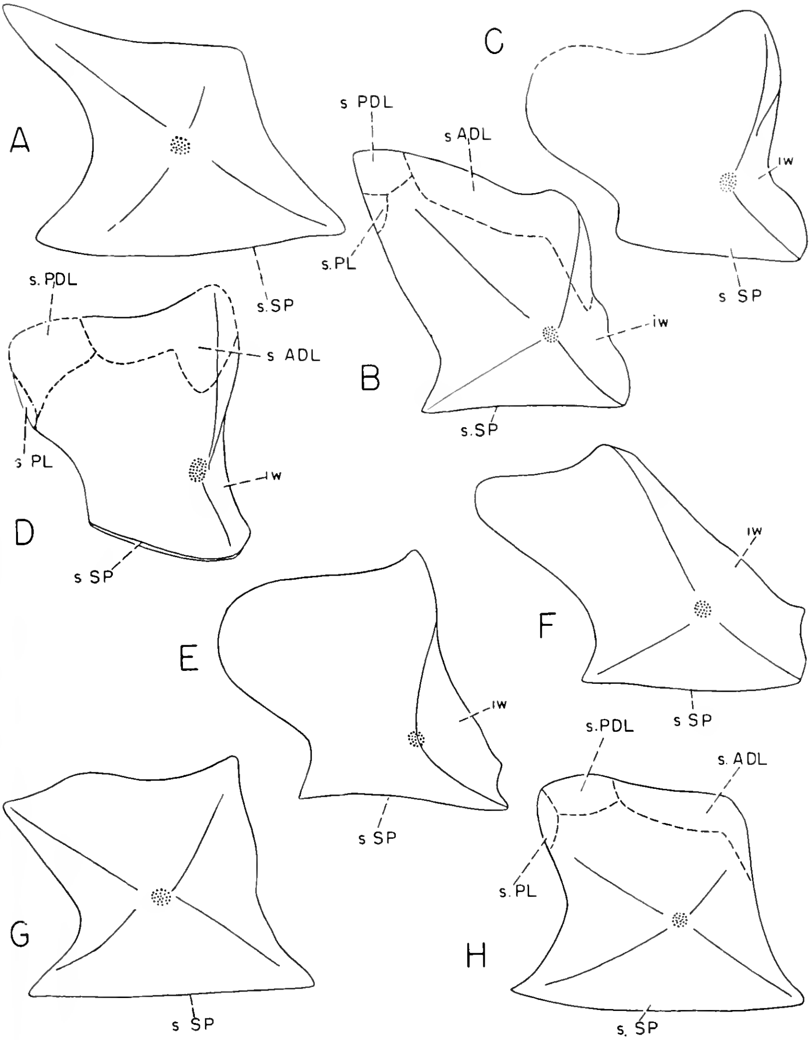


FIG. 110. Right anterior lateral plates of Arctolepida, all reduced to the same area; centers of ossification stippled. A, *Arctolepis decipiens*, after Heintz, 1938 (× 1.3); B, *Phlyctaenaspis acadica*, after Heintz, 1933 (× 0.8); C, *Simblaspis cachensis*, PF 562 (× 0.6); D, *Aethaspis major*, restored from PF 560, 561 (× 0.5); E, *Bryantolepis brachycephalus*, restored from PF 1549, 1553, UC 2210 (× 2.1); F, *Anarthraspis* sp., restored from PF 255, 1524 (× 0.9); G, "*Phlyctaenaspis*" *pusilla*, after Gross, 1937 (× 10.9); H, *Kujdanowiaspis* sp., restored from casts of Podolian specimens, PF 1163, 1164, 1166, 1176 (× 1.5).

iw, inner wing; *s. ADL*, *s. PDL*, *s. PL*, extent of inner overlap areas for anterior and posterior dorso-laterals and posterior lateral; *s. SP*, edge for spinal.

may meet both mediad and laterad to a relatively small fenestra, as in *Arctolepis*. In other forms the pectoral fenestra extends medially to reach the posterior ventro-lateral and posterior lateral, while the anterior ventro-lateral and anterior lateral meet laterally near the spinal. This is probably the case in *Aethaspis*, where an internal thickening of the posterior edge of the anterior lateral indicates the presumed extent of the attachment of the pectoral fin. As restored, *Phlyctaenaspis sherwoodi* shows the same situation. It may be true in *Kujdanowiaspis*, since Stensiö's specimen is incomplete laterally. The significance of the development of the pectoral fenestra will be deferred to the discussion of the pectoral fin.

The *posterior lateral plates* have hitherto been recognized among the Arctolepida only in *Phlyctaenaspis acadica* (Heintz, 1933, fig. 3), *"P." heintzi* (Gross, 1933a, fig. 7:5), and *Williamsaspis* (White, 1952). In the course of the present study the posterior lateral has been found also in *Aethaspis*, *Anarthraspis*, and *Bryantolepis*. In all except *Williamsaspis* it is a small plate. In *Phlyctaenaspis* (fig. 111, A, B) it is relatively long and low, overlapping the posterior dorsolateral dorsally, with a long external overlap area for the posterior ventro-lateral along its whole ventral edge, and with a small external overlap area anteriorly or antero-dorsally for the posterior tip of the anterior lateral. The posterior lateral of *Anarthraspis* (fig. 111, D) is similar except that it is relatively higher and has a longer overlap area for the anterior lateral. A plate figured by Bryant (1934, pl. 13, fig. 4) as a posterior ventro-lateral of *Bryantolepis* is probably a posterior lateral of *Anarthraspis*. In all of these the anterior lateral and posterior ventro-lateral overlap areas meet, signifying that the pectoral fenestra did not reach the posterior lateral. In *Bryantolepis* (fig. 111, E) the posterior lateral is long and low with its exposed face high posteriorly but very low anteriorly; the anterior lateral overlap area is long and does not meet the ventral overlap area, being separated by a forward extension of the exposed face that must have bounded the pectoral fenestra; as will be shown below, both the anterior and posterior ventro-laterals appear to overlap the posterior lateral in this genus. *Aethaspis* (fig. 111, C) has a short, high posterior lateral with a very small anterior lateral overlap area that is widely separated from the posterior ventro-lateral area; the posterior lateral must have had a wide contact with the pectoral fenestra. *Kujdanowiaspis* may have been incorrectly restored by Stensiö (1944, fig. 17, A) as far as the relationships of the anterior lateral, posterior lateral, and posterior ventro-lateral are concerned; it seems probable that the posterior lateral bounded the pectoral fenestra, at least in the form upon which this part of the restoration was based. *Williamsaspis* has a very large posterior lateral, relatively short and very high, peculiarly shaped, laterally ridged, and with a rather large edge for the pectoral fenestra; presumably this is a specialized condition, since nothing approaching it is found in other euarthrodires. In the Brachythoraci the posterior lateral is almost invariably reduced in connection with the posterior reduction of the trunk shield. A small but well-developed posterior lateral, relatively long and low in proportions, is believed to be primitive in the Arctolepida.

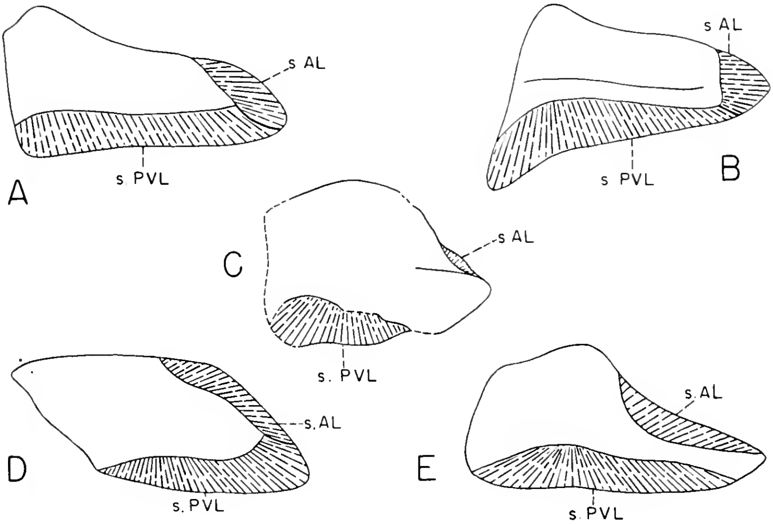


FIG. 111. Right posterior lateral plates of Arctolepida, all reduced to the same area. A, *Phlyctaenaspis acadica*, after Heintz, 1933 (× 1.1); B, "*P.*" *heintzi*, after Gross, 1933b (× 1.2); C, *Aethaspis major*, restored from PF 924 (× 0.5); D, *Anarthraspis* sp., PF 1541 (× 1.4); E, *Bryantolepis brachycephalus*, PF 183 (× 2.2).

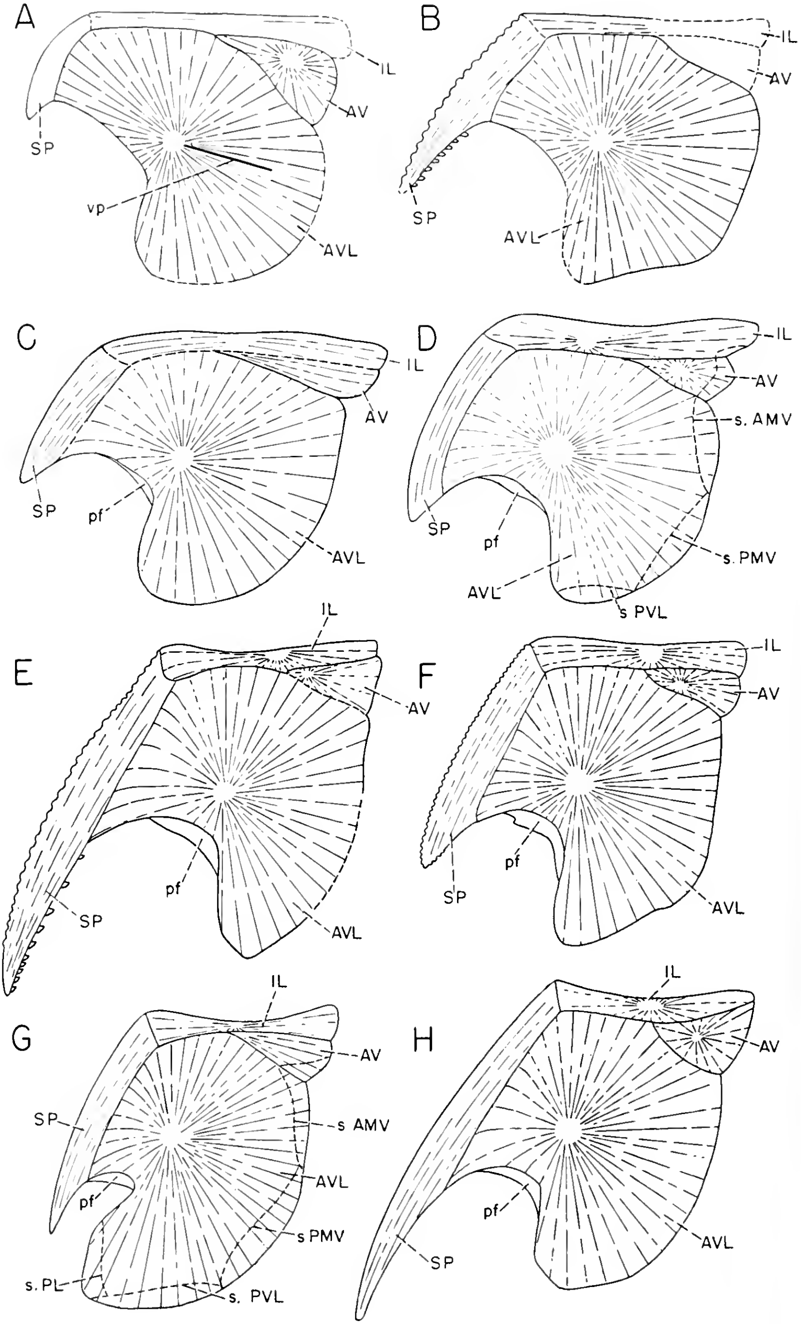
s. AL, *s. PVL*, external overlap areas for anterior lateral and posterior ventro-lateral.

The *anterior ventro-lateral* plates (fig. 112, *AVL*) are constructed on a plan very similar to that of the anterior laterals. The lateral border attaches to the spinal in a simple harmonic suture and shows modifications similar to those of the spinal edge of the anterior lateral; it is long in forms with a long spinal and tends to be short in those with a short spinal. The anterior border unites with the intero-lateral in a harmonic suture, while the antero-medial, medial, and postero-medial borders overlap the antero-ventral (in Actinolepinae), anterior and posterior medio-ventrals, and posterior ventro-lateral. The postero-lateral part of the plate is of particular interest. It is arched inward to bound the pectoral fenestra ventrally, while its posterior edge is concave to form the boundary of the pectoral sinus, which lies between the body wall and the spinal. The extent of the pectoral fenestra has been considered in the discussion of the anterior lateral, but additional evidence may be obtained from the anterior ventro-lateral. The fenestra may extend all of the way from the spinal to the point where the anterior ventro-lateral overlies the posterior ventro-lateral, as in *Williamsaspis*. In *Arctolepis*, at the other extreme, it is probable that the anterior ventro-lateral and anterior lateral meet both medially and laterally to the small pectoral fenestra (fig. 115). An anterior ventro-lateral of *Bryantolepis* (PF 194, fig. 112, G, *s. PL*) shows very distinctly an internal overlap area in its postero-lateral corner, which could only have overlapped the anterior lateral or the posterior lateral; an overlap of the anterior lateral by the anterior ventro-lateral is most improbable, and while the anterior ventro-lateral is not known to suture with the posterior lateral in other Arctolepida, possibly excepting *Williamsaspis*, this appears to be the more probable explanation of this overlap. Above the ornamented edge of the pectoral sinus of *Aethaspis* and *Anarthraspis* there rises a smooth, unornamented flange (fig. 112, C, D, F, *pf*) attached to the anterior ventro-lateral and probably representing the endoskeletal attachment of the pectoral fin; this occupies the antero-medial part of the pectoral sinus and does not extend to the spinal, suggesting that the pectoral fin base was considerably more restricted than in *Williamsaspis*.

The postero-lateral part of the anterior ventro-lateral also varies in the shape and position of the pectoral sinus. In many forms (*Arctaspis, Arctolepis, Kujdanowiaspis, "Phlyctaenaspis" heintzi, P. sherwoodi, Prosphymaspis, Heterogaspis,* and *Huginaspis*) the sinus is rather narrow laterally and deep antero-posteriorly, with its lateral edge bounded by the spinal and its anterior and medial edges bounded by the anterior ventro-lateral and anterior lateral. *Bryantolepis* (fig. 112, G) differs in having an extremely narrow sinus. In other genera the pectoral sinus is more open laterally because of the shortness of the spinal and of the spinal edge of the anterior lateral and anterior ventro-lateral, and also takes a more anterior position as a result of the shortening of the antero-lateral part of the anterior ventro-lateral. This situation is found in *Aethaspis, Anarthraspis, Actinolepis, Lataspis, Phlyctaenaspis acadica,* and *Mediaspis;* its greatest development is seen in a relative of *Actinolepis* from Spitsbergen (fig. 112, A), where the spinal projects only slightly, and in *Williamsaspis* (fig. 112, J), where the sinus is not bounded laterally by the spinal. Among the Brachythoraci, only the Coccosteidae and *Pholidosteus* resemble the Arctolepida in the development of the pectoral sinus. The deep pectoral sinus is considered to be primitive within the Arctolepida, while the relatively open sinus with a more laterally directed pectoral fin is considered to be specialized.

The *spinal plates* (fig. 112, *SP*) are invariably present in Arctolepida, and for that matter in all Arthrodira, except for certain Brachythoraci where their absence is due to secondary loss. This alone is sufficient demonstration that the spinal represents part of the heritage of the ancestral arthrodire. Within the Euarthrodira there are all variations, from the extremely long, slender spinal of *Arctolepis* and *Elegantaspis* (Heintz, 1929, pls. 2, 16) to a mere vestige in *Dinichthys* and to complete loss in a number of Brachythoraci. Opinions differ as to what represents the primitive condition. Stensiö (1944) maintains that the large spinal is specialized and was formed from the exoskeleton of the anterior part of a once more extensive pectoral fin, while White (1952, pp. 296–297) considers the small spinal of *Williamsaspis* to represent a primitive condition in Arctolepida. On the other hand, Heintz (1932a, 1938), Westoll (1945), and Gross (1954) consider the long spinal to be primitive. This matter will be considered in more detail in the discussion of the pectoral fin. In my opinion the primitive euarthrodires had spinals of moderate length, such as occur in *Arctaspis* (fig. 112, I) and *Kujdanowiaspis* (fig. 112, H). The Phlyctaenaspinae tended to retain long spinals and even to lengthen them in *Elegantaspis* and *Arctolepis,* while the short spinals of certain Actinolepinae such as *Aethaspis, Anarthraspis, Actinolepis,* and *Williamsaspis* are believed to indicate a tendency toward reduction, leading to the conditions found in the Brachythoraci. This belief fits in well with the stratigraphic occurrence and also receives some support from a possible ontogenetic development. As was shown above (p. 487), there is a suggestion in certain forms from the Water Canyon Formation that the spinals were relatively large in small individuals and relatively small in large individuals. If this is actually a growth phenomenon, the long-spined juveniles may be recapitulating a long-spined ancestral stage.

The *intero-lateral plates* (fig. 112, *IL*) are adequately known in very few Arctolepida. They have been described above (p. 488) in *Aethaspis,* where they were shown to consist of a ventral or external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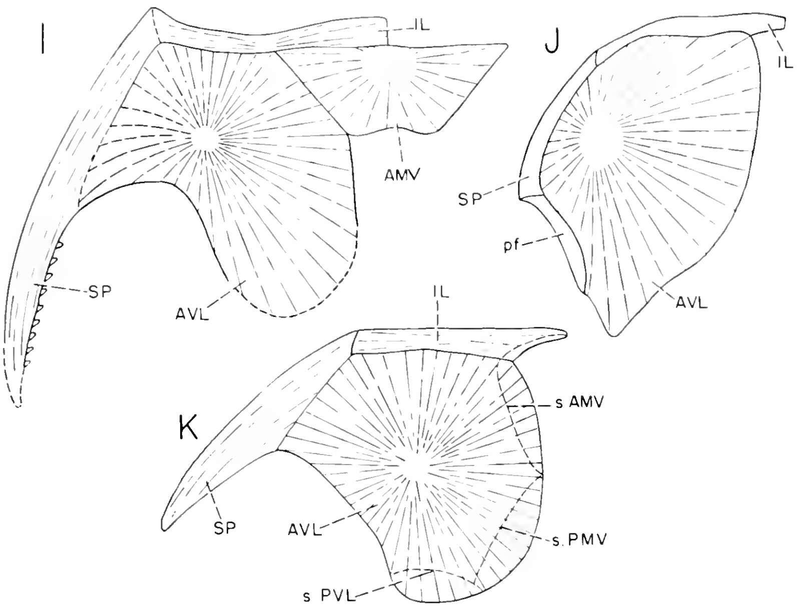

FIG. 112. Right anterior ventro-lateral, antero-ventral, intero-lateral, and spinal plates of Arctolepida, the AVL's all reduced to the same area. A, genus from Spitsbergen related to *Actinolepis*, from cast, PF 1171 (× 0.6); B, *Actinolepis tuberculata*, modified from Gross, 1940 (× 1.3); C, *Anarthraspis* sp., restored from PF 262, 1525, 1528 (× 0.4); D, *Aethaspis major*, restored from PF 939, 940, 983, 988–990 (× 0.6); E, undetermined arctolepid from Utah, PF 923 (× 1.9); F, *Aethaspis utahensis*, PF 321 (× 1.0); G, *Bryantolepis brachycephalus*, restored from PF 189, 194, 1543 (× 1.7); H, *Kujdanowiaspis* sp., modified from Stensiö, 1944 (× 1.1); I, *Arctaspis hoegi*, interpreted from Heintz, 1929 (× 0.6); J, *Williamsaspis bedfordi*, modified from White, 1952 (× 1.1); K, *Phlyctaenaspis acadica*, after Heintz, 1933 (× 0.6).

AMV, anterior medio-ventral; *AV*, antero-ventral; *AVL*, anterior ventro-lateral; *IL*, intero-lateral; *SP*, spinal; *pf*, endoskeletal attachment for pectoral fin; *s. AMV*, *s. PMV*, *s. PVL*, extent of internal overlap areas for anterior and posterior medio-ventrals and posterior ventro-lateral; *s. PL*, internal overlap area, probably for posterior lateral; *vp*, transverse ventral pit line.

lamina and a dorsal or internal lamina; the latter meets the infolded anterior quadrant of the anterior lateral, and together they form the inner wing of the trunk shield. This intero-lateral agrees in all essential respects with that of *Phlyctaenaspis acadica* as described by Heintz (1933, figs. 3, 5). The intero-lateral of *Bryantolepis* is probably similar. *Williamsaspis* has a very well-developed inner wing and I believe, contrary to the opinion of White (1952, p. 257), that the intero-lateral had a strong dorsal lamina which contributed importantly to its formation. In *Arctolepis* the inner wing is rather small, and was probably formed as usual of both the intero-lateral and anterior lateral; figures of Heintz (1929, figs. 12, 13) show a distinct dorsal lamina on the intero-lateral. A specimen of *Kujdanowiaspis* that has been figured by Stensiö (1944, fig. 16) is interesting in that it shows the inner wing in an incipient stage of development; the anterior quadrant of the anterior lateral is turned in only slightly and meets the dorsal lamina of the intero-lateral, which is small and restricted to the lateral half of the plate. Presumably, the inner wing was small or absent in the primitive euarthrodiran.

The paired *antero-ventral plates* (figs. 94, E; 99; 112, *AV*), as stated above, have not been recognized previously, or have been confused with the anterior medio-ventral. Characteristically they are present in the Actinolepinae and absent in the Phlyctaenaspinae, Williamsaspidae, and Brachythoraci. It is possible that they represent a new ossification in the Actinolepinae that was never developed in the other groups, but I know of no evidence to support this. On the other hand, they may have been a primitive character that was lost in most later Euarthrodira. This loss may have been a result simply of failure to ossify, or it could have resulted from fusion with the neighboring intero-lateral, anterior medio-ventral, or anterior ventro-lateral. A fusion with the medial part of the intero-lateral is suggested in certain cases. The center of ossification of the antero-ventral is near its lateral point and approaches that of the intero-lateral in *Bryantolepis* (fig. 112, G) and some undetermined arthrodires from Utah, PF 536 and 923 (fig. 112, E). In *Anarthraspis* (fig. 112, C) the antero-ventral is not clearly distinguishable from the intero-lateral in any specimen that I have seen and complete fusion may have taken place, although the presence of the antero-ventral is still indicated by the expanded medial end of the combined intero-lateral and antero-ventral. I know of no case where there has been a fusion of the antero-ventral with the anterior ventro-lateral, resulting in a single center of ossification. Evidence for fusion with the anterior medio-ventral is also absent, although in *Phlyctaenaspis acadica* the expanded anterior end of the anterior medio-ventral may include antero-ventral equivalents. Another possibility is that the paired antero-ventrals fused to a single median plate and that the original anterior medio-ventral was reduced and lost. If the bone radiation is correctly indicated in Heintz's photograph of *Arctaspis hoegi* (1929, pl. 12, fig. 1), the antero-ventrals may have fused so as to have a common center of radiation at the midline anteriorly (fig. 112, I). If this is so, the median plate just behind may be the posterior medio-ventral as Heintz identified it, or the anterior medio-ventral which has been crowded posteriorly. All of these points favor the view that the antero-ventrals were present primitively in the Arctolepida and that their loss in various ways is secondary in the Phlyctaenaspinae, Williamsaspidae, and Brachythoraci.

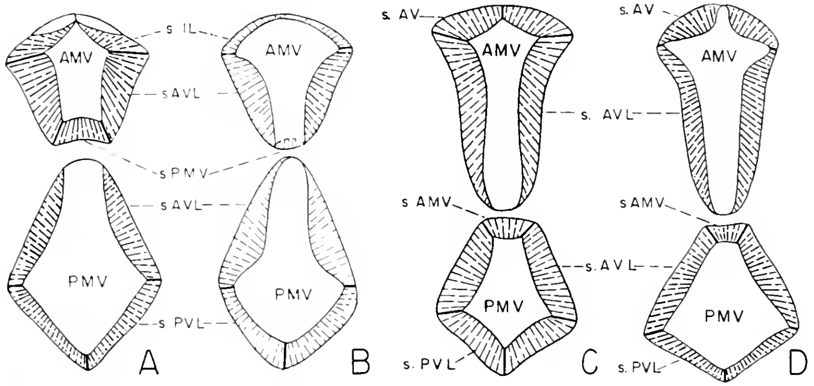

FIG. 113. Anterior medio-ventrals (*AMV*) and posterior medio-ventrals (*PMV*) of Arctolepida, all reduced to the same area. A, "*Phlyctaenaspis*" *heintzi*, after Gross, 1933b (× 0.8); B, *P. acadica*, after Heintz, 1933 (× 0.6); C, *Bryantolepis* sp., AMV from Bryant, 1934, PMV from PF 1551 (× 2.2); D, *Anarthraspis* sp., AMV from Bryant, 1932, PMV from PF 258 (× 0.6).

s. AMV, *s. AV*, *s. AVL*, *s. IL*, *s. PMV*, *s. PVL*, external overlap areas for anterior medio-ventral, antero-ventral, anterior ventro-lateral, intero-lateral, posterior medio-ventral, and posterior ventro-lateral.

The *anterior medio-ventral* and *posterior medio-ventral plates* (fig. 113, *AMV*, *PMV*) lie in the midline largely between the anterior ventro-laterals; the posterior medio-ventral is also bounded posteriorly by the posterior ventro-laterals, while the anterior medio-ventral is bounded anteriorly by the intero-laterals and in the Actinolepinae by the antero-ventrals. The anterior and posterior medio-ventrals are without known exception overlapped externally by all of these paired plates. There appears to be less consistency about the overlap between the two median ventral plates. In *Coccosteus, Dinichthys, Pholidosteus,* and probably in other Brachythoraci the anterior medio-ventral externally overlaps the posterior medio-ventral. The same appears to be the case in *Anarthraspis* (fig. 113, D) and in *Bryantolepis* (fig. 113, C). However, in *Phlyctaenaspis acadica* (fig. 113, B), *"P" heintzi* (fig. 113, A), and *Prosphymaspis* the reverse is true, and the posterior medio-ventral overlaps the anterior medio-ventral. In *Phlyctaenaspis* the two anterior sutural areas of the anterior medio-ventral are overlapped by the intero-lateral. Two similar overlap areas occur in *Bryantolepis* and *Anarthraspis,* but here they are probably overlain by the antero-ventrals; if this is so, the anterior medio-ventral would not meet the intero-laterals except perhaps in the midline. In *Aethaspis* (fig. 99) the anterior medio-ventral is not known, but its approximate shape is indicated by the overlap areas and margins of the anterior ventro-lateral, antero-ventral, and intero-lateral in PF 940. The anterior medio-ventral must have had a quite distinctive form with two pairs of lateral points bounding the antero-ventral overlaps, and with sharply distinct intero-lateral overlaps anteriorly.

The *posterior ventro-lateral plates* (fig. 114, *PVL*) are interesting for the manner in which they overlap each other near the midline. Usually the left posterior ventro-lateral externally overlaps the right, but in *Williamsaspis* (White, 1952, p. 257) the reverse is true, and in *Prosphymaspis* (fig. 114, G) the right plate overlaps the left anteriorly, though posteriorly the normal overlap occurs. Otherwise the posterior ventro-laterals are overlapped by the anterior ventro-laterals and overlap the posterior medio-ventral and posterior laterals.

The upward bend of the posterior ventro-lateral at the ventro-lateral edge serves to separate a lateral and a ventral face. These plates are often somewhat flattened in preservation and are so drawn in figure 114. In Brachythoraci, where the lateral trunk shield is reduced posteriorly, the lateral face of the posterior ventro-lateral is small or absent, but in the Arctolepida it is usually strongly developed; it is particularly long in several Phlyctaenaspinae (*Arctolepis, Phlyctaenaspis, Prosphymaspis, Huginaspis*) and in *Williamsaspis,* while in the Actinolepinae it is of moderate length in some (*Kujdanowiaspis, Aethaspis,* and *Bryantolepis*) and quite short in a few (*Actinolepis* and *Anarthraspis*). The short lateral face is believed to be specialized within the Arctolepida.

The ventral face of the posterior ventro-lateral is short and broad in *Kujdanowiaspis, Arctaspis, Aethaspis, Prosphymaspis, Phlyctaen-*

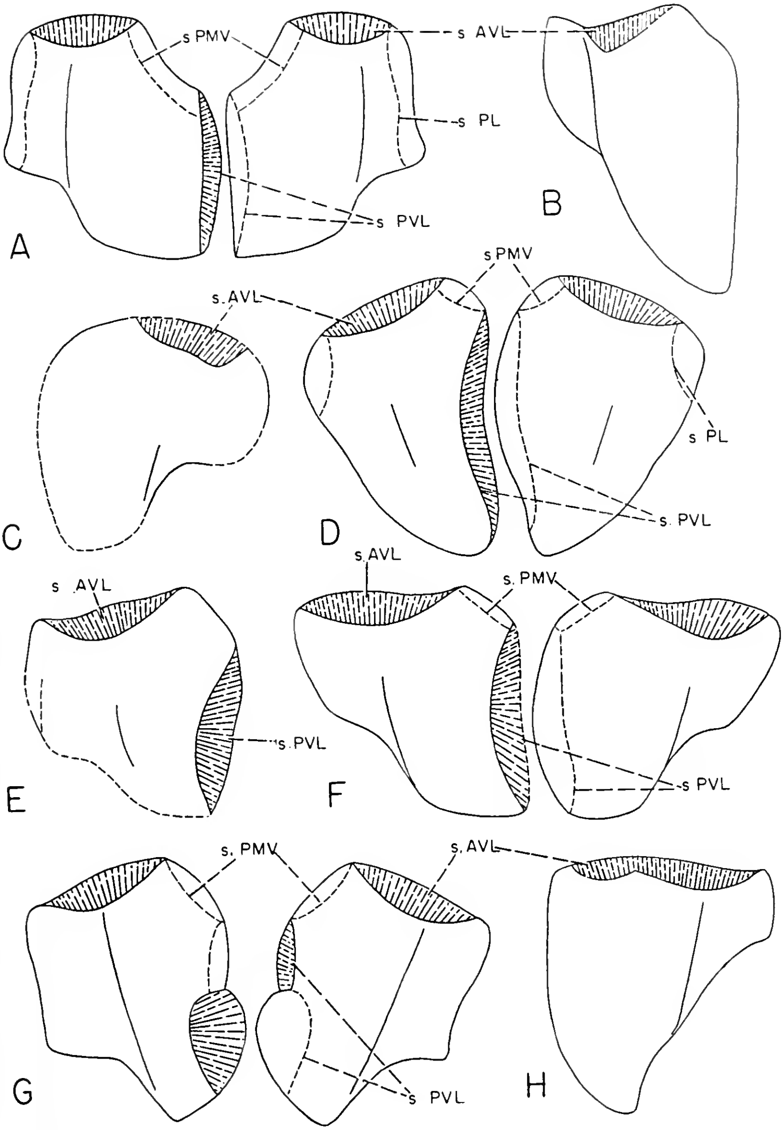

FIG. 114. Posterior ventro-lateral plates of Arctolepida, flattened and all reduced to the same area. A, *Phlyctaenaspis acadica*, modified from Heintz, 1933 (× 0.6); B, *Anarthraspis* sp., right PVL, from Bryant, 1934 (× 0.7); C, *Aethaspis major*, left PVL, restored from PF 913 (× 0.4); D, *Bryantolepis* sp., restored from PF 166, 1546, 1547 (× 1.4); E, *Aethaspis utahensis*, right PVL, restored from PF 322 (× 0.8); F, *Kujdanowiaspis* sp., based on casts of Podolian specimens, PF 1177, 1179 (× 1.6); G, *Prosphymaspis subtilis*, from Gross, 1937 (× 1.6); H, *Actinolepis tuberculata*, left PVL, after Gross, 1940 (× 4.2).

s. AVL, s. PVL, external overlap areas for anterior ventro-lateral and opposite posterior ventro-lateral; *s. PL, s. PMV, s. PVL,* extent of internal overlap areas for posterior lateral, posterior medio-ventral, and opposite posterior ventro-lateral.

aspis acadica, and some *Heterogaspis;* it is long and narrow in *Anarthraspis, Actinolepis, "Phlyctaenaspis" heintzi, P. sherwoodi,* and *Williamsaspis,* while in *Arctolepis, Huginaspis,* and *Bryantolepis* it is intermediate in proportions. The Brachythoraci typically have long, slender posterior ventro-laterals, indicating a slender trunk region. The rather short, broad trunk may be primitive in Euarthrodira. The two posterior ventro-laterals usually form a bluntly rounded posterior end to the trunk shield; however, in *Arctolepis, Prosphymaspis,* and especially in *Huginaspis,* the posterior ventro-laterals are incut posteriorly to form a concave posterior end of the shield.

Pectoral Fins

A difference of opinion regarding the origin and evolution of their pectoral fins has led to widely divergent views on the phylogeny and classification of the placoderms. Heintz (1932a, 1938) believed that the Arctolepida were primitive and possessed a simple pectoral fin consisting of an immovable skin fold from the spinal to the posterior corners of the anterior lateral and anterior ventro-lateral. From them he derived the Brachythoraci with a reduced spinal and enlarged or open pectoral fenestra, suggesting the presence of a large pectoral fin. Gregory and Raven (1941) agreed with Heintz that the long-spined Arctolepida were primitive, as did Westoll (1945), Romer (1946), and Gross (1954), although Westoll thought that a fin membrane was absent in early Arctolepida. On the other hand, Stensiö (1944) has argued that a long-based pectoral fin such as is found among the Brachythoraci is primitive in arthrodires. He interpreted the stenobasal fin, whose presence he demonstrated in Arctolepida, as the result of a reduction of a long-based fin. The endoskeleton lying between the anterior lateral and anterior vento-lateral represents, according to Stensiö, the anterior part of the originally eurybasal fin, while the spinal is believed to represent the skeleton of the anterior part of the fin. White (1952) has accepted this theory of Stensiö.

The evidence of the nature of the pectoral fin in arthrodires is of three types:

(1) The radials of the pectoral fin skeleton are rarely preserved. They were first noted by Heintz (1932a, p. 198, fig. 86) in an undetermined arthrodire which displayed four radials lying parallel to each other between the anterior ventro-lateral and anterior lateral. Later (1938, p. 21, fig. 5) he found in *Coccosteus decipiens* six or seven radials arranged parallel to each other along the posterior border of the anterior lateral. Gross (1938, p. 199, fig. 5, A) described a specimen of

the nearly related *Rachiosteus* which shows five pectoral fin radials, probably somewhat displaced yet still adjoining the anterior lateral. The specimen of *Coccosteus* indicates the presence of a pectoral fin with a moderately broad, unconstricted base, which must have attached at a pectoral fenestra between the anterior lateral and anterior ventro-lateral. The pectoral fin was probably similar in the other two specimens. Fin radials were presumably cartilaginous in other arthrodires and thus not preserved. They are known, however, in *Gemundina*, which had extremely eurybasal, ray-like pectoral fins, and in *Pseudopetalichthys*, in which these fins were rather short-based.

(2) The endoskeletal shoulder girdle bearing an articular crest for the pectoral fin has been described by Stensiö (1944) in a few arthrodires. In *Enseosteus* (op. cit., fig. 14) both the shoulder girdle and the articular crest are very long, demonstrating the presence of a eurybasal pectoral fin. In *Palaeacanthaspis* (op. cit., fig. 9) and in *Kujdanowiaspis* (op. cit., fig. 16) the articular area for the pectoral fin was short and the fin must have been stenobasal. White (1952, figs. 16–19) has described the endoskeletal shoulder girdle of *Williamsaspis*, which has an articular ridge of intermediate length for the pectoral fin. In *Aethaspis* an unornamented flange of the anterior ventro-lateral has been interpreted above (p. 490) as an ossification of the endoskeletal attachment of the pectoral fin, and indicates that the latter was narrow-based. Westoll (1945, p. 384) believed that *Arctolepis* lacked a pectoral fenestra and fin, but both were present, as is proved by a section of a specimen in Naturhistoriska Riksmuseet in Stockholm (fig. 115, B) which shows the perichondrally ossified articulation of the pectoral fins; the latter must have been very narrow-based in this genus.

(3) In the many arthrodires where neither the pectoral fins nor their endoskeletal girdles are known, evidence of the fin development may be obtained from the structure of the lateral wall of the trunk shield. In *Kujdanowiaspis* (Stensiö, 1944, fig. 17) the anterior lateral, anterior ventro-lateral and probably posterior lateral (see p. 526) bound a small pectoral fenestra through which the pectoral fin attached to its endoskeletal girdle; the size of the fenestra necessarily indicates a narrow-based pectoral fin. In *Phlyctaenaspis sherwoodi* a reconstruction (Denison, 1950, pl. 3) indicates that a similar pectoral fenestra was present here. The section of *Arctolepis* mentioned above shows that this genus also had a small pectoral fenestra. Presumably this fenestra was present in all Arctolepida, and there is evidence of its presence in *Aethaspis*, *Anarthraspis*, and *Bryantolepis*. It is well shown

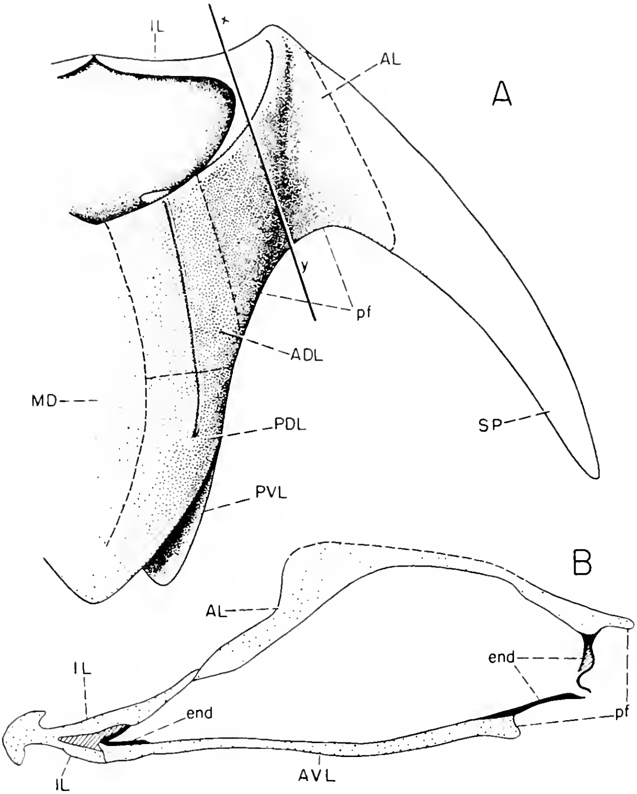

FIG. 115. *Arctolepis* sp. A, right half of trunk shield in dorsal view (× 3/2) showing position of section, *x-y*, and extent of pectoral fenestra, *pf;* B, section through lateral part of trunk shield (× 3), demonstrating the presence of a pectoral fenestra, *pf;* bones stippled, presumed cartilage cross-hatched; endoskeletal perichondral bone (*end*) black.

ADL, anterior dorso-lateral; *AL,* anterior lateral; *AVL,* anterior ventrolateral; *IL,* intero-lateral; *MD,* median dorsal; *PDL,* posterior dorso-lateral; *PVL,* posterior ventro-lateral; *SP,* spinal.

in *Williamsaspis* (White, 1952, figs. 3, 4), where it is relatively larger than in other Arctolepida, its size indicating the longer base of the pectoral fin. Among the Brachythoraci, the situation must have been similar in the Coccosteidae, Pholidosteidae, and perhaps the Holonemidae. The size of the pectoral fenestra is not known exactly in these forms, but it was certainly present and perhaps somewhat larger than in typical Arctolepida. In most Brachythoraci the pectoral fenestra is widely open behind, forming a pectoral incisure. This results from absence of contact between the ventral and lateral parts of the trunk shield behind the anterior lateral and anterior ventro-lateral. Although the open pectoral incisure cannot be taken as proof of the presence of a long-based pectoral fin, such a fin could occur only in forms that have the lateral wall of the trunk shield incompletely covered by dermal bones.

If we return to the theory of Stensiö that the eurybasal fin is primitive in the Arthrodira, we may inquire with what sort of trunk shield it occurred originally. As far as I know, Stensiö has not published his opinion on this matter. White (1952, p. 286) believed that the primitive form had not only a long-based pectoral fin, but a full body armor as in the Arctolepida. It is difficult to imagine how this could be. The primitive fin of Stensiö's theory extended forward to the anterior end of the trunk shield and included the ancestral spinal at its anterior edge. A fin of this sort would completely separate the lateral and ventral trunk shields and leave them with only a cartilaginous endoskeletal connection. Such a shield would have been so inefficient either as a protective armor or as an external shoulder girdle that it is hardly to be considered as a possible ancestral condition.

Another possibility, if we follow Stensiö's theory, is that the long-based, primitive pectoral fin occurred in forms with the lateral wall of the trunk shield little developed. Such a condition is exemplified by many Brachythoraci, and it is necessary to consider whether these forms, though clearly specialized in other respects, could have had primitive trunk shields. One difficulty of this possibility has to do with the spinal. This plate is always very small or completely absent in those Brachythoraci that have the deep pectoral incisure. It is surely a vestigial plate rather than a rudiment that could give rise to the large and functional spinal of the Arctolepida, Coccosteidae, and Pholidosteidae. The spinal was certainly a part of the ancestral inheritance of arthrodires, since it is present in all orders, and possibly was present in the placoderm ancestor, if its homologue is represented in the Antiarcha and Rhenanida. A primitive euarthrodiran should possess a well-developed spinal, which is not present in those Brachythoraci with eurybasal pectoral fins. In known euarthrodires the size of the spinal is inversely correlated with the size of the pectoral fin, so it seems improbable that there ever was a long-finned member of the group with a large spinal. The posterior dorso-lateral and posterior lateral may be very small in the Brachythoraci, and the anterior lateral may be very narrow and produced far under the head. These features appear to be the result of reduction and specialization and are difficult to picture as a primitive condition. Finally, the closure of a pectoral fenestra in Arctolepida and Coccosteidae requires the junction of the posterior lateral and posterior ventro-lateral. But how can one explain the presence of the posterior ventro-laterals in the long-finned Brachythoraci where they have no apparent function and are sometimes lost, unless it is as an inheritance from an ancestor with a fully developed trunk shield?

It is also possible according to the Stensiö theory that the ancestral arthrodire was unarmored and that the exoskeleton was independently acquired in the various orders, as well as in the suborders Arctolepida and Brachythoraci. This seems hardly worthy of serious consideration since the armor is universally present in placoderms and is so similar in general plan that it was undoubtedly derived by modifications of a common armored ancestor.

The discussion above indicates some of the difficulties in Stensiö's theory, and these are not overbalanced by evidence to support it. None of these problems arise if the Arctolepida are considered as primitive Euarthrodira, ancestral as a group to the Brachythoraci. All of the elements of the trunk shield of the Brachythoraci are present and well developed in the Arctolepida. A small pectoral fenestra is the primitive place of attachment of the narrow-based pectoral fin. As the fin lengthens, the pectoral fenestra enlarges and finally becomes open behind, a change accomplished by the posterior reduction of the lateral trunk shield and the loss of its original posterior connection to the ventral shield. The opening of the pectoral fenestra allows the lengthening of the pectoral fin, and this change is accompanied by a reduction and sometimes the loss of the spinal. A number of genera are known that are intermediate not only in their trunk shield and pectoral fins but also in cranial characters, and these are strong support for the derivation of the Brachythoraci from the Arctolepida. Thus *Williamsaspis* is an arctolepid with a reduced spinal and slightly elongate pectoral fin base. *Coccosteus* and *Pholidosteus* are Brachythoraci as regards their cranial structure yet they still retain the trunk shield of an arctolepid with a closed pectoral fenestra; they approach the Brachythoraci, however, in the probable enlargement of the fenestra and in the posterior reduction of the lateral trunk shield.

Finally, the stratigraphic occurrence of arthrodires presents major difficulties to Stensiö's theory. A small pectoral fenestra indicating a stenobasal fin, and a relatively large spinal are characteristic of Early Devonian Arctolepida. A narrow-based fin also occurs in the Early Devonian Acanthothoraci and in *Pseudopetalichthys* but is exceptional in later Arthrodira, occurring in the Middle Devonian *Actinolepis* (where it may be somewhat enlarged), and in the Late Devonian *Phlyctaenaspis sherwoodi*. A somewhat longer fin base associated with a reduced spinal may occur in *"Coccosteus" angustus* from the Early Devonian Hunsrückschiefer; it is typically developed in the Middle Devonian *Williamsaspis*, Coccosteidae, and probably in the Holonemidae; it persists into the Late Devonian in the Coccosteidae, Holonemidae, and *Pholidosteus*. The Brachythoraci with an open pectoral incisure and very small or no spinal are the characteristic forms of the Late Devonian, although a few of them appear in the Middle Devonian (Heterosteidae and Homosteidae). The only placoderm known to have a eurybasal fin in the Early Devonian is the rhenanid, *Gemundina*, which is a ray-like form of undoubtedly extreme specialization. The paleontological evidence thus strongly supports the primitive nature of the stenobasal pectoral fin in arthrodires and indicates that the eurybasal fin was specialized in this group.

Sensory Canal System

The lateral line canals are developed very uniformly among the Euarthrodira. The deeper canals, which form marked grooves in the dermal bones, are rather consistently present, although they may be reduced in a few of the Wildungen Brachythoraci. The pit lines may form shallow grooves on the dermal bones or they may be entirely superficial, in which case there is no record of their presence in fossils.

The supraorbital canal (fig. 105, *soc*) in Arctolepida almost always begins at the center of ossification of the preorbital and extends anteriorly onto the postnasal. In the Brachythoraci (as well as the Petalichthyida and Phyllolepida) it also extends posteriorly toward the center of ossification of the central. In one specimen of *Arctolepis* (fig. 105, I, *soc*) from Wijde Bay, Spitsbergen, the supraorbital canal extends onto the central, although this is not usually the case in this genus. In the coccosteid, *Rachiosteus* (Gross, 1938, p. 186), the supraorbital canal extends forward from the center of the preorbital as a wide canal, while its posterior part, which extends onto the central, is narrow and probably shallow. Many Arctolepida may have possessed the posterior part of this canal as a superficial pit line, but whether this condition was primitive or a secondary reduction is not clear. In either case the Wijde Bay *Arctolepis* and *Rachiosteus* represent intermediate conditions.

The canal called premarginal by Bryant (1934, p. 137) was considered by Stensiö (1945, p. 50) to have been supplied by the profundus nerve and was named by him the profundus canal. It is well developed only in *Bryantolepis* (fig. 105, C, *pfc*) although traces of it are seen as a pit line on the preorbital and postorbital of *Kujdanowiaspis* and *Simblaspis* (fig. 105, D, *pfc*). This canal may have been present as a superficial pit line in other Arctolepida. It has not been detected in Brachythoraci.

The central, infraorbital, and preopercular canals, as well as the cephalic division of the main lateral line canal, are with few exceptions well developed in Euarthrodira, but the middle and posterior pit lines and the supratemporal cross commissure are less commonly indicated. Among the Arctolepida, *Actinolepis* shows a full development of the posterior pit line and supratemporal commissure (fig. 105, H, *pp, stc*); *Simblaspis* (fig. 105, D) sometimes shows the antero-medial portions of the middle and posterior pit lines and the postero-lateral portions of the posterior pit line and supratemporal commissure; *Kujdanowiaspis* (Stensiö, 1945, pp. 50–51) may display the antero-medial part of the middle pit line and both ends of the posterior pit line. In the Brachythoraci the ends of the middle and posterior pit lines are not uncommonly indicated, as in Coccosteidae, *Rhinosteus, Brachyosteus, Leiosteus,* and *Pholidosteus;* the supratemporal cross commissure is known only in *Coccosteus minor, Brachyosteus,* and *Rhinosteus,* where medially it passes onto the gap between the nuchal and median dorsal.

The groove or grooves on the lateral part of the paranuchal of *Aethaspis* (fig. 105, B, *opc*) probably indicate a pit line and may, as suggested above (p. 478), be homologous to the canal that crosses the posterior part of the gill cover in *Acanthodes.* It is not known in any other arthrodire. In Acanthodii, Watson (1937, p. 121) identified it as the opercular canal, while Stensiö (1947, pp. 40–41) compared it to the scapular canal of Batoidea.

Little is known of the sensory canals of the cheek in Arctolepida. The infraorbital canal (fig. 106) passes behind and under the eye on the suborbital and is usually well developed, though on the dorsal part of the suborbital it may be only a shallow pit line. The supramaxillary (or jugal) line may be a deep canal or may be a shallow pit line that leaves no mark on the bone, as in *Anarthraspis* and *Bryantolepis* (fig. 106, E, C).

On the trunk shield the main lateral line canal passes posteriorly across the anterior and posterior dorso-laterals (figs. 108, 109), although commonly the posterior part is superficial and leaves no mark on the bones. Usually this is the only post-cranial canal to be seen, but in a few cases others are indicated. On the lateral trunk shield a canal or groove may branch dorsally from the main lateral line canal on the anterior dorso-lateral, cross the antero-dorsal corner of the posterior dorso-lateral, and pass onto the median dorsal probably nearly to its center of ossification. This canal is not known in Arctolepida but is seen in some Coccosteidae where it may represent a vestige of the dorsal lateral line. A probable homologue occurs in some Antiarcha in the anterior oblique abdominal pit line (Stensiö, 1948, pp. 185–186). On the ventral shield a sensory line may originate on the anterior medio-ventral, pass laterally onto the anterior ventro-lateral, and curve anteriorly to cross the lateral part of the interolateral. A part of this canal is seen on the anterior ventro-lateral of a relative of *Actinolepis* from Spitsbergen (fig. 112, A, *vp*), and it is also known in some Coccosteidae and in *Holonema*. It is probably a vestige of a transverse ventral pit line and has a homologue among Antiarcha on the anterior ventro-lateral of *Bothriolepis* (Stensiö, 1948, pp. 187–188).

It is probable that the sensory canal system was more fully developed in the ancestral placoderms and that it has been reduced to some extent in known arthrodires. The reduction may have involved merely a transformation into superficial pit lines or in many cases it may have led to complete loss of a canal. The Arctolepida and Coccosteidae retain a number of canals otherwise not indicated or rare in placoderms. These include the profundus canal, the middle and posterior pit lines, the supratemporal cross commissure, the opercular canal, a part of the dorsal lateral line, and a ventral pit line. On the other hand, in certain of the Late Devonian Wildungen arthrodires, especially *Oxyosteus*, *Synauchenia*, and *Brachydirus*, the sensory canals are greatly reduced. According to Geuenich (1939) these were free-swimming forms, living under favorable light conditions, and no longer had as great a need for the lateral line sensory system.

EVOLUTION OF THE ARCTOLEPIDA

From the preceding discussion of arctolepid morphology, the characters of a primitive member of the group may be summarized as follows:

In the cranial roof, the nuchal was moderately long and narrow. The paranuchals were rather large and lacked differentiated glenoids for the anterior dorso-laterals. The centrals were six-sided. The preorbitals were wider than long and five-sided. The rostral, pineal, and postnasals were rather small, possibly not fused to the cranial roof behind, and the pineal notched the preorbitals only slightly. The bones had for the most part nearly central ossification centers. The orbits were small, and the suborbitals had short suborbital processes and large blades. The sensory canal system was quite fully developed, though many canals may have been present only as pit lines. The endocranium was low and broad, with large suborbital shelves and supraorbital processes and a short occipital region; probably it was perichondrally ossified, with the nasal capsules separately ossified. The possible arrangement of the cranial plates of a primitive euarthrodire is shown in figure 116.

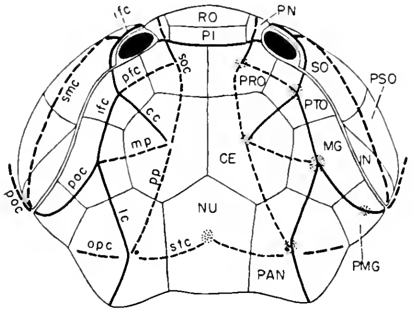

FIG. 116. Cranial roof and cheek plates of hypothetical primitive arctolepid. *CE*, central; *IN*, internal; *MG*, marginal; *NU*, nuchal; *PAN*, paranuchal; *PI*, pineal; *PMG*, postmarginal; *PN*, postnasal; *PRO*, preorbital; *PSO*, postsuborbital; *PTO*, postorbital; *RO*, rostral; *SO*, suborbital; *cc*, central canal; *ifc*, infraorbital canal; *lc*, main lateral line; *mp*, middle pit line; *opc*, "opercular" canal; *pfc*, profundus canal; *poc*, preopercular canal; *pp*, posterior pit line; *smc*, supramaxillary canal; *soc*, supraorbital canal; *stc*, supratemporal commissure.

The trunk shield was low and broad. The median dorsal was short and broad with a central growth center, and the posterior dorsals were large. The anterior dorso-laterals lacked trochleae for the cranial roof, and both the anterior and posterior dorso-laterals were probably relatively long and low. The anterior laterals had nearly central ossification centers, their anterior triangles were not modified into an inner wing, and their ventral triangles were large. The posterior laterals were well developed and probably rather long and low. The spinals were of moderate length. The anterior ventro-laterals had long spinal edges and bounded deep pectoral sinuses. The dorsal laminae of the intero-laterals were small and formed little or no inner wings. Paired antero-ventrals were present, and the posterior ventro-laterals had well-developed lateral faces and rather short ventral faces. The pectoral fenestrae were small and the pectoral fins were narrow-based.

Kujdanowiaspis approaches most closely to this ideally primitive condition and both in its early appearance and in its structure can be considered to be near the ancestry of other Arctolepida. This suborder is not well enough known at present to permit any detailed determination of its phyletic development. However, certain general evolutionary trends are clear, and some specific phyletic lines may be distinguished. The Arctolepinae as a group retain a number of primitive features, including the short, broad median dorsal, the paired antero-ventrals, and the lack of any differentiated articulations between the anterior dorso-laterals and paranuchals. *Kujdanowiaspis* itself is considered to be the most primitive, while "*Svalbardaspis*" *angulatus* and some undescribed forms from the lower part of the Wood Bay Series of Spitsbergen are very similar in known cranial characters. *Simblaspis* and *Bryantolepis* are possibly related primitive forms that show only a few distinctive specializations. In both, the nuchal and paranuchals are shortened posteriorly, the preorbitals are relatively large, and the anterior laterals have well-developed inner wings; *Bryantolepis* is also specialized in its large postnasals and pineal and very narrow pectoral sinuses. *Anarthraspis*, while it retains a rather primitive cranial roof, is advanced in having a high trunk shield with well-developed inner wings on the anterior laterals, shortened spinals and pectoral sinuses, and probably a long ventral shield. *Aethaspis* is specialized both in its cranial roof and its trunk shield. The former has a greatly elongate nuchal completely separating the centrals, preorbitals much elongated posteriorly, and reduced postmarginals, rostral, pineal and postnasals. Its trunk shield is high, the anterior laterals have inner wings, the spinals are reduced, and the pectoral fenestrae slightly enlarged. One distinct phyletic line of Actinolepinae is represented by the Middle Devonian *Actinolepis* and related forms from the Lykta and Stjørdalen Divisions of the Wood Bay Series of Spitsbergen, including "*Svalbardaspis*" *rotundus* and "*S.*" *polaris*. All are characterized by the position of the centers of ossification of the preorbitals, far posterior and near the midline, resulting in *Actinolepis* in the fusion of the two plates. The fused rostral and pineal notch the anterior edges of the preorbitals rather deeply. The trunk shield is high, the spinals are reduced, and the pectoral sinuses become quite shallow.

The Phlyctaenaspinae were derived presumably from the Actinolepinae and may be considered as advanced in the development of articulations between the paranuchals and anterior dorso-laterals, and in the loss of the antero-ventrals. The elongate, narrow median dorsal and the usually elongate spinals are considered as specializations. *Arctaspis*, from the lower part of the Wood Bay Series, is the earliest of known Phlyctaenaspinae and is intermediate to the Actinolepinae in some respects; its median dorsal and its spinals are not as elongate as in other Phlyctaenaspinae, the pattern of the cranial roof bones is similar to that of *Kujdanowiaspis*, and the anterior medio-ventral may represent recently fused antero-ventrals (see p. 533, fig. 112, I). Undescribed material from Spitsbergen may illustrate an intermediate condition even better. *Arctolepis* and related forms from Spitsbergen, including *"Svalbardaspis" stensioi*, form a well-marked phyletic line, characterized particularly by the enlargement of the rostral and pineal, and their extension posteriorly to meet the centrals and to separate the relatively narrow preorbitals. The orbits, though small, may notch the cranial roof deeply, the trunk shield is relatively long, and the spinals very long. The interrelationships of other Phlyctaenaspinae are not clear, and many of them are inadequately known. *Phlyctaenaspis* has rather minor specializations of the cranial roof; the nuchal and paranuchals are shortened posteriorly and the postmarginals are large. The trunk shield is high, the pectoral sinuses are rather shallow, the ventral shield is rather long, and the articulations between the trunk shield and cranial roof are well developed and spaced more widely than is usual in Arctolepida. *Diadsomaspis* is characterized by its peculiarly shaped median dorsal and long, low anterior dorso-laterals. *Elegantaspis* has extremely long, slender spinals. *Huginaspis* is specialized in its high median crest on the median dorsal. *Gronlandaspis* has a short, high posterior dorso-lateral like that of *Prosphymaspis*. The latter shows a number of specializations, including the laterally notched median dorsal, the angulate contours of the sides of the trunk shield, and the peculiar overlap relations of the posterior ventro-laterals. Most of these genera clearly represent distinct phyletic lines and emphasize the inadequacy of our present knowledge of the group.

Williamsaspis exhibits a number of unique characteristics that are clearly specializations. None of these suggest any close relationship to other Arctolepida, and for this reason it must at present be considered as an isolated phyletic line and placed in its own family.

The origin of the Brachythoraci is perhaps not within the scope of this paper, but inasmuch as it concerns the Arctolepida it will be discussed briefly. If one follows Stensiö in considering a wide-based pectoral fin to be primitive among arthrodires, the Arctolepida could not have been ancestral to Brachythoraci. But with the exception of this purely theoretical consideration, there seems to be every reason for believing that the Brachythoraci were derived from Arctolepida. In the first place, Arctolepida lived at the right time. Secondly, there are several forms known that are intermediate in structure. The Early Devonian "*Coccosteus*" *angustus* (Traquair, 1903, pp. 732–733, pl. 6, figs. 1, 2) resembles the Coccosteidae in its cranial roof, in its long slender ventral shield, and in the presence of a small keel on the inner side of the median dorsal. On the other hand, it resembles the Arctolepida in the slight reduction of the spinals, the long spinal edges of the anterior laterals and anterior ventro-laterals, the suborbitals with short suborbital processes, and the rather long, narrow median dorsal with an external crest. The Middle Devonian *Buchanosteus* (White, 1952, figs. 21, 27) has a cranial roof that is typically coccosteid, yet its endocranium is that of an arctolepid, with a platybasic form, large suborbital shelves, both anterior and posterior suborbital processes, a short occipital region, and circumcapsular bones not fused to the postethmoid ossification. The Coccosteidae and Pholidosteidae are intermediate between Arctolepida and typical Brachythoraci in possessing pectoral fenestrae closed behind by the junction of the posterior laterals and posterior ventro-laterals.

The ancestral position of the Arctolepida is also supported by the large number of characters in which they approach the Brachythoraci. The more obvious are:

(1) The pineal and part of the rostral have pushed back between the preorbitals in *Arctolepis*.

(2) The posterior part of the cranial roof is shortened in *Bryantolepis*, *Simblaspis*, *Arctolepis*, and *Phlyctaenaspis*.

(3) The orbits notch the sides of the cranial roof deeply in *Arctolepis* and "*Svalbardaspis*" *stensioi*.

(4) The supraorbital sensory lines may extend posteriorly onto the centrals in *Arctolepis*.

(5) The trunk shield is rather high in *Aethaspis*, *Anarthraspis*, *Phlyctaenaspis*, and probably *Actinolepis*.

(6) The median dorsal of *Phlyctaenaspis acadica* approaches in shape that of *Coccosteus minor*.

(7) The paired articulations between the head and trunk shields are well developed and rather widely spaced in *Phlyctaenaspis acadica*.

(8) The spinals and spinal edges of the anterior laterals and anterior ventro-laterals are reduced in *Aethaspis*, *Anarthraspis*, *Lataspis*,

Actinolepis, and especially in *Williamsaspis* and a relative of *Actinolepis* from Spitsbergen.

(9) The pectoral fenestrae are enlarged in *Williamsaspis* and probably to some extent in *Aethaspis, Phlyctaenaspis,* and others.

(10) The ventral shield is long in *Anarthraspis, Actinolepis, Phlyctaenaspis,* and *Williamsaspis.*

No single genus of arctolepids combines all of these characters, from which we may conclude that we do not know the actual ancestor of the Brachythoraci, although an evolutionary trend toward the latter is indicated in a general way. It is probable that the ancestor of the Brachythoraci is to be found among the Phlyctaenaspinae, since they possess a differentiated articulation between the head and trunk shield. *Phlyctaenaspis acadica,* as far as its trunk shield is concerned, approaches very closely to *Coccosteus minor,* as Heintz (1938) has pointed out, but its cranial roof shows little resemblance to that of the Coccosteidae. The Brachythoraci must have originated fairly early in the Early Devonian, but the actual ancestral forms have not yet been discovered.

SUMMARY

The classification of the Placodermi is discussed and a new classification of the suborder Arctolepida is proposed. *Williamsaspis* is retained in a family of its own, the Williamsaspidae. Other arctolepids are referred to the family Phlyctaenaspidae, which is divided into two subfamilies, Actinolepinae and Phlyctaenaspinae.

The Arctolepida from the Water Canyon Formation of Utah are described as *Simblaspis cachensis,* new gen. and sp., a rather primitive member of the Actinolepinae, and *Aethaspis major,* new gen. and sp., and *A. utahensis,* new sp., more specialized members of the same subfamily, and *Bryantolepis,* sp. indet. A number of undetermined infragnathals, supragnathals, and cheek plates are described.

The geological occurrence of Arctolepida is considered, and their general morphology is discussed with particular reference to primitive features and specializations within the Euarthrodira. It is concluded that *Kujdanowiaspis,* one of the Actinolepinae, is the most primitive of known Arctolepida, that the Phlyctaenaspinae were derived from the Actinolepinae, and that the ancestry of the Brachythoraci is to be looked for among the Phlyctaenaspinae.

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