Taxonomy of the arthrodire *Phlyctaenius* from the Lower or Middle Devonian of Campbellton, New Brunswick, Canada

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Synopsis

The species of the Lower/Middle Devonian arthrodire *Phlyctaenius* are reviewed in the light of new material. The new species *P. stenosus* is described and diagnoses of previous species are emended. A multivariate analysis is used to support species recognition. It is suggested that some features hitherto used to distinguish species are invalid, since they are shown to be highly variable. It is also suggested that previous restorations of *Phlyctaenius* are composites of more than one species: a new restoration is given here.

Introduction

In 1971 the British Museum (Natural History) received a collection of fossil fishes collected by Dr W. Graham-Smith and Professor T. S. Westoll from the Devonian of Campbellton, New Brunswick, Canada. Amongst the collection there were many specimens of the arthrodire placoderm *Phlyctaenius*, including twelve skull roofs and many isolated but well-preserved thoracic plates.

It became evident that three species of Campbellton *Phlyctaenius* could be recognized: the type species *P. acadicus* (Whiteaves), *P. atholi* (Pageau) and a new species described below. It also became apparent that the most comprehensive description (Heintz 1933) of *P. acadicus* is based on information from more than one species. Further anatomical information is also provided by these additional specimens. Since *P. acadicus* is often cited in discussions of arthrodire phylogeny it is desirable to revise the taxonomy and to attempt a new restoration of the Campbellton species. These are the primary objectives of this paper.

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Specimens of *Phlyctaenius* from Campbellton were first described by Whiteaves (1881, 1888) as *Coccosteus acadicus*. Further material was described by Traquair (1890*a*, *b*, *c*, 1893) who proposed the name *Phlyctaenius*; Woodward (1891, 1892*a*, *b*) commented on these early descriptions. Heintz (1933) provided a detailed description, used by subsequent authors (Denison 1958, 1978; Goujet 1975; Miles & Dennis 1979; Dennis & Miles 1979*a*, *b*, 1980; Young 1979, 1980, 1981; Young & Gorter 1981) as the basis for comparisons with presumed relatives (*Dicksonosteus*, groenlandaspids). Since Heintz' description many species from the Devonian of Europe have been assigned to *Phlyctaenius*, but these are now placed in other genera (Denison 1978: 60).

Materials and methods

The material used in this study is in the British Museum (Natural History), London, the Royal Scottish Museum, Edinburgh, and the National Museum of Canada, Ottawa. Specimens in the two latter institutions are referred to by register number, prefixed by RSM or NMC respectively. Specimens in the British Museum (Natural History) are referred to simply by register number. All of the material is from Campbellton, New Brunswick, Canada. The early collections are not precisely localized, but the material collected by Graham-Smith and Westoll comes from half a mile west of Campbellton. The similarity of the matrix between this material and that previously collected suggests that all of it is from the same locality.

The fish material comes from the Gaspé Sandstone Series (described by Logan 1846, 1863), the age of which is uncertain (Alcock 1935, McGerrigle 1950, Pageau 1968), being considered by some authors Lower Devonian and others Middle Devonian. Alcock (1935) proposed that the base of the Gaspé Sandstone marks the beginning of the Middle Devonian; McGerrigle (1950) divided the middle part of the Gaspé Sandstone into the older York River and younger Battery Point Formations, which together he believed were of Middle Devonian age. According to Pageau (1968) the fish fauna occurs in the Battery Point Formation, which he suggests belongs to the lower part of the Middle Devonian, with the Gaspé Sandstone Series crossing the Lower/Middle Devonian boundary. The Gaspé Sandstone Series contains abundant, well-preserved spores (McGregor 1973, 1977) which indicate that the Lower/Middle Devonian boundary lies in the upper part of the Battery Point Formation (McGregor 1973: fig. 4). The fish fauna is therefore considered to be of latest Lower or earliest Middle Devonian age.

In the following study the specimens were sorted into three groups and original observations were tested by a multivariate analysis. As with many primitive arthrodires the skull roofs tend to remain intact and, in this instance, provide the bulk of the evidence for species recognition. The abbreviations of the separate plates are mainly those of Miles (1971); see list below.

Explanation of abbreviations used in text and figures:

ADL	anterior dorsolateral	PM	postmarginal
AL	anterior lateral	PMV	posterior median ventral
AMV	anterior median ventral	PN	postnasal
AV	anteroventral	PNu	paranuchal
AVL	anterior ventrolateral	PrO	preorbital
C	central	PtO	postorbital
IL	interolateral	PVL	posterior ventrolateral
M	marginal	R	rostral
MD	median dorsal	RP	rostralo-pineal
Nu	nuchal	SM	submarginal
P	pineal	SO	suborbital
PDL	posterior dorsolateral	Sp	spinal
PL	posterior lateral		

The specimens were prepared using a mechanical drilling tool. Where impressions only remain, positive casts were made using silicone or latex rubber. Casts of ornament tubercles were studied with the aid of a scanning electron microscope. Because of the difficulty of examining large bone fragments in the SEM, 'Araldite' casts were made from latex rubber moulds. The casts were coated with 360 Å (36 nm) of gold palladium. Drawings were made with the aid of a Grant Projector and with the drawing tube attached to the Wild stereo microscope.

Taxonomy

Identification of the species

The specimens of skull roofs studied here belong to more than one morphological group. They were divided visually into three groups, based on proportions and characters, corresponding to *Phlyctaenius acadicus*, *P. atholi* and the new species *P. stenosus*.

A multivariate analysis was carried out, using qualitative characters and measurements (numbered 1–10, Fig. 1) of the skull roofs. The characters used in the analysis were those visible in the majority of specimens. They were coded for their alternative states and are discussed in the text below. These characters include the nature of the sutures; the nature of the occipital cross commissural groove and position of the growth centre and the shape of the posterolateral margin of the PNu; the skull roof length relative to the width; the presence or absence of the median postpineal and the nature and arrangement of the ornament tubercles. Ten measurements (Fig. 1) were used; the raw data are deposited on file in the Palaeontology Library, British Museum (Natural History).

The percentage similarity between each pair of specimens was calculated using Gower's (1971) coefficient of similarity. The results were used in a principal co-ordinates analysis to produce a two-dimensional plot in which the distances between the points (representing specimens) most closely correspond to the calculated similarities between the specimens.

The first plot (Fig. 2) used qualitative characters and measurements for 41 specimens out of a total of 43 (two very fragmentary specimens were excluded). From the plot it seems that the specimens may be divided into three groups. One incomplete specimen (P6573d, Fig. 2), at first assigned to *P. acadicus*, appears to have a higher similarity to *P. atholi*: it is uncertain to which group it belongs. A second specimen (P6573e, Fig. 2), probably belonging to *P. stenosus* sp. nov., appears to have a higher similarity to *P. acadicus* or *P. atholi*, but it is incomplete and the lack of data may account for its unexpected position on the plot.

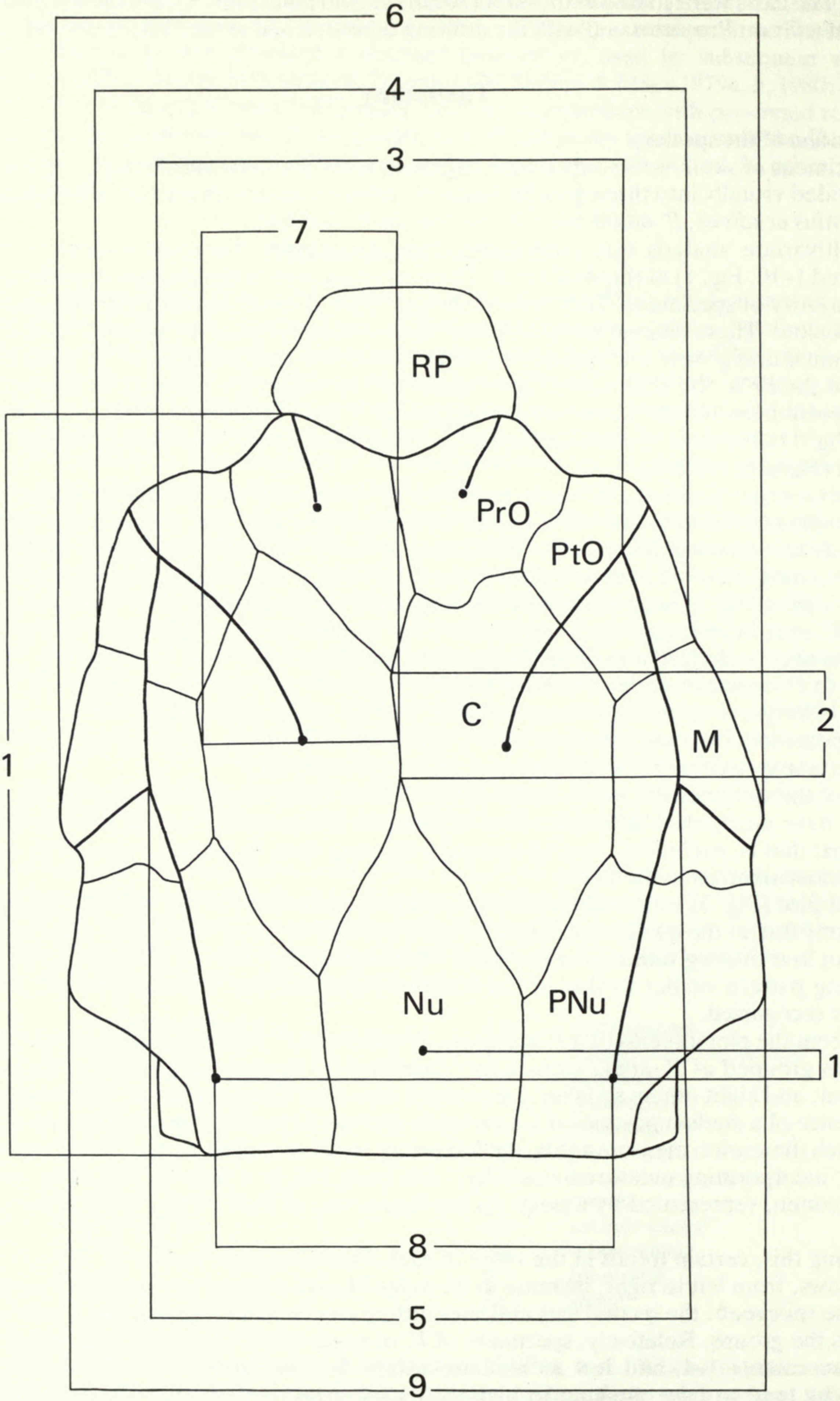
Some of the specimens included on this first plot have many missing values and it was felt that this may have introduced distortion. So a second plot was prepared for the 34 most complete specimens; that is, excluding those specimens with more than 10 missing values. The resulting plot is almost identical to the first.

A third plot (Fig. 3) was constructed from measurements only, to test whether the grouping was entirely due to the qualitative characters and whether or not it was biased. Specimens with more than four missing values were excluded. Although this left only 22 specimens, the result is a grouping pattern similar to that of the first two plots, and corresponding to the groupings originally recognized.

Thus from the plot it seems that *P. acadicus*, *P. atholi* and *P. stenosus* are distinct groups. The specimens grouped as *P. atholi* include two described by Pageau (1969), both with a median postpineal, and eight others showing the anterior area all without this plate. This suggests that the presence of a median postpineal is a variation and not a specific character (see pp. 12–13).

For each dimension measured (Fig. 1), a separate sheet of tracing paper was laid over Fig. 3 (the plot incorporating measurements only), and using this as a basis the measured value for each specimen, represented by a point on the figure, was plotted on the sheet at the relevant point.

By doing this, certain trends in the value of each dimension were indicated. The first axis of Fig. 3 shows, from left to right, increase in the value of each dimension corresponding with the size of the specimen: the second axis indicates differences in shape between the specimens and separates the groups. Relatively, specimens of *P. stenosus* tend to have medium to high values for measurements 1–4, and low to medium values for measurements 5–10. Specimens of *P. acadicus* tend to have medium to high values for measurements 1–3 and high values for measurements 4–10. Specimens of *P. atholi* tend to have low to medium values for measure-


6
4
3
7
RP
PrO
PtO
C
2
M
1
Nu
PNu
10
8
5
9

ments 1–4 and medium to high values for measurements 5–10. These character tendencies, interpreted as a result of overlaying measurements on the plot, as described above, can be summarized as follows:

1. Skull roofs of *P. acadicus* tend to be larger overall than those of the other two species;
2. Skull roofs of *P. acadicus* and *P. stenosus* tend to be relatively longer than those of *P. atholi*;
3. Skull roofs of *P. atholi* tend to be relatively narrower anteriorly compared with those of the other two species;
4. Skull roofs of *P. atholi* and *P. acadicus* tend to be relatively wider posteriorly than those of *P. stenosus*; and
5. The growth centre of the PNu occurs in the same transverse plane as that of the Nu in *P. stenosus* but further posteriorly in the other two species.

Diagnoses

Order **ARTHRODIRA** Woodward, 1891

Suborder **PHLYCTAENIOIDEI** Miles, 1973

Infraorder **PHLYCTAENII** Miles, 1973

Family **PHLYCTAENIIDAE** Fowler, 1947

Genus ***PHLYCTAENIUS*** Traquair, 1890*a*

[= *Phlyctaenaspis* Traquair, 1890*c*]

DIAGNOSIS. See Denison (1978: 59).

TYPE SPECIES. *Phlyctaenius acadicus* (Whiteaves 1881).

REMARKS. The name *Phlyctaenius* was originated by Traquair (1890*a*: 20), but he later (1890*c*: 144) changed it to *Phlyctaenaspis* since he believed the name *Phlyctaenius* to be preoccupied by *Phlyctaenium* Zittel, a fossil sponge. However, *Phlyctaenius* is the valid name for this genus (White 1969: 302 footnote; Fowler 1947: 6).

Two points in Denison's 1978 diagnosis could not be confirmed in material examined here: the PMs were stated to be large, and the endocranium perichondrally ossified (see p. 17). The source of the reference to the size of the PMs seems to be Denison (1958: 511, fig. 105, specimen number P5972), where he records an impression of a plate suspected to be large, although he does not say that the PM is from an impression.

Phlyctaenius acadicus (Whiteaves 1881)

Figs 4; 5A, D; 9A; 10; 11A; 12A; 16D; 18A, D, F

1881 *Coccosteus acadicus* Whiteaves: 94; text-fig. 1.
1888 *Coccosteus acadicus* Whiteaves; Whiteaves: 93; pl. 9, figs 1, 3 (not figs 2, 4); text-fig. 2.
1890*a* *Phlyctaenius acadicus* (Whiteaves) Traquair: 20.
1890*b* *Phlyctaenius acadicus* (Whiteaves); Traquair: 60.
1890*c* *Phlyctaenaspis acadica* (Whiteaves) Traquair: 144.
1891 *Phlyctaenaspis acadica* (Whiteaves); Woodward: 295 (in part).
1892*a* *Phlyctaenaspis acadica* (Whiteaves); Woodward: 5; pl. 1, fig. 8 (not fig. 7).
1892*b* *Phlyctaenaspis acadica* (Whiteaves); Woodward: 481, text-fig. 1.

Fig. 1 Outline drawing of skull roof to show measurement parameters used in multivariate analysis: 1. PrO–PNu length of skull roof; 2. Length of mutual C suture; 3. Distance between growth centres of PtOs; 4. Width of skull roof at level of PtOs; 5. Distance between growth centres of Ms; 6. Width of skull roof at level of Ms; 7. Width of C (where possible measured on left C); 8. Distance between growth centres of PNus; 9. Width of skull roof at level of PNus; 10. Longitudinal distance between the growth centres of Nu and PNu. The breadth/length index (100B/L) used in the species diagnoses was obtained by expressing measurement 6 as a percentage of measurement 1. The abbreviations for plate names follow those used by Miles (1971); see p. 2.

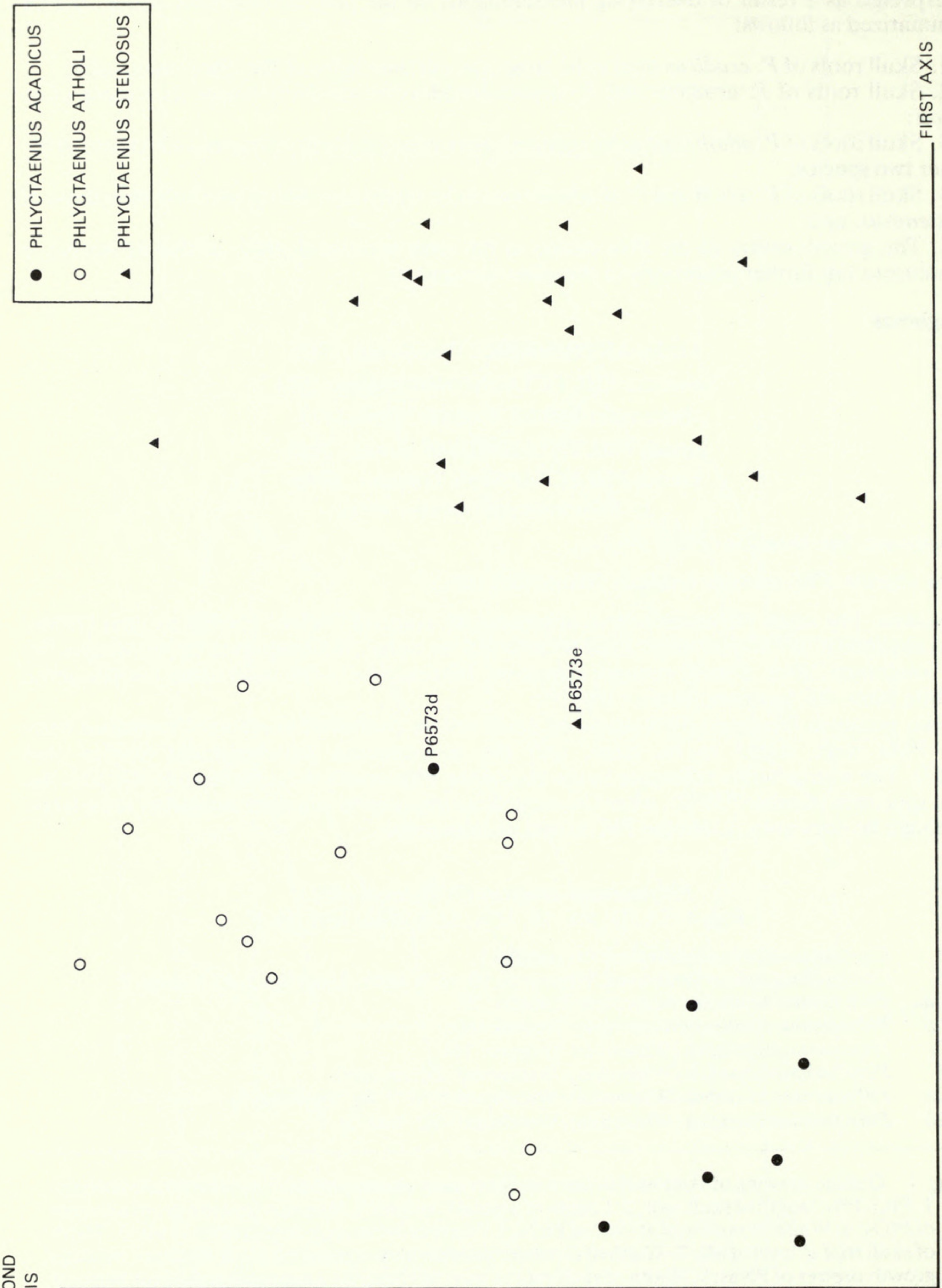


Fig. 2 A plot of the first two principal co-ordinates axes using qualitative characters and measurements.

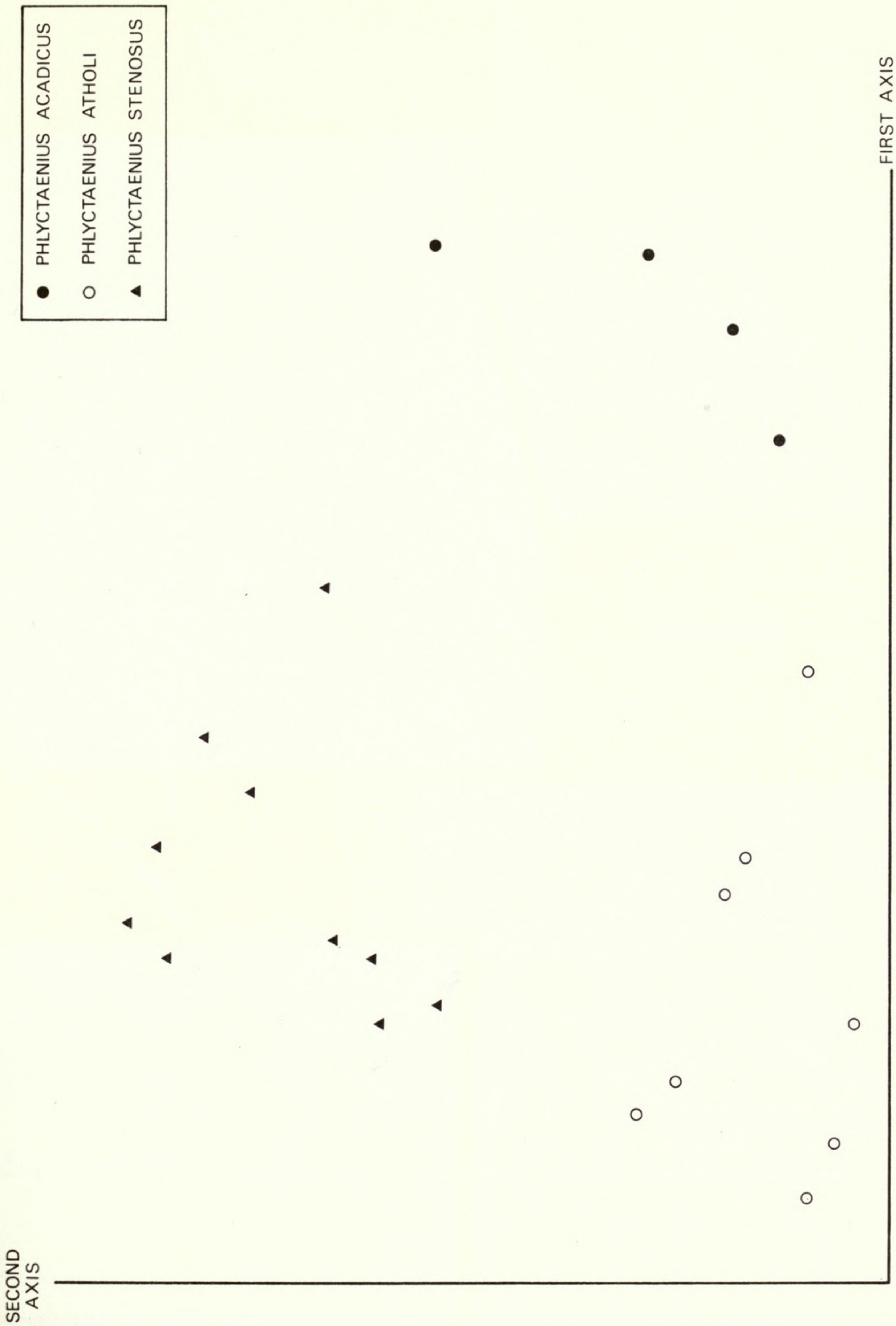
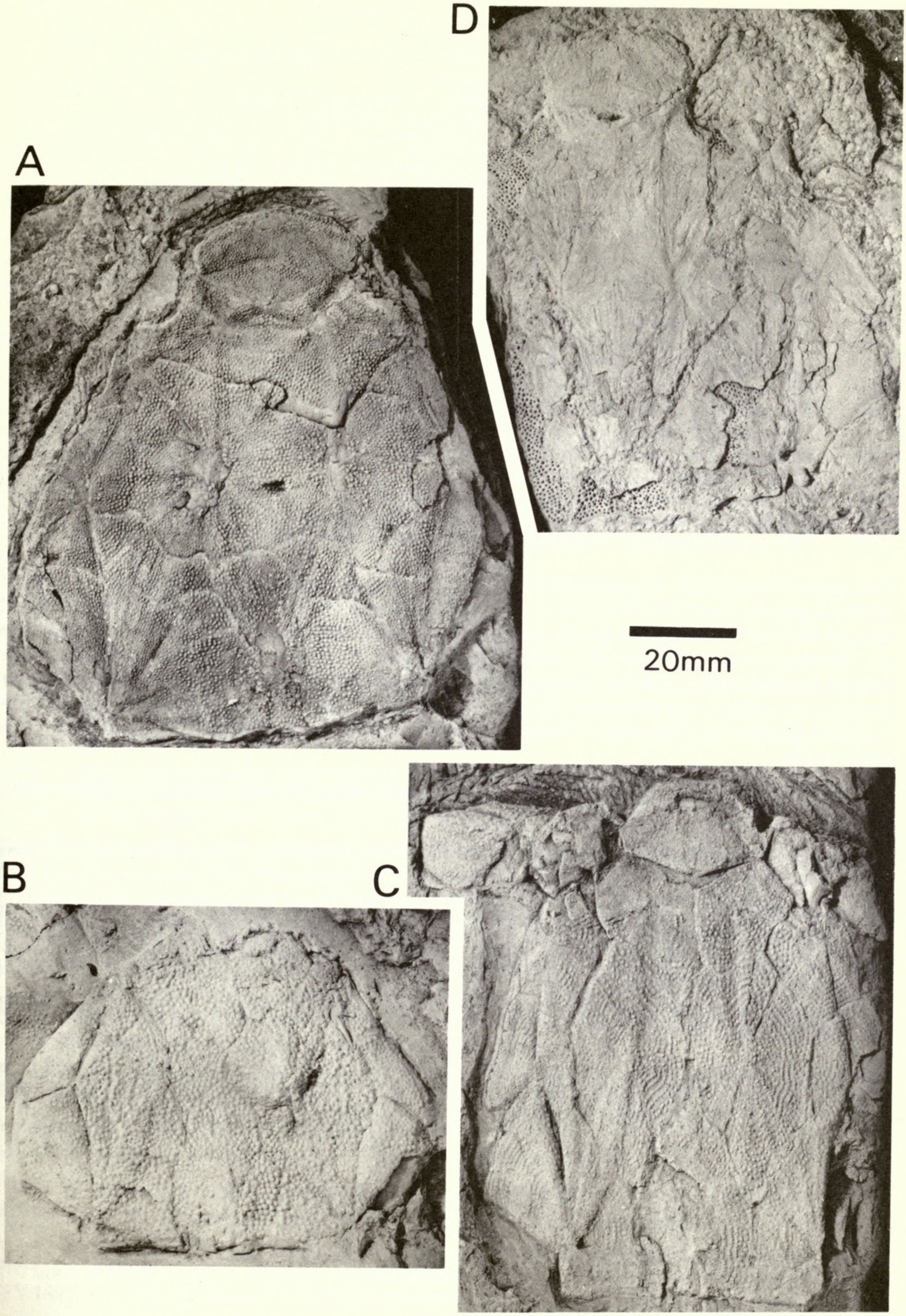


Fig. 3 A plot of the first two principal co-ordinates axes using measurements only.

Fig. 4 *Phlyctaenius acadicus* (Whiteaves). Restoration of skull roof based on RSM GY 1897.51.129.

Fig. 5 A. *Phlyctaenius acadicus* (Whiteaves), skull roof, RSM GY 1897.51.129. B. *Phlyctaenius atholi* (Pageau), skull roof, **lectotype** RSM GY 1897.51.123. C. *Phlyctaenius stenosus* sp. nov., skull roof, **holotype** P6555. D. *Phlyctaenius acadicus* (Whiteaves), skull roof, visceral surface, P6554.


D
A
20mm
B
C

1893 *Phlyctaenaspis acadica* (Whiteaves); Traquair: 147, text-fig. 1.
1894 *Phlyctaenaspis acadica* (Whiteaves); Traquair: 370.
1907 *Phlyctaenaspis acadica* (Whiteaves); Whiteaves: 265; pl. 4, figs 3, 4 (not figs 1, 2).
1916 *Phlyctaenaspis acadica* (Whiteaves); Chapman: 212.
1925 *Phlyctaenaspis acadica* (Whiteaves); Stensiö: 165; text-fig. 20 (not fig. 21).
1932 *Phlyctaenaspis acadica* (Whiteaves); Woodward *in* Zittel: 42.
1933 *Phlyctaenaspis acadica* (Whiteaves); Heintz: 127; (not pl. 1), pl. 2, figs 1–8; pl. 3, figs 4–6 (not figs 1–3); text-figs 3 (in part), 5 (in part), 6 (in part) (not text-figs 1, 2, 4).
1938 *Phlyctaenaspis acadica* (Whiteaves); Hussakof: 280.
1951 *Phlyctaenaspis acadica* (Whiteaves); Ørvig: 408; pl. 7, fig. 1.
1957 *Phlyctaenaspis acadica* (Whiteaves); Ørvig: text-fig. 9A.
1957 *Phlyctaenaspis acadica* (Whiteaves); Gross: 20; pl. 6, figs 5–7, 9.
1958 *Phlyctaenaspis acadica* (Whiteaves); Denison: text-figs 107B, 110B, 112K, 113B.
1959 *Phlyctaenaspis acadica* (Whiteaves); Stensiö: 13.
1962 *Phlyctaenaspis acadica* (Whiteaves); Miles: 65.
1963 *Phlyctaenaspis acadica* (Whiteaves); Westoll & Miles: 146; text-fig. 6a.
1964 *Phlyctaenaspis acadica* (Whiteaves); Lehman: 194; pl. 1, fig. E.
1966 *Phlyctaenaspis acadica* (Whiteaves); Gardiner: 32.
1968 *Phlyctaenaspis acadica* (Whiteaves); Miles & Westoll: 399.
1969 *Phlyctaenaspis acadica* (Whiteaves); Miles: 132; text-figs 9f–g (not 9h).
1969 *Phlyctaenaspis acadica* (Whiteaves); Pageau: 810; pl. 25, fig. 1; pl. 29, fig. 5; pl. 30, figs 1, 2, 4–7, 10; text-figs 19.5, 20.7, 21M.
1975 *Phlyctaenius acadicus* (Whiteaves); Goujet: text-fig. 1B.
1978 *Phlyctaenius acadicus* (Whiteaves); Denison: 59; text-fig. 42.
1979*a* *Phlyctaenius acadicus* (Whiteaves); Dennis & Miles: text-fig. 1.

Diagnosis (emended). A species of *Phlyctaenius* in which the skull roof breadth at the level of the M is greater than the PrO–PNu length; 100 B/L index = 110 (excluding RP); posterolateral margin of the PNu straight or gently curved; anterior and lateral margins of the R convex; sutures not evident; ornament tubercles uniformly arranged; tubercles small with pointed, angular peaks; growth centre of PNu at posterolateral margin of the plate, and close to the posterior margin; occipital cross-commissural groove on PNu clearly indicated; postoccipital para-articular process on PNu small; infraorbital canals converge anteriorly; AL more than twice as tall as wide.

Holotype. NMC 2774, a cranial shield. Restigouche River, Campbellton, New Brunswick, Canada.

Horizon and locality. Latest Lower or earliest Middle Devonian, Campbellton, New Brunswick, Canada.

Material. Specimens showing skull roofs: a cast of the holotype; RSM GY 1897.51.129, an almost complete specimen; P6554, the visceral surface of the skull roof; and four other incomplete specimens, P5474, P6572, P56113a, b and P56115a, b. P6577a is probably *P. acadicus*, and possibly also P6573d and P6577d.

Specimens showing only thoracic plates: P6576, P7083, P56131, P56137 and RSM GY 1897.51.123, 124, 128.

Remarks. *Batteraspis fulgens* Pageau 1969, known only by an incomplete AL, may well be a separate species of *Phlyctaenius* (Denison 1978: 60). I have not included it in the formal synonymy since I have not had the opportunity to examine the specimen at first hand.

Phlyctaenius atholi (Pageau 1969)

Figs 5B; 6; 7C, D; 9B; 11B; 12D; 16B, E; 17A; 18B

1888 *Coccosteus acadicus* Whiteaves; Whiteaves: 94; pl. 9, fig. 2.
1890*b* *Phlyctaenius acadicus* (Whiteaves) Traquair: pl. 3, fig. 2.
1892*b* *Phlyctaenaspis acadica* (Whiteaves) Woodward: 481.

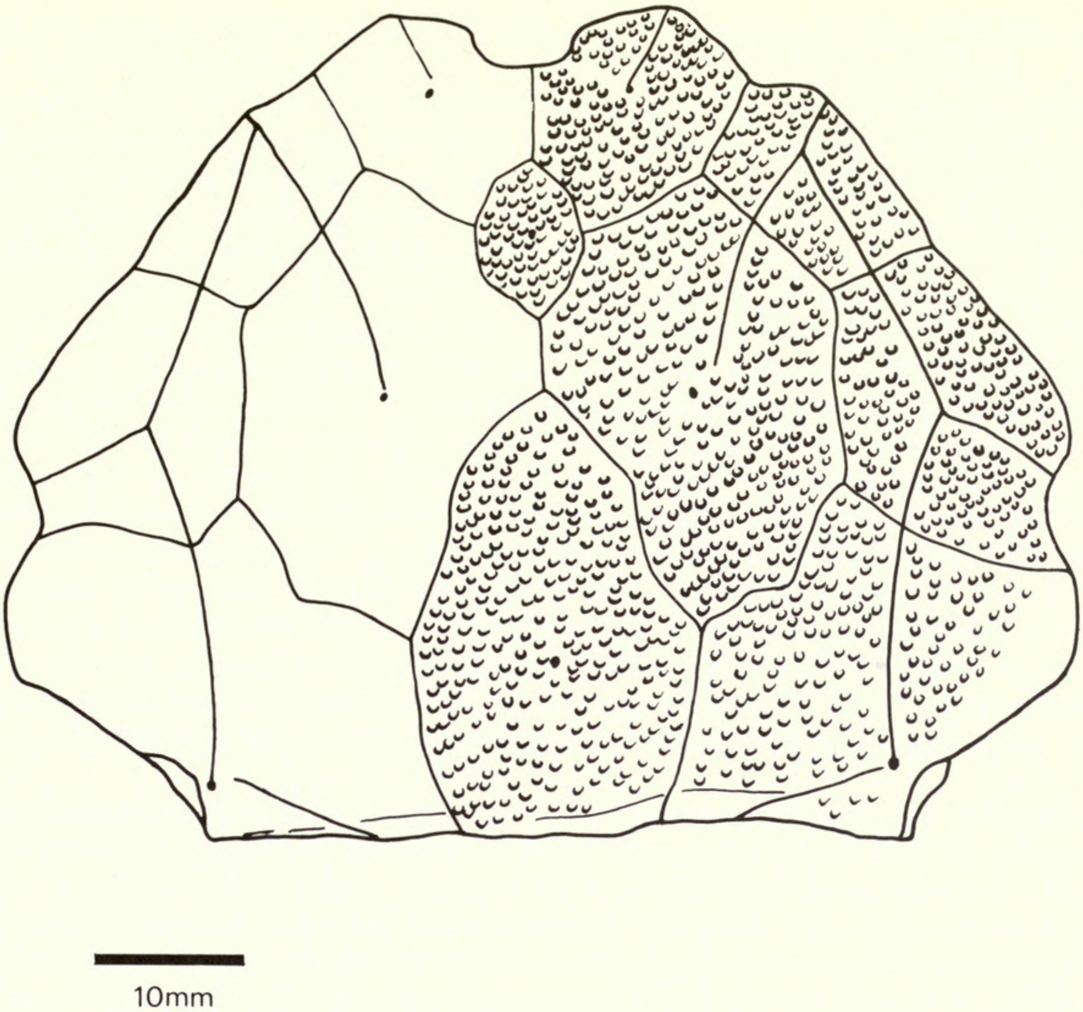


Fig. 6 *Phlyctaenius atholi* (Pageau). Restoration of skull roof based on the lectotype, RSM GY 1897.51.123.

1916 *Phlyctaenaspis acadica* (Whiteaves); Chapman: pl. 21, fig. 6.
1933 *Phlyctaenaspis acadica* (Whiteaves); Heintz: pl. 3, fig. 1.
1969 *Phlyctaenaspis atholi* Pageau: 819; pl. 25, fig. 2; pl. 28, fig. 5; text-fig. 19.1, 4.

Diagnosis (emended). Species of *Phlyctaenius* in which the skull roof breadth at the level of the M is greater than the PrO–PNu length; 100 B/L index = 110–142 (excluding RP); posterolateral margin of PNu divided by an angle into two sections; ornament tubercles uniformly arranged; tubercles large with rounded peaks; growth centre of PNu inside posterolateral margin of plate and fairly close to posterior margin; occipital cross-commissural groove on PNu clearly indicated; postoccipital para-articular process on PNu well developed; infraorbital sensory canals converging strongly anteriorly; anterior point of Nu approximately in line with growth centres of Cs; Nu length greater than half PrO–PNu length of skull roof; AL equidimensional; ADL with prominent posterior process above lateral line groove.

Lectotype. Pageau based *P. atholi* upon two skull roofs (Pageau 1969, specimens RSM GY 1897.51.113, 123) but he did not specify which was the holotype. I therefore here select as **lectotype** the better-preserved specimen, RSM GY 1897.51.123, a skull roof from the Lower or Middle Devonian, Campbellton, New Brunswick, Canada. Fig. 5B.

Horizon and locality. Latest Lower or earliest Middle Devonian, Campbellton, New Brunswick, Canada.

Material. Specimens showing skull roofs: nine fairly complete specimens; P6556, P6573a, P6573g, P6574, a (part and counterpart), P56120, RSM GY 1887.20.44a, RSM GY 1897.51.113, 123, RSM GY 1978.30.3. Also five others which are poorly preserved.

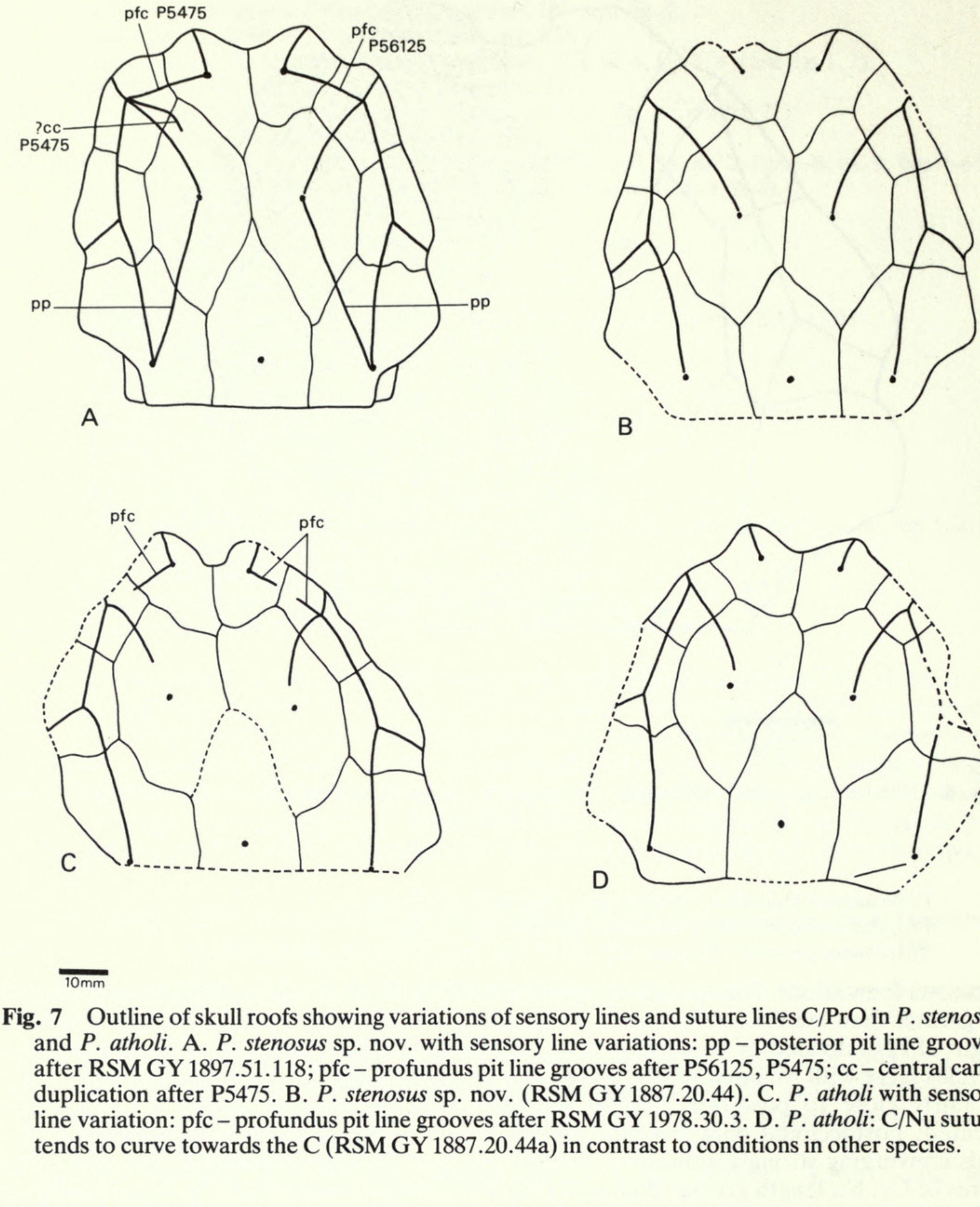


Fig. 7 Outline of skull roofs showing variations of sensory lines and suture lines C/PrO in *P. stenosus* and *P. atholi*. A. *P. stenosus* sp. nov. with sensory line variations: pp – posterior pit line grooves after RSM GY 1897.51.118; pfc – profundus pit line grooves after P56125, P5475; cc – central canal duplication after P5475. B. *P. stenosus* sp. nov. (RSM GY 1887.20.44). C. *P. atholi* with sensory line variation: pfc – profundus pit line grooves after RSM GY 1978.30.3. D. *P. atholi*: C/Nu suture tends to curve towards the C (RSM GY 1887.20.44a) in contrast to conditions in other species.

Specimens showing only thoracic plates: P6559, P6575e, P6577e, h, P56126b, P56127, RSM GY 1887.20.45, RSM GY 1897.51.126, 130, 131, 132, 142, 143, RSM GY 1978.30.8, 12, 13.

REMARKS. Pageau (1969: 820) specified three characters in erecting this species:

1. Ornament of large, uniformly arranged tubercles with rounded peaks;
2. RP not attached to skull roof; and
3. Presence of a median postpineal.

The first of these characters is valid but the remaining two are omitted from the emended diagnosis presented here, for the following reasons.

The detachment of the RP is not a distinguishing character since skull roofs without attached RP elements are also known for both *P. acadicus* and *P. stenosus*. In RSM GY 1897.51.113, 123 and P6556 a median postpineal is present. This plate is hexagonal (Figs 5, 6) with the smallest tubercles, indicating the growth centre, at the centre of the plate. However, a number of specimens which do not possess this plate are similar to *P. atholi* in all other characters by which they were compared, and group with that species in a multivariate analysis (see p. 3). On these specimens, where the postpineal is absent, the suture line pattern between the PrOs and Cs is very variable in *P. atholi* as it is in *P. stenosus* (Fig. 7), and the right or left PrO may extend between the two Cs (RSM GY 1887.20.44a, RSM GY 1978.30.3). Denison (1958:507) remarked that the PrO, and possibly the R, P and PNs, '. . . show the most variable development of any of the dermal bones of the arctolepid cranial roof', and that this may be 'an indication of the relative plasticity of the anterior part of the skull'. Miles & Westoll (1968: 390) commented that in *Coccosteus* 'the pineal region is by far the most variable part of the dermal bone-pattern', although they never found a separate postpineal 'in any of the several hundred individuals of *C. cuspidatus* examined' or, indeed, in any other coccosteomorph. They conclude that 'differential growth rates of the bones from their radiation centres is considered sufficient to explain all observed conditions . . .'. Species closely related to *Phlyctaenius*, such as *Heightingtonaspis anglica* (Traquair) (White 1961, 1969) and *Aggeraspis heintzi* (Gross) (Gross 1962) sometimes show a postpineal between the PrO and C. I also note considerable variation in the presence or absence of small roofing bones in *Acipenser* (Jarvik 1948), *Eusthenopteron* (Jarvik 1944), dipnoans (Miles 1977) and *Osteolepis* (Graham-Smith 1978b). It is concluded that the presence of a postpineal is an individual variation rather than a distinguishing character of *P. atholi*.

The figures and description by Pageau (1969) of the skull roof and several thoracic plates of *Gaspeaspis cassivii* Pageau from the Battery Point formation, Gaspé Bay, Quebec suggest that this species should be considered a synonym of *P. atholi*. I have not included it in the formal synonymy since I have not examined the material at first hand. Pageau specified two characters for *Gaspeaspis cassivii*, the form of the sub-paranuchal depression on the visceral surface of the skull roof and the superficial ornament. The visceral surface of the PNu of *P. atholi* is unknown and this first character cannot be compared. The superficial ornament of *G. cassivii* is of large, uniformly distributed tubercles with rounded peaks. This is a character of *P. atholi* (compare Pageau 1969: pl. 28, fig. 5, *P. atholi*, with his pl. 27, fig. 2, *G. cassivii*). There are also several other points of similarity from which I infer that these species are conspecific:

1. The breadth of the skull roof at the M is considerably greater than the length (Pageau 1969: pl. 27, fig. 2; pl. 28, figs 1, 2);
2. The posterolateral margin of the PNu is divided by an angle into two sections (Pageau 1969: pl. 28, fig. 2);
3. The postoccipital para-articular process on the PNu is well developed (Pageau 1969: pl. 28, fig. 2); and
4. The infraorbital sensory canals tend to converge anteriorly (Pageau 1969: pl. 27, fig. 2; pl. 28, fig. 1).

Phlyctaenius stenosus sp. nov.

Figs 5C; 7A, B; 8; 9C; 11C; 12C; 13; 14; 15; 16A, C, F; 17B–F; 18A, C–E

1888 *Coccosteus acadicus* Whiteaves; Whiteaves: 94; pl. 9, fig. 4.
1890*b* *Phlyctaenius acadicus* (Whiteaves) Traquair: pl. 3, fig. 1.
1891 *Phlyctaenaspis acadica* (Whiteaves) Woodward: 296.
1892*a* *Phlyctaenaspis acadica* (Whiteaves); Woodward: pl. 1, fig. 7.
1907 *Phlyctaenaspis acadica* (Whiteaves); Whiteaves: pl. 4, figs 1, 2.
1925 *Phlyctaenaspis acadica* (Whiteaves); Stensiö: text-fig. 21.
1933 *Phlyctaenaspis acadica* (Whiteaves); Heintz: 128; text-figs 1, 2, 3 (in part), 4, 5 (in part), 6 (in part); pl. 1, figs 1–4; pl. 3, figs 2, 3.
1958 *Phlyctaenaspis acadica* (Whiteaves); Denison: text-figs 105G, 106D, 108B, 109A, 111A, 114A.
1969 *Phlyctaenaspis acadica* (Whiteaves); Pageau: 814.
1969 *Phlyctaenaspis acadica* (Whiteaves); Miles: 147; text-fig. 9h.

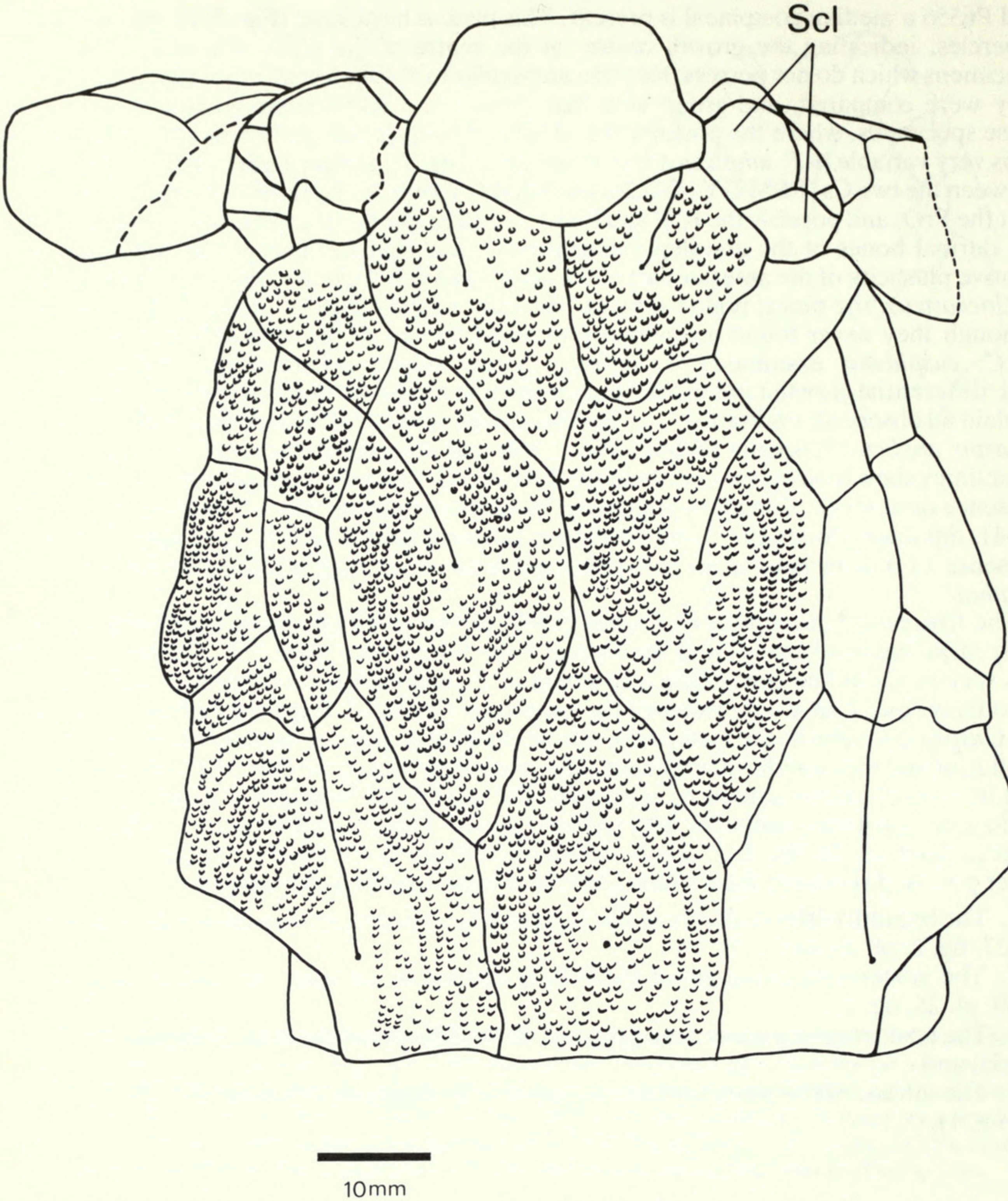


Fig. 8 *Phlyctaenius stenosus* sp. nov. Restoration of skull roof based on the holotype P6555 and P56125 and P56116a. Scl – sclerotic plates.

DIAGNOSIS. Species of *Phlyctaenius* in which the skull roof breadth at the level of the M is equal to, or a little less than, the PrO–PNu length; 100 B/L index = 90–99 (excluding RP), posterolateral margin of PNu marked by an internal angle; anterior and lateral margins of RP gently concave; sutures evident; ornament tubercles form regular concentric rows parallel to the plate margins; tubercles generally medium-sized with sharp to rounded peaks; growth centre of PNu inside posterolateral margin of plate and fairly close to posterior margin; postoccipital para-articular process on PNu well developed; infraorbital canals subparallel, or converging anteriorly; anterior point of Nu posterior to growth centres of C; Nu length less than half PrO–PNu length of skull roof; AL equidimensional.

NAME. *Stenosus* is from the Greek στενός, narrow, in reference to the most striking feature of this species, the narrowness of the skull roof at the level of the M and the PNu.

HOLOTYPE. P6555, a skull roof, Lower or Middle Devonian, Campbellton, New Brunswick, Canada. Fig. 5C.

HORIZON AND LOCALITY. Latest Lower or earliest Middle Devonian, Campbellton, New Brunswick, Canada.

MATERIAL. Specimens showing skull roofs: holotype P6555, P5475, P5972, P6573h, P6573i, P56114a, b, P56116a, b, P56117a, b, P56121, P56122, P56123, P56125, RSM GY 1887.20.44, RSM GY 1897.51.118, RSM GY 1897.51.125, RSM GY 1898.180.24, RSM GY 1978.30.5, RSM GY 1978.30.7; and possibly P6573e, P56124.

Specimens showing only thoracic plates: P5973, P6559a, c, P6577b, d, P56126a, b, P56131, P56134, P56142, P56144, P56146, P56148, P60900, RSM GY 1897.51.120, 121, 134, 135, 136, 139, 140, RSM GY 1978.30.10, 11.

Comparative description

This section is intended to supplement and amplify the information included in the species diagnoses and accompanying remarks.

The plates forming the skull roof of *Phlyctaenius* are normal for arthrodires. They are strongly sutured together, except for the PM, of which a fragment is questionably identified on P6577a, here referred to *P. acadicus*. As with other primitive (non-brachythoracid) arthrodires the orbital notches are shallow, the sutures show very little overlap, the Cs are hexagonal and the Nu is parallel-sided and anteriorly wedged between the Cs. The shape and proportions of the head shield and constituent plates, particularly the Nu and PNu, vary between the three species. These differences are best seen by comparing Figs 4, 5, 6 and 8.

The suture lines are clearly visible on the ornamented surface in *P. stenosus* (Figs 5C, 8), normally visible on *P. atholi* (Figs 5B, 6) and are not evident on *P. acadicus* (Figs 5A, 4), where the path of the sutures is deduced from the ornament pattern, and, on the visceral surface, by the junctions of radiating lines (Figs 5D, 10). The dorsal surface immediately adjacent to the posterior margin of the skull roof of *P. acadicus* is unornamented and bevelled and was probably covered with skin. The skull roof specimens of *Phlyctaenius* have been flattened in preservation. A paper model of the thoracic shield was made by restoring to best fit drawings of individual plates. This suggests that in life the head showed a marked transverse curvature, the highest point coinciding with the growth centre of the Nu. From here ridges run to the growth centre of each C thus delimiting a dorsal flattened triangular area. From the sides of this area the skull roof slopes laterally. The RP (not known in *P. atholi*) differs in *P. acadicus* and *P. stenosus*. In the former the anterior and lateral margins are convex (Figs 4, 5A) while in the latter these margins are gently concave (Figs 5C, 8) and where they meet the resulting corners turn downwards – a feature noted by Heintz. Heintz (1933: 130) also noted indistinct impressions on P6555, here referred to *P. stenosus*, as evidence of nasal apertures. However, nasal apertures were not recognized in the specimens studied. The limit between the R and P components of the RP is obvious in *P. acadicus* where there is a clear break in the ornament (RSM GY 1897.51.129) and a suture line on the visceral surface (P6554), but in *P. stenosus* the ornament is continuous.

The shape of the PrO appears highly variable in *Phlyctaenius*, particularly along the contact with the C (p. 13) and there may be marked asymmetry in this region of the roof of *P. stenosus* (Fig. 7A, B) and *P. atholi* (Fig. 7C, D). The variation in this region of the skull roof is discussed more fully on p. 13. The anterior margin of the PrO of *P. atholi* is strongly concave (Figs 5B, 6) and this contrasts with the more gently concave anterior margin of the PrO of *P. acadicus* (Figs 4, 5A) and *P. stenosus* (Figs 5C, 8).

Towards the posterior end of the head shield further differences between the three species are seen in the shape of the PNu (Figs 4, 5A–D, 6, 8). The posterior margin meets the lateral margin at varying angles: between 40° and 50° in *P. acadicus*, between 60° and 77° in *P. atholi*, 90° in

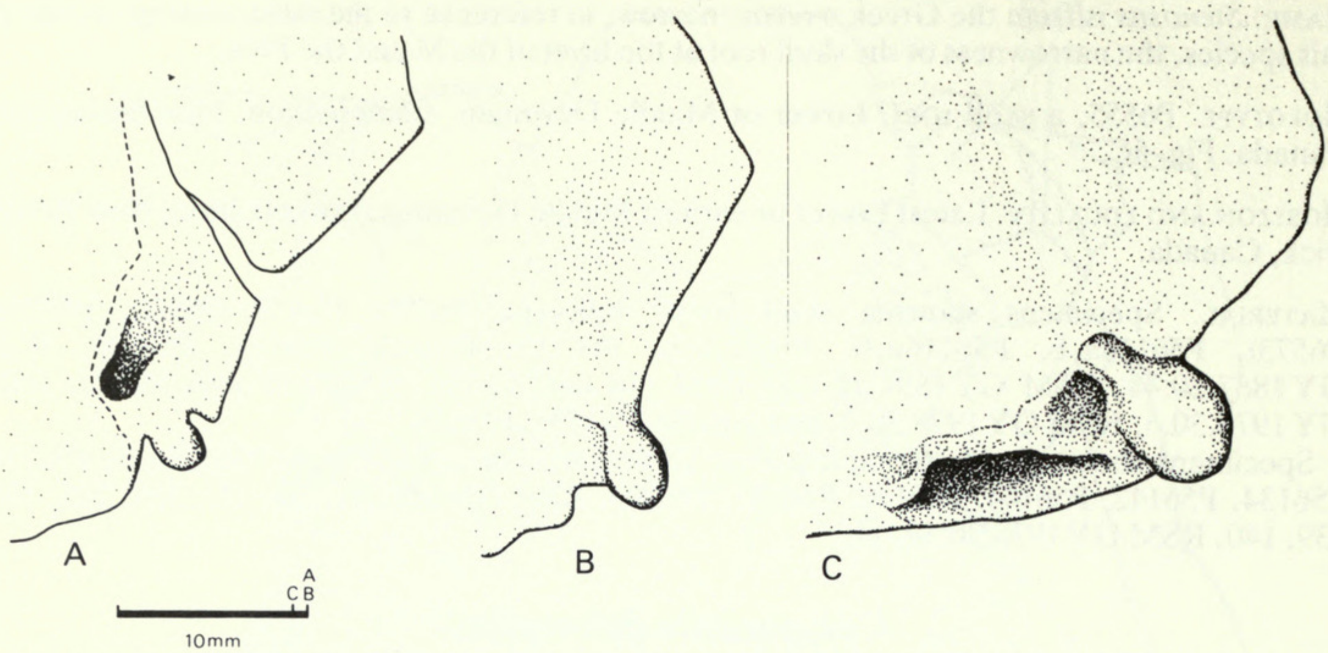


Fig. 9 Different development of the para-articular process on the visceral surface of the PNu in the three species of *Phlyctaenius*: A. *P. acadicus* (Whiteaves), P6554. B. *P. atholi* (Pageau), P6573b. C. *P. stenosus* sp. nov., RSM GY 1898.180.24.

P. stenosus. Beneath the surface of the PNu the cranial division of the craniothoracic joint is seen as the development of a para-articular process and a glenoid fossa which receives the trochlear of the ADL. The relative sizes of the process differ in the three species and are best seen in Fig. 9. Of particular diagnostic significance is the margin of the dorsal ornamented surface above the joint, where it shows a marked inside angle in *P. stenosus* and *P. atholi* absent in *P. acadicus* (Figs 4, 5A–C, 6, 8).

A cucullaris depression was recognized on one specimen (P6554, *P. acadicus*) showing the visceral surface, and is similar to that described for *Buchanosteus* by Young (1979: fig. 2). A pineal foramen is only recognized in one specimen of *P. stenosus* (P6555) and the broken margin suggests that it was quite small. The visceral surface of the skull roof of *P. acadicus* (P6554, P6572) suggests that both a pineal fontanelle within the neurocranium and a shallow pineal pit in the visceral surface of the P are developed.

The external opening for the endolymphatic duct is only recognized in *P. atholi* (RSM GY 1887.20.44a); this occurs just mesial to the growth centre of the PNu. Although an opening for the endolymphatic duct was not recognized in *P. acadicus* it is possible that the duct ran for some distance through the PNu. In RSM GY 1897.51.129 this is indicated by a slight linear indentation which runs from a point mesial to the growth centre of the PNu to the C/PNu/Nu junction (Figs 4, 5A). It may have been formed by the collapse of the roofing bone of the duct (D. Goujet, personal communication).

Little evidence of the neurocranium is preserved, as with '*Phlyctaenius*' sp. (Gross 1937: pl. 2, fig. 10; text-fig. 21q). Stensiö (1925: 165) suggested that this indicates that the neurocranium was either entirely cartilaginous or only slightly ossified. The outline of the neurocranium in *P. acadicus* is evident as the boundary between two types of surface on the underside of the skull roof and by the surface relief. Specimen P6554 shows the outline most clearly (Fig. 10) but remnants occur on several other specimens. Where present the outline appears to be generally similar in all three species of *Phlyctaenius*. The bone surface which must have lain beyond the limits of the neurocranium is dark-coloured, smooth and with few canals for blood vessels and nerves. It is present around the skull roof margins. The surface which originally lay above the neurocranium is lighter in colour, uneven and marked by numerous grooves. The radiating growth pattern of the individual dermal plates is very clear (Figs 5D, 10). This surface is covered in places by a thin layer of lighter-coloured bone with a shiny, uneven surface. This might

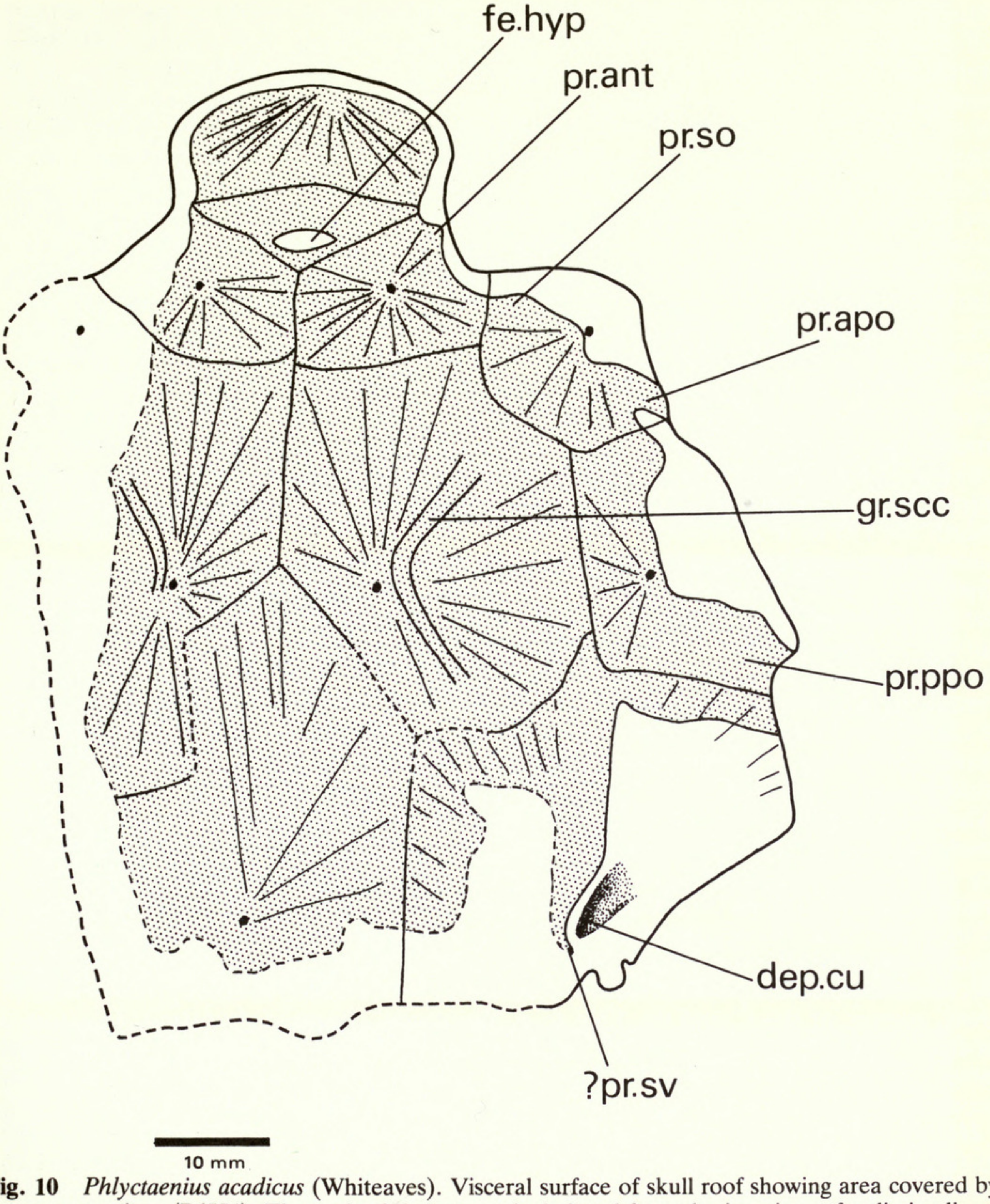


Fig. 10 *Phlyctaenius acadicus* (Whiteaves). Visceral surface of skull roof showing area covered by neurocranium (P6554). The path of the sutures is deduced from the junctions of radiating lines. dep.cu – cucullaris depression; fe.hyp – hypophysial fenestra; gr.scc – groove for semicircular canal; pr.ant – antorbital process; pr.apo – anterior postorbital process; pr.ppo – posterior postorbital process; pr.so – supraorbital process; ? pr.sv – possible supravagal process. Scale bar 10 mm.

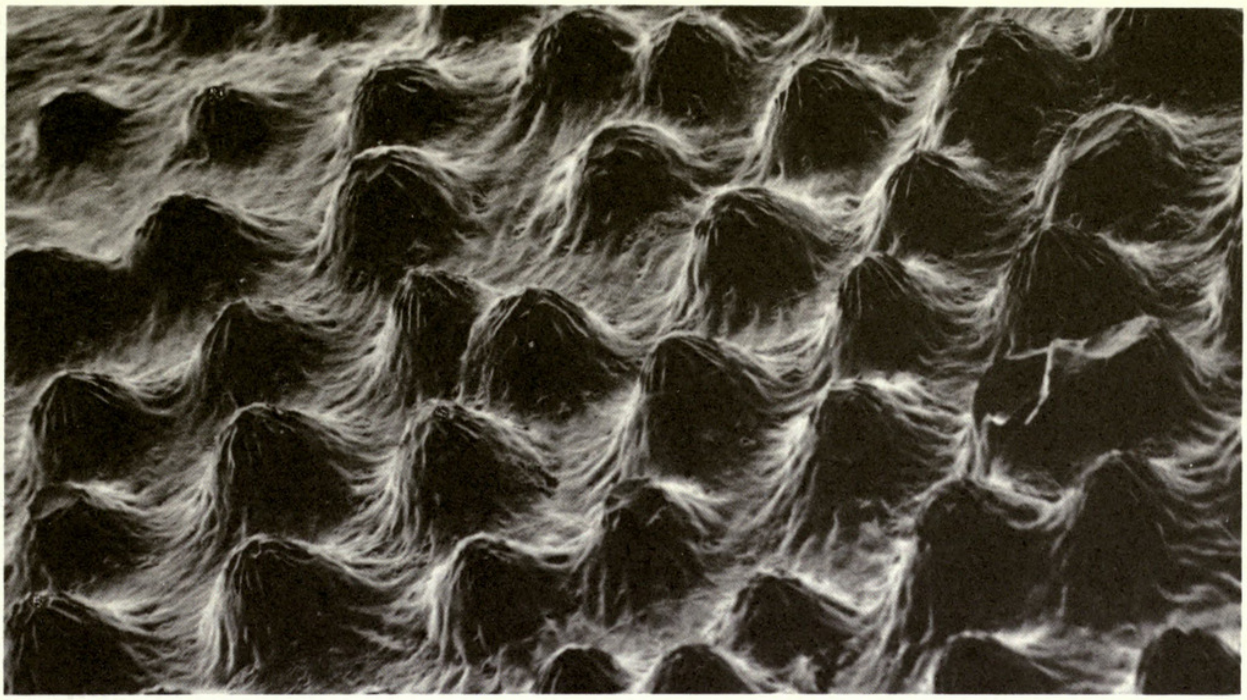
represent isolated areas of perichondral ossification. Denison (1978: 59) comments that '. . . the neurocranium . . . of *Phlyctaenius* . . . is perichondrally ossified'. The original source is Ørvig (1951: 408; pl. 7, fig. 1), where he says that the endocranium of *P. acadicus* is ossified to a large extent, and has a lining consisting of thin perichondral bone, and a thin basal layer of globular calcified cartilage. He goes on to say that the skull roof bone has fused with the perichondral bone layer of the dorsal endocranial wall beneath the growth centres. However, perichondral bone was not certainly recognized in the material examined here.

The RP is often detached from the remainder of the skull roof in all three species studied here (in *P. acadicus* it is detached in two out of six suitable specimens, in *P. stenosus* in 13 out of 14 suitable specimens and in *P. atholi* in all eight suitable specimens). This suggests that the nasal capsules were units independent of the orbital and occipital region of the neurocranium. This type of neurocranium would seem to belong to Stensiö's (1963: 820) 'type B' group. The dorsal outline of the postethmo-occipital portion of the neurocranium differs in many respects from the reconstruction of that of *P. acadicus* provided by Stensiö (1925: text-fig. 20). It is broader, has more processes and a wider occipital region (Figs 5D, 10). The postethmoidal region is generally similar in outline to that of *Kujdanowiaspis* (Stensiö 1945, 1963), though it differs in details. It is broad throughout. The remaining fragments of the occipital region indicate that it appears to be wider than in *Actinolepis magna* (Mark-Kurik 1973: fig. 7a, b), and *Kujdanowiaspis* (Stensiö 1945, 1963). The antorbital, supra-orbital, anterior and posterior postorbital and possibly supravagal processes are developed (Fig. 10). Between the antorbital and supra-orbital processes is a notch for the orbital recess. The anterior postorbital process is situated at the PtO/M suture, and the posterior postorbital process at the M/PNu suture. The latter process does not bifurcate as it does in *Kujdanowiaspis* (Stensiö 1945, 1963), *Actinolepis* (Mark-Kurik 1973: fig. 7a, b) and *Dicksonosteus* (Goujet 1975: fig. 4). However, the impression left by this process ends abruptly at the lateral margin of the skull roof, between the M and the PNu. It may well bifurcate beneath the PM as in *Actinolepis* (Mark-Kurik 1973: fig. 7a, b), although no evidence of the neurocranium is indicated on the fragment of the PM of specimen P6577a.

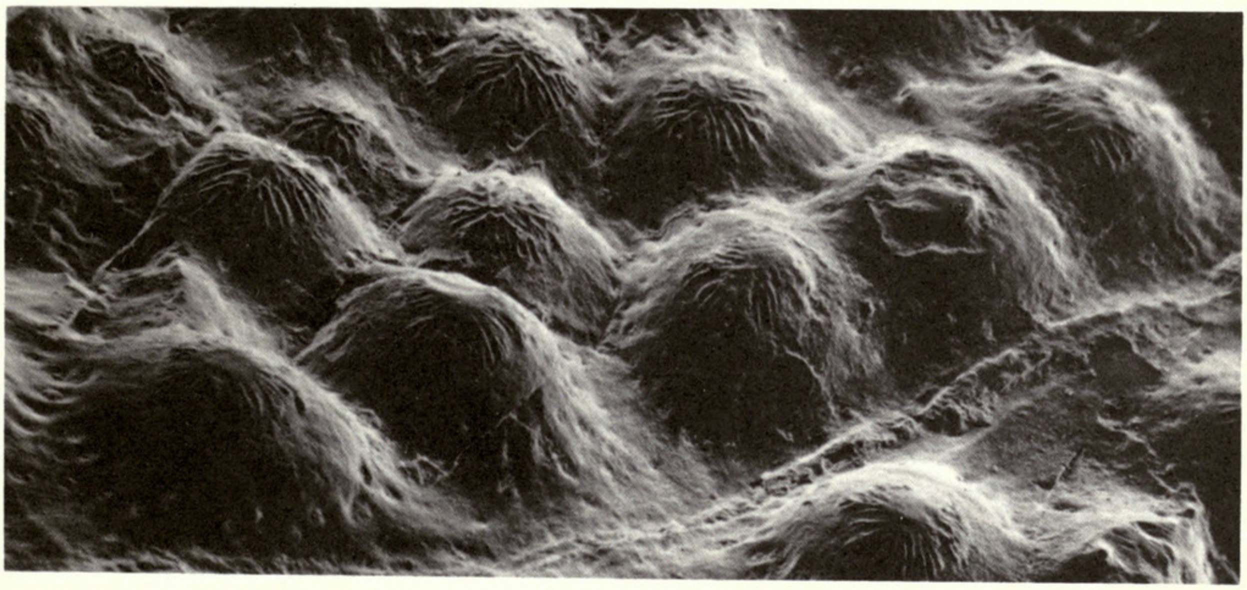
Specimen P56120 is here identified as *P. atholi*; although poorly preserved it has several interesting features. Impressions are present for the infra-orbital and lateral sensory canals, and impressions of a number of other canals are preserved. From a comparison with those of *Kujdanowiaspis rectiformis* (Brotzen) (Stensiö 1945: fig. 1) they can be interpreted: antero-laterally there are dorsal canals for cutaneous nerves and vessels, lateral to the growth centres of the Cs there are canals for a dorsal branch of the glossopharyngeal and vessels, and postero-laterally canals for a supratemporal branch of the vagus and for vessels. Other canals are indistinct on this specimen.

The general pattern of sensory lines on the skull roof is seen in Figs 4, 5A–C, 6, 8. In *P. stenosus* the infraorbital canals run nearly parallel to one another while in the other two species they converge anteriorly, particularly in *P. atholi*. Several specimens of *P. stenosus* show variations in the sensory canals: paired posterior pit-line grooves, not normally identified in *Phlyctaenius*, occur on specimen RSM GY 1897.51.118 (Fig. 7A). Each occurs as a paired row of tubercles extending between the growth centres of the C and PNu. In many actinolepids and phlyctaeniids posterior pit-lines are not evident, or are indicated as short grooves near to the growth centres of the C and the PNu (e.g. *Simblaspis, Sigaspis, Arctolepis*; Denison 1978: text-figs 31, 38). A posterior pit-line is evident on *Actinolepis* extending between the growth centres of the C and the PNu (Denison 1978: text-fig. 31). Posterior pit-lines may occur as discontinuous grooves between the growth centres of the C and the PNu of brachythoracids such as *Holonema, Buchanosteus, Millerosteus, Coccosteus* and *Dicksonosteus* (Denison 1978: text-figs 45, 49, 57). Specimen P5475, *P. stenosus*, has a short groove which runs from the growth centre of the PtO to the PtO/C border, which may be a short duplication of the central canal (Fig. 7A). Although not typical of *Phlyctaenius*, shallow traces of grooves, which may be profundus pit-line grooves, run between the growth centres of the PrOs and PtOs of *P. stenosus* (P5475; P6573i; P56125, Fig. 7A). This is also seen in one specimen of *P. atholi* (RSM GY 1978.30.3, Fig. 7C). Profundus grooves occur in some other actinolepids (e.g. *Bryantolepis brachycephalus* and *Simblaspis cachensis* Denison, 1958: 508). Graham-Smith (1978*a*: 26) suggests that 'profundus' grooves in some dolichothoracids may be produced as a result of an extension of the suborbital canal becoming anchored ontogenetically to a rudiment of the PtO.

Fig. 11 *Phlyctaenius*, ornament tubercles: A. *P. acadicus* (Whiteaves) (RSM GY 1897.51.129) ×22, SEM SP5/407. B. *P. atholi* (Pageau) (RSM GY 1897.51.123) ×25, SEM SP5/428. C. *P. stenosus* sp. nov. (P6573h) ×25, SEM SP5/415.



A



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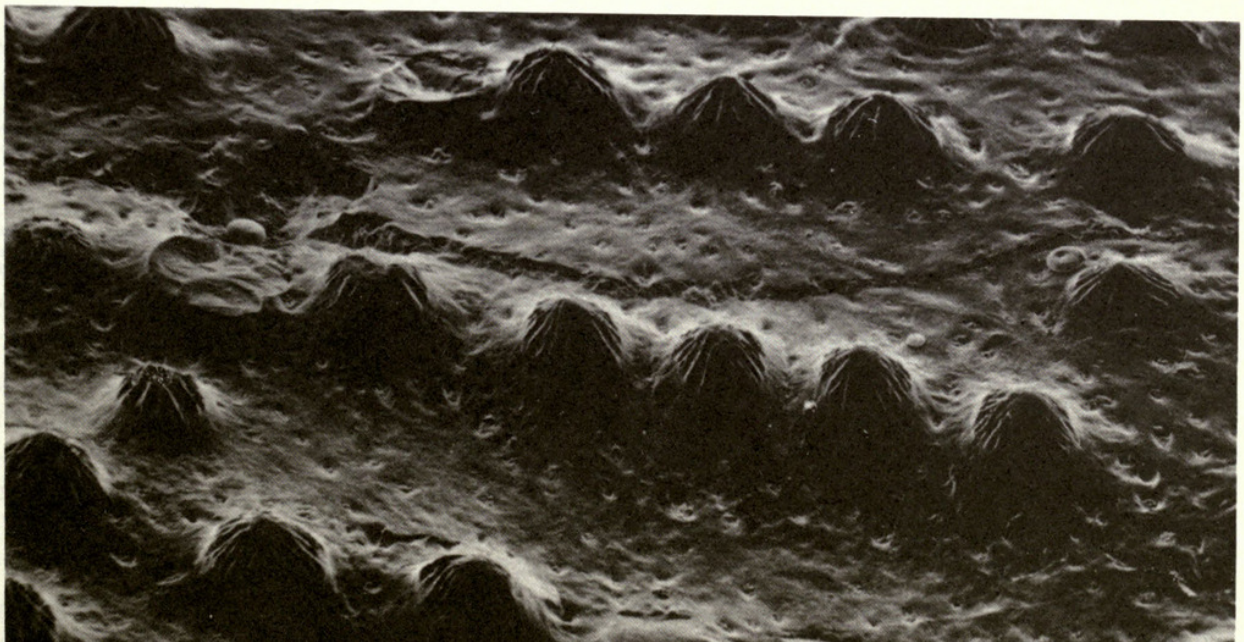

C

In some specimens of *P. stenosus* (P6555, P56125, P5972) the suture line between the PtO and the M on one side of the infraorbital canal is displaced relative to that on the other side (Figs 7A, 8). In each case the section of the suture line lateral to the infraorbital canal is more anterior than the mesial section. Similar displacement at the junctions of sensory canal grooves has been figured by Gross (1941: text-fig. 7a) for several species of *Bothriolepis*, and Graham-Smith (1978*a*: 23–25) has proposed an explanation of how this may have occurred.

The occipital cross-commissural groove is seen in *P. acadicus* and *P. atholi* where it runs from the growth centre of the PNu posteromesially to notch the posterior margin about half-way along. It is possible that the path of this groove may indicate the presence of extrascapular plates, as suggested by Miles & Dennis (1979: 45). However, extrascapular plates were not seen in any species of *Phlyctaenius*.

The ornament of *Phlyctaenius* is of individual tubercles, the shape, size and arrangement of which differ among the three species (Fig. 11A–C). In each species the ornament tubercles of individual plates are smallest around the growth centre and largest at the plate margins. Tubercles are uniformly arranged and are close together in *P. acadicus*, and normally uniformly arranged in *P. atholi*. In *P. stenosus* they are arranged in rows parallel to the plate margins. Thus it is usually possible to distinguish the approximate outlines of the plates in the three species. In all three species tubercles lateral to the infraorbital sensory canal are smaller than those mesial. In several areas of specimen RSM GY 1897.51.129 it seems that tubercles have overgrown earlier tubercles. This feature was noticed in *P. acadicus* by Gross (1957: pl. 6, fig. 7), and by Ørvig (1957: fig. 9a) who figured a section of *P. acadicus* which shows two generations of tubercles separated by a thin layer of laminar bone. In *Arctolepis magna* Mark-Kurik tubercles often overgrow other tubercles so that 'the concentric arrangement of the tubercles is often considerably confused' (Mark-Kurik 1973: 97).

SOs (Fig. 12C, D) occur on P6555 (*P. stenosus*) and as isolated fragments of *Phlyctaenius* sp., RSM GY 1897.51.118 and 126. Areas missing, due to fracture, from specimen P6555 are present

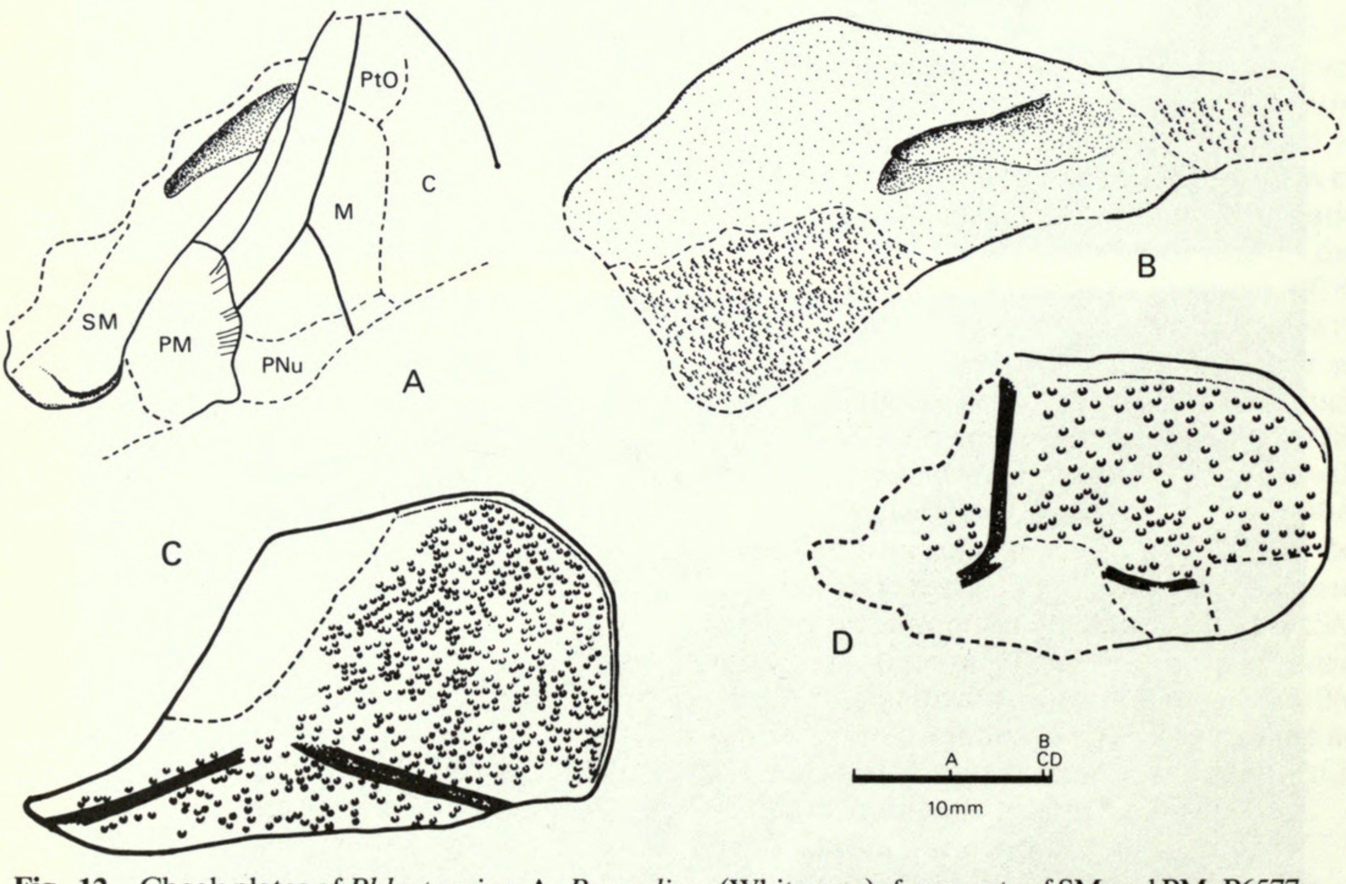

Fig. 12 Cheek plates of *Phlyctaenius*. A. *P. acadicus* (Whiteaves), fragments of SM and PM, P6577a. B. *P.* sp. SM showing groove for hyomandibular, P6573d. C. *P. stenosus* sp. nov., SO, holotype P6555. D. *P. atholi* (Pageau), SO, RSM GY 1897.51.126.

on the isolated fragments of the SO (Fig. 12D). In section the SO may be divided into two laminae which lie at an angle to one another (Heintz 1933: fig. 1). The bend between the two laminae runs horizontally across the 'blade' to the orbital margin. The postorbital branch of the infraorbital canal has not previously been recorded for *Phlyctaenius* but it is present in RSM GY1897.51.118 and 126, and in each it runs in usual arthrodire fashion (Fig. 12D). A post-suborbital was not found.

The sclerotic plates (Fig. 8, Scl) occur as fragments on specimen P6555, *P. stenosus*, where there are apparently four on each side, as is usual for arthrodires (Denison 1978: 2). Each is thick and strongly arched, similar to those of *Arctolepis* (Heintz 1962: 36–38). Heintz (1933: 130) commented that 'the sclerotic ring in *Phlyctaenaspis* must form something like a more or less strong capsule protruding from the orbital opening of the head roof'. The sclerotic plates of Placodermi are sometimes ornamented (Denison 1978: 2; *Arctolepis*, Heintz 1962: 36–38), and the outer surface of those of *Phlyctaenius* have an ornament of uniformly arranged tubercles. Heintz (1933: 129) commented on the presence of fragments of possible PNs occurring near the orbit on P6555. However, they are poorly preserved and cannot be positively identified.

The remains of three isolated gnathal elements are recognized (Heintz 1933: pl. 2, figs 2–4). All three are poorly preserved, fractured and incomplete. Two are believed to be inferognathals, and one a superognathal, and are believed, by association, to belong to *P. stenosus* (RSM GY1897.51.125), and *P. atholi* (RSM GY1897.51.126). The inferognathal elements (RSM GY1897.51.125, 126) are small and slender and consist of an anterior tooth-bearing section and a posterior blade, without teeth. RSM GY1897.51.126 is narrow posteriorly, becoming wider anteriorly. On the tooth-bearing section of this specimen about 25 to 30 teeth are evident. In both elements the teeth are of varying sizes, are conical and tend to become larger towards what is presumed to be the anterior end. Broken sections confirm Heintz' (1933: 132) comment that the teeth appear to have no pulp cavity.

Other cranial elements of *Phlyctaenius* are preserved as fragments. Four poorly-preserved specimens are identified as submarginals (Fig. 12A, B): P6577a (Heintz 1933: pl. 2, fig. 1), P6573d – both *P. acadicus*; RSM GY1897.51.125 – *P. stenosus*; RSM GY1897.51.118 – *Phlyctaenius* sp. All plates show the visceral surface and show small traces of ornament as impression. The first two specimens mentioned show a shallow longitudinal groove anteriorly which probably represents the point of attachment for the hyomandibular.

A small fragment of the visceral surface of a plate, possibly a PM, is attached to the margin of the skull roof of P6577a, *P. acadicus* (Fig. 12A herein and Heintz 1933: pl. 2, fig. 1) and an impression of the visceral surface of the PM is present on P5972, *P. stenosus*. The outline of the impression is indistinct.

Specimens of the thoracic shield of *Phlyctaenius* are represented mostly as isolated plates, although some occur in association and a few with a skull roof. The ornament of individual plates may be matched, in most cases, with one or other of the three types of skull roof ornament.

Previous restorations of the trunk shield of *Phlyctaenius* (Heintz 1933) were based upon information from more than one species. The present reconstruction of the thoracic shield (Figs 13, 14, 15) is based upon *Phlyctaenius stenosus* since, of the three species, the specimens of this show the most complete series of thoracic plates. The reconstruction was difficult because of variation in size, and the incompleteness of many of the individual plates, and because associations of trunk plates from one individual are rare and never complete. The reconstruction was done by making outline tracings of individual plates. The size of the tracings was adjusted with the Grant Projector to relate to those of one of the more complete associations of plates belonging to a single individual. The relative sizes of the overlap areas were taken into consideration. The resulting composite plate outlines were traced onto thin card, cut out individually, and from these the thoracic shield was reconstructed.

The ventral surface of the thoracic shield is flat with the remaining plates forming an arch. Sections vertically through the thoracic shield show an anterior triangular cross section and a posterior seven-sided section, similar to those described and figured by Heintz (1933: 141, fig. 5).

The mutual relationships of constituent plates is that typical of primitive arthrodires (Denison

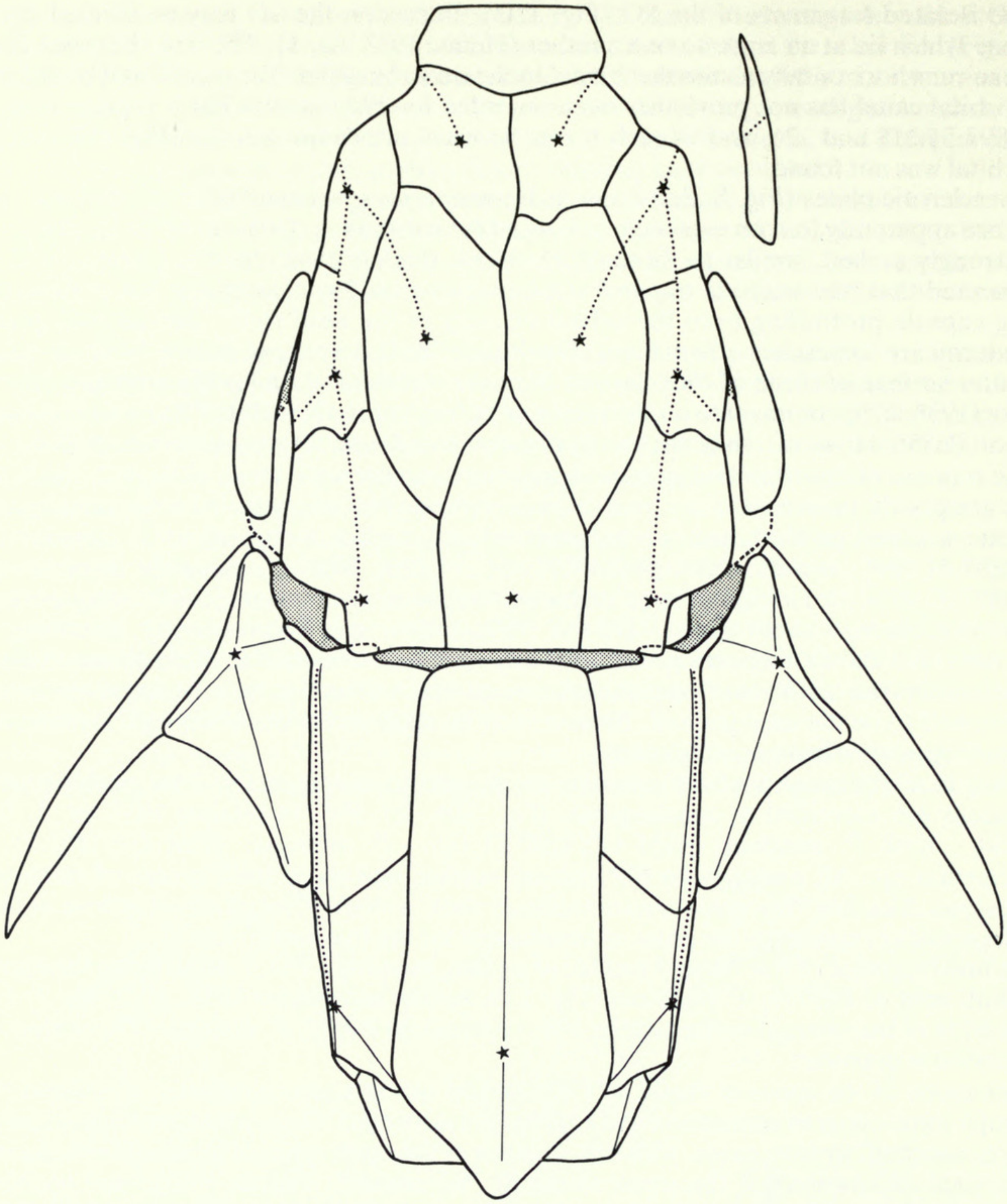

Fig. 13 *Phlyctaenius stenosus* sp. nov. Restoration of skull roof and trunk shield in dorsal view. The SO is drawn separately since its exact position is unknown. The sensory lines are dotted and the growth centres starred.

1950, 1978), in which the PL and PVL contact one another to enclose a pectoral fenestra. However, the extent of the overlap areas of constituent plates suggests that the margin of the pectoral fenestra is bounded by the AVL, AL and possibly the PVL (Figs 13, 14). There is a well-developed 'Dorsolateralkante' and 'Ventrolateralkante' (Gross 1932) and a postbrachial lamina on the AVL and PVL.

The differences between the thoracic shields of the three species are most conspicuous in the shapes of the MD, AL and ADL. The MD of *P. stenosus* (Figs 13, 16A) shows a square anterior end in contrast to the rounded margin in *P. atholi* (Fig. 16B). In both, there is a low dorsal crest (more developed in *P. stenosus*) and the visceral surface shows a small median ridge which might

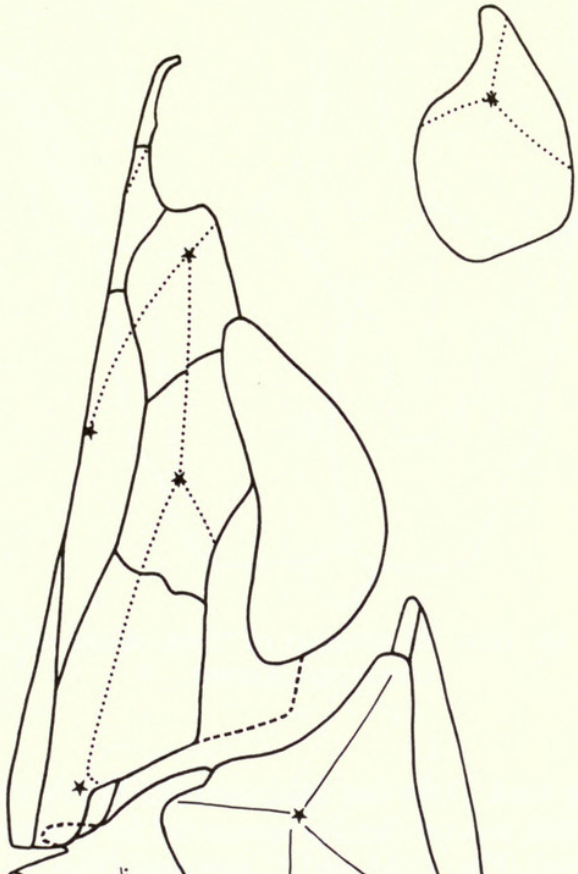

Fig. 14 *Phlyctaenius stenosus* sp. nov. Restoration of skull roof and trunk shield in lateral view. The SO is drawn separately since its exact position is unknown. The sensory lines are dotted and the growth centres starred.

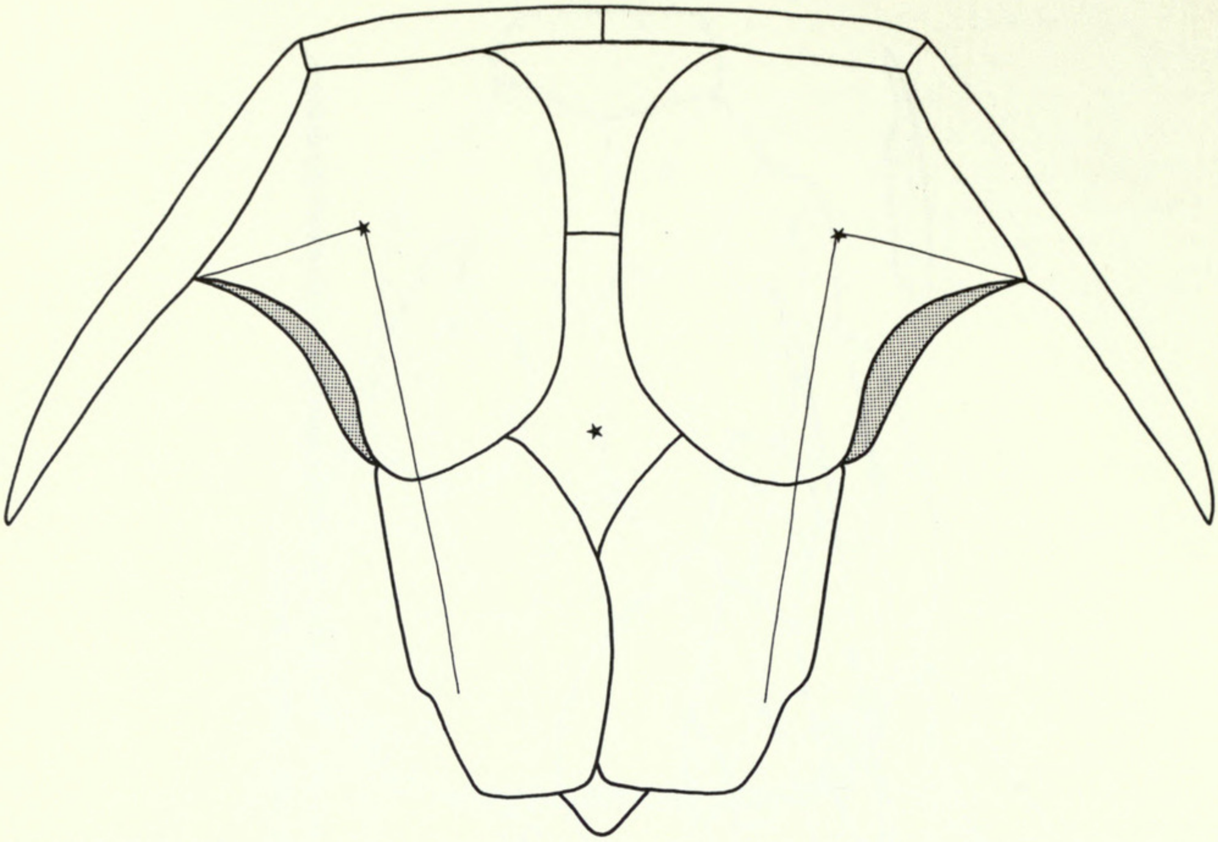

Fig. 15 *Phlyctaenius stenosus* sp. nov. Restoration of trunk shield in ventral view. The growth centres are starred.

be interpreted as a rudimentary keel. Only one specimen (RSM GY 1897.51.128) of the MD of *P. acadicus* was examined and this was too poorly preserved for comment.

The ADL is known in *P. atholi* (Fig. 17A) and *P. stenosus* (Figs 14, 17B, C). Both show an articular condyle below which there is, in *P. stenosus*, a swollen anterior margin resembling an obstantic process, although it is not as well developed as that process in *Holonema* (Miles 1971: 158). Similarly, there is no obvious development of a para-articular face but the shape of the matching angle of the paranuchal suggests that there must have been some articulation with the ADL ventrolateral to the articular condyle articulation. Specimens of the visceral surface of the ADL include: RSM GY 1897.51.124, 125, 126; P6575; P56143. The specimens are incomplete and it is not possible to identify them to species by their outline. On these specimens the swollen process running from below the articular condyle anteroventrally is very prominent as a ridge along the anterior margin of the lower lamina of the plate, and is similar to the 'ventral ridge' on the ADL of *Holonema* (Miles 1971: text-fig. 68). It borders the upper part of the anterior margin of the AL (Figs 13, 14, 17A–C). There appears to be a small para-articular face of rough-surfaced bone on the visceral surface of RSM GY 1897.51.125 and P56143. The differences in shape of the ADL of *P. atholi* and *P. stenosus* are seen in Fig. 17A–C. In both, the plate is divided by a pronounced ridge beneath which the lateral line groove runs to notch the posterior margin. The main lateral line is continued as a groove as far as the growth centre of the PDL of both *P. stenosus* (Figs 14, 17D, E) and *P. atholi*; thereafter it does not mark the bone (cf. Heintz 1933: fig. 3). The PDL of these two species (unknown for *P. acadicus*) is very similar except that the groove for the lateral line is not accompanied by a ridge in *P. atholi* as it is in *P. stenosus*. The PDL of *P. stenosus* is interesting in showing a small triangular area posteriorly in which the arrangement of the tubercular ornament differs from (P56126a, b), or is similar to (P6577d, Fig. 17E), that on the rest of the plate.

I thank Dr Gavin Young for drawing my attention to an unusual PDL figured and described by Pageau (1969: 819; pl. 30, fig. 10; fig. 21M; specimen LTC-29D in Laboratoire Teilhard de Chardin, Univ. Québec, Montreal). The specimen is from a horizon yielding specimens of

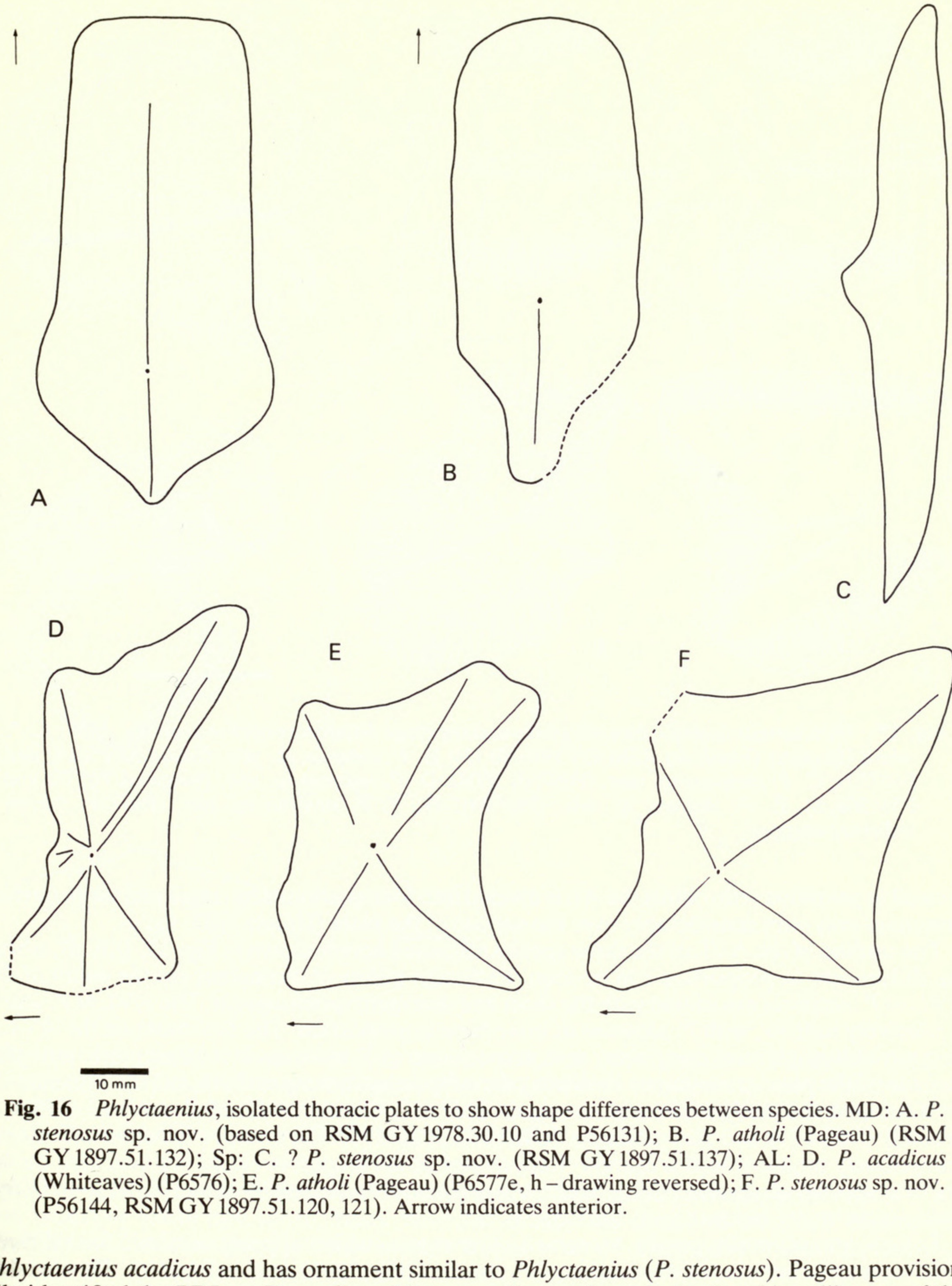

Fig. 16 *Phlyctaenius*, isolated thoracic plates to show shape differences between species. MD: A. *P. stenosus* sp. nov. (based on RSM GY 1978.30.10 and P56131); B. *P. atholi* (Pageau) (RSM GY 1897.51.132); Sp: C. ? *P. stenosus* sp. nov. (RSM GY 1897.51.137); AL: D. *P. acadicus* (Whiteaves) (P6576); E. *P. atholi* (Pageau) (P6577e, h – drawing reversed); F. *P. stenosus* sp. nov. (P56144, RSM GY 1897.51.120, 121). Arrow indicates anterior.

Phlyctaenius acadicus and has ornament similar to *Phlyctaenius* (*P. stenosus*). Pageau provisionally identified the PDL as *P. acadicus*. However, the specimen is short and is unlike any of the specimens of PDLs of *Phlyctaenius* studied here (Figs 14, 17D, E).

The AL is known for all three species and comparative outlines are given in Fig. 16D–F, from which it may be seen that the AL of *P. acadicus* is very tall and narrow with a short spinal margin. This contrasts with the relatively long plate of *P. stenosus*; *P. atholi* is intermediate in these dimensions. The posterodorsal corner of the AL of *P. atholi* is distinctive in being truncated. As

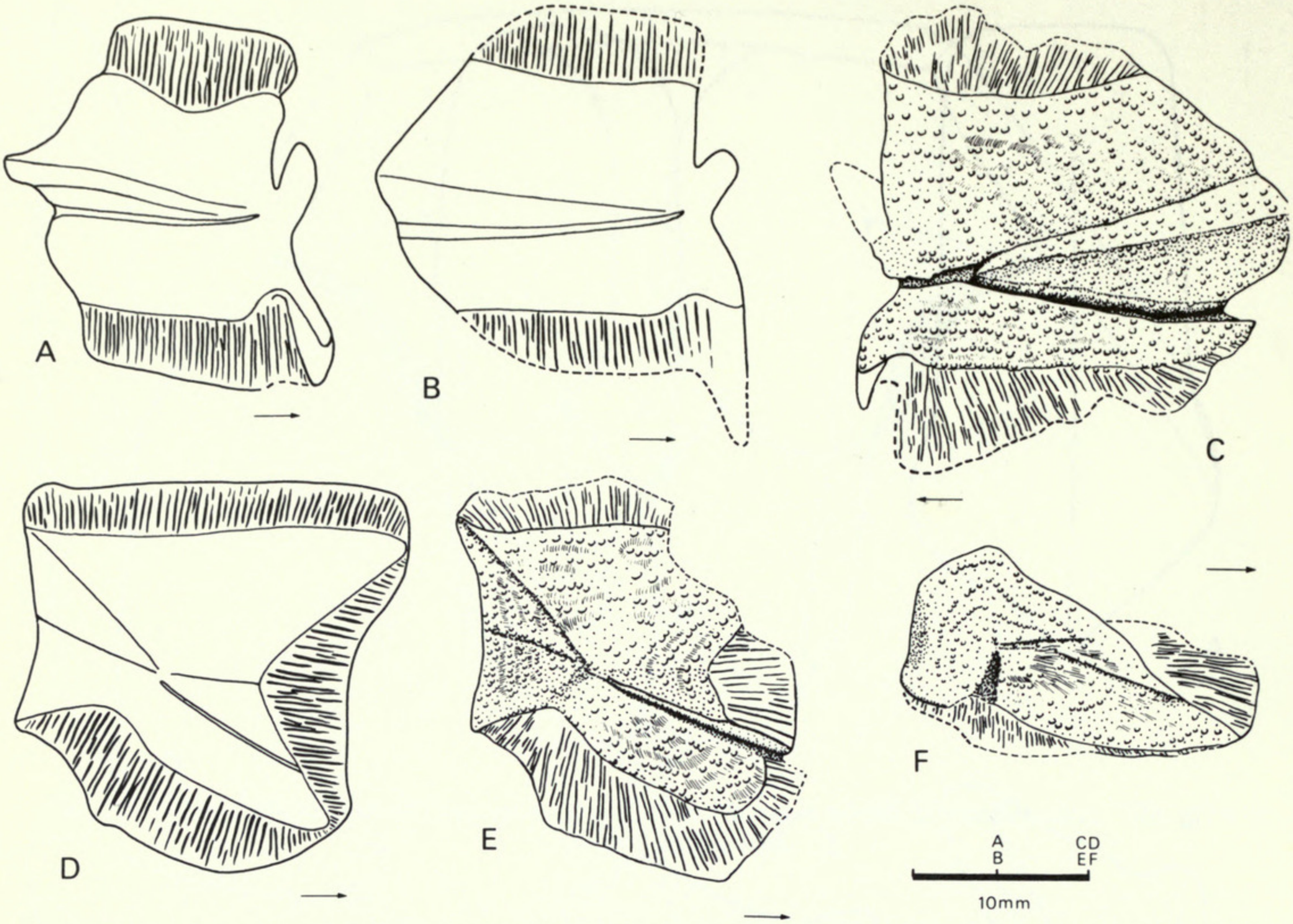

Fig. 17 *Phlyctaenius*, isolated thoracic plates to show shape differences between species. ADL: A. *P. atholi* (Pageau) (based on RSM GY 1978.30.13); B. *P. stenosus* sp. nov. (based on P56142 and P6577d); C. *P. stenosus* sp. nov. (P6577d). PDL: D. *P. stenosus* sp. nov. (based on P6577d and P56126a, b); E. *P. stenosus* sp. nov. (P6577d). PL: F. *P. stenosus* sp. nov. (P6577d). Arrow indicates anterior.

is usual in primitive arthrodires the AL is divided into four quadrants by ridges and the pattern of ornament may vary considerably over the surface of the plate (Heintz 1933: fig. 4).

The outline of the AVL of the three species discussed here is shown in Figs 15, 18A, B, where the differences in proportion can be seen. Particular points of distinction are the width of the AVL in *P. acadicus* associated with the short and divergent spinal margin. The AVL of *P. atholi* is relatively narrow, with *P. stenosus* intermediate in proportion. The ornament on the AVL is very variable but is most completely seen in specimens of *P. stenosus*. It is of interest to note that the side of the plate immediately bordering the subpectoral emargination is heavily ornamented with tubercles, usually uniformly arranged. This is unlike the AVL of *Coccosteus* (Miles & Westoll 1968: 434) and *Barrydalaspis* (Chaloner *et al.* 1980: 131), where tubercles are absent immediately adjacent to this margin. Impressions of the scapulocoracoid are indicated on the visceral surface of several AVLs, and are approximately similar in outline to that of *Barrydalaspis theroni* (Chaloner *et al.* 1980: fig. 3).

Spinals are generally poorly preserved. The shape, which appears constant for all three species, may be seen in the restoration of *P. stenosus* (Figs 13–15) and in Fig. 16C. The spinal of *P. stenosus* is the best known. The ornament over the inner and central areas is of small- to medium-sized tubercles. These may be rounded or elongated, sometimes forming rows parallel, or slightly inclined, to the longitudinal axis of the plate; occasionally they are uniformly arranged. The outer margin of the plate is covered by larger tubercles. Although Heintz (1933: 138) commented that spines were not evident on either the inner or outer margins of the Sp, small spine-like projections, possibly modified tubercles, are present on the inner margin of P6576b

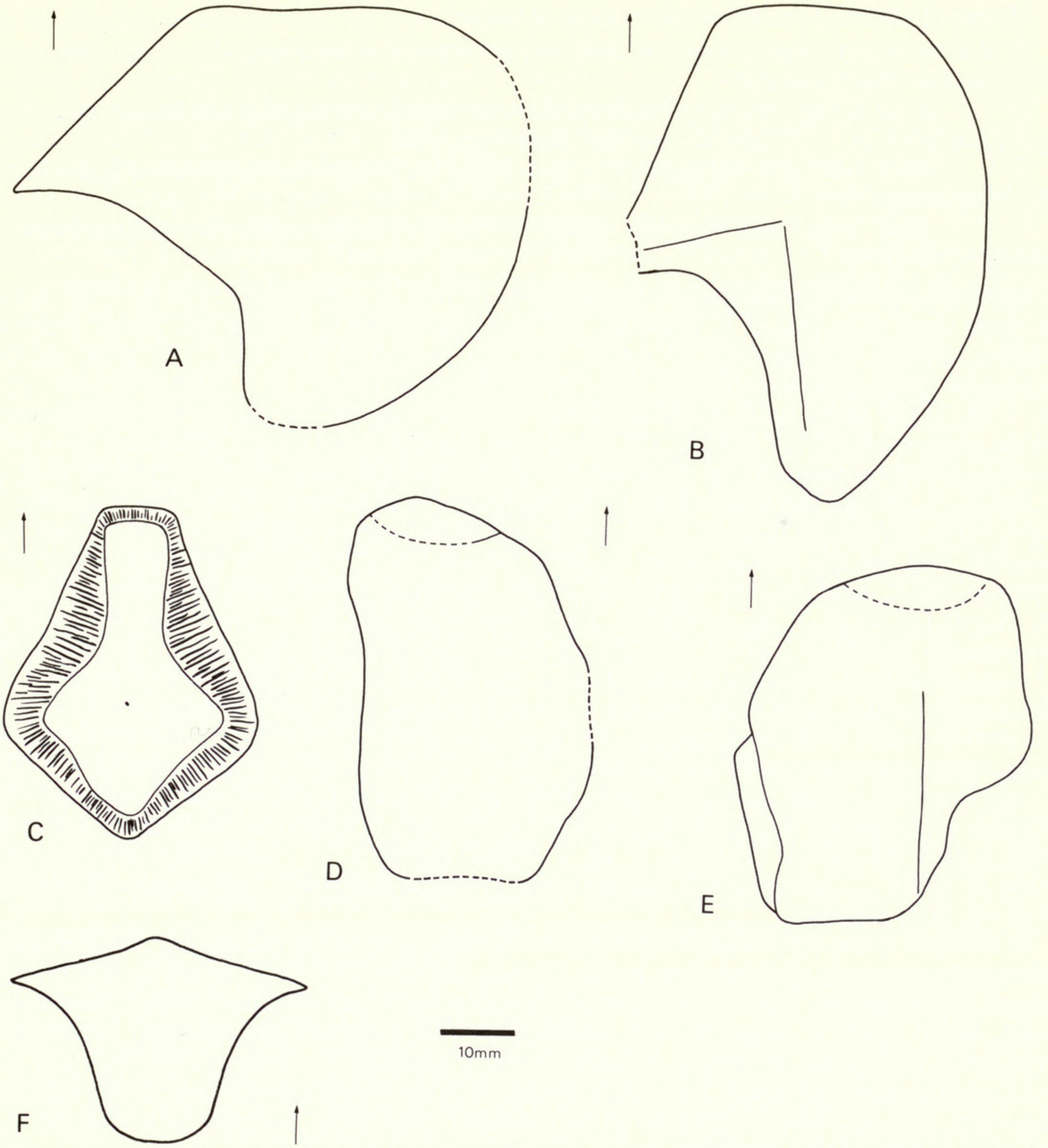

Fig. 18 *Phlyctaenius*, isolated thoracic plates. AVL: A. ? *P. acadicus* (Whiteaves) (RSM GY 1897.51.123); B. ? *P. atholi* (Pageau) (P56126b). PMV: C. *P. stenosus* sp. nov. (P56126a, b). PVL: D. *P. acadicus* (Whiteaves) (P56131); E. *P. stenosus* sp. nov. (RSM GY 1897.51.118). AMV: F. *P. acadicus* (Whiteaves) (P6577a). Arrow indicates anterior.

and RSM GY 1897.51.134. Specimen P6576 is possibly that figured by Heintz (1933: figs 3, 5, 6). It is relatively small and short. Small tubercles occupy the centre of the plate, and larger tubercles the outer margin. The plate is situated close to an AL assigned to *P. acadicus* and may belong to this species.

The IL is very incompletely known. Several specimens (RSM GY 1897.51.134–136) of *P. stenosus* displaying this bone show that the ventral surface is narrow (Fig. 15) and has a rounded recess for the AMV towards the mid-line. A mesial section of the IL is present on RSM GY 1897.51.134 and two laminae of the IL, set at an angle to each other, seem to be indistinctly indicated. What little of the surface ornament is preserved seems to be of uniformly arranged tubercles.

Heintz (1933: 142) recognized four kinds of scales:

1. Rhomboidal or quadrangular scales without evidence of overlap margins, and with typical *Phlyctaenius*-like ornament.
2. '. . . more or less oblong triangular scales with clearly overlapping margins along both the longitudinal sides . . .'. They are strongly arched and thick.
3. '. . . fulcra-like quite big scales . . . bent along the longitudinal axis with a deep incut in the hind margin'.
4. '. . . quite large, thin roundish scales . . . on the outside covered with concentrically arranged tubercles.'

The rhomboidal or quadrangular scales on RSM GY 1897.51.128 (Heintz 1933: pl. 3, fig. 6a) are situated close to an MD of *P. acadicus*, and probably belong to this species. Scales which are similar, though subtriangular or round, are also present in this area. The long, narrow, triangular scales figured by Heintz (1933) are associated with plates of *P. stenosus* (Heintz 1933: pl. 3, fig. 5) and an MD of *P. acadicus* (Heintz 1933: pl. 3, fig. 6b). At each of the longer margins of the scales on RSM GY 1897.51.125 is a narrow, sloping lateral surface which may be overlap surface. Heintz comments that the scales are ornamented with large tubercles (Heintz 1933: pl. 2, figs 6, 7), though this is not clear on the specimens he described. These scales resemble the flank scales of *Sigaspis* (Goujet 1973), which are tall and narrow and overlap one another. It is possible that the tall narrow scales on RSM GY 1897.51.125 and 128 are flank scales of *P. stenosus* and *P. acadicus*. The 'fulcra-like' scales, examples of which were described and figured by Heintz (1933: pl. 3, fig. 4: P6559b, an isolated scale, and fig. 5, lower right corner of his photograph: RSM GY 1897.51.127, 128) are believed to be dorsal ridge scales. The ornament is of *P. acadicus* type. The scale is heart-shaped, conical and deep in section. Its deepest point is at the growth centre. At its wider end is a V-shaped opening with rounded edges extending from the growth centre to the scale margins. On specimens RSM GY 1897.51.127 and 128 two dorsal ridge scales, which are mentioned by Miles (1969: 132), are present, associated with an MD of *P. acadicus* and a large cluster of scales. Both specimens are fractured and compressed. The outlines are indistinct and the V-shaped notch is not seen. It seems that the pointed end of the scale is anterior. Heintz (1933: pl. 3, fig. 3; P7084) figured a '. . . quite large, thin, roundish scale' or 'plate . . . covered with concentrically arranged tubercles'. This specimen is believed to be a C of *P. stenosus*.

In addition to the scales described above two further varieties are recognized. Small round or ellipsoidal scales are situated close to the thoracic shield of P6577a, *P. acadicus*, and possibly belong to this species. There is no evidence of overlap surfaces or ornament. Also a small, round scale, about 8 mm in diameter and ornamented with concentrically arranged tubercles, is associated with small, presumed juvenile, thoracic plates of *P. stenosus* (P6577a), and may belong to the same individual. Two ridges diverge from the central growth centre to the margin of the scale. This specimen is believed to be a median ridge scale, and may be a juvenile, or a different variety of that described above.

Discussion

Traditional classifications of *Phlyctaenius* (often as *Phlyctaenaspis*: see pp. 5, 10) have been provided by Woodward (1891), Zittel (1895, 1932), Fowler (1947), Denison (1958, 1975), Obruchev (1964, 1967), Miles (1969, 1973) and Stensiö (1969). Woodward (1891) and Zittel (1895) placed *Phlyctaenius* in the family Coccosteidae; later Woodward *in* Zittel (1932), followed by Obruchev (1964, 1967) and Miles (1973), placed the genus in the family Phlyctaenaspidae; Fowler (1947), followed by Denison (1978), placed it in the family Phlyctaeniidae. Stensiö (1969) placed *Phlyctaenius* in the order Dolichothoraci.

In attempting to reconstruct the phylogeny of arthrodires Miles (1969), Stensiö (1969) and Denison (1975) identified evolutionary trends in order to establish characters by which taxa could be grouped. Miles (1969) divided the arthrodires into four main groups, which he recognized as grades of taxa at a particular level of biological organization, each successively more 'biologically efficient' than the last. *Phlyctaenius acadicus* (Whiteaves), representing the phlyctaenaspid level of organization, was regarded as intermediate between the presumed more primitive, actinolepid, and the more advanced, brachythoracid, levels of organization. More recently placoderm interrelationships have been expressed in the form of cladograms, proposed by Denison (1978), Miles & Dennis (1979), Dennis & Miles (1979*a*, *b*, 1980) and Young (1979, 1980, 1981). The cladogram of Denison (1978) is a general cladogram for the Arthrodira. That of Miles & Dennis (1979) and Dennis & Miles (1979*a*, *b*, 1980) (with slight variations) is concerned mainly with the brachythoracid arthrodires. The cladogram of Young (1981) is concerned with phlyctaenioids. The cladograms of Denison (1978) and of Young (1979, 1981) agree generally in the relationships of the Phlyctaeniidae. In all three cladograms the suborders Phlyctaeniina, Heterosteina, Coccosteina and Pachyosteina (Denison 1978: fig. 30), or representative taxa, are grouped together on the possession of a hinged dermal neck-joint. Young (1979, 1981) adds the loss of AV plates (if primitive for placoderms), although Denison (1978: fig. 30) suggests that the presence of paired AVs is a specialization of the Actinolepidae. Miles & Dennis (1979: 43) and Dennis & Miles (1979*a*: 19, 1979*b*: 308) proposed the presence of a ventral ridge on the MD as a phlyctaenioid synapomorphy, but Young & Gorter (1981) reject this since a ventral ridge on the MD is present also in some actinolepids (e.g. *Aethaspis, Sigaspis, Actinolepis*). Denison (1978) separated the suborder Phlyctaeniina, including the families Phlyctaeniidae, Holonematidae and possibly the Williamsaspidae, on the basis of a long, narrow MD. He also suggested that the elongation of the Sps is a specialization of the Phlyctaeniidae. However, as Young & Gorter (1981: 109) remark, neither of these characters is reliable since the Sps of some actinolepids and phlyctaeniids are of similar length; a long narrow MD is also present in some brachythoracids, e.g. *Gemuendenaspis*. They conclude, therefore, that both characters are plesiomorphous and this leaves the Phlyctaeniina without a character. They also recognize that the family Phlyctaeniidae can only be defined on the basis of primitive characters, and cannot therefore be justified as a monophyletic group.

Within the family Phlyctaeniidae Dennis & Miles (1979*a*: 19, 1979*b*: 308, 1980: 47) have proposed a specialization to separate *Phlyctaenius* together with more advanced taxa; the occipital cross-commissure passing off the posterior margin of the PNu. However, this character seems unacceptable since, as Young & Gorter (1981) have commented, in the brachythoracid *Buchanosteus* this sensory groove has the supposed primitive position. As Young & Gorter (1981) conclude, within the family Phlyctaeniidae subgroups do not seem to be readily defined and the family may be a paraphyletic group.

Of the phlyctaeniids (listed by Denison, 1978) some genera may be more closely related to *Holonema* or *Groenlandaspis*. The genera *Huginaspis, Kolpaspis* and *Prosphymaspis*, each known only by trunk plates, resemble *Groenlandaspis* and *Tiaraspis* in having a high trunk shield and a convex, high-crested MD. *Diadsomaspis*, based on trunk plates, resembles *Groenlandaspis* and *Tiaraspis* in the highly arched MD, and it has a holonematid-like ornament of ridges, though unlike *Groenlandaspis* the ADL is narrow. Denison (1978) comments that the head shield of *Arctolepis* resembles those of the Holonematidae in the wide, fused rostral and postnasals, the large pineal separating the PrOs, and in the shape of the Nu. This genus was included by Young (1981: fig. 17) as the sister-group of a group including *Holonema*. Denison (1978: 55) remarks that *Aggeraspis* includes skull roofs and trunk plates which indicate both phlyctaeniid and actinolepid characters, and may include two genera, or 'might represent a derivative of Actinolepidae that had attained some of the phlyctaeniid specializations'. Of the remaining genera of the family Phlyctaeniidae listed by Denison (1978), *Phlyctaenius* may be distinguished from *Arctaspis* and *Svalbardaspis* in the characteristic shield-shape, and wider proportions, at the M and PNu, of the skull roof. The trunk shield of *Heterogaspis* is short and broad compared with that of *Phlyctaenius*, while that of *Neophlyctaenius sherwoodi* Denison is proportionately longer, and shapes of the plates differ from those of *Phlyctaenius* (cf. Figs 13–15 herein with Denison 1950: pl. 2, figs 1, 2; pl. 3, figs 1, 2). The Sp of *Elegantaspis* is very long in comparison with that of *Phlyctaenius*.

However, I have found no unique derived character shared by these genera, and so they cannot form a monophyletic group. The best known species of the Phlyctaeniidae is *Dickso-*

nosteus arctica Goujet. The general shape of the skull roof and pattern of plates is similar to those of *Phlyctaenius*, although *D. arcticus* is more slender overall. The widths of the skull roof at the levels of the rostral and of the occipital are about equal in *D. arcticus*, contrasting with the condition in *Phlyctaenius* where the rostral region is narrower. The lateral margin of the skull roof of *Phlyctaenius* gently narrows anteriorly at the level of the M and PtO, contrasting with that of *D. arcticus* where it is strongly indented. The R of *Phlyctaenius* is relatively narrower than that of *D. arcticus* and the P is shorter. The PNus of *Phlyctaenius* are wider than those of *D. arcticus*, and the PrO/C margins slope posteromesially, unlike those of *D. arcticus* where they are more transverse. The main differences in the thoracic plates of *Phlyctaenius* and *D. arcticus* concern the MD, Sps and PVLs. The posteriorly pointed MD of *Phlyctaenius* differs from the rounded posterior margin of the MD of *D. arcticus*. The Sps of *D. arcticus* are more slender and curved than those of *Phlyctaenius* and have distinct spines on their inner surface. The mutual PVL overlap of *Phlyctaenius* is simple, while in *D. arcticus* each PVL overlaps the other in a complex S-shaped suture.

The other Phlyctaeniidae include *Denisonosteus weejasperensis* Young & Gorter (1981) from the Middle Devonian near Wee Jasper, New South Wales, Australia, and genera described by Pageau (1969) from the Battery Point formation of Gaspé Bay, Quebec. *D. weejasperensis* may be distinguished from *Phlyctaenius* by the shape of the Nu, the convex posterior margin of the skull roof, and by differences in the shapes of some of the thoracic plates (cf. Figs 4, 5, 6, 8, 13, 14, 16, 17 herein, and Young & Gorter 1981: figs 22, 24). In addition to *P. atholi* from Campbellton, Pageau described six new species from beds contemporaneous with material described here, and some comments are necessary. However, I have not examined the material at first hand, and my comments are based solely on published information. Three of the species are based on trunk plates only: *Kolpaspis beaudryi*, based on an MD and other thoracic plates, is more reminiscent of *Groenlandaspis* as discussed above. *Batteraspis fulgens*, known only by an AL plate, may well be a separate species of *Phlyctaenius* (Denison 1978: 60). However, there is little basis for comparison. *Laurentaspis splendida* is based on an MD, PVL and AL, and an isolated C. There is no basis for considering this species to be closely related to *Phlyctaenius*, and Denison (1978: 105) placed it in Arthrodira *incertae sedis*. *Quebecaspis russelli* (renamed by Denison (1978: 59) as *Pageauaspis*) and *Cartieraspis nigra*, each based on a skull roof and isolated thoracic plates, differ from *Phlyctaenius* species in the shapes of some of the skull roof plates, particularly the long, slender Nu. The posterior margin of the PNu of *C. nigra* slopes anterolaterally, unlike that of *Phlyctaenius* where it slopes very gently posterolaterally. The ADL of *C. nigra* is very long and narrow, unlike that of *Phlyctaenius*. *Gaspeaspis cassivii* is based on a skull roof and thoracic plates and, as Denison (1978: 58) remarks, is doubtfully distinct from *Phlyctaenius*. It should probably be considered synonymous with *P. atholi*. The reasons are discussed under *P. atholi* (p. 13).

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