Age	Acme-zones (ZAJÍC 1990)	Central andf Western Bohemian Basins (HOLUB & PEŠEK 1991)			*Acanthodes fritschi* n. sp.	*Acanthodes* sp.	Krkonoše Piedmont Basin (HOLUB & PEŠEK 1991)		*Acanthodes* sp.
		Formation	Member				Formation	Member	
Stephanian C		Líně ♦ ♥			│	│ │	Semily	Upper	
								Middle ♣	│
								Lower	
Stephanian B	*Sphaerolepis*	Slaný	Kamenný Most	Otruby	│	│	Syřenov	Upper	
			Kounov						
			Ledce						
	Watsonichthys		Hředle	Malesice	│	│			
			Mšec					♠	
			Jelenice					Lower	

Fig. 2. Lithostratigraphic table of the Central and Western Bohemian region and Krkonoše Piedmont Basin with the subzones (acme-zones) of the *Sphaerolepis-Watsonichthys* range-zone and with acanthodian occurrence. The suits indicate important fossiliferous horizons: ♥ – Zdětín Horizon, ♦ – Klobuky Horizon, ♠ – Black Shale Horizon, ♣ – Ploužnice and Štěpanice-Čikvásky Horizons. For biostratigraphic details see chapter 4.

* Klobuky Horizon (isolated remains)
Klobuky (12-213)
Páleček (12-213; OBRHEL 1959)
Peruc (12-122)

* Ploužnice Horizon (isolated remains)
– Krkonoše Piedmont Basin
HK-1 borehole (Horní Kalná; 03-414)
Ploužnice (03-431)

* Štěpanice-Čikvásky Horizon (isolated remains)
– Krkonoše Piedmont Basin
Dolní Štěpanice (03-414; HOLUB 1961)
Nedvězí (03-413)

Acknowledgements

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2. DESCRIPTION

2.1. Index of abbreviations

a – zone without canals
ag – anterior groove of the pectoral fin spine
alb – axial lobe of the caudal fin
art. cs – articular cotylus
asp – anal fin spine
b – zone of canals oblique to the longitudinal axis of spine
ba – scale base
bra – branchial arch
c – "pith" cavity zone
can – canal
cmo – circumorbital bones
c. pi – "pith" cavity
cr – scale crown
crh – ceratohyal
d – zone of canals running parallel with the longitudinal spine axis
dmt – dermotrichia

dpl – dorsal plate
dsp – dorsal fin spine
e – zone of the proximal canals
e. pm – posteromesial elevation
fop – pectoral fossa
fo. sbsc – subscapular fossa
glr – gill rakers
g. Hm – groove for the hyomandibula
gr. Ch – groove for the ceratohyal
g. pi – "pith" groove
Hm. v – ventral ossification of the hyomandibula
jc – fragment of a jaw cartilage
l – lateral process
ld – longitudinal division of the hypochordal lobe
m. add – surface for the dorsal adductor muscles
mc – meckelian cartilage
mca – anterior ossification of the meckelian cartilage (mentomandibular)
mcp – posterior ossification of the meckelian cartilage (articular)
mdo – mandibular bone (mandibular splint)
mll – main lateral line
n – notch
p – pore
pgl – pectoral girdle
po – perichondral ossification
p. p – posterior projection of the scale crown
p. pr – procoracoid process
pr – procoracoid
pr. art – articular process
pr. gl. f – preglenoid fossa
pr. preart – prearticular process
pr. pregl – preglenoid process
pr. ptart – postarticular process
ps. gr – groove for the pectoral fin spine
psp – pectoral fin spine
qu – quadrate
rbr – branchiostegal ray
rdl – radials
sc – scapular blade
ssc – suprascapula
sl – sensory line
vl – ventrolateral sensory line
vlb – ventral lobe of the caudal fin
vsp – ventral fin spine
x – zone of poorly preserved scales
Z1, Z2, Z2'', Z3, Z4 – HEYLER's scale zones of the caudal fin

2.2. Methods of measurement

The proportions of specimens (see Fig. 3) are taken from ZIDEK (1976, 1980), LONG (1986b), and SCHULTZE (1990). The detailed method of measurement of the individual parameters was checked (ZIDEK, personal communications) in order to be certain of correct correlation with measurements of earlier described genera and species. The prepectoral length (l_{PR}) was measured between the anterior margin of the head and the longitudinal axis of the scapulocoracoid. The distances between the fin spines (v_{x-y}) were measured between the middles of their proximal terminations. The fin spine lengths (l_x) were measured between their proximal and distal terminations regardless of the spine distortion. I prefer the term spine length (considerably longest dimension) to the term spine height (considering the position in the body). Acanthodian specimens are usually bent postmortem. The total specimen length (l_T) or the standard specimen length (l_S) and the other often deformed proportions (v_{P-A}, v_{P-D}, v_{V-A}, etc.) were measured along the longitudinal body axis, mostly along the lateral sensory line and its imaginary continuation on the head or the tail. The number of scales per millimetre in a row (y) is measured in the region of the largest (oldest) trunk scales (near the lateral sensory line, after the dorsal fin spine) in the natural (oblique) row. The below figured (Fig. 3) proportions form the basis for calculation of the following ratios:

$$A^1 = \frac{l_A}{l_P} = \frac{\text{anal spine length}}{\text{pectoral spine length}}$$

$$A^2 = \frac{l_D}{l_P} = \frac{\text{dorsal spine length}}{\text{pectoral spine length}}$$

$$B = \frac{l_V}{l_P} = \frac{\text{ventral spine length}}{\text{pectoral spine length}}$$

$$C = \frac{l_P}{l_T} = \frac{\text{pectoral spine length}}{\text{total specimen length}}$$

$$D^1 = \frac{l_A}{l_T} = \frac{\text{anal spine length}}{\text{total specimen length}}$$

$$D^2 = \frac{l_D}{l_T} = \frac{\text{dorsal spine length}}{\text{total specimen length}}$$

$$E = \frac{l_V}{l_T} = \frac{\text{ventral spine length}}{\text{total specimen length}}$$

$$F = \frac{v_{P-A}}{l_T} = \frac{\text{distance between pectoral and anal spines}}{\text{total specimen length}}$$

$$G = \frac{v_{V-A}}{l_T} = \frac{\text{distance between ventral and anal spines}}{\text{total specimen length}}$$

$$H = \frac{l_{PR}}{l_T} = \frac{\text{prepectoral length}}{\text{total specimen length}}$$

$$I = \frac{v_{D-Z}}{l_T} = \frac{\text{distance from dorsal spine to caudal cleft}}{\text{total specimen length}}$$

$$J = \frac{v_{Z-O}}{l_T} = \frac{\text{distance from caudal cleft to tip of axial lobe}}{\text{total specimen length}}$$

$$K = \frac{d_O}{l_{PR}} = \frac{\text{outer diameter of circumorbital ring}}{\text{prepectoral length}}$$

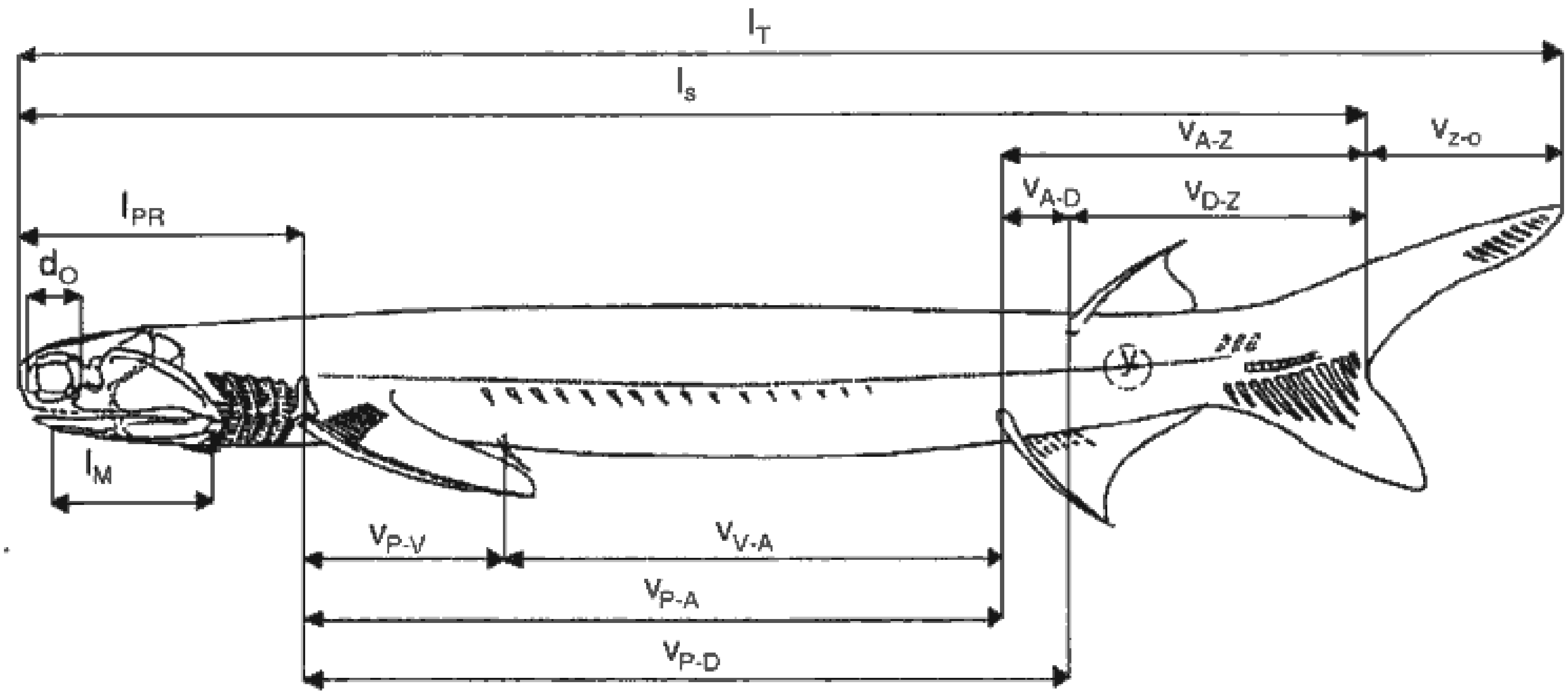


Fig. 3. The restoration of *Acanthodes bronni* (according to HEIDTKE 1990a, Fig. 39) with indicated distances: d_O – outer diameter of circumorbital ring; l_A – anal spine length; l_D – dorsal spine length; l_M – mandibular bone length; l_P – pectoral spine length; l_{PR} – prepectoral distance; l_S – standard specimen length; l_T – total specimen length; l_V – ventral spine length; v_{A-D} – anal-dorsal spine distance; v_{A-Z} – distance from anal spine to caudal cleft; v_{D-Z} – distance from dorsal spine to caudal cleft; v_{P-A} – pectoral-anal spine distance; v_{P-D} – pectoral-dorsal spine distance; v_{P-V} – pectoral-ventral spine distance; v_{V-A} – ventral-anal spine distance; v_{Z-O} – distance from caudal cleft to tip of axial lobe; y – number of scales per millimetre in a row (the scale count is from the proximity of the main lateral sensory line in the postdorsal-precaudal region).

$$L = \frac{l_M}{l_P} = \frac{\text{mandibular bone length}}{\text{pectoral spine length}}$$

$$M = \frac{v_{P-V}}{v_{V-A}} = \frac{\text{distance between pectoral and ventral spines}}{\text{distance between ventral and anal spines}}$$

$$N = \frac{l_M}{l_{PR}} = \frac{\text{mandibular bone length}}{\text{prepectoral length}}$$

$$O = \frac{l_M}{l_T} = \frac{\text{mandibular bone length}}{\text{total specimen length}}$$

The values of the above mentioned ratios can be given as a decimal or as a percentage. ZIDEK (1985) estimated importance of the ratios A^1, A^2, B, C, D^1, D^2, E, F, G, K, L, N, O, l_D, l_A, maximum diameter : height of scapular blade, minimum diameter : height of scapular blade, maximum height : total length of specimen for taxonomy. I agree with his estimation and add the following notes. Suprascapulae are undoubtedly present in pectoral girdles of Bohemian Stephanian specimens. They are crushed and almost always need careful preparation because they are covered with rather thick layer of sediment. However, articulated specimens are often not prepared at all and these delicate structures therefore pass unnoticed. Such specimens are often described as having the suprascapula missing because the visible dorsal borders of scapular blades are mostly concave. Very similar condition may be found in the procoracoids.

2.3. *Acanthodes fritschi* n. sp.

Acanthodes fritschi n. sp.

(Figures 4–52, 64–77; Plates 1–17)

1893 *Acanthodes Bronni?* (partim): A. Fritsch, Fauna der Gaskohle etc.; p. 61; Pls. 106/9–12, 1–5.

1981 *Acanthodes* cf. *punctatus* Fritsch, 1893 (partim): J. Zajíc, Možnosti interpretace etc.; p. 13–24; Fig. 4; Pls. 1–4, 7/1.

1985 *Acanthodes* sp. indet. (partim): J. Zajíc, New finds etc.; p. 278–284; Figs. 2, 4; Pls. I, II, III/1.

1988 *Acanthodes* sp. indet. (partim): J. Zajíc, Acanthodian (Acanthodii) jaws etc.; p. 222–224; Fig. 2; Pls. I, II/1, 2.

Etymology: Named in honour of the prominent Czech paleontologist Prof. Antonín Frič who often used the German transcription of his name – Anton Fritsch.

Holotype: Specimen YA 2397 (Czech Geological Survey, Prague).

Type locality: Drill core of the Ři–22 (Řisuty) borehole; depth 54.30 m; Kladno Basin; 6 km WSW of Slaný; Kladno district; Czech Republic.

Horizon: Mšec Member; Stephanian B.

Paratypes: JZ 1/11, JZ 1/13, JZ 2/24, M 1117, M 3629, M 3630, M 3633, M 3635, P 30 675/šv., P 30 676/šv., P 30 678/šv., P 30 705/šv., YA 1347, YA 1378, YA 1379, YA 2347, YA 2356, YA 2381, YA 2384, YA 2406, YA 2459, YA 2460, YA 2461, YA 2470, YA 2491.

Diagnosis: Medium-sized acanthodian (estimated length up to 350 mm). Squamation extends anteriorly to pectoral area (laterally on the fish body). Dorsal fin slightly more posterior than anal. Anal : pectoral spine length ratio (A^1) = 0.70; ventral : pectoral spine length ratio (B) = 0.31–0.33;

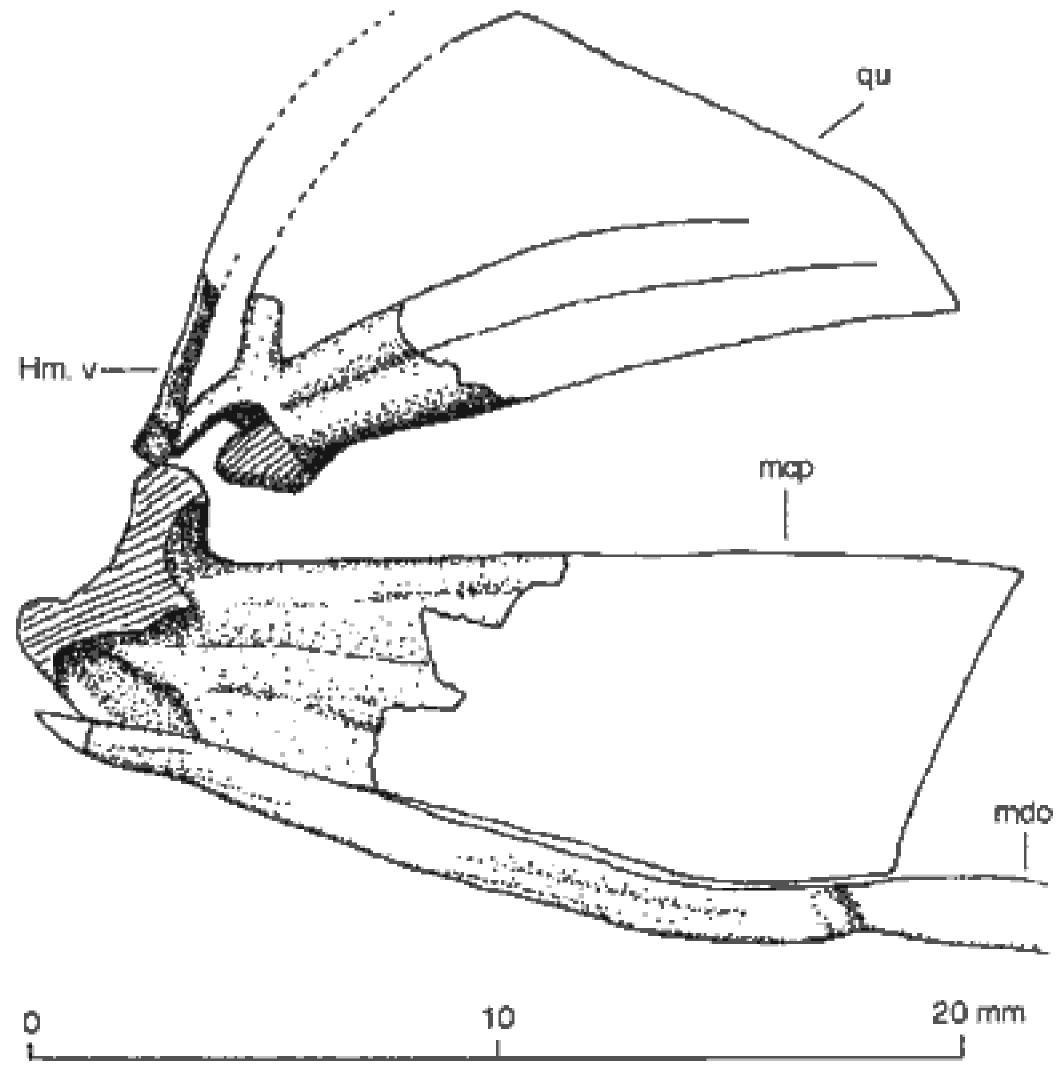


Fig. 4. *Acanthodes fritschi* n. sp., the association of quadrate, ventral ossification of hyomandibula, articular, and mandibular bone; YA 2397 (holotype), Mšec Member.

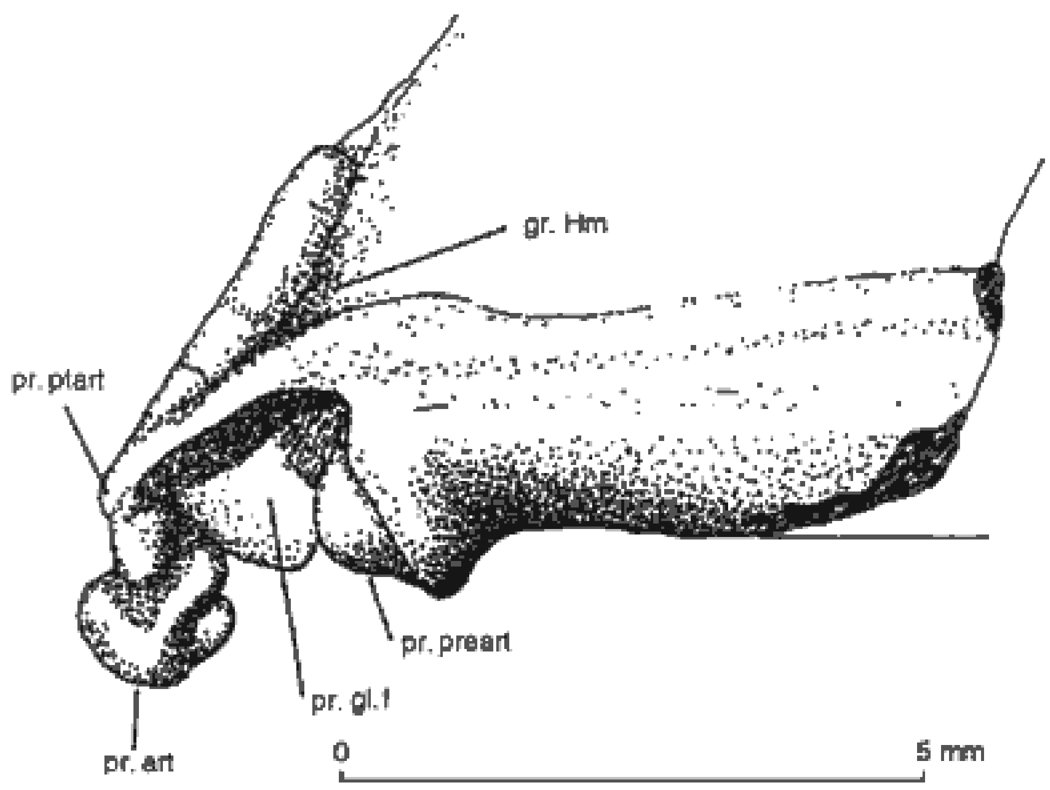


Fig. 5. *Acanthodes fritschi* n. sp., the caudal portion of quadrate with jaw articulation; YA 2384, Mšec Member.

outer diameter of circumorbital ring : prepectoral length ratio (K) = 0.21–0.23; mandibular bone length: pectoral spine length ratio (L) = 0.73–0.78; mandibular bone length: prepectoral distance ratio (N) = 0.52–0.60. At least part of endocranium (basisphenoid) starts ossification in specimens about 350 mm long. Meckelian cartilage have 2 ossifications; distinctive shaped branchial gill rakers; circumorbital ring with 5 segments; tesserae absent; branchiostegal rays long and slender; suprascapula co-ossified with scapula; procoracoid long (from three to five quarters of scapulocoracoid length); pectoral, anal, and dorsal fins supported by dermotrichia; pectoral fin with radialia; dorsal spine supported by basal plate; caudal fin with extended distal termination of axial lobe; unossified backbone; smooth scale crown with very thin pointed posterior projection.

Description: The body is fusiform and rather long - characteristic of the genus *Acanthodes*. The total lengths were estimated with the aid of the ratio C because no complete specimen is known. The amounts of this ratio are 0.15–0.23 in adults and or subadults, the most frequent ones are 0.17–0.20. I used the amount 0.17 as the basis of estimation of the maximum total length of *Acanthodes fritschi* n. sp. Some total lengths were also estimated with the help of the ratios B or D^1. In the event of incomplete pectoral spines (as in the holotype) I estimated their lengths with the aid of the fin spines maximum width/length diagram (Fig. 33). All measured sizes are stated in the Fig. 49. All ratios (estimated total specimen lengths not use) are shown in Fig. 50. The comparison of ratios with other *Acanthodes* species is shown in the Fig. 51.

The longest known specimen (holotype) shows a fragment of ossified neurocranium – basisphenoid (sensu HEIDTKE 1990a). The ventral side of this element is visible on Pls. 2A and 2B. The rostral region is rounded like in HEIDTKE's restoration of *Acanthodes bronni* (1990a, Fig. 5). The basal foramen seems to be somewhat larger than in *Acanthodes bronni*. The caudal part is not preserved.

Only some posterior parts of the quadrates are preserved (Figs. 4–6; Pls. 2A, 3B, 15C). No other part of the upper jaw is known. The prearticular process is oriented more posteriorly than in *Acanthodes bronni*. The articular process, the postarticular process and the preglenoid fossa are also well preserved in the jaw joint (Fig. 5). In Fig. 6, it is possible to see the posterior part of the quadrate jointed with the preglenoid process of the caudal part of the articular.

The meckelian cartilage consists of two separated ossifications (see Figs. 7, 8; Pls. 9, 10A, 10B) – the anterior (mentomandibular) and the posterior (articular). All known specimens show this arrangement but we cannot determine whether both ossifications are co-ossificated in adults or not. In any case, the gap between both ossifications diminishes during ontogeny. The preglenoid process is somewhat small and rounded (Fig. 9) and tends more anteriorly than is shown in most restorations. A very similar situation can be seen in JARVIK's (1977; Fig. 6) jaw restoration of *Acanthodes bronni*. The articular cotylus is not so conspicuous as in other *Acanthodes* species.

The fragment of the ventral ossification of hyomandibula (Fig. 4) is the only preserved portion of the hyoid arch. The presence of a hyoid arch is also documented by the groove for the hyomandibula on the quadrate (Fig. 5) and by the groove for the ceratohyal on the articular (Fig. 9).

The gill arches are not preserved but articulated gill rakers partly trace their course on some specimens (Figs. 8, 10, 11; Pls. 3B, 4B, 13A, 14C, 14D). The precise number of gill arches is not possible to establish with confidence. Both branchial and hyoid gill rakers have distinctive features in comparison with other *Acanthodes* species (Fig. 52). The exact shape is not always the same (Figs. 12–14) – it depends on its position on gill arch and probably also on the ontogenetic age of the fish. The most common is the slender type of branchial gill raker (Figs. 11, 12, 52) which have a very flat, long, pointed, and sabre-shaped body and an asymmetric base with a half-moon-shaped lower border. The whole surface is covered by fine striae separated each other by tiny ridges (Fig. 12 shows gill rakers without describing the structure which was lost during preparation of galvanoplastic replicas). The striae are parallel with longitudinal axis. They are expanded like a fan on the base. Gill rakers articulate with gill arches by the concave border of their bases and each other by their flats (Figs. 11, 12).

The dermal bones of the head are represented by five circumorbital bones arranged around the orbit as the circumorbital ring. The individual segments are numbered according to Heidtke (1990a; Fig. 15) on the Fig. 15. The smallest segment number 4 overlaps segment number 3 in contrast to *Acanthodes bronni*. However, few specimens of circumorbital rings are preserved complete and the arrangement described above could be the result of postmortem dislocation. The convex outer surface of the segments is ornamented with tubercles and radiating striae. The individual segments are crescent-shaped, each with an elevated rim along the inner margin. The rim is also covered by abundance of the largest tubercles which connect into short concentric ridges near the inner border of the larger segments. The radially arranged rows of tubercles are concentrated on the wider three-quarters of the segments. The ornament becomes more robust during ontogeny because the tubercles grow and become fused into ridges, and the number of radial striae increases.

The mandibular bone (or splint) is the only dermal bone of the head. We often find it very as an isolated skeletal element. The characteristic shaped slender bone (Figs. 16–19; Pls. 2A, 5B, 5C, 9, 10, 11, 13A) is thin and bent along about half its length. The short longitudinal groove is situated on the curve, under the gap between the anterior and posterior ossifications of meckelian cartilage. Both (anterior and posterior) parts of the mandibular bone are almost horizontally situated in the lower jaw, although the anterior one lies somewhat higher. *Acanthodes fritschi* n. sp. differs from *Acanthodes bronni* (Heidtke 1990a, Fig. 18B; Miles 1973, Fig. 12 etc.) in the curve of the mandibular bone. The most similar situation is shown by *Acanthodes lundi* (Zidek 1980, Fig. 4A) in this feature. This bone of *Acanthodes fritschi* n. sp. is pointed in the front and extended and flattened at the back (Figs. 16, 17). The anterior part of the posterior extension sometimes shows a shallow poorly expressed groove on lateral (?) side. The detail of problematic sculpture (probably a postmortem structure) of the posterior part of mandibular bone, originally pictured by Fritsch (1893; Pl. 106/10), is shown in Fig. 18. The bone reinforces both ossifications of the meckelian cartilage (on

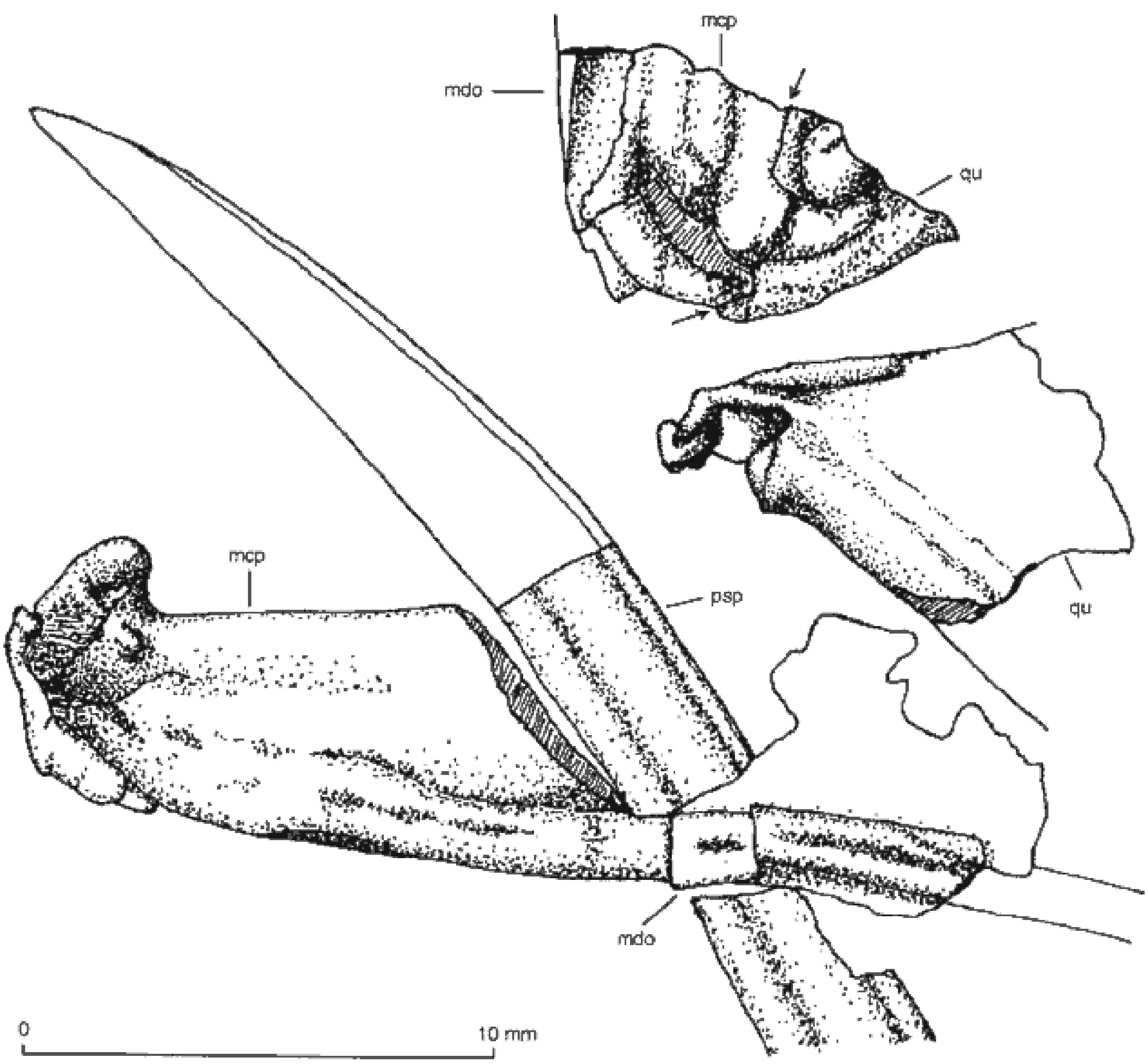


Fig. 6. *Acanthodes fritschi* n. sp., the association of right and left quadrate, articular, and pectoral fin spine; the arrows indicate the course of articular/quadrate boundary; YA 2384, Mšec Member.

Fig. 7. *Acanthodes fritschi* n. sp., both lower jaws according to ZAJÍC (1988b; Fig. 2); YA 1347, Mšec Member.

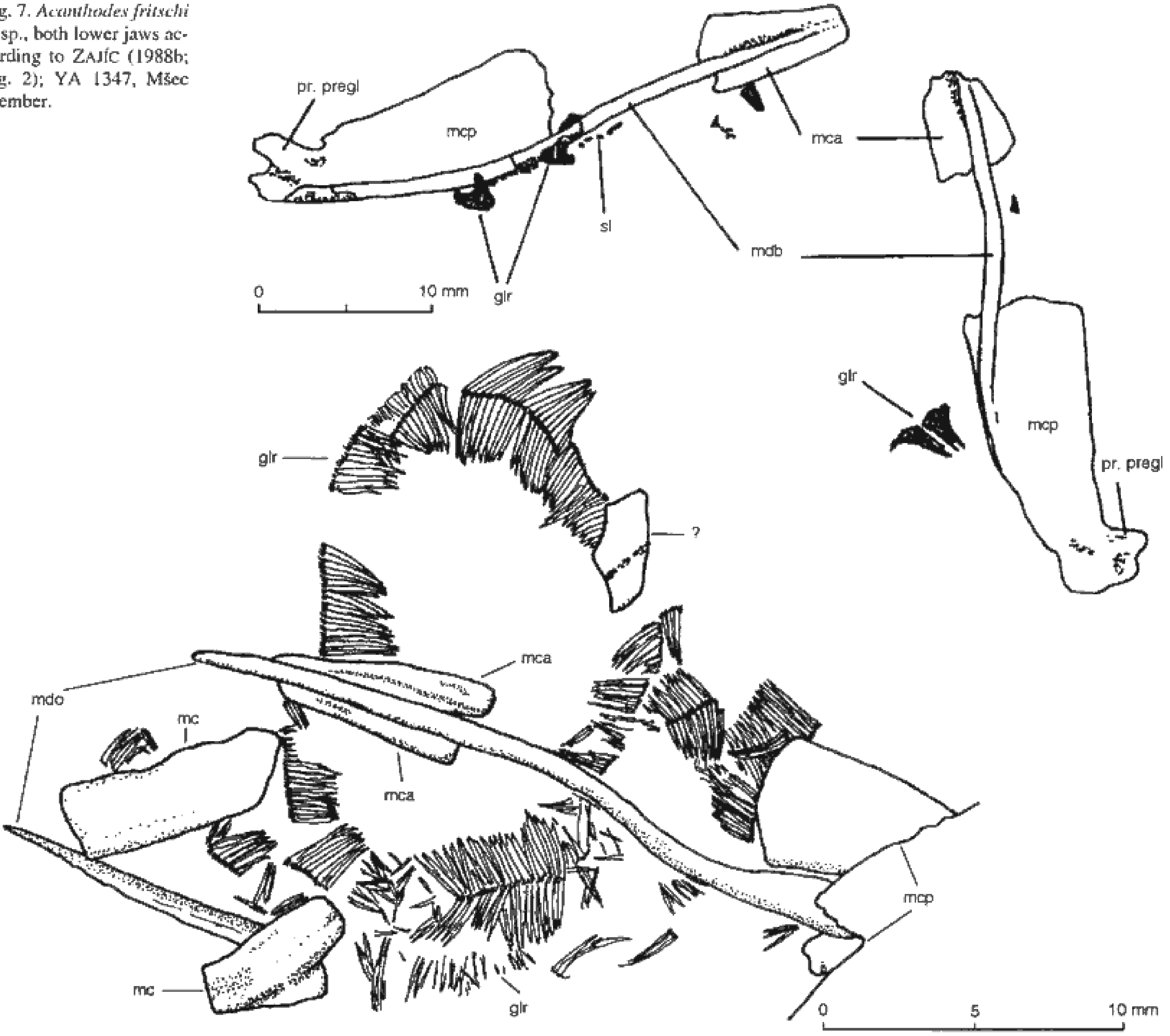


Fig. 8. *Acanthodes fritschi* n. sp., fragments of lower jaws and articulated gill rackers that indicate the course of the gill arches; YA 1379, Mšec Member.

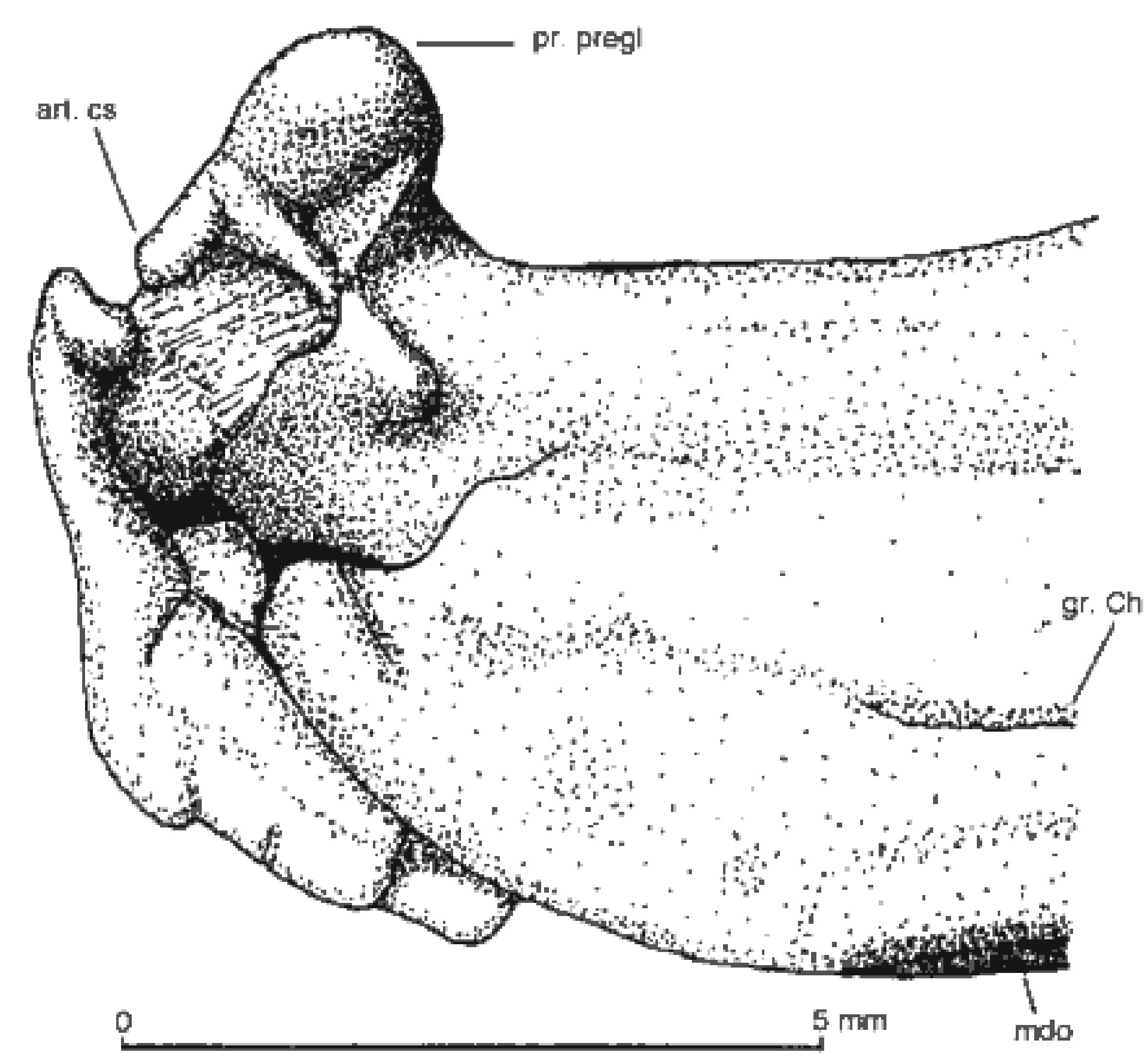


Fig. 9. *Acanthodes fritschi* n. sp., the detail of posterior portion of articular with jaw articulation; YA 2384, Mšec Member.

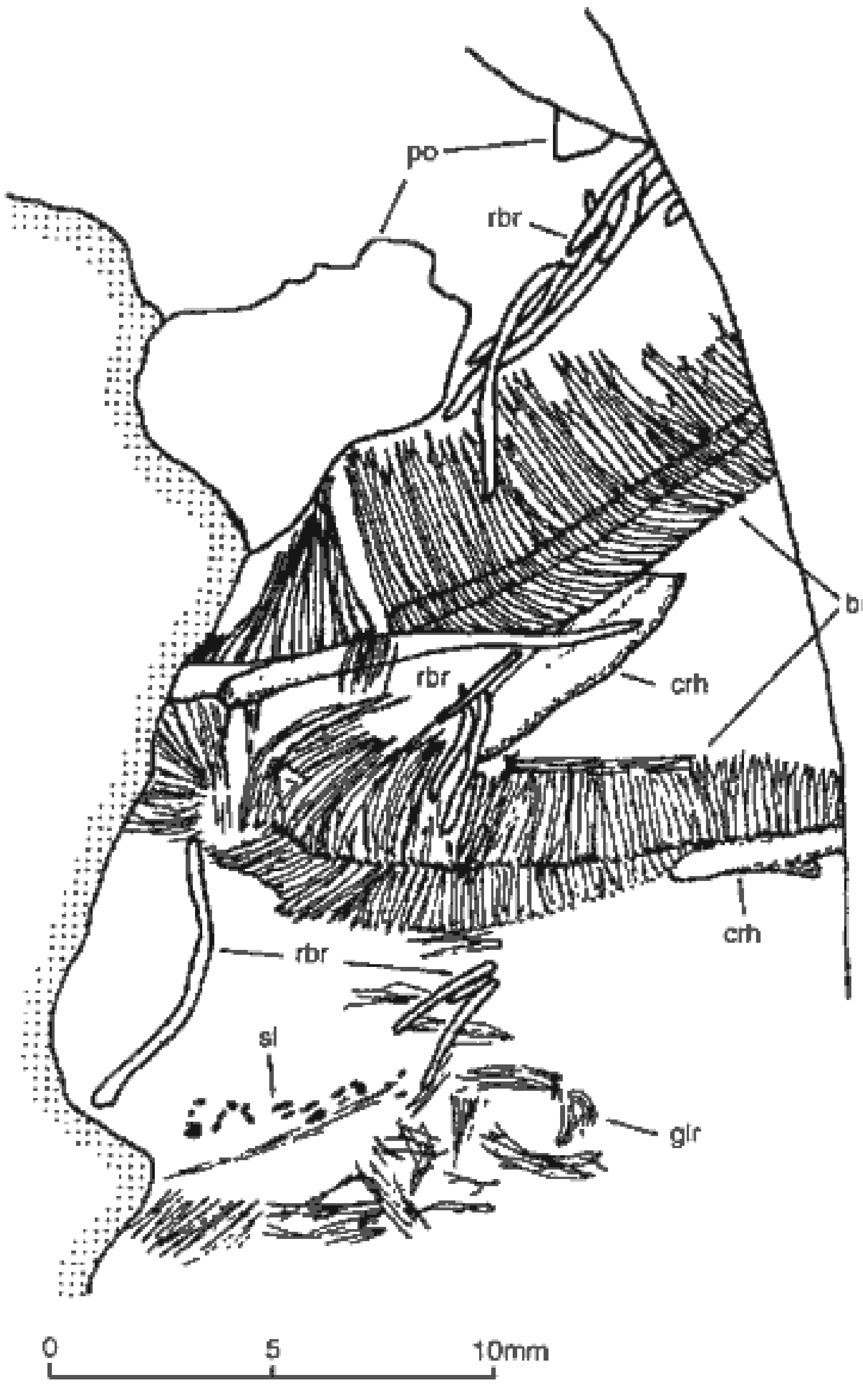
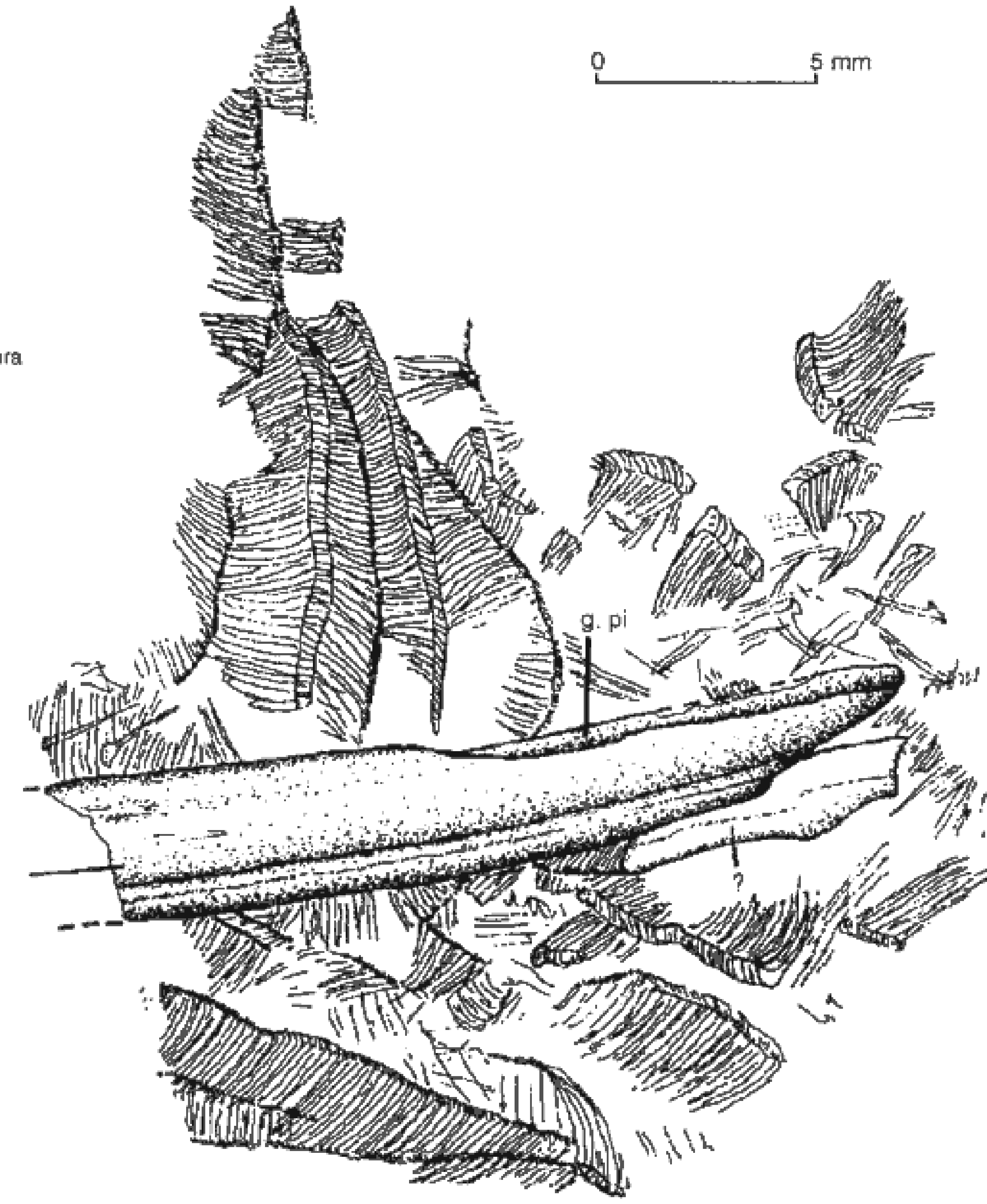


Fig. 10. *Acanthodes fritschi* n. sp., part of gill area; YA 2381, Mšec Member.

Fig. 11. *Acanthodes fritschi* n. sp., part of gill area with proximal part of the pectoral fin spine; M 1117 (the galvanoplasty), Mšec Member.



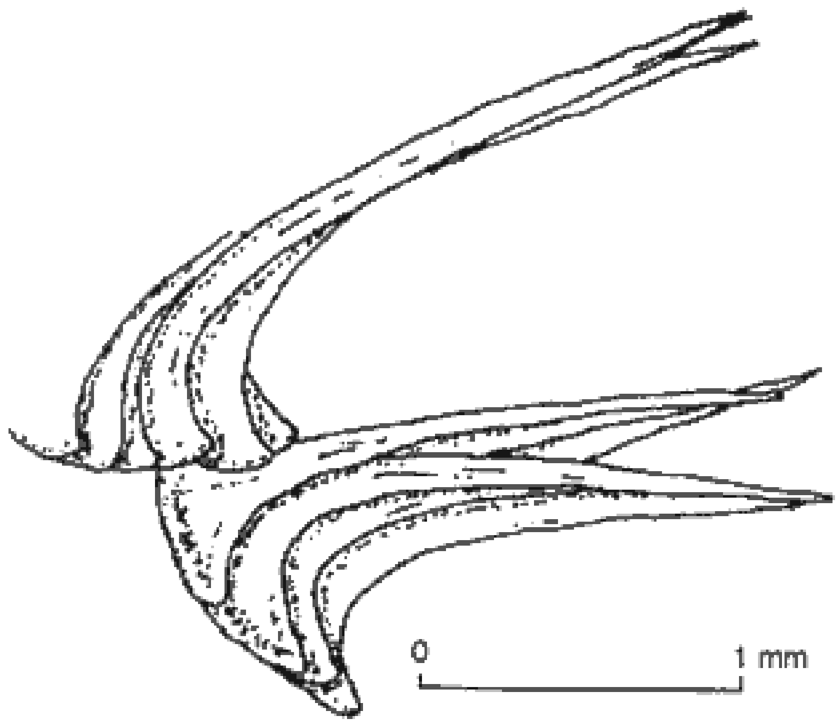


Fig. 12. *Acanthodes fritschi* n. sp., articulated branchial gill rakers; M1117 (the galvanoplasty), Mšec Member.

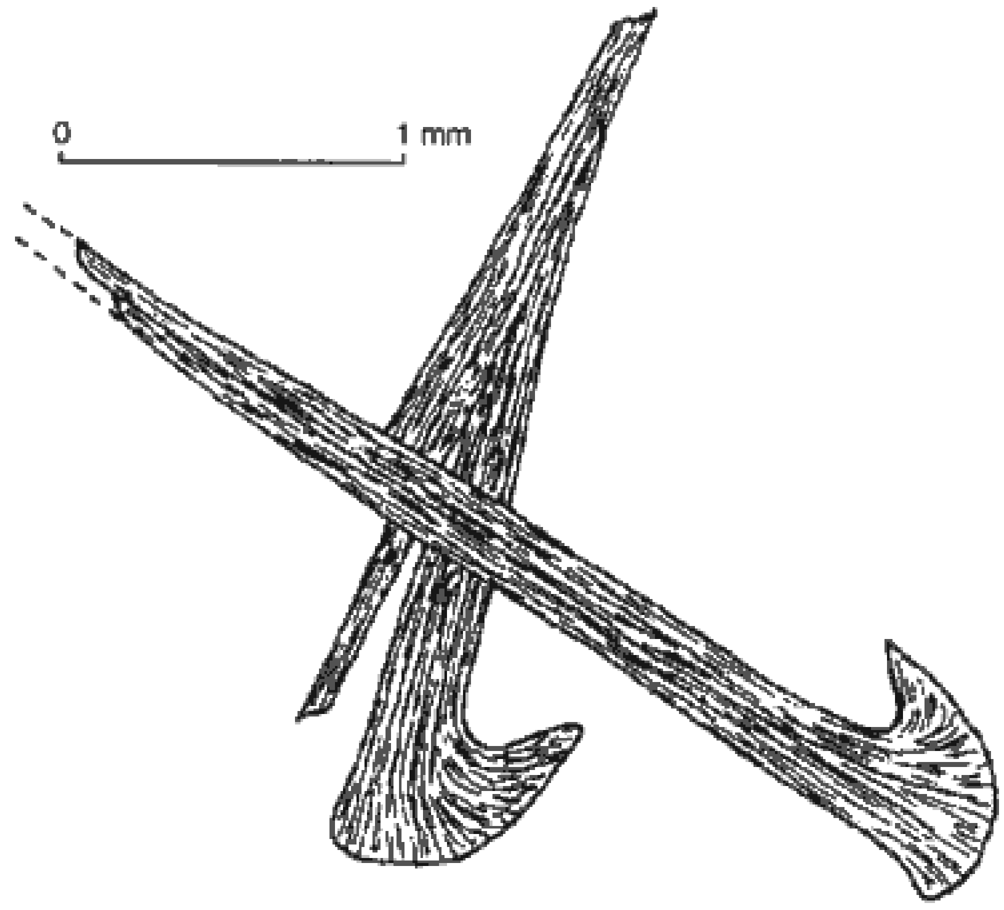


Fig. 13. *Acanthodes fritschi* n. sp., branchial gill rakers; M 3629, Kounov Member.

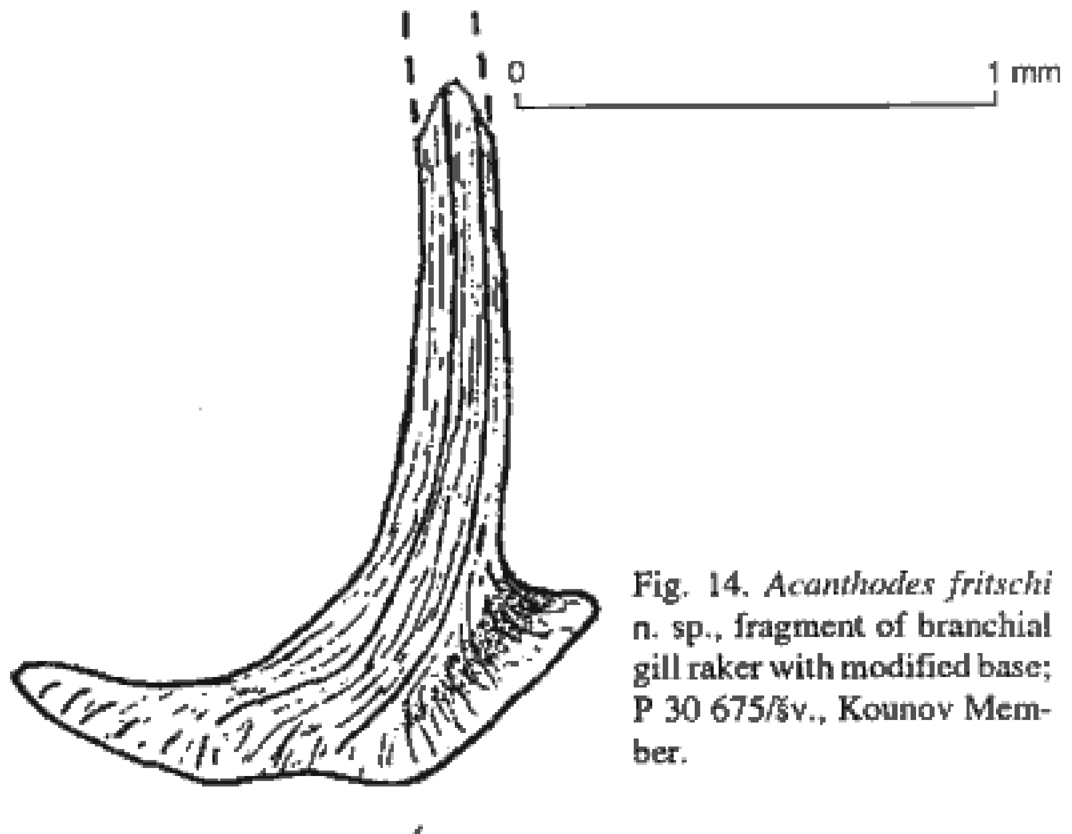


Fig. 14. *Acanthodes fritschi* n. sp., fragment of branchial gill raker with modified base; P 30 675/šv., Kounov Member.

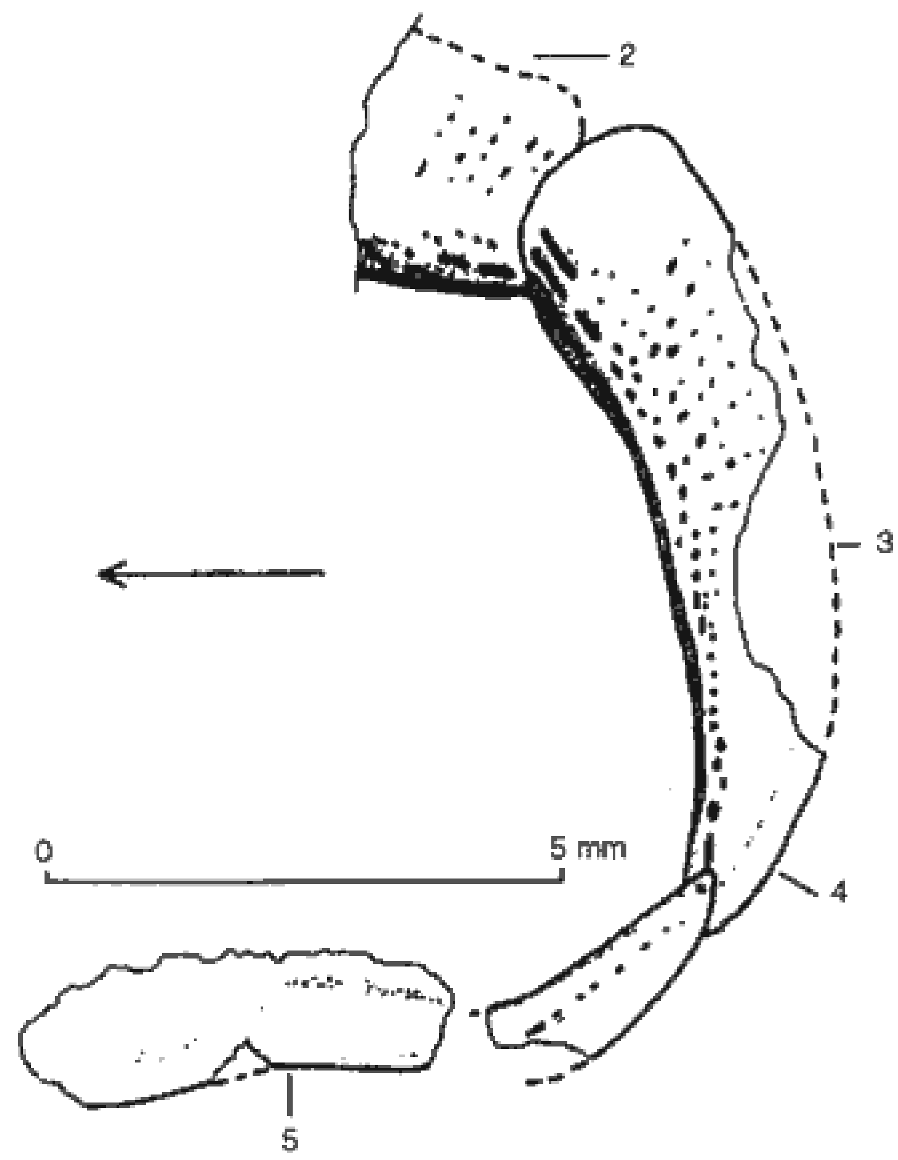


Fig. 15. *Acanthodes fritschi* n. sp., the incomplete circumorbital ring; the arrow marks the anterior direction; M 1117 (the galvanoplasty), Mšec Member.

their lower parts) from medial side. The detail of this connection is shown in Fig. 19.

The gill covers are represented by very thin branchiostegal rays (Figs. 10, 16, 17, 20) of different length. They are distinctly shaped, from straight to variously curved (Fig. 20 shows two of them). The proximal end is sometimes flattened. Shorter branchiostegals are situated ventrally and longer ones posteriorly (they reach up to the anterior half of gill chamber) from the articular.

The pectoral girdle is composed of the central scapulocoracoid, dorsal suprascapula, and ventral procoracoid. The procoracoid is co-ossified with the slender dorsal scapular blade and the wide ventral coracoid. The opening for articulation with the pectoral fin spine (pectoral fossa) is bordered by the scapular blade, coracoid, and procoracoid (Figs. 21–24). The articulation of the pectoral girdle with the pectoral fin spine is clearly visible on Fig. 25. The spine was seated in the opening and in the groove passing along the scapular blade/coracoid boundary. The scapular blade is a slender bone and its narrowest part is situated closely dorsally of the wide coracoid plate. The dorsal termination of the scapular blade is somewhat extended and concave in lateral view. The well ossified suprascapula (its shape is similar to that of *Acanthodes bronni*) is jointed to the above-mentioned dorsal termination of the scapular blade. This bone is somewhat wider than the dorsal termination of the suprascapula. Their degree of ossification is, however, clearly less than that of the scapulocoracoid. The dorsal termination of the suprascapula was apparently cartilaginous. The cross section of the suprascapula is very flat in contrast to the circular cross section of the scapular blade. The longitudinal section of scapular blade shows, in its narrowest part, an almost hair-like constriction of the "pith" cavity (Fig. 27). The ventrally situated coracoid is almost always fragmentarily preserved but it was significantly larger than is depicted on restorations of other species of *Acanthodes*. This bone was thin and probably mostly cartilaginous. The procoracoid process on the scapulocoracoid is jointed with the dorsolateral branch of procoracoid. The procoracoid is long and mostly well ossified. The caudal and ventral parts

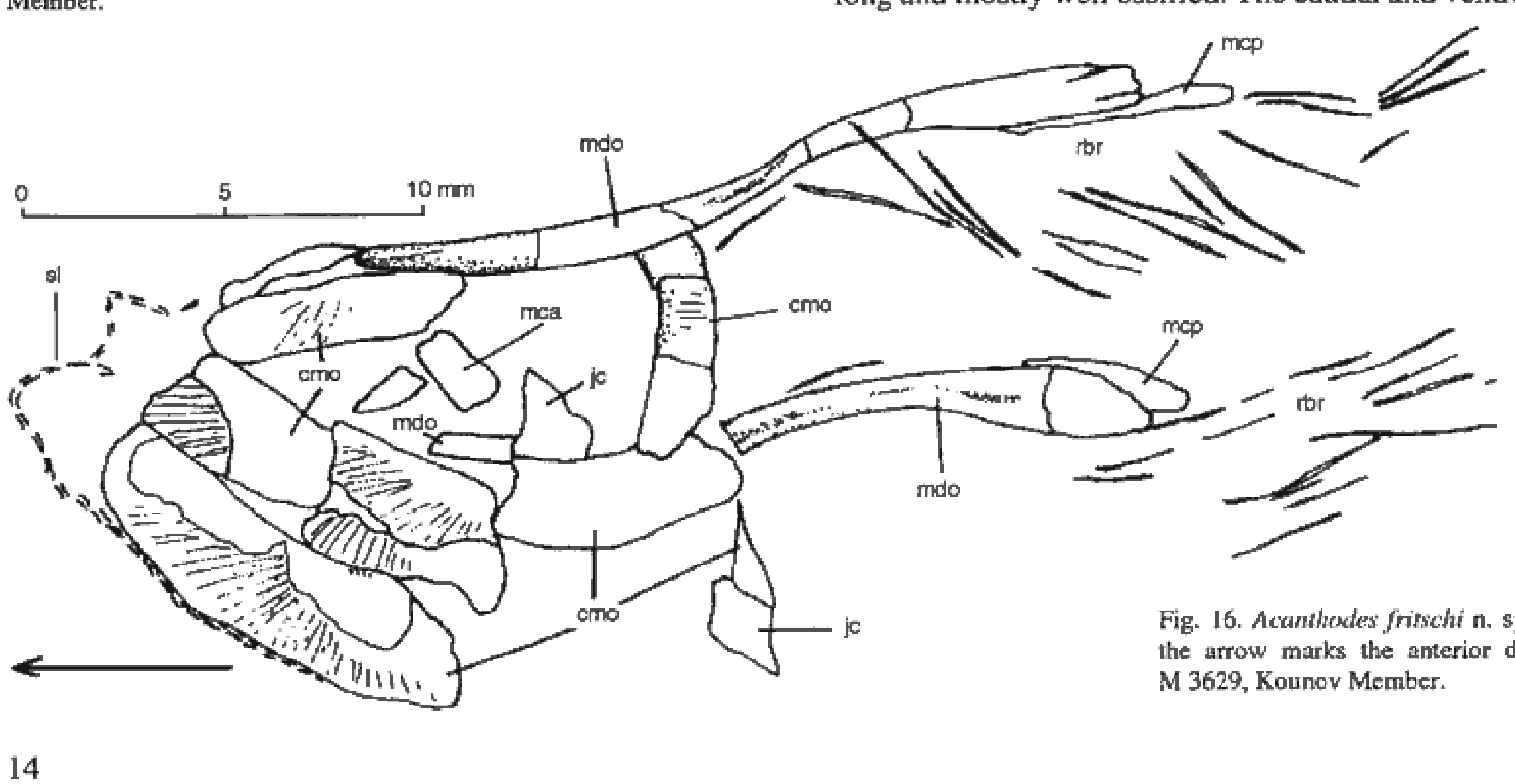


Fig. 16. *Acanthodes fritschi* n. sp., head; the arrow marks the anterior direction; M 3629, Kounov Member.

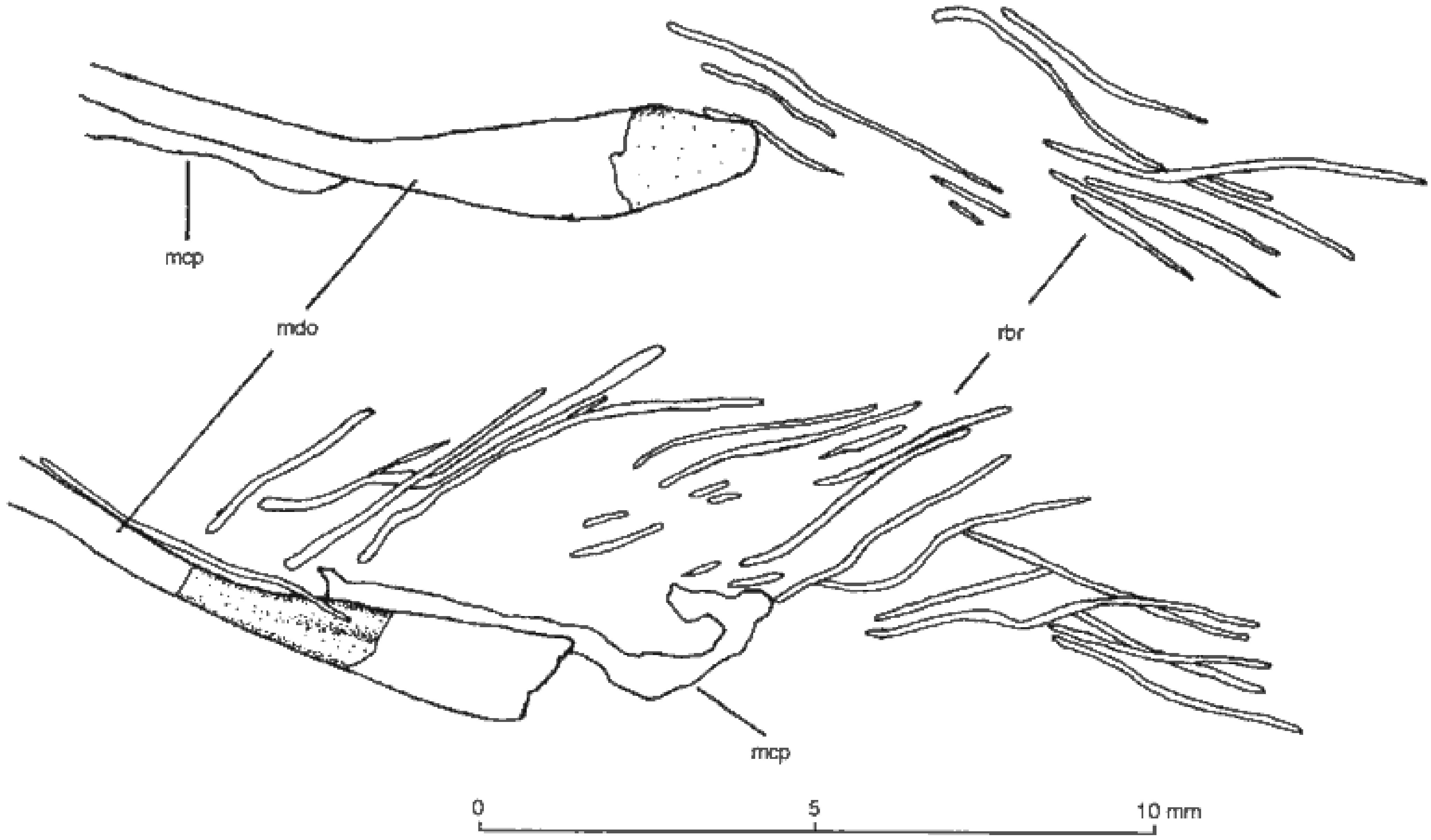


Fig. 17. *Acanthodes fritschi* n. sp., mandibular bones and branchiostegal rays; M 3630, Kounov Member.

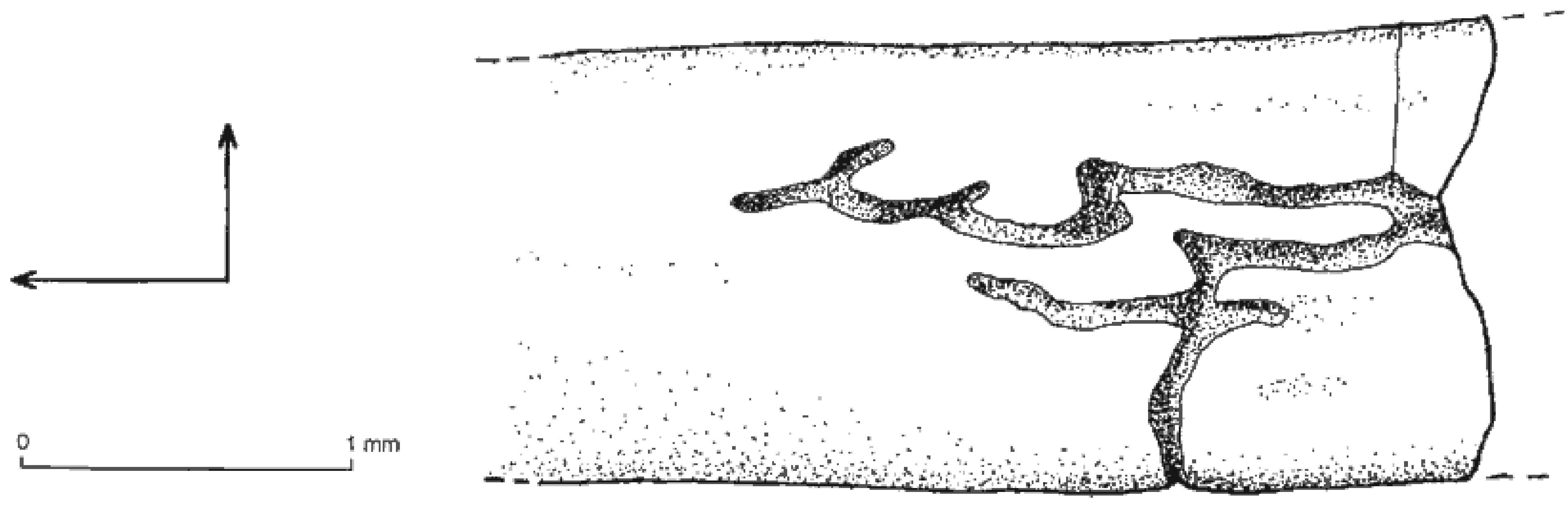


Fig. 18. *Acanthodes fritschi* n. sp., detail of problematic sculpture of the posterior part of mandibular bone, the vertical structure most probably corresponds to a fracture, the arrows indicate the anterior and dorsal directions; M 1117 (the galvanoplasty), Mšec Member.

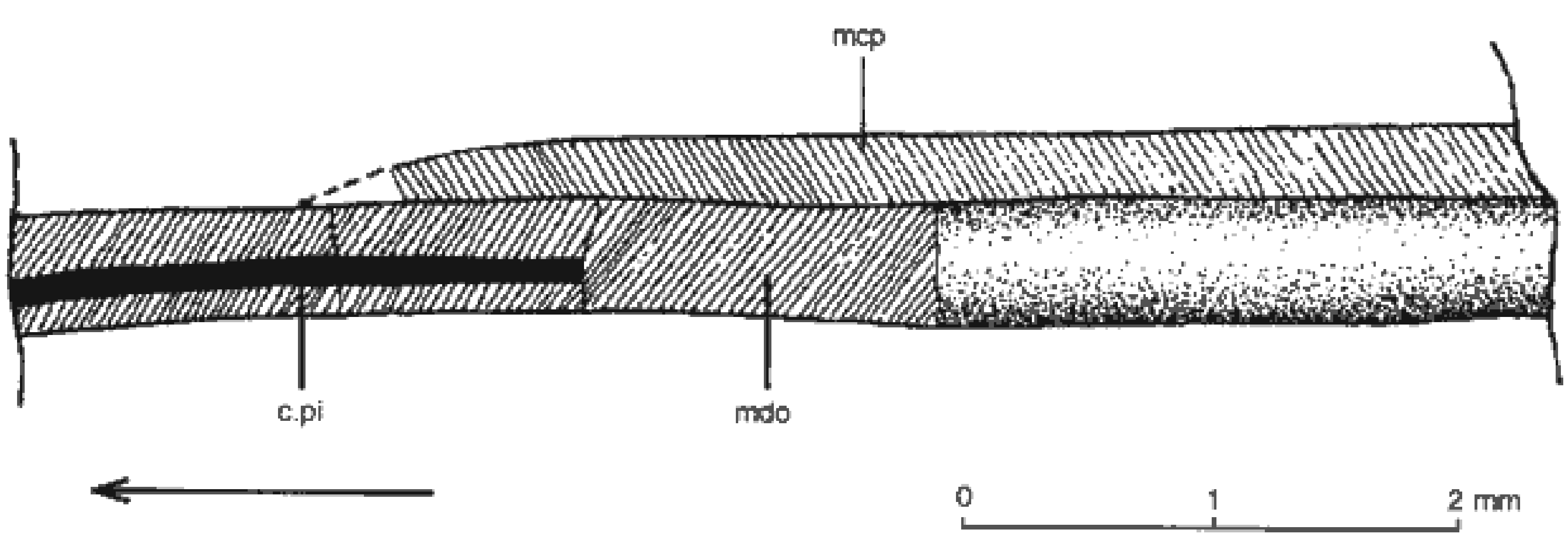


Fig. 19. *Acanthodes fritschi* n. sp., detail of mandibular bone contacting with articular in dorsal or ventral view (it is not possible to decide), hatching refers to cracked bone, the arrow indicates the anterior direction; YA 2459, Mšec Member.

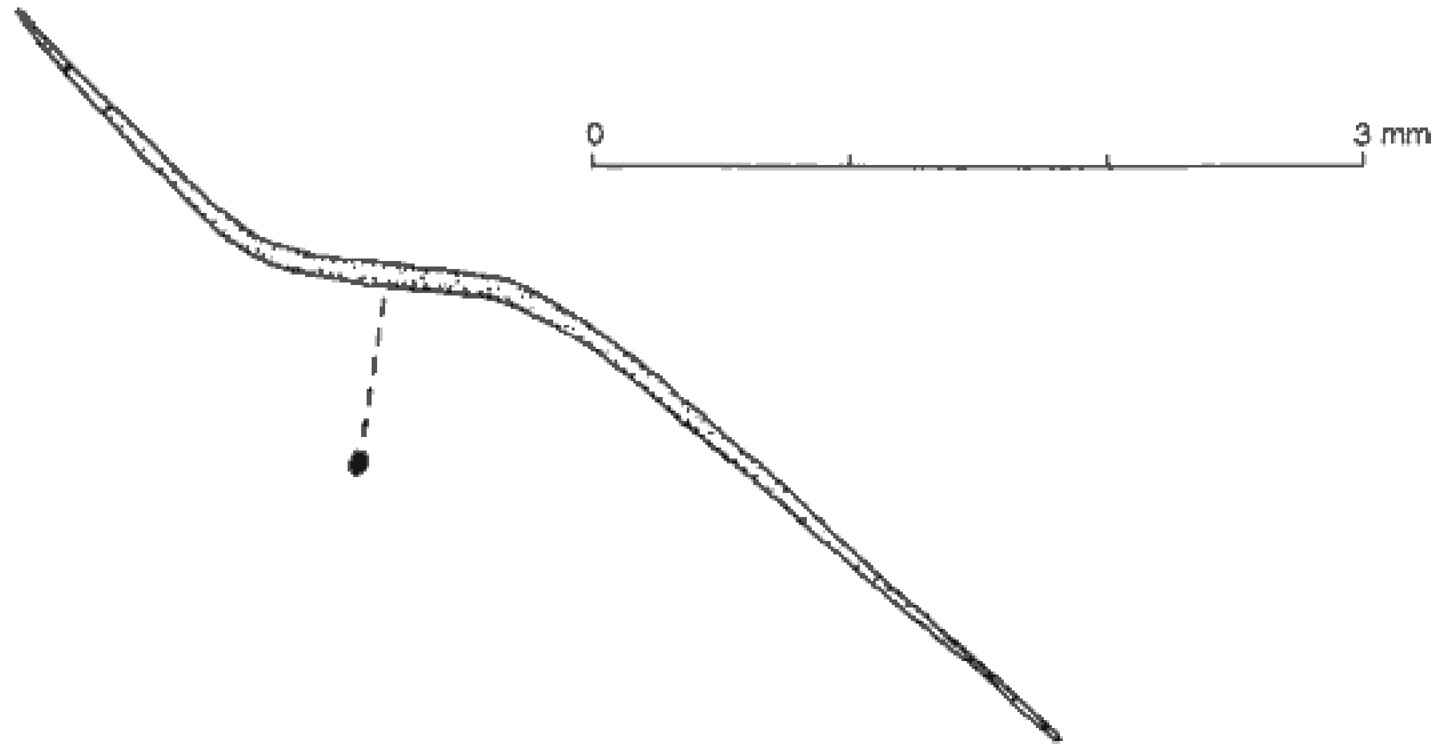
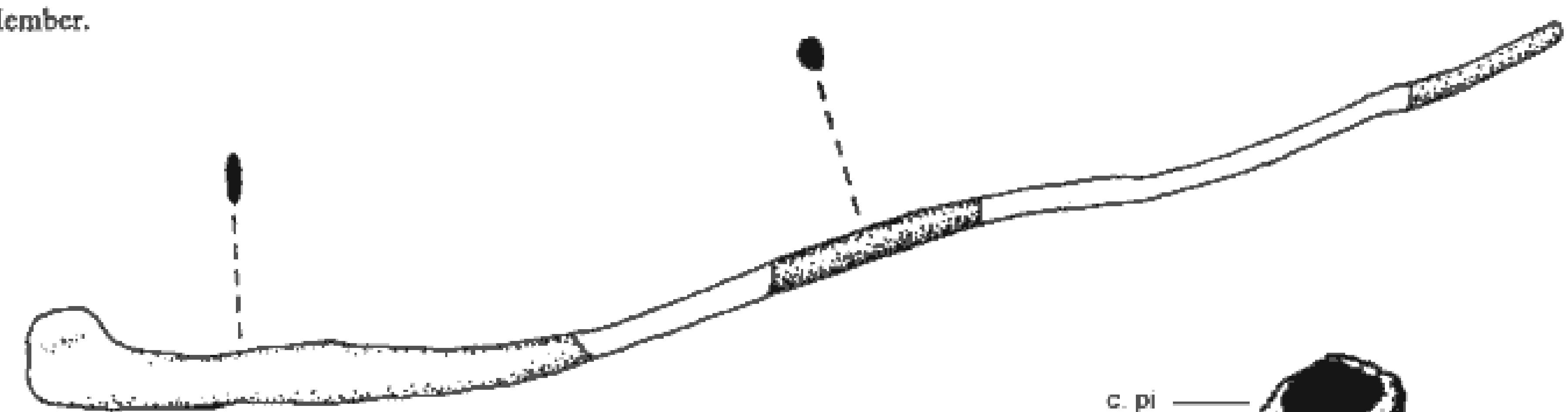


Fig. 20. *Acanthodes fritschi* n. sp., the two branchiostegal rays with marked cross sections; M 3630, Kounov Member.



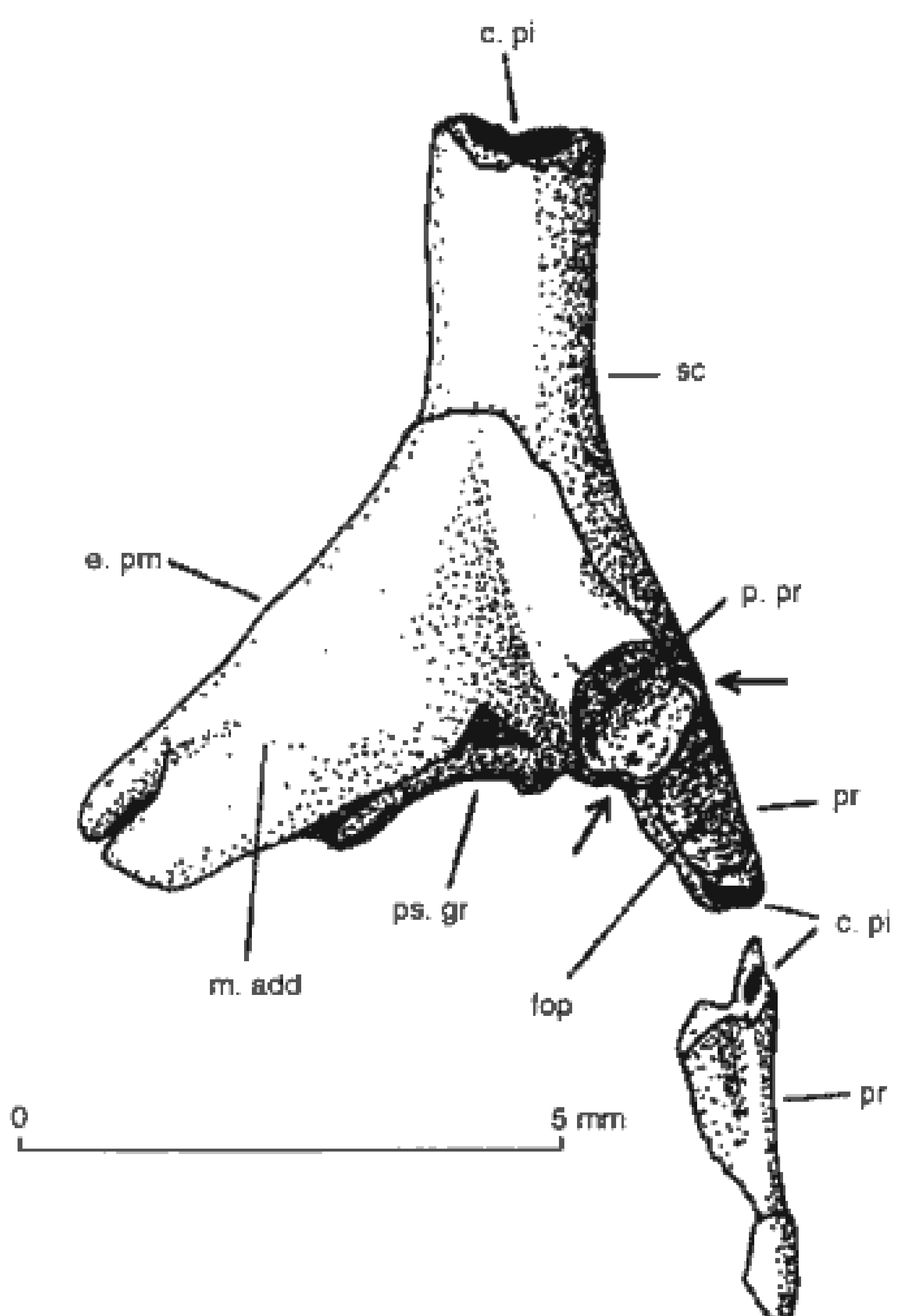


Fig. 21. *Acanthodes fritschi* n. sp., the pectoral girdle in anterolateral view, the dorsal termination of the scapular blade is missing; YA 2384, Mšec Member.

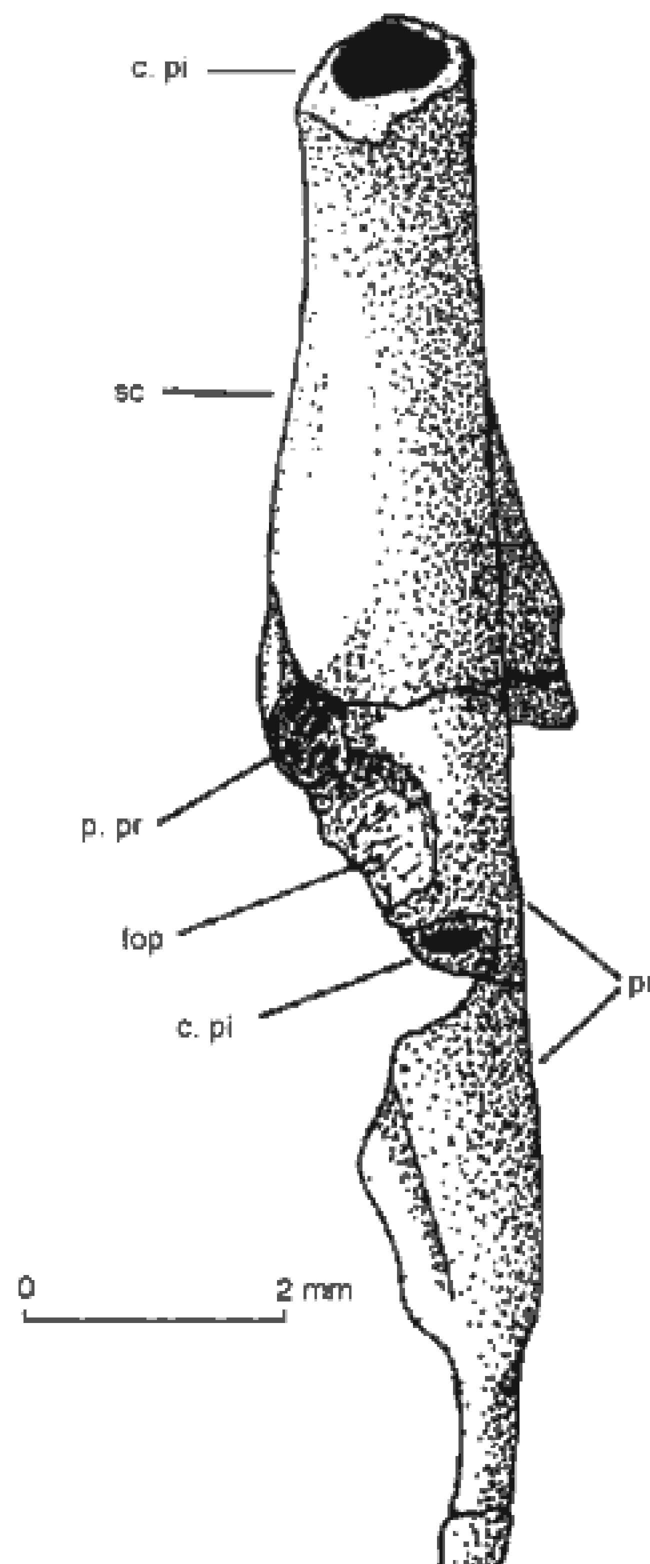


Fig. 22. *Acanthodes fritschi* n. sp., the pectoral girdle in oral view, the dorsal termination of the scapular blade is missing; YA 2384, Mšec Member.

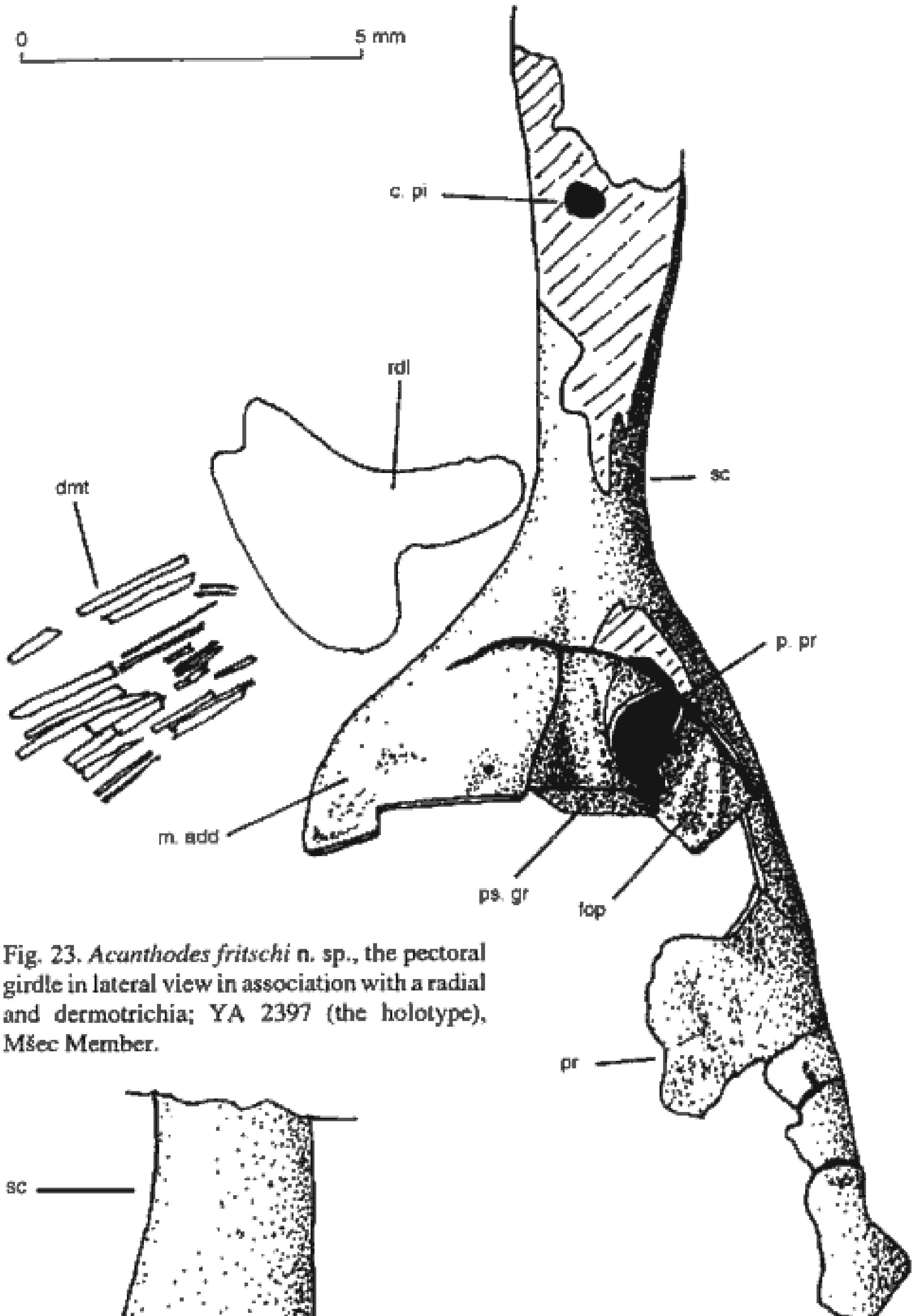


Fig. 23. *Acanthodes fritschi* n. sp., the pectoral girdle in lateral view in association with a radial and dermotrichia; YA 2397 (the holotype), Mšec Member.

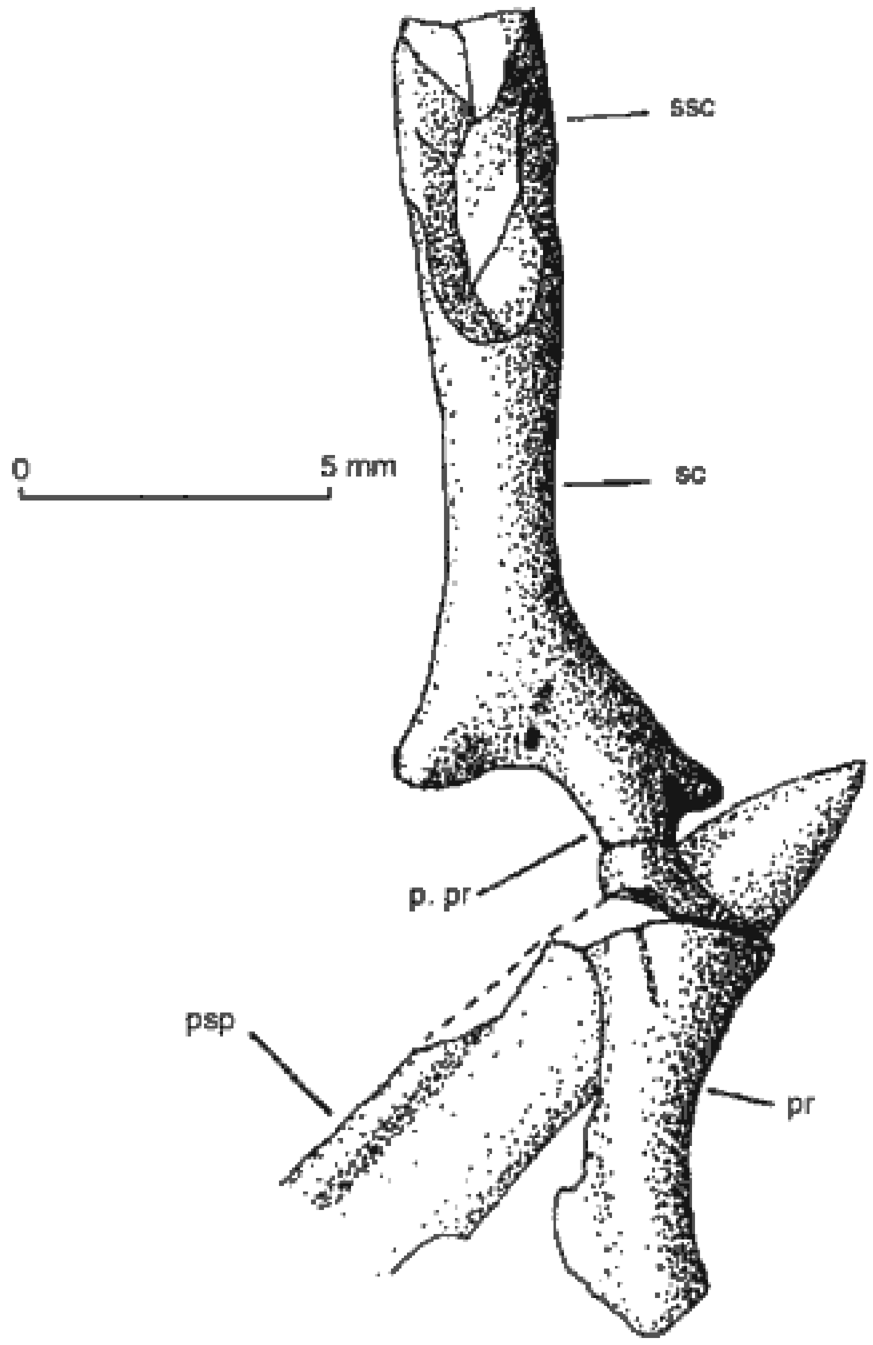


Fig. 25. *Acanthodes fritschi* n. sp., the pectoral girdle articulated with the pectoral fin spine in lateral view; YA 2397 (the holotype), Mšec Member.

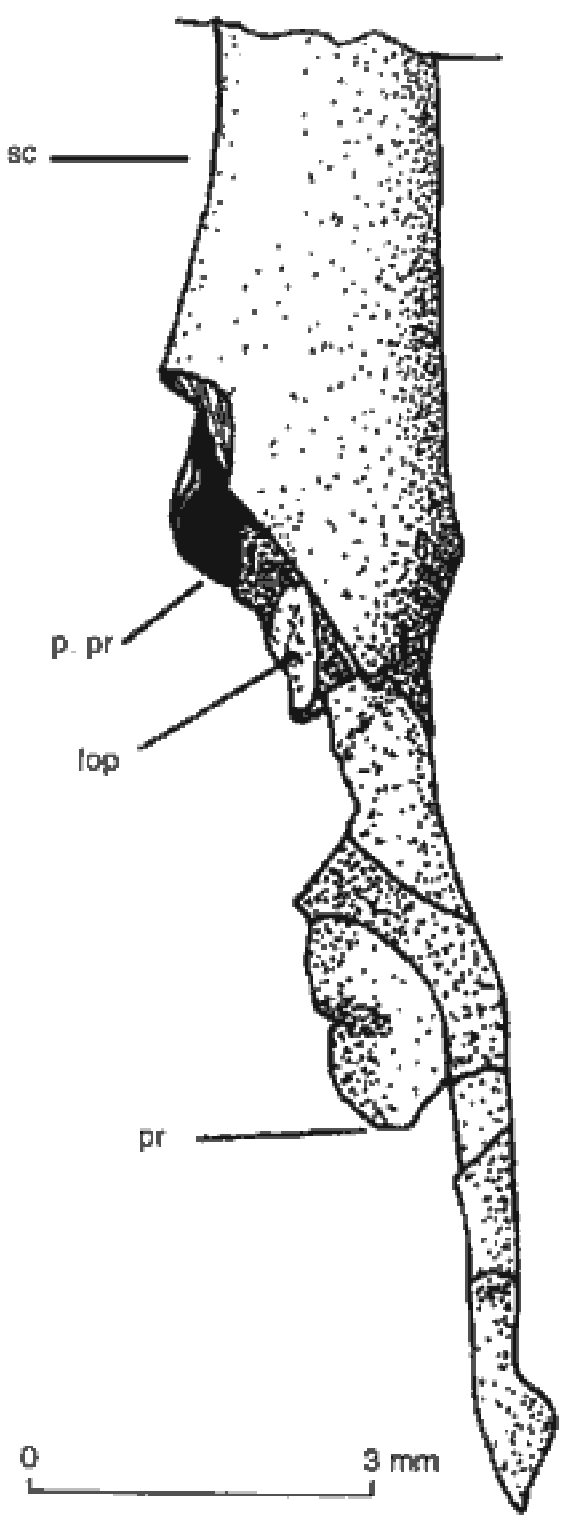


Fig. 24. *Acanthodes fritschi* n. sp., the pectoral girdle in oral view; YA 2397 (the holotype), Mšec Member.

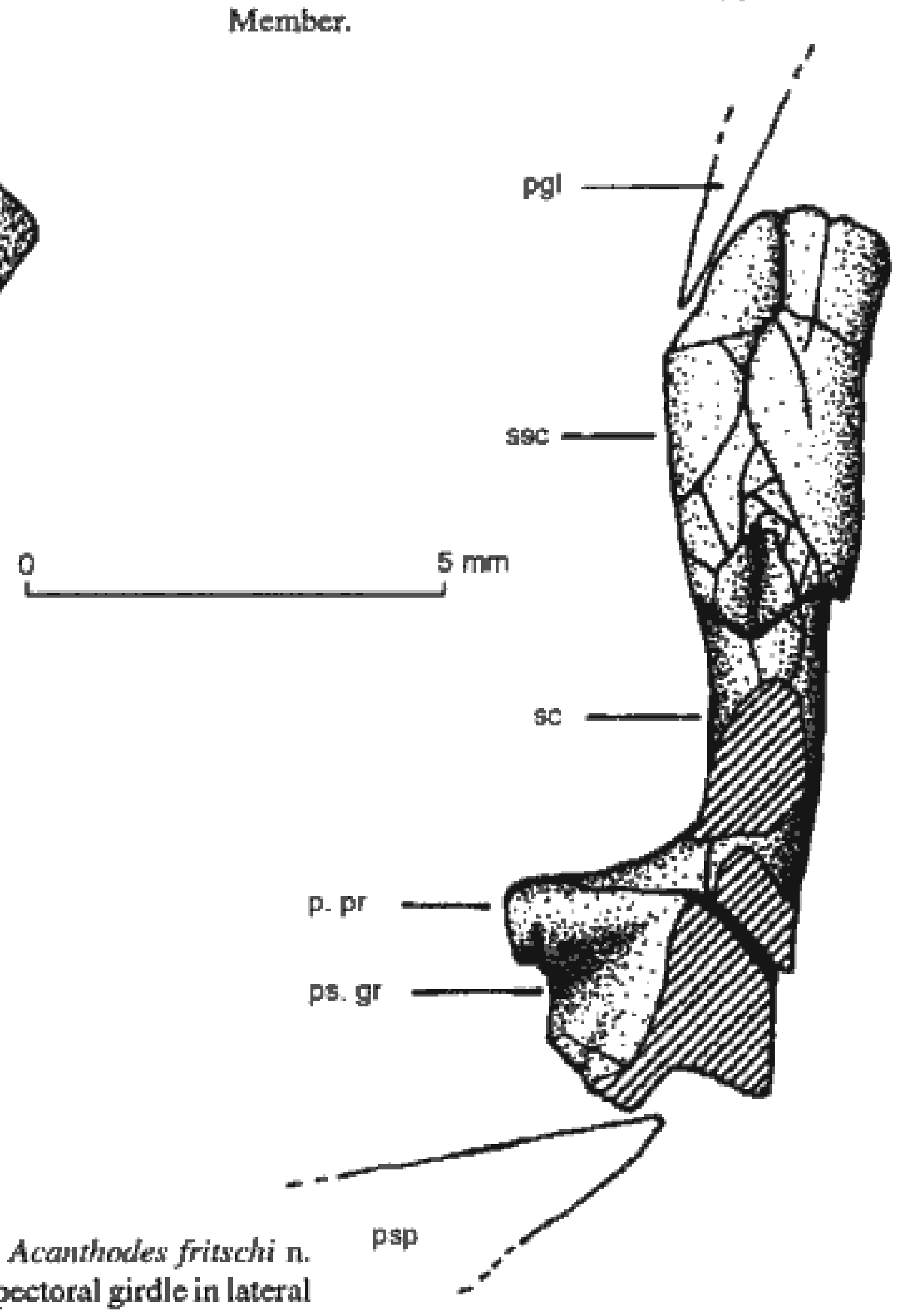


Fig. 26. *Acanthodes fritschi* n. sp., the pectoral girdle in lateral view; M 3629, Kounov Member.

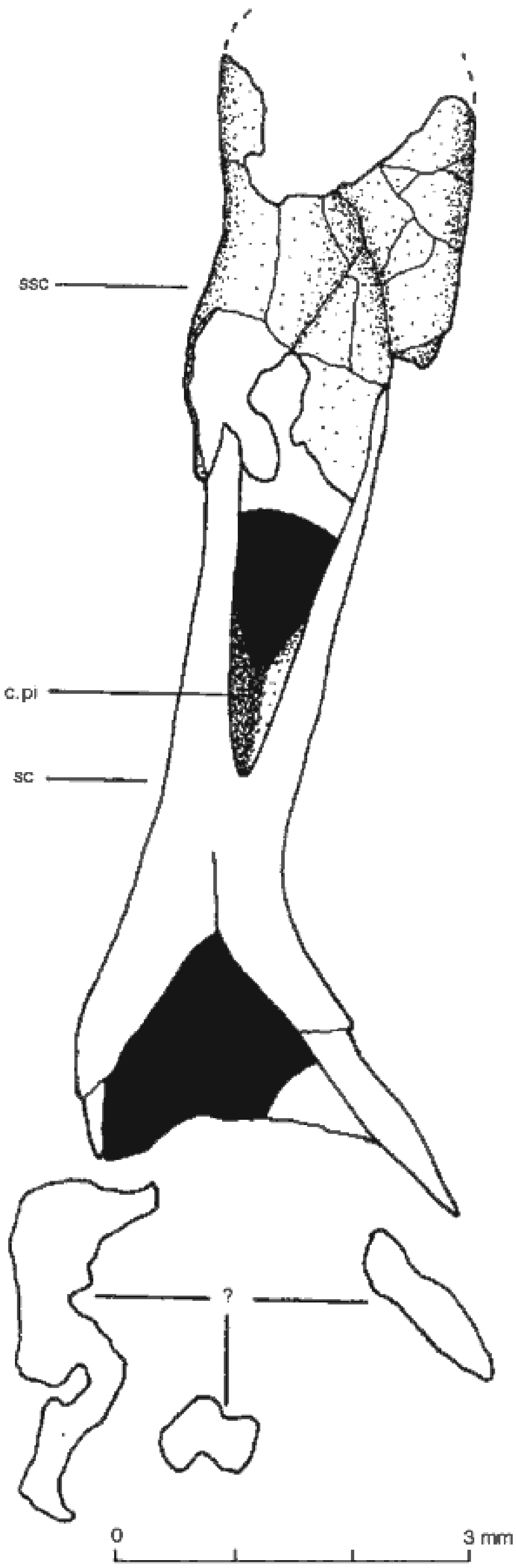


Fig. 27. *Acanthodes fritschi* n. sp., the broken pectoral girdle; M 3629, Kounov Member.

of this bone are, however, thin and less well ossified. The procoracoid is considerably longer and tends ventrolaterally in contrast to the situation in *Acanthodes bronni* (the orientation of its procoracoid is more or less orocaudal). The length of procoracoid is from three to five quarters of scapulocoracoid length.

One perichondrally ossified basal plate supports the dorsal fin spine (Fig. 29). This element was found in only one specimen (M 3633). Both *Acanthodes boyi* and *Acan-*

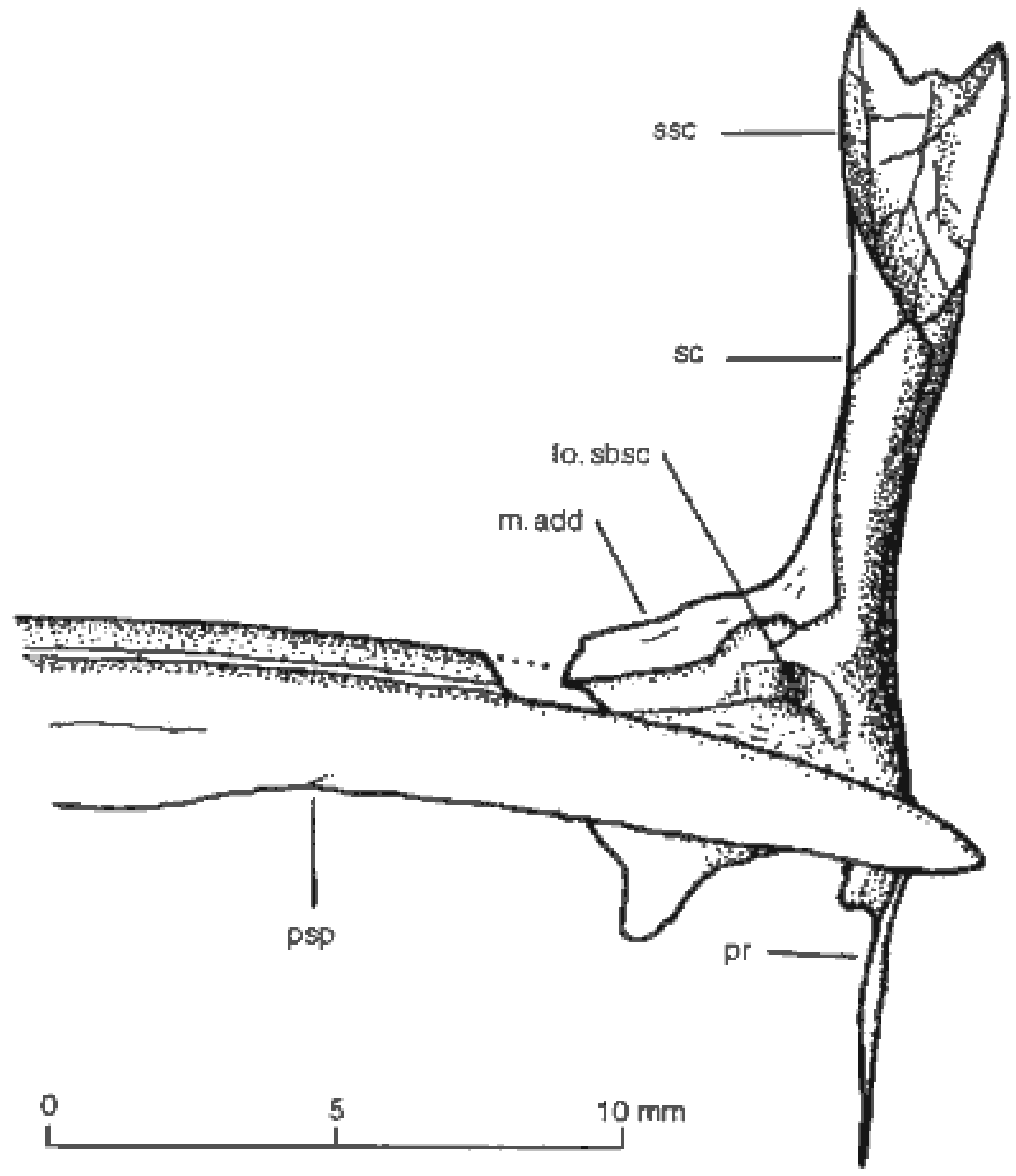


Fig. 28. *Acanthodes fritschi* n. sp., the pectoral girdle articulated with the pectoral fin spine in mesial view; YA 2347, Mšec Member.

thodes bridgei have two more slender dorsal basal plates in contrast to *Acanthodes fritschi* n. sp.

The pectoral fin spines are both the longest and the only paired fin spines of the genus *Acanthodes*. They are moderately sabre-shaped and distally pointed. Their widest part is situated near the proximal termination. All the fin spines have a pronounced rib along the anterior margin. The rib is separated from the lateral and mesial sides of the spine by longitudinal grooves containing abundant irregularly spaced pores. Spine thickness diminishes distally. A less distinct rib is situated along the posterior margin with poorly defined bordering longitudinal grooves. The proper posterior margin contains an eccentric posterior groove containing numerous pores. This groove (as well as the posterior margin) proximally extends and gradually changes into a deep symmetrical "pith" groove in the proximal fourth of the spine length (which was embedded in the animal´s musculature). The U-shaped "pith" groove represents the "pith" cavity. The two cross-sections of the fin spines of *Acanthodes luedersensis* (Dalquest, Kocurko & Grimes 1988; Fig. 4) also show the open "pith" groove. However, the anterior rib is more robust than in *Acanthodes fritschi* n. sp. and the open "pith" groove reaches up to two-thirds of the spine length. The inner structure of the spine is formed by the above-mentioned "pith" cavity and by a complicated canal system which communicates with the outer environment by pores. The detailed description of the inner structure of the fin spines is presented below, within the framework of description of *Acanthodes* sp. because most of the spines suitable for this study are isolated. The relationship of the length and maxi-

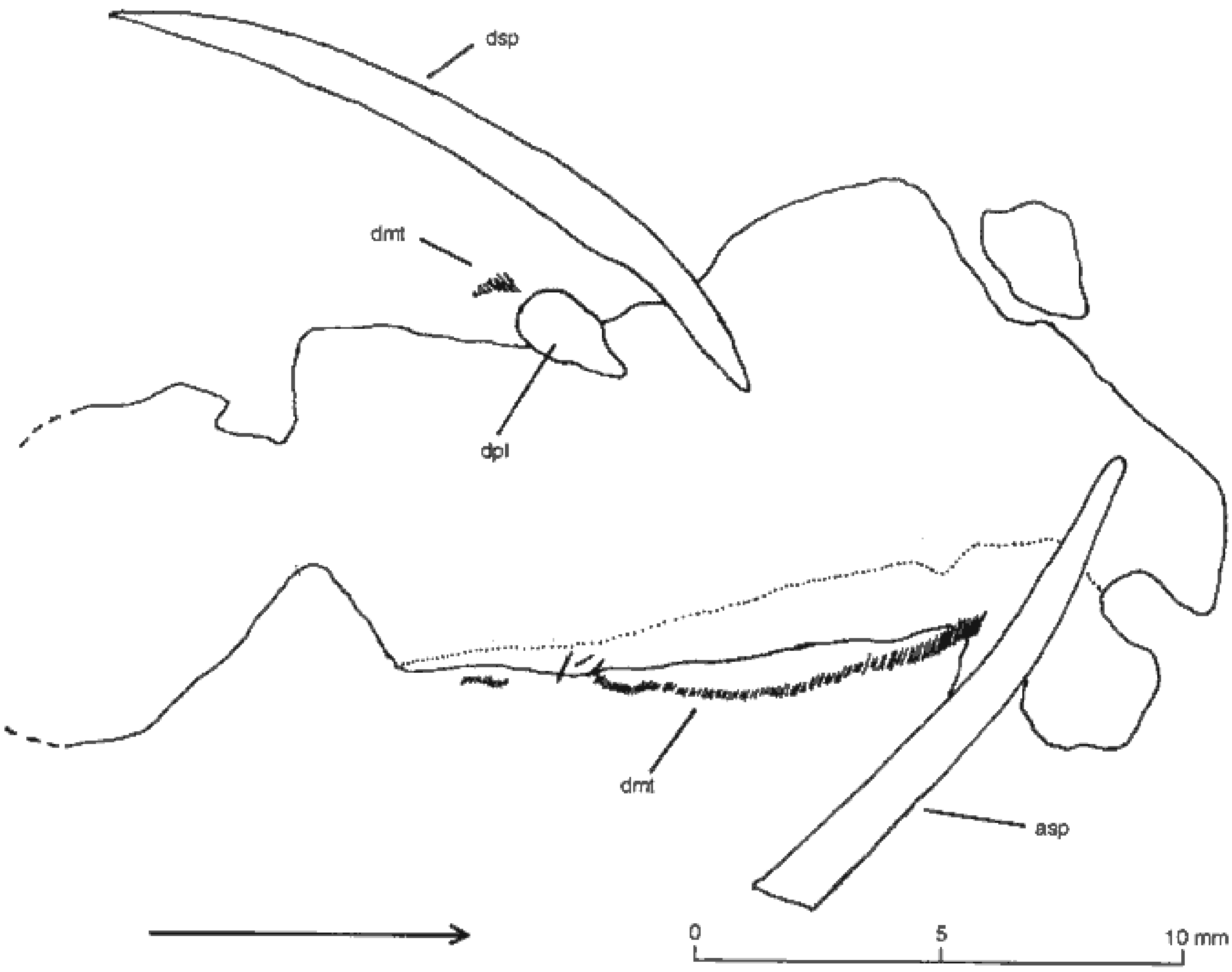


Fig. 29. *Acanthodes fritschi* n. sp., the posterior part of the body with dorsal and anal fin remains, the arrow marks the anterior direction, the extent of tiny scales of the anal fin is indicated by the dotted line; M 3633, Kounov Member.

mum width of spines is shown in Figs. 33 and 34. The spine maximum width : length ratio has no taxonomical significance. The measured values referred in *Acanthodes kinneyi* (ZIDEK 1975b; Tab. on the p. 15) and measured by the author in *Acanthodes bronni* (collection of the Museum für Naturkunde der Humboldt-Universität, Berlin) are in agreement with Figs. 33 and 34. The maximum width of the pectoral fin spine is potentially suitable for estimation of the total specimen length. The total lengths are roughly one hundred times the maximum widths of the pectoral spines in *Acanthodes kinneyi*. This relationship needs verifications at others *Acanthodes* species though. If the relationship is generally valid than the total lengths of *Acanthodes fritschi* n. sp. are underestimated here.

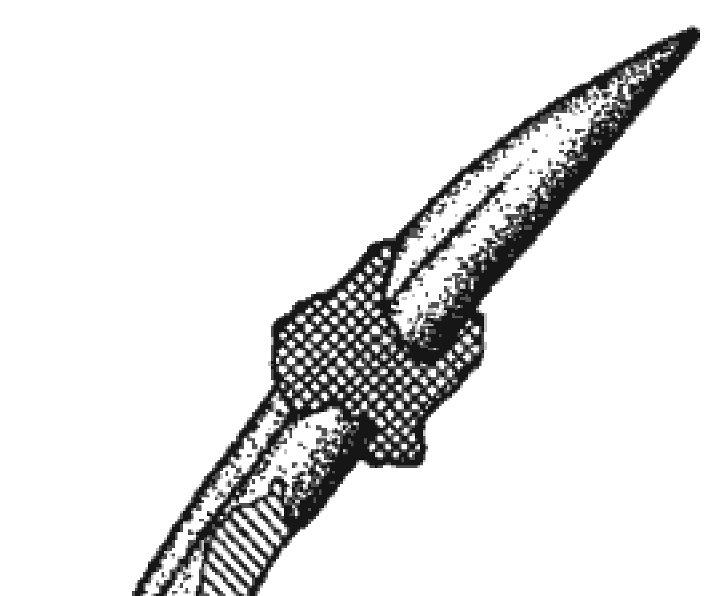


Fig. 30. *Acanthodes fritschi* n. sp., the ventral spine, the broken part is indicated by simple hatching, the overlapping tiny scales are indicated by double hatching; YA 2459, Mšec Member.

The ventral spine (Figs. 30–32; Tabs. 5A, 10C, 11A, 12B, 16A, 16B, 17A) differs from other fin spines not only in its length (the ventral spines are considerably shorter) but also in morphology. The ventral spine is also moderately sabre-shaped like the pectoral one, but widest in relation to its length. The circular cross section extends further distally than in other fin spines. Both proximal and distal terminations are pointed. The inner canal system is simpler than in other fin spines (Fig. 32). The inner structure is formed by simple canals (with pore-like cross sections) in its proximal part at least.

The anal and dorsal fin spines are about the same lengths. Both are shorter and slightly straighter than the pectoral one. The outer morphology and the inner structure are very similar or almost the same. However, only ventral spines are safely distinguishable among isolated spines.

The radialia of the pectoral fins were found in three specimens (Figs. 23, 35, 36). Three perichondrally ossified elements were originally present in each pectoral fin. The ossification of radialia is poor and their exact shape is not

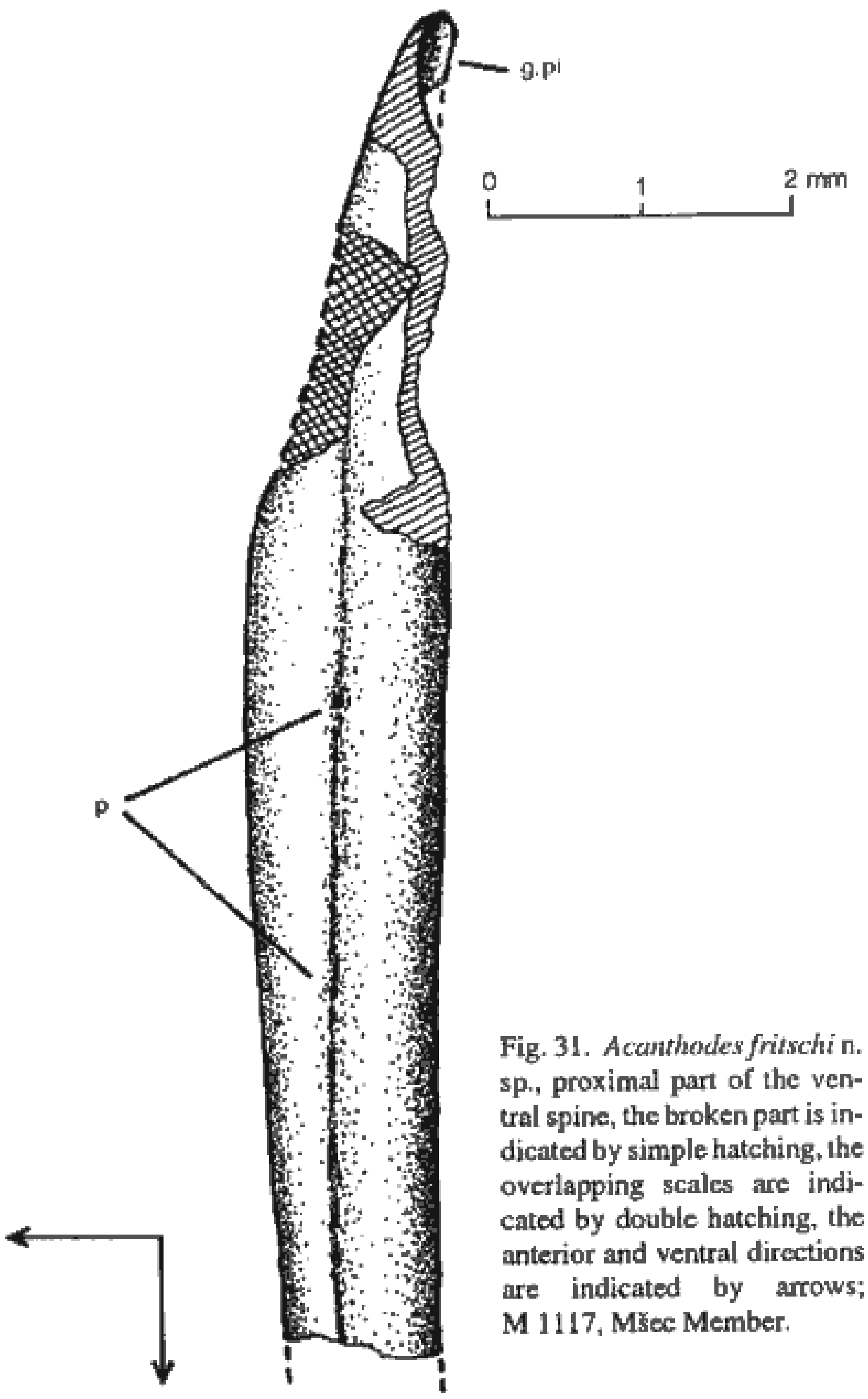


Fig. 31. *Acanthodes fritschi* n. sp., proximal part of the ventral spine, the broken part is indicated by simple hatching, the overlapping scales are indicated by double hatching, the anterior and ventral directions are indicated by arrows; M 1117, Mšec Member.

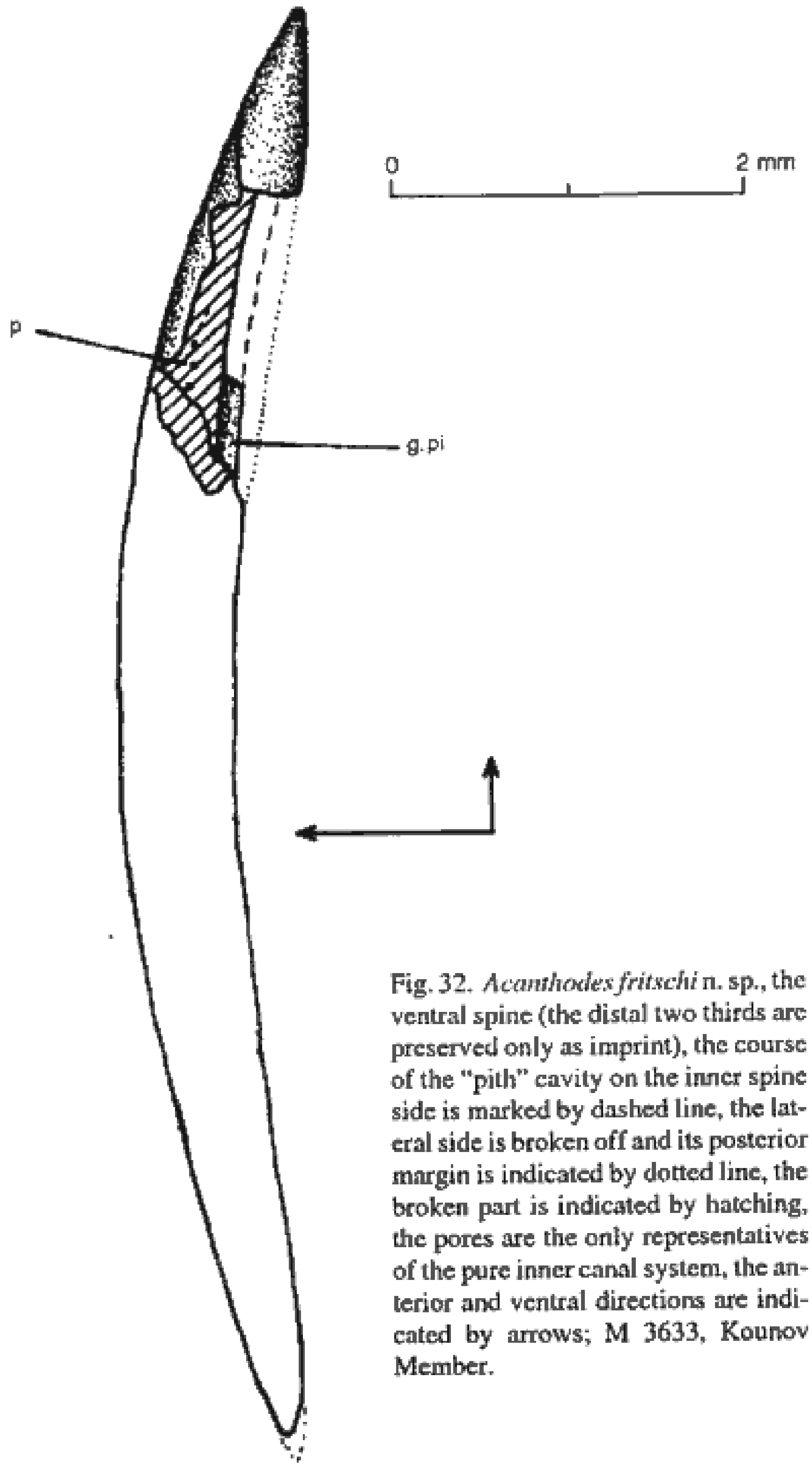


Fig. 32. *Acanthodes fritschi* n. sp., the ventral spine (the distal two thirds are preserved only as imprint), the course of the "pith" cavity on the inner spine side is marked by dashed line, the lateral side is broken off and its posterior margin is indicated by dotted line, the broken part is indicated by hatching, the pores are the only representatives of the pure inner canal system, the anterior and ventral directions are indicated by arrows; M 3633, Kounov Member.

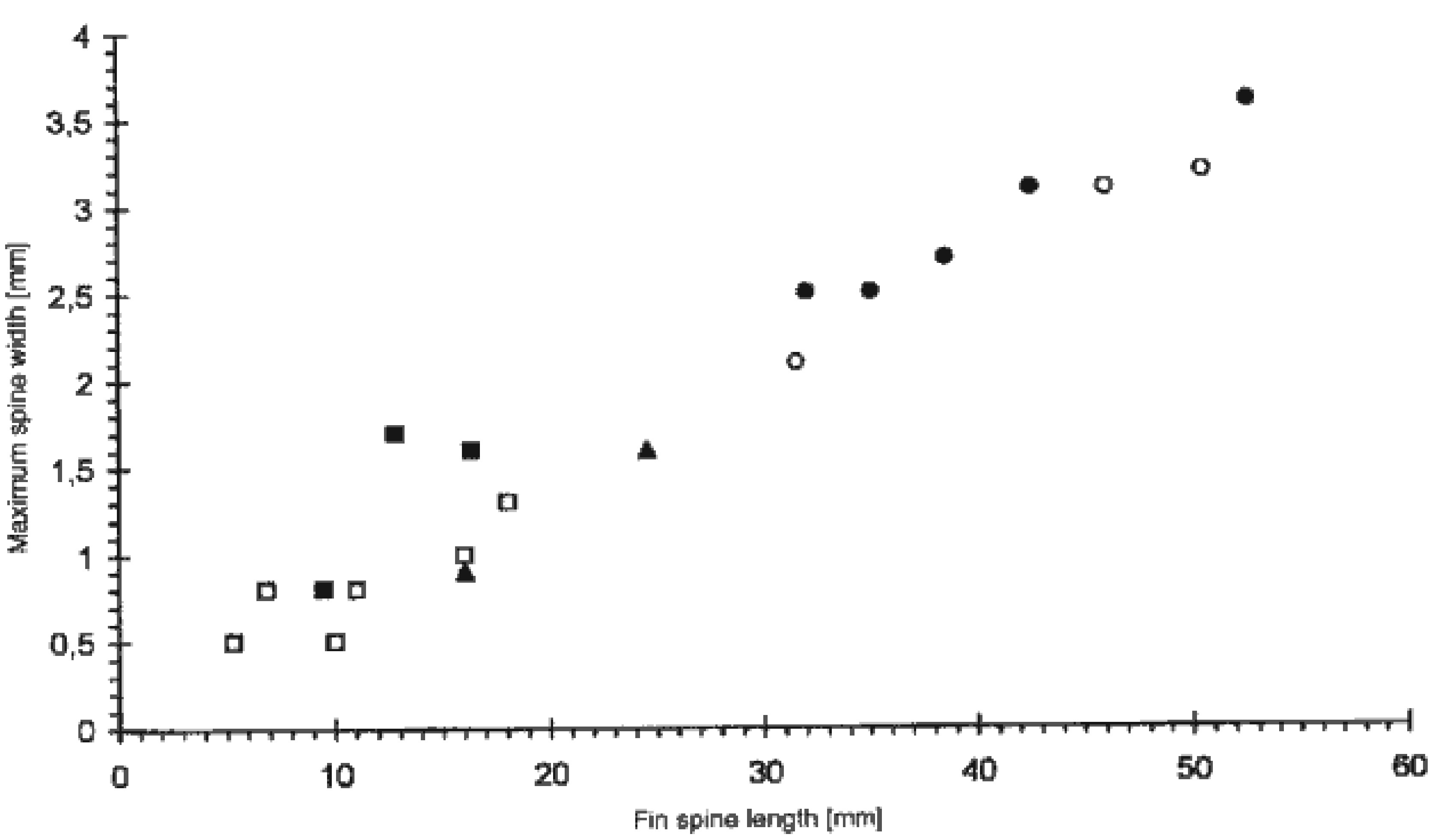


Fig. 33. Relationship between the length and the maximum width of fin spines. The spines of *Acanthodes fritschi* n. sp. are shown by solid symbols, *Acanthodes* sp. by open symbols, the pectoral fin spines are shown by circles, the ventral spines by squares, the anal and dorsal fin spines by triangles.

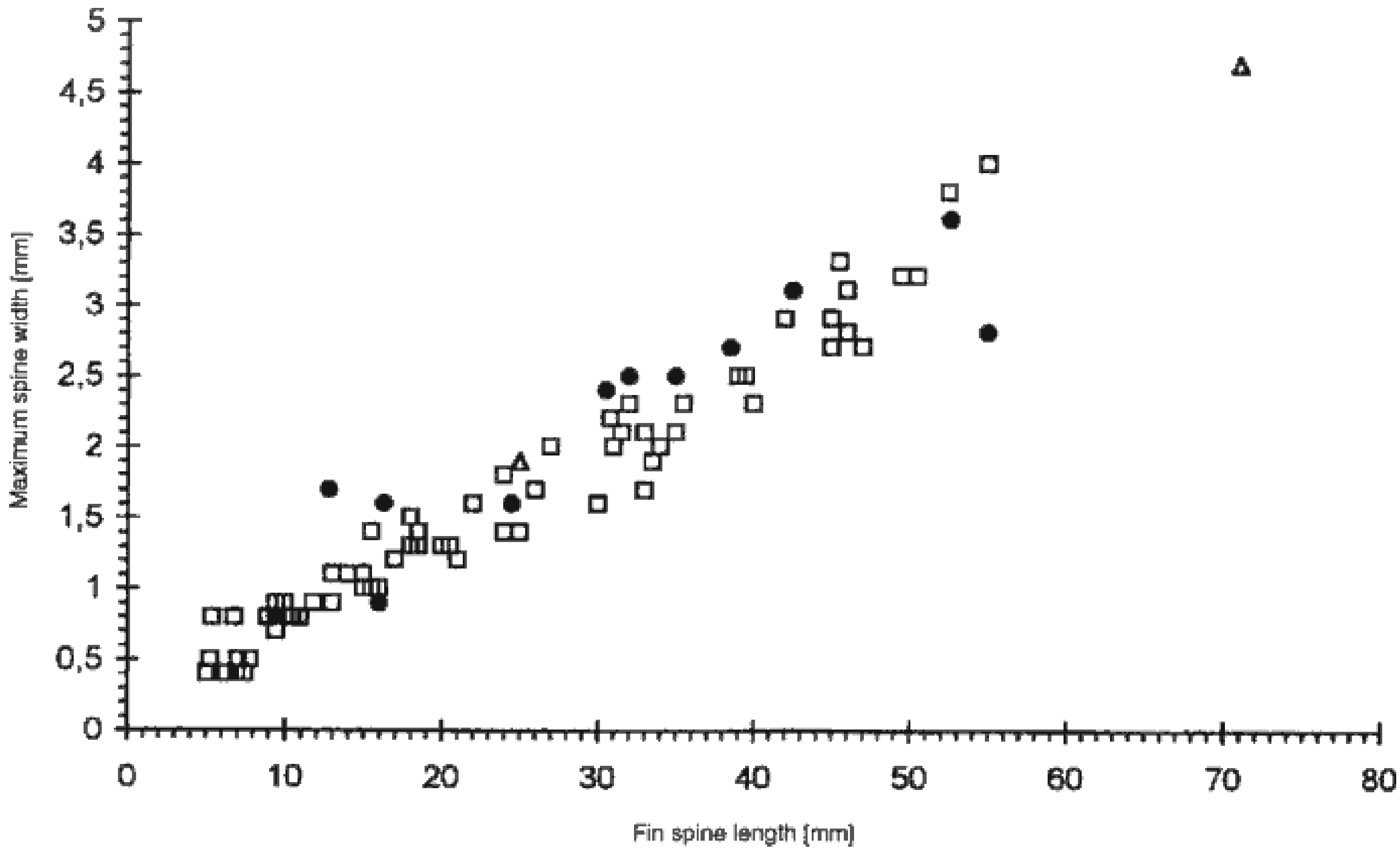


Fig. 34. Relationship between the length and the maximum width of fin spines. The spines of *Acanthodes fritschi* n. sp. are shown by solid circles, the spines of *Acanthodes* sp. from Stephanian B age by open squares, the spines of *Acanthodes* sp. from Stephanian C age by open triangles.

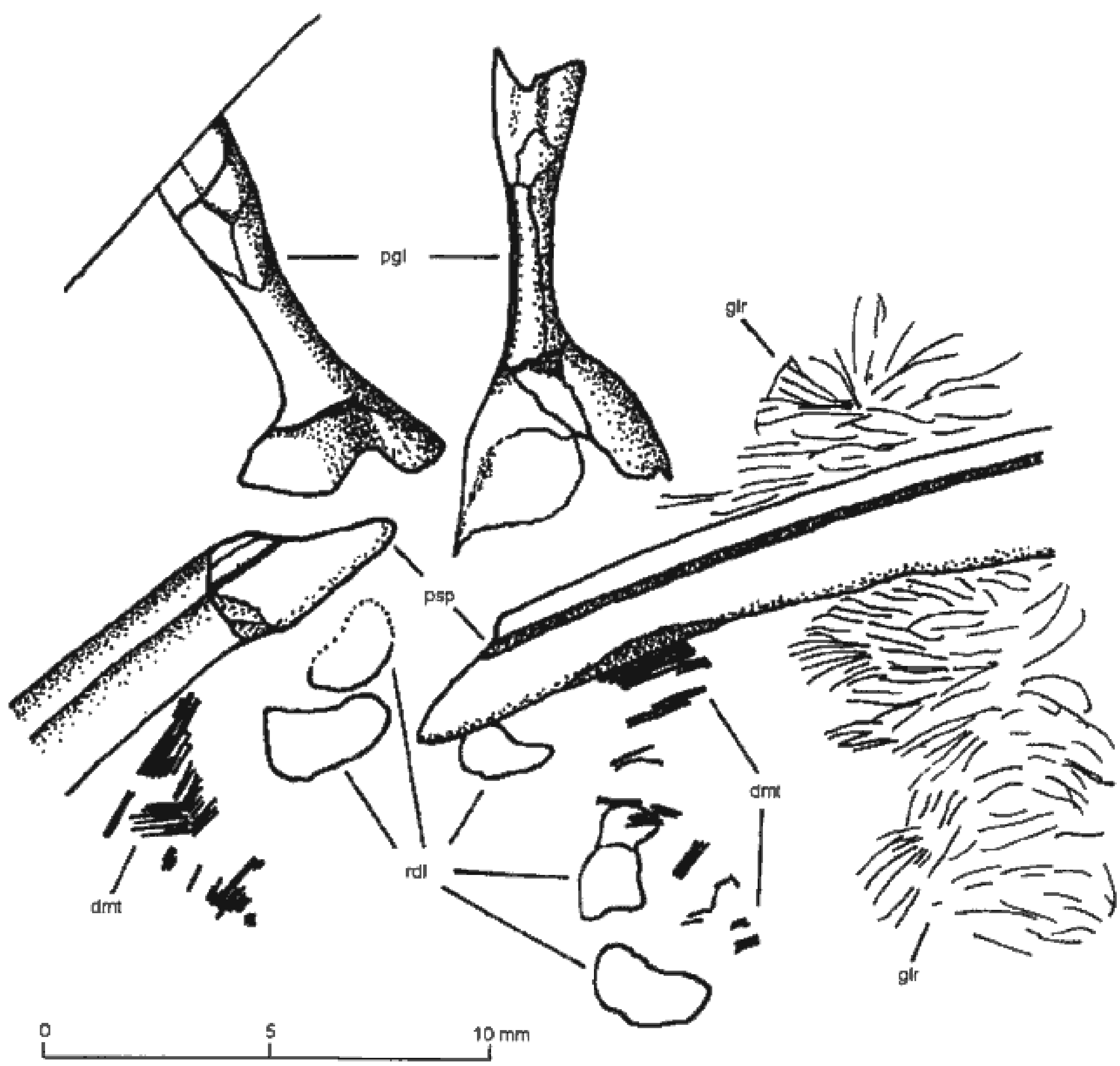


Fig. 35. *Acanthodes fritschi* n. sp., the pectoral girdles associated with pectoral fin spines, radialia, dermotrichia, and gill rakers; YA 1378, Mšec Member.

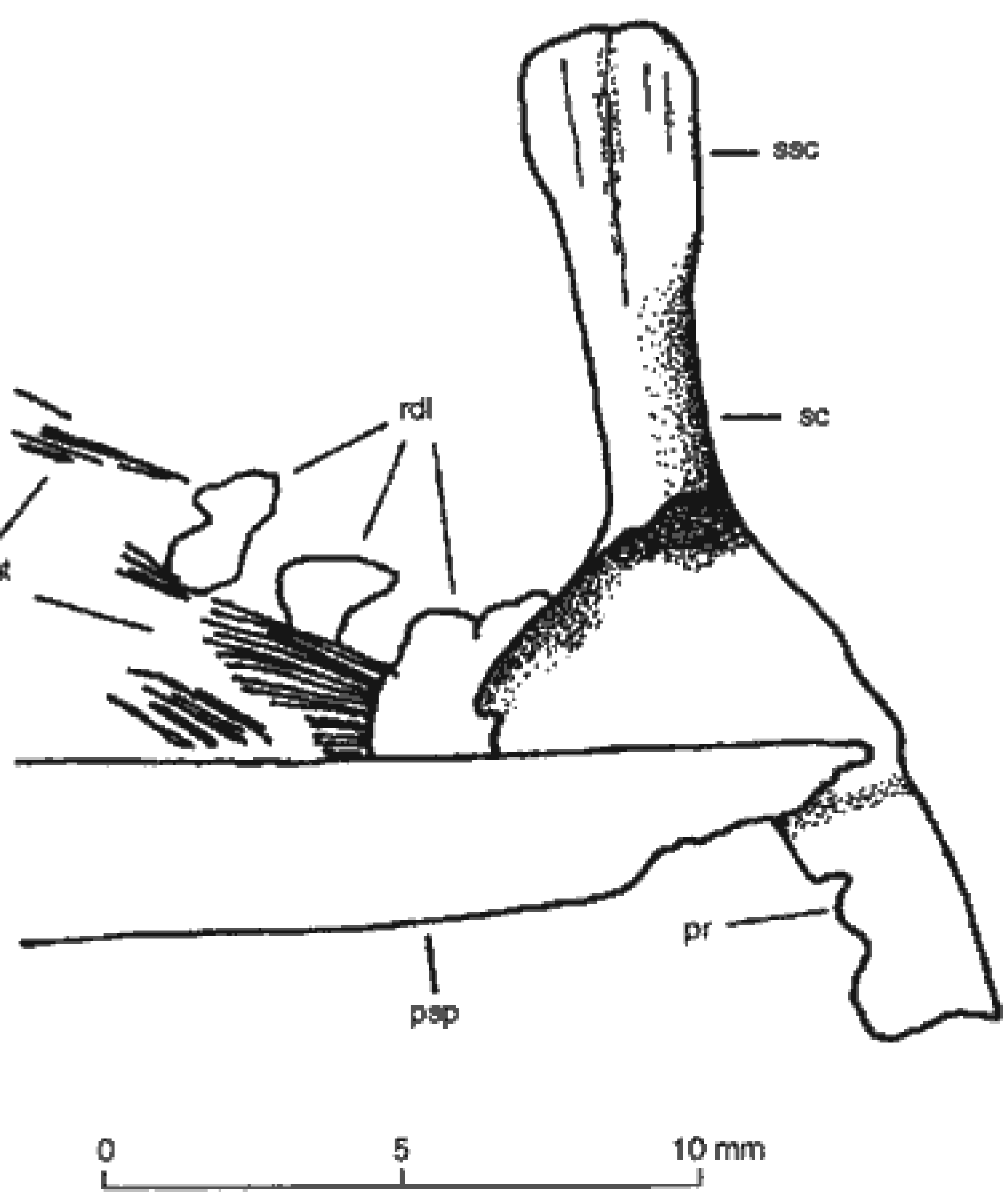


Fig. 36. *Acanthodes fritschi* n. sp., the pectoral girdle in mesial view articulated with the pectoral fin spine, radialia, and dermotrichia; YA 2356, Mšec Member.

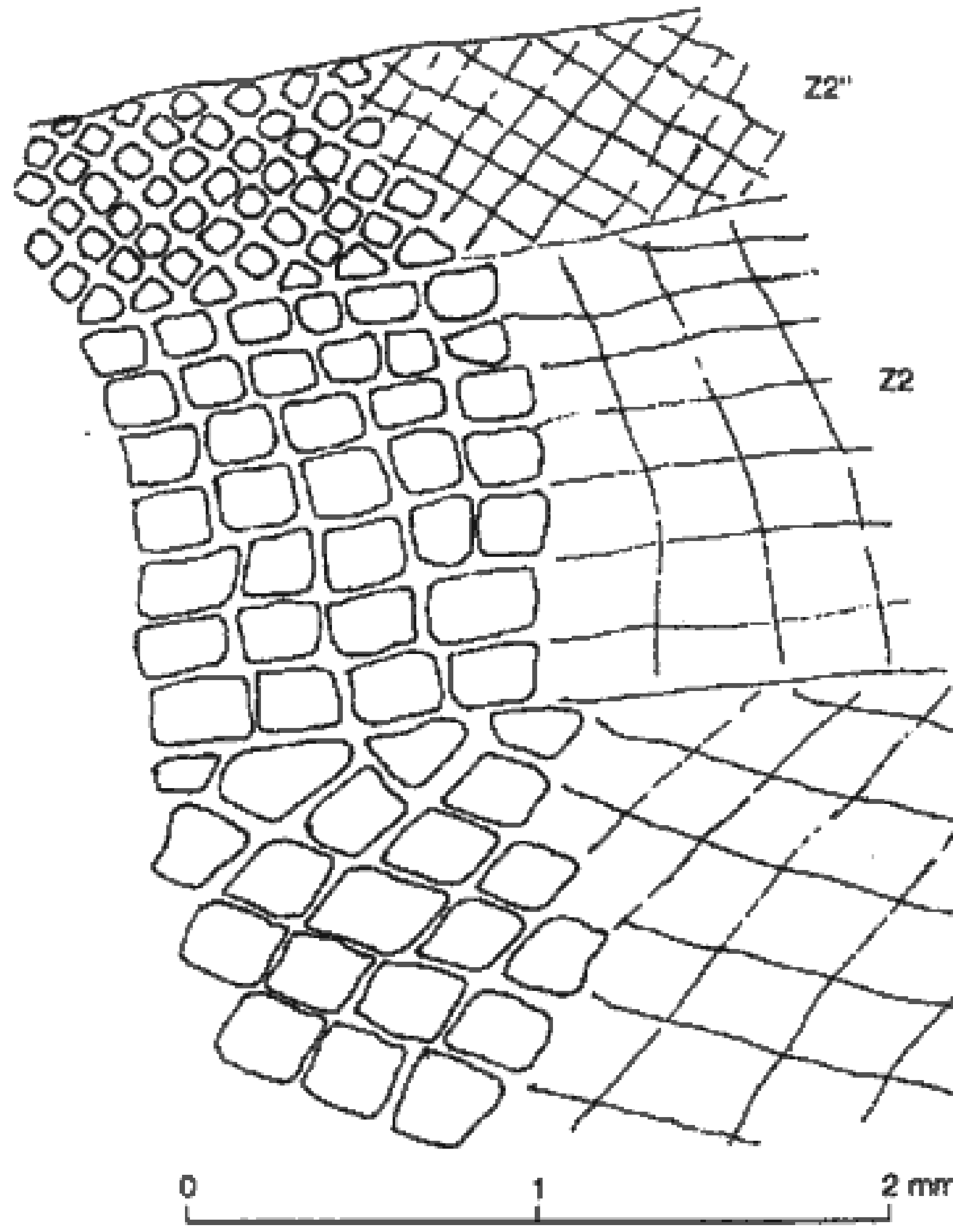


Fig. 38. *Acanthodes fritschi* n. sp., the detail of scale arrangement of the Heyler's zones Z1, Z2, and Z2'' on the axial lobe (the position of the detail is indicated by an asterisk in Fig. 37); YA 2406, Mšec Member.

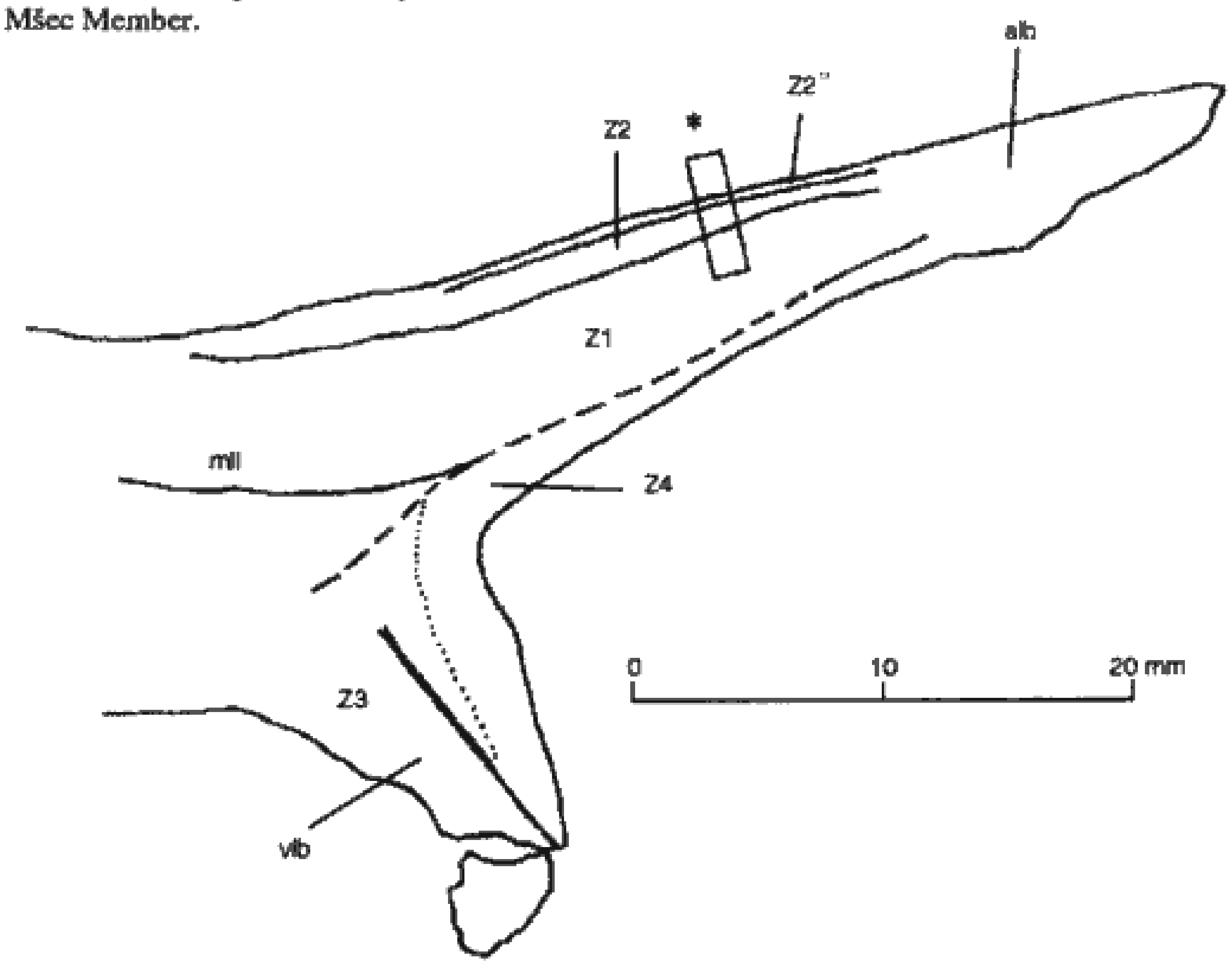


Fig. 37. *Acanthodes fritschi* n. sp., the caudal fin including some data obtained from the counterpart, the detail drawn in the Fig. 38 is indicated by an asterisk; YA 2406, Mšec Member.

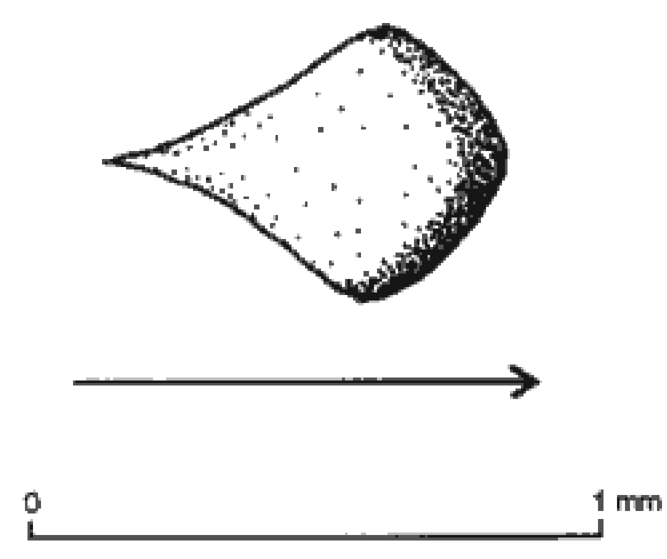


Fig. 39. *Acanthodes fritschi* n. sp., the scale crown from the top, anterior direction is marked by an arrow; YA 2461, Kounov Member.

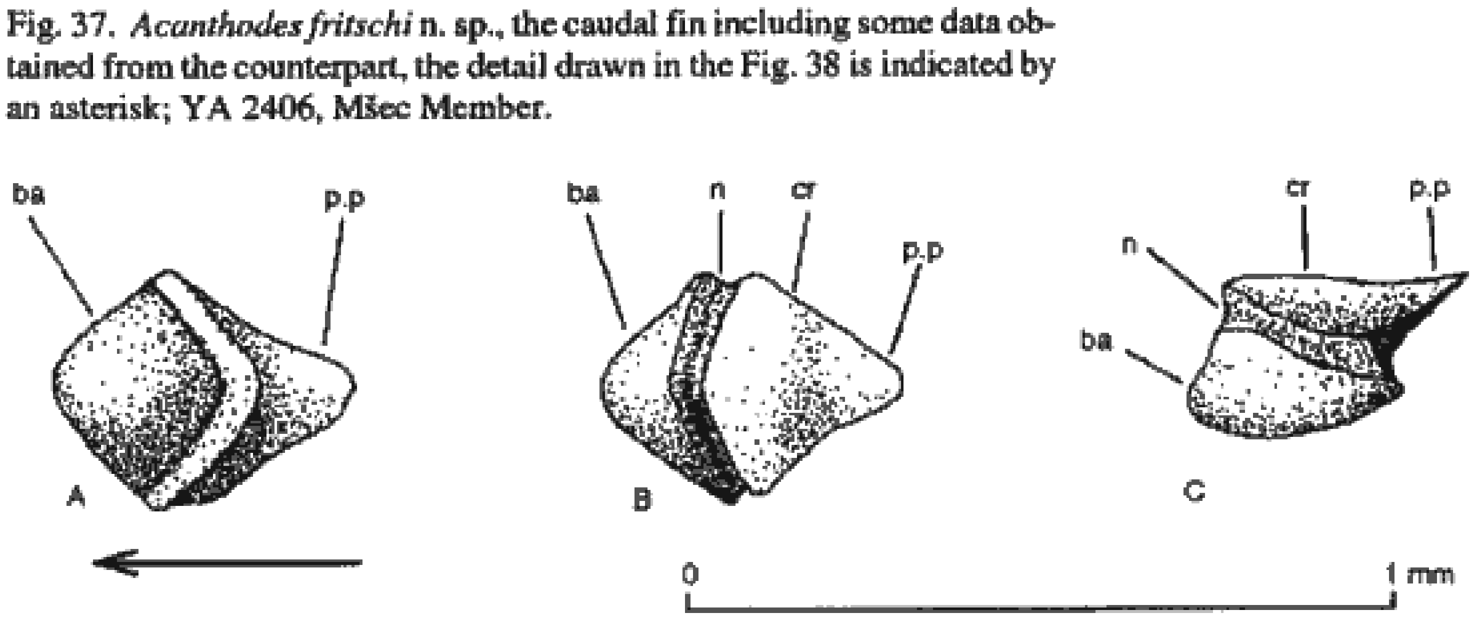


Fig. 40. *Acanthodes fritschi* n. sp., the isolated scale, A – the posterobasal view, B – anterocoronal view, C – lateral view; YA 2491, Kounov Member.

known up to date. Their approximate shape is probably bean-like.

Dermotrichia are long, narrow, non-articulating rods with oval cross section. The formerly described rectangular cross section (ZAJÍC 1985b) is secondary because it was caused by compaction of sediment (the associated dermotrichia were compressed until they resemble a compact and flexible piece). Dermotrichia and radialia were found together in some specimens (Figs. 23, 35, 36). Dermotrichia of the anal fin (Fig. 29) are short and form a relatively long row. They indicate (together with tiny fin scales) at least 15 mm long anal fin with estimated total specimen length 160 mm. A very similar row of short dermotrichia of the anal fin is described in *Acanthodes bridgei* (ZIDEK 1976; Fig. 9) and somewhat shorter one in *Acanthodes bourbonensis* (HEIDTKE 1996; Figs. 1b, 5). Dermotrichia of the dorsal fin are short and few on the same specimen (Fig. 29).

The only two caudal fins were found in specimens from the Bohemian Stephanian. Only one of them (Figs. 37 and 38; Pls. 16C and 16D) is possible to classify as *Acanthodes fritschi* n. sp. on the basis of the presence of spiny scales in the postdorsal-precaudal region. No supporting elements were found in the caudal fin. The proximally widened termination of the axial lobe of the caudal fin is not so conspicuous as in *Acanthodes bourbonensis* (HEYLER 1969b, Pl. 7; HEIDTKE 1996, Figs. 1a, 1b, 6). No similar structure is known from other *Acanthodes* specimens to date. Heyler's zones are drawn on Figs. 37 and 38.

The *Acanthodes*-type scales have smooth scale crowns which terminate in posteriorly orientated spiny projections (Figs. 39–41; Pls. 17B-E). Similar projections were described in *Acanthodes luedersensis* (DALQUEST, KOCURKO & GRIMES 1988, Figs. 7 and 9). Various other isolated scales of *Acanthodes* sp. have been figured (SCHULTZE 1985, Fig. 5; TWAY 1979, Figs. 7a, b; TWAY & ZIDEK 1982, Figs. 53a–d). Two other representatives of the family Acanthodidae have scales with the posterior spiny projection: *Traquairichthys pygmaeus* (FRITSCH 1893, Fig. 266d) and *Pseudacanthodes pinnatus* (FRITSCH 1893, Fig. 266c). The imprints of the articulated flank scales (Fig. 41) show that the very thin spiny posterior projections which overlapped the back scales were in the majority of cases broken (either during the life or during postmortem transport or as a consequence of the sediment splitting). This important feature can therefore easily pass unnoticed.

The body sensory lines are represented by the paired lateral (main) sensory line and by the paired ventrolateral sensory line. The lateral sensory line is formed by two scale "rows" (the true scale rows are oblique) which are somewhat larger than the surrounding scales. The largest body scales are situated just in the lateral sensory line. These scales overlap each other in the same way as in *Acanthodes gracilis* (Fig. 42) and form a characteristic elevation. Imprints of the lateral surfaces of the lateral sensory lines show broken posterior projections, imprints of median surfaces form characteristic zig-zag lines (Fig. 43). Neither lateral nor ventrolateral sensory lines show the structure pictured by FRITSCH (1893, Pl. 107/3). The short sections of both parallel ventrolateral sensory lines are well preserved in M 3633 (Fig. 44). Ventrolateral sensory lines are formed by noticeably larger scales than the surrounding ones. The lateral view shows scales overlapping by often broken posterior projections. The inner view shows two rows of aslant turned scale bases with longitudinal axes intersecting anteriorly. Both sides of the ventrolateral sensory line (outer and inner) form an elevation. Both ventrolateral sensory lines (left and right) are united into the unpaired and anteriorly orientated medioventral sensory line on the ventral part of the body under the posterior part of the gill chamber. This structure, similar to that in *Acanthodes bridgei* (ZIDEK 1976, Fig. 4C), was found in the specimen YA 2459. The short row of enlarged scales of elongated oval shape described in the pectoral fin of *Acanthodes bourbonensis* by HEIDTKE (1996; Fig. 5) seems more likely to be a fragment (one scale row only) of the ventrolateral sensory line (similar to *Acanthodes fritschi* n. sp. and *Acanthodes gracilis*).

The sensory lines of the head are preserved only in short sections which are not possible to determine exactly (Fig. 47). These sensory lines are composed of individual segments (modified scales) with very interesting morphology (Figs. 45 and 46). No complete segment was found. The broken elements are formed by central semi-cylindrical bodies (concave in lateral view). The connected segments form, in that way, an interrupted sensory groove. Each body of the segment bears two flat and very thin and fragile "lateral" wing-shaped processes. The segments of different *Acanthodes* species were always figured without "lateral" processes which were preserved rather rarely. The appearance of each of such fragments is similar (FRITSCH 1893, Fig. 262; HEIDTKE 1990a, Fig. 46; ZIDEK 1976, Fig. 5 etc.).

Type series:

(For the measured data see Figs. 49 and 50)

1. Holotype YA 2397 (Figs. 4, 23–25, 45; Pls. 1 and 2); Ři-22 (Řisuty) borehole, depth 54.30 m, Kladno Basin, Mšec Member; head and pectoral region of the body, the largest specimen (estimated length = 350 mm), subadult stage.

2. Paratype M 1117 (the nodule + galvanoplasty; Figs. 11, 12, 15, 18, 31, 43; Pls. 3, 4, 5A); Žilov, Plzeň Basin, Mšec Member; the head and anterior part of body; FRITSCH (1893) described this specimen as *Acanthodes* sp. (Pl. 106/9–12) and as *Acanthodes Bronni?* (Pl. 107/1–5).

3. Paratypes M 3629 + M 3630 (original + counterpart; Figs. 13, 16, 17, 20, 26, 27; Pls. 5B, 5C, 6A); Záboř near Slaný, the mine of Baron Reis, Kladno Basin, Kounov Member; the head and the pectoral part of body.

4. Paratype M 3633 (Figs. 29, 32, 44; Pls. 6B, 6C); Záboř, Kladno Basin, Kounov Member; the posterior part of body (from the ventral fin spine to the caudal fin).

5. Paratype M 3635 (Fig. 41); Záboř near Slaný, the mine of baron Reis, Kladno Basin, Kounov Member; skin fragment with distinctive scales.

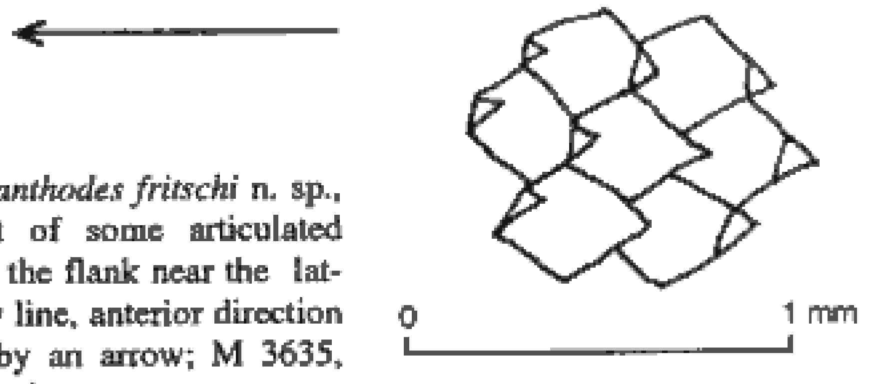


Fig. 41. *Acanthodes fritschi* n. sp., the imprint of some articulated scales from the flank near the lateral sensory line, anterior direction is marked by an arrow; M 3635, Kounov Member.

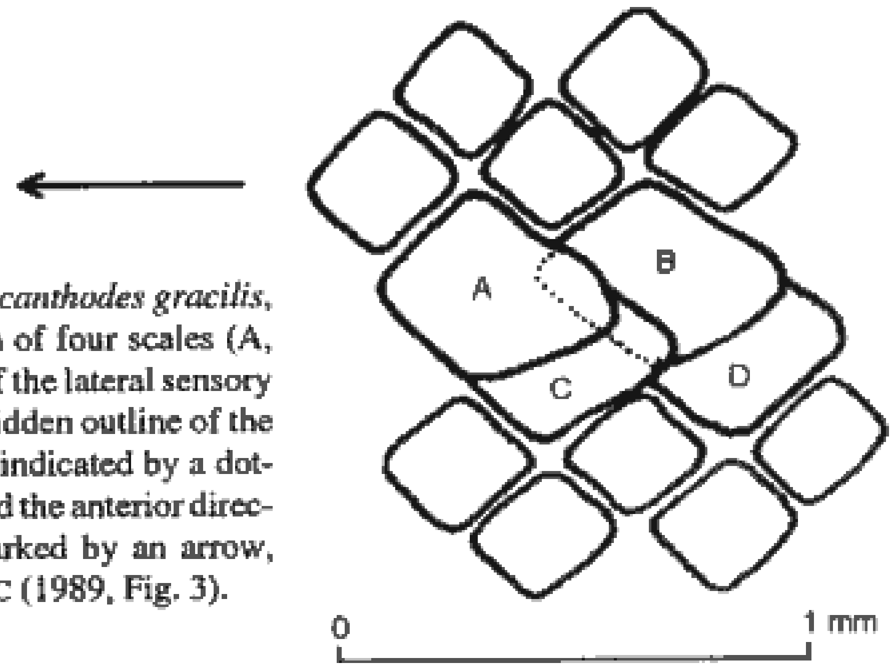


Fig. 42. *Acanthodes gracilis*, restoration of four scales (A, B, C, D) of the lateral sensory line, the hidden outline of the scale B is indicated by a dotted line and the anterior direction is marked by an arrow, after ZAJÍC (1989, Fig. 3).

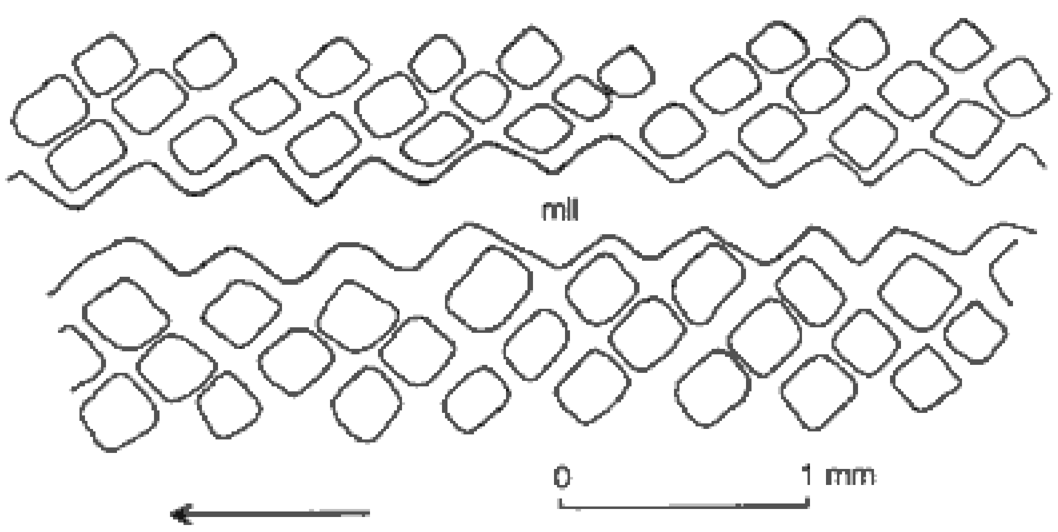


Fig. 43. *Acanthodes fritschi* n. sp., imprint of the median side of the lateral sensory line with surrounding scale bases, the anterior direction is marked by an arrow; M 1117, Mšec Member.

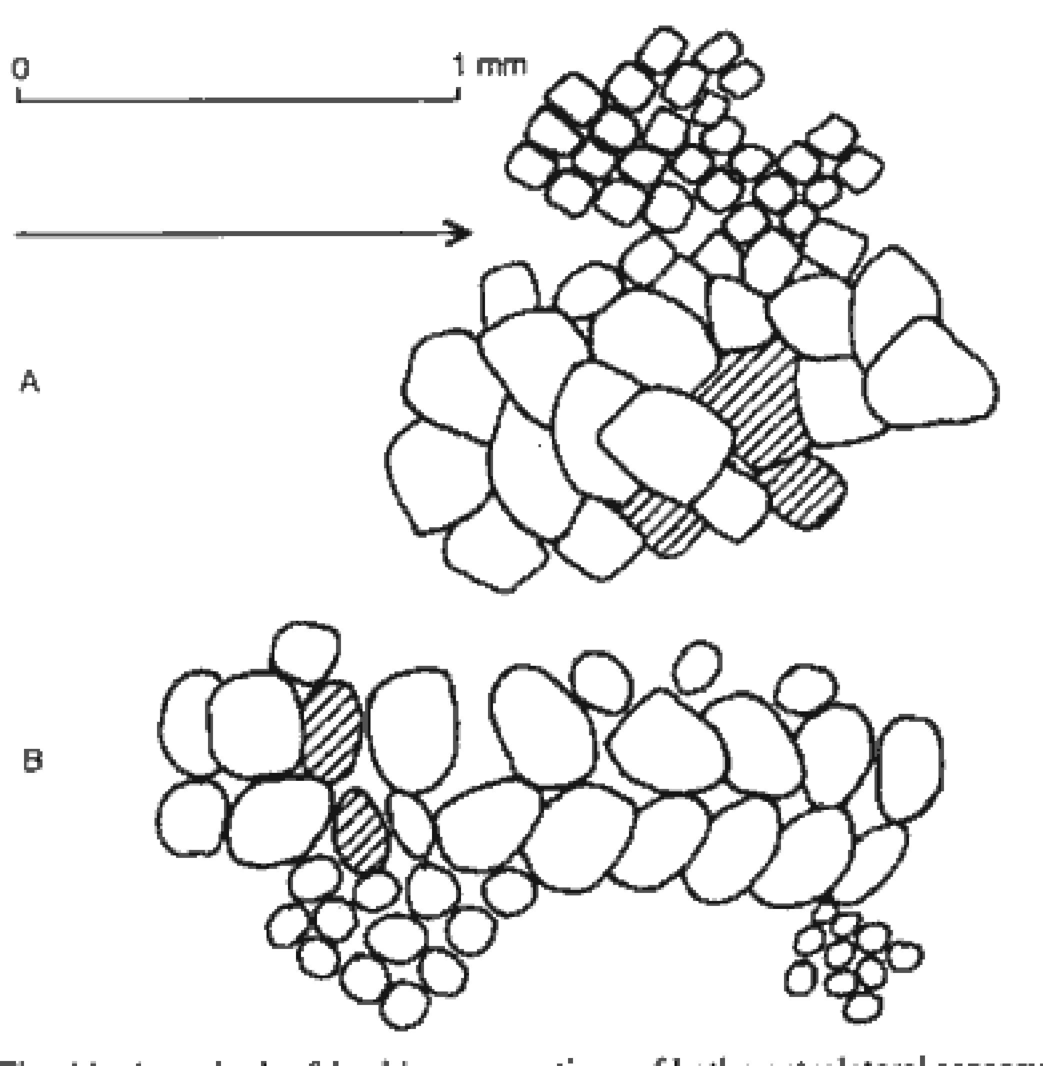


Fig. 44. *Acanthodes fritschi* n. sp., sections of both ventrolateral sensory lines near the ventral fin spine of the same specimen, A – lateral view, B – inner view, broken scales are hatched, anterior direction is marked by an arrow; M 3633, Kounov Member.

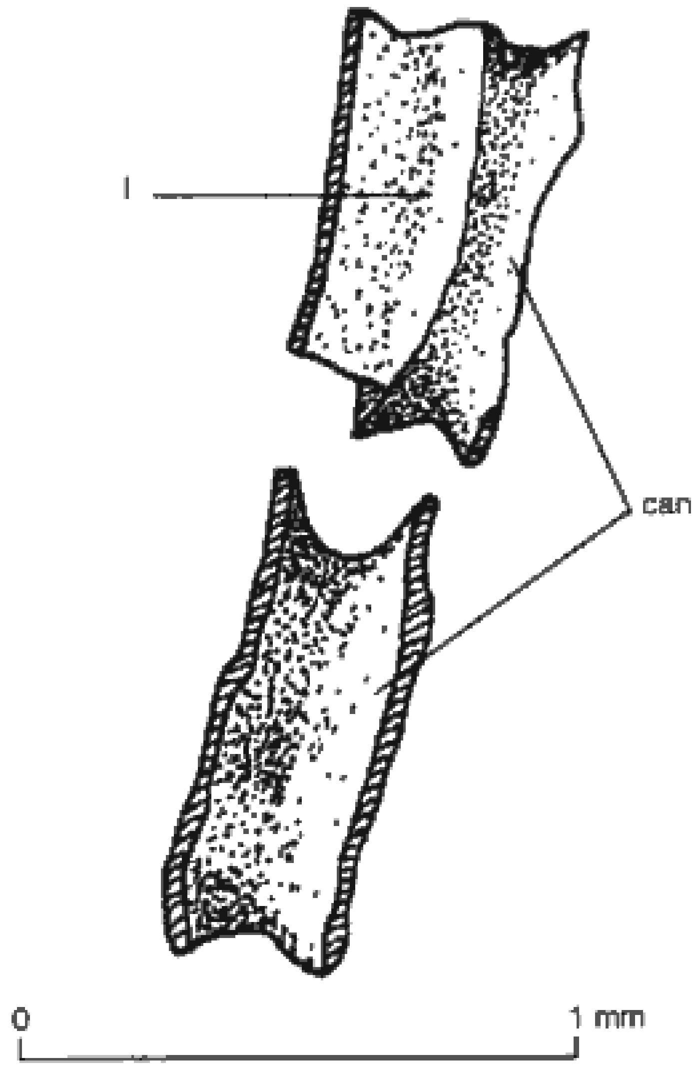


Fig. 45. *Acanthodes fritschi* n. sp., fragments of two segments of a sensory line of the head, broken parts are indicated by hatching, lateral view; YA 2397 (the holotype), Mšec Member.

Fig. 46. *Acanthodes fritschi* n. sp., segment of a sensory line of the head, median view; M 3629, Kounov Member.

6. Paratypes P 30 675/šv. + P 30 676/šv. (original + counterpart; Fig. 14; Pls. 7 and 8); Jedomělice, Kladno Basin, Kounov Member; the part of body between the pectoral girdles and anal fin spine; this specimen was first illustrated by ZAJÍC (1985b; Fig. 4; Pls. I, II/2, III/1).

7. Paratype P 30 678/šv. (Fig. 52); Jedomělice, Kladno Basin, Kounov Member; branchial and hyoid gill rakers; this specimen was first illustrated by ZAJÍC (1985b; Fig. 2).

8. Paratype 30 705/šv.; Jedomělice, Kladno Basin, Kounov Member; complex of scales, branchiostegal rays, and branchial gill rakers.

9. Paratype YA 1347 (Fig. 7; Pls. 9, 10A, 10B); Sa-2a (Slaný) borehole, depth 162.00–163.00 m, Kladno Basin, Mšec Member; the lower jaw; this specimen was first illustrated by ZAJÍC (1988b; Fig. 2; Pls. I, II/1–2).

10. Paratype YA 1378 (Figs. 35, 47; Pls. 10C, 11, 12); Ři-20 (Řisuty) borehole, depth 51.40 m, Kladno Basin, Mšec Member; the head, pectoral portion, and ventral spine.

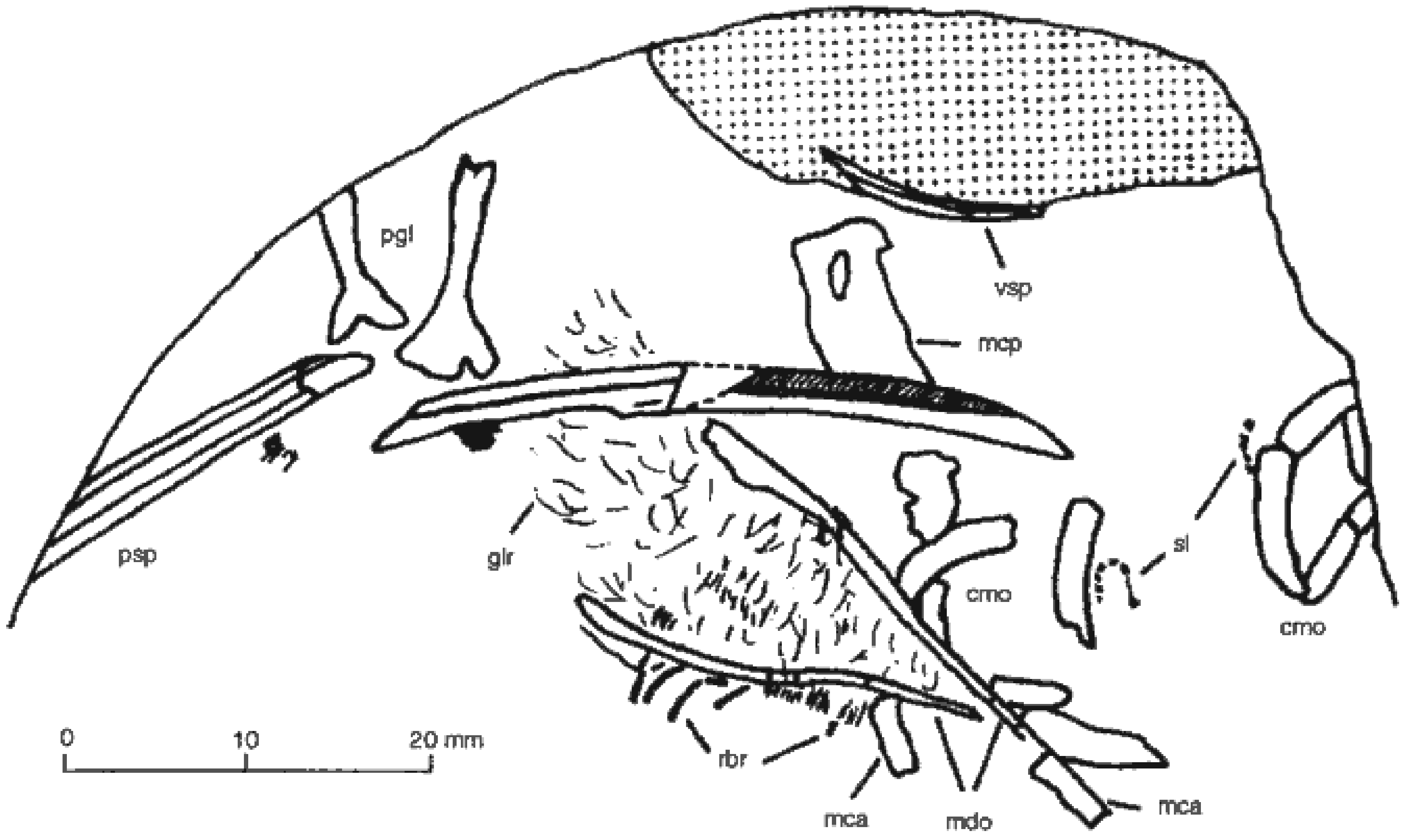


Fig. 47. *Acanthodes fritschi* n. sp., the incomplete head and the pectoral region of the body, the dotted area indicates body scales; YA 1378, Mšec Member.

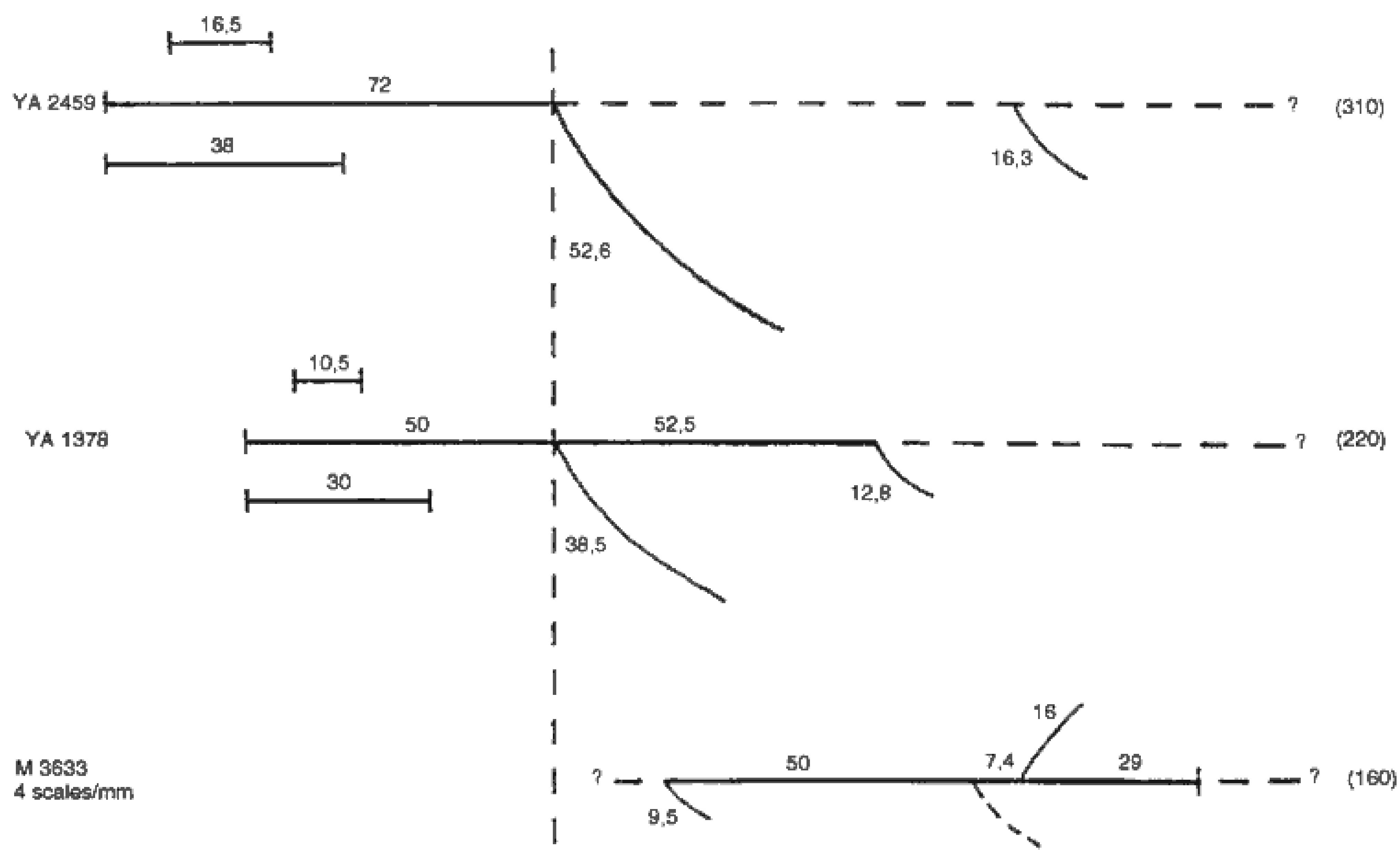


Fig. 48. *Acanthodes fritschi* n. sp.; schematic presentation of the body proportions (ZIDEK's diagrams) of the most complete specimens.

11. Paratype YA 1379 (Fig. 8; Pl. 13A); Bc-1 (Brodce) borehole, depth 511.20 m, Mšeno Basin, Mšec Member; the lower jaw and articulated branchial gill rakers.

12. Paratype YA 2347 (Fig. 28; Pls. 14A, 14B); Lo-6 (Lotouš) borehole, depth 309.40 m, Kladno Basin, Mšec Member; the pectoral girdle articulated with the pectoral fin spine.

13. Paratype YA 2356 (Fig. 36; Pl. 13B); Bc-1 (Brodce) borehole, depth 510.10 m, Mšeno Basin, Mšec Member; the pectoral girdle, pectoral fin spine, radialia, and dermotrichia.

14. Paratype YA 2381 (Fig. 10; Pls. 14C and 14D); MV-1 (Mělnické Vtelno) borehole, depth 739.20 m, Mšeno Basin, Mšec Member; the posterior part of the head with the pectoral region.

	l_P	l_V	l_A	l_D	$v_{P\text{-}V}$	$v_{V\text{-}A}$	$v_{P\text{-}A}$	$v_{A\text{-}D}$	$v_{A\text{-}Z}$	$v_{D\text{-}Z}$	$v_{Z\text{-}O}$	l_{PR}	l_M	d_O	y	l_T
YA 2397 (holotype)	? 3,8	–	–	–	–	–	–	–	–	–	–	–	?	(20)	–	(350)
YA 2459	52.6 3.6	16.3 1.6	–	–	–	–	–	–	–	–	–	(72)	(38)	(16.5)	–	(310)
YA1347	–	–	–	–	–	–	–	–	–	–	–	–	>35.2	–	–	–
YA 1379	–	–	–	–	–	–	–	–	–	–	–	–	>34	–	–	–
YA 2384	42.5 3.1	–	–	–	–	–	–	–	–	–	–	–	?	–	–	(250)
M 1117	? 2.7	? 1.6	–	–	–	–	–	–	–	–	–	–	?	(11)	–	(220)
YA 1378	38.5 2.7	12.8 1.7	–	–	(52.5)	–	–	–	–	–	–	(50)	>30	(10.5)	–	(220)
P 30675/šv. P 30676/šv.	>35 2.5	–	24.5 1.6	–	–	–	?(45)	–	–	–	–	–	–	–	–	(205)
M 3629 M 3630	32 2.5	–	–	–	–	–	–	–	–	–	–	?(65)	–	–	–	(190)
M 3633	–	79.5 ?0.8	? 1.2	16 0.9	–	(50)	–	7.4	36.4	29	–	–	–	–	4	(160)
YA 2406	–	–	–	–	–	–	–	–	–	–	28	–	–	–	–	–

Fig. 49. *Acanthodes fritschi* n. sp. ; summary of all measured values of the holotype and paratypes; spine lengths are situated at the top of cells, their maximum widths at the bottom; estimated values are in brackets (for explanation see chapter 2.2).

	A^1	B	K	L	N	y	l_T
YA 2459	–	31	23	73	52	–	(310)
YA 1378	–	33	21	78	60	–	(220)
P 30675/šv. + P 30676/šv.	70	–	–	–	–	–	(205)
M 3633	–	–	–	–	–	4	(160)

Fig. 50. *Acanthodes fritschi* n. sp.; calculated ratios (for explanation see chapter 2.2).

15. Paratype YA 2384 (Figs. 5, 6, 9, 21, 22; Pl. 15); Hředle, Rakovník Basin, Mšec Member; the posterior part of the head with the pectoral region.

16. Paratype YA 2406 (Figs. 37, 38; Pls. 16C, 16D); MV-1 (Mělnické Vtelno) borehole, depth 739.05 m, Mšeno Basin, Mšec Member; the caudal fin.

17. Paratype YA 2459 (Figs. 19, 30; Pls. 16A and 16B); Ři-25 (Řisuty) borehole, depth 72.40 m, Kladno Basin, Mšec Member; the head and the anterior part of the body.

18. Paratypes YA 2460 + YA 2461 (original + counterpart; Fig. 39); Jedomělice, Kladno Basin, Kounov Member; scales.

19. Paratype YA 2470 (Pl. 17A); Jedomělice, Kladno Basin, Kounov Member; scales.

20. Paratype YA 2491 (Fig. 40); Jedomělice, Kladno Basin, Kounov Member; the isolated scale.

21. Paratype JZ 1/11 (Pl. 17F); Klobuky, Kladno Basin, Klobuky Horizon; the branchial gill raker.

22. Paratype JZ 1/13 (Pls. 17B and 17C); Klobuky, Kladno Basin, Klobuky Horizon; the scale.

23. Paratype JZ 2/24 (Pls. 17D and 17E); Klobuky, Kladno Basin, Klobuky Horizon; the scale.

	A[1]	A[2]	B	C	D[1]	D[2]	E	F	G	H	I	J	K	L	M	N	O
Acanthodes "beecheri"	–	–	–	–	8–12	11–12	4	35	24	–	–	–	–	–	46	–	9–11
Acanthodes bourbonensis	59–88 61–71	50–64 56–69	36–43 29	17–20 18	11–18 13	9–13 11	6–8 9	– –	– 35	– 19	– –	– –	– –	– 50	– 36–42	– 43–48	– 9
Acanthodes bridgei	64–74 –		37–45 –	16–20 –	12–14 –		7–8 –	42–58 –	28–41 –	16–24 –	15–20 –	8–13 –	20–35 –	53–75 –	– 29–52	– 43–58	– 10–14
Acanthodes bronni	58–65 65–95		– 32–47	10–22 11–16	6–12 7–10		– 9	– 44–46	– 36	– 18–24	– –	– –	18–23 15–24	– 61–85	– 35–44	* 56–60	** 11
Acanthodes fritschi n. sp.	70	–	31–33	–	–	–	–	–	–	–	–	–	21–23	73–78	–	52–60	–
Acanthodes gracilis	– 60	– 50	– 36	– 16–17	– 9–10	– 8	– 6	– –	– –	– –	– –	– –	– –	49–54 –	– –	50 –	– –
Acanthodes kinneyi	42	42–55	26	18–21	9	9–10	5	52–55	36	–	–	–	30	49–50	–	–	9–10
Acanthodes lundi	72–77	64–74	27–35	15–21	11–16	11–13	5–6	46–52	38	21–29	?13	?12	27	63–86	33–35	48–53	11–14
Acanthodes ovensis	~90		~50		–	–	–	–	–	–	–	–	–	–	–	–	–
Acanthodes sippeli	– 57	– –	– –	<17 –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	– –	15 –
Acanthodes sulcatus	20		29	17	–		–	–	–	41	–	–	–	–	~100	–	–
Acanthodes wardi	65	60	–	20	10–13	7–12	5	41–48	29	18–29	–	–	24	–	67	54	–
Acanthodes sp. Kansas (HQ)	67		35	20	14		7	51	37	16	21	9	44	74	38	44	15
Acanthodes sp. Okla., Texas	75		–	–	–		–	–	–	–	–	–	–	–	–	–	–
Acanthodes sp. Spain	50	–	–	20	10	–	–	44	32	24	–	–	–	–	40	–	–

Fig. 51. Comparison of the values of individual ratios in *Acanthodes*; * indicates HEIDTKE (1990a, Fig. 54); ** indicates HEIDTKE (1990a, Fig. 53); *Acanthodes "beecheri"* – the numerical values were computed from data in ZIDEK (1976, p. 37); *Acanthodes bourbonensis* – the upper line of values were computed according to measurements of HEYLER (1969b, p. 40), the lower one with help of photographs of HEYLER (1969b, Pls. III/1–2, IV/1); *Acanthodes bridgei* – the upper line contains the data of ZIDEK (1976, 1988), the lower one the computed values according to the data of ZIDEK (1976); *Acanthodes bronni* – the upper line of values were computed according to HEIDTKE (1990a), the lower one with help of illustrations of BOY (1976, Fig. 12), DEAN (1907, Fig. 28), HEIDTKE (1990a, Figs. 2C, 30, 39, 47, 49), KNER (1868, Pl. 5/1), and REIS (1895, Pl. I/4); *Acanthodes gracilis* – for the upper line of values, the figure of FRITSCH (1893, Fig. 265) was used, the values of the lower one were computed according to the data of AUGUSTA (1939b); *Acanthodes kinneyi* – from ZIDEK (1992); *Acanthodes lundi* – from ZIDEK (1980); *Acanthodes ovensis* – see FOREY & YOUNG (1985a); *Acanthodes sippeli* – for the upper row of values see HEIDTKE (1995), the lower one was computed according to HEIDTKE (1995, Fig. 26); *Acanthodes sulcatus* – from ZIDEK (1980, p. 67); *Acanthodes wardi* – measured according to DAVIS (1894, Pls. 27/1, 28/1, 29/2); *Acanthodes* sp. from Kansas (Hamilton Quarry) – see ZIDEK (1976); *Acanthodes* sp. from Oklahoma and Texas – see ZIDEK (1975a); *Acanthodes* sp. from Spain - values were measured from an unpublished photograph supplied by SOLER–GIJÓN, University of Madrid.

Ontogeny: The determination of ontogenetic stages is difficult because no complete specimens were found. Only relationship of estimated total length to size and stage of development of individual structures can help us. Partly articulated specimens are often deformed and some measurements therefore seem not to be trustworthy such as $v_{P\text{-}A}$ in the specimen P 30 675/šv. and l_{PR} in the specimen M 3629 (see Fig. 49). The possibility of utilising Zidek's diagrams is therefore very limited. The first parts of the neurocranium which commenced ossification in *Acanthodes bronni* specimens of estimated length 130–150 mm were according WATSON (1937; p. 102) the labyrinth and the anterior part of basisphenoid. However, HEIDTKE (1990a; Fig. 50) figured the partly ossified labyrinth, dorsal ossification of the neurocranium, basisphenoid, "central" ossification of the neurocranium, and ventrooccipital ossification of the neurocranium in specimens of *Acanthodes bronni* which were only 50 mm in length. The labyrinth and basisphenoid were not the first ossified parts of the neurocranium in *Acanthodes bridgei* and *Acanthodes* sp. from Hamilton Quarry (ZIDEK 1976; p. 8). The largest specimen of *Acanthodes fritschi* n. sp. (holotype; estimated length is 350 mm) shows a part of the neurocranium – basisphenoid. Development of squamation can be examined only in the following specimens:

1. YA 1378 (estimated length is 220 mm) – scales extend forward ahead of the ventral spine.
2. YA 2459 (estimated length is 310 mm) – scales extend to the pectoral region.
3. YA 2397 (holotype; estimated length is 350 mm) – scales reach to pectoral region.

For full resolution of *Acanthodes fritschi* n. sp. ontogeny, it is, however, necessary to obtain more complete material.

Stratigraphic occurrence: Stephanian B (Mšec – Kounov Members) – Stephanian C (Klobuky Horizon).

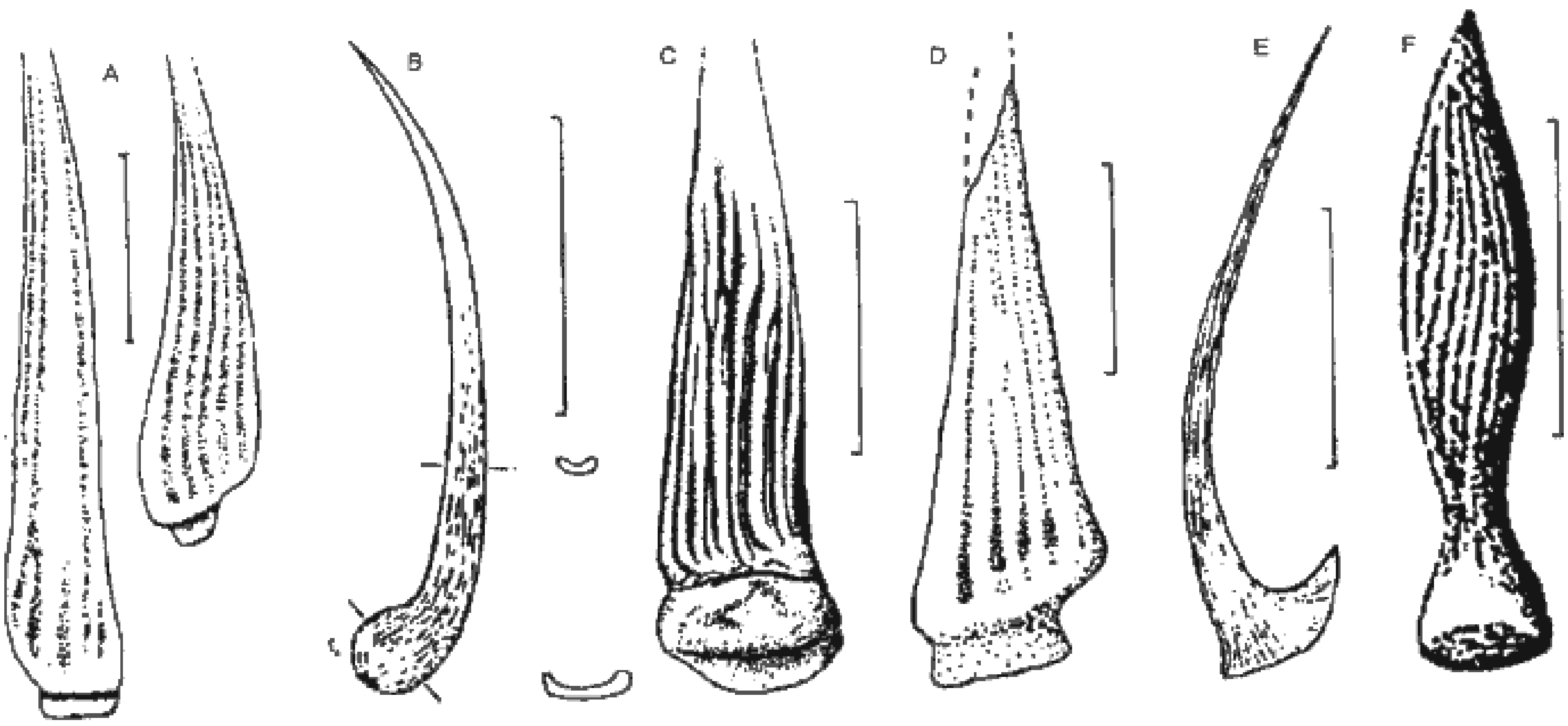


Fig. 52. Gill rakers of *Acanthodes* (from ZIDEK 1992, Fig. 12); A – branchial gill rakers of *Acanthodes kinneyi*; B – ceratohyal gill raker of *Acanthodes bridgei* (from ZIDEK 1976, Fig. 4B); C – hyoid gill raker of *Acanthodes lundi* (from ZIDEK 1980, Fig. 4C); D – hyoid gill raker of *Acanthodes* sp. (from ZAJÍC 1985b, Fig. 1); E – branchial gill raker of *Acanthodes fritschi* n. sp. (from ZAJÍC 1985b, Fig. 2); F – gill raker of *Acanthodes bronni* (from REIS 1896, Pl. 6/18); scale bars equal 1 mm.

Geographic occurrence: Czech Republic, Bohemia; Plzeň, Rakovník, Kladno, and Mšeno Basins.

Sites: Hředle, Jedomělice, Klobuky, Záboř, Žilov, and boreholes Bc-1 (Brodce), Lo-6 (Lotouš), MV-1 (Mělnické Vtelno), Ři-20, 22, 25 (Řisuty), Sa-2a (Slaný).

Remarks and relationship: The extensive acanthodian material from the Bohemian Stephanian provides only a limited number of specimens usable for description of *Acanthodes fritschi* n. sp. Significant features are missing in majority of mostly very fragmentary material which must therefore be classified as *Acanthodes* sp. All these acanthodian remains are, however, very similar and their attribution to *Acanthodes fritschi* n. sp. is therefore very probable. All measured values are mentioned in Fig. 49 and calculated ratios are shown in Fig. 50. Figure 51 presents a comparison of individual ratios of various *Acanthodes* species. The value of ratio B is close to those in *Acanthodes bronni*, *Acanthodes tholeyi*, and *Acanthodes lundi*. The most similar values among the Stephanian representatives of the genus are shared by *Acanthodes* sp. from Kansas, *Acanthodes bourbonensis*, and *Acanthodes bridgei*. The most different value was computed in *Acanthodes kinneyi*. The value of the ratio K corresponds to range of values mentioned in *Acanthodes bronni* and *Acanthodes bridgei*. Rather close values are shown by the Stephanian representatives *Acanthodes bridgei* and *Acanthodes bourbonensis*. The most different values were measured in *Acanthodes kinneyi* and above all in *Acanthodes* sp. from Kansas. The value of the ratio L is in accordance with the values measured in *Acanthodes bronni*, *Acanthodes bridgei*, *Acanthodes lundi*, *Acanthodes sp.* from Kansas, and also in *Traquairichthys pygmaeus*. *Acanthodes kinneyi* shows the most different value among the Stephanian representatives. The value of ratio N corresponds with the values in *Acanthodes bronni*, *Acanthodes boyi*, *Acanthodes tholeyi*, *Acanthodes bridgei*, *Acanthodes lundi*, *Acanthodes wardi*. Very different values of this ratio are shown by Stephanian *Acanthodes* sp. from Spain and *Acanthodes* sp. from Kansas.

The basal foramen of the basisphenoid of *Acanthodes fritschi* n. sp. seems to be somewhat larger than in *Acanthodes bronni*. The prearticular process of the palatoquadrate is orientated somewhat more posteriorly than in *Acanthodes bronni*. The jaw joint on the articulare is orientated more anteriorly than is shown in most restorations of the genus *Acanthodes* apart from that of JARVIK (1977; Fig. 6) of *Acanthodes bronni*. The articular cotylus is rather less conspicuous than is illustrated in other *Acanthodes* species. The branchial gill rakers are of characteristic shape. Their comparison with gill rakers of some other species (*Acanthodes bronni*, *Acanthodes bridgei*, *Acanthodes kinneyi*) is shown on the Fig. 52. The smallest segment of the circumorbital ring (No 4 according to HEIDTKE 1990a) overlaps segment No 3 in contrast to *Acanthodes bronni*. This feature was, however, observed in only one specimen and may therefore be the result of postmortem dislocation. The mandibular bone is more strongly curved than that of *Acanthodes bronni*, but similar to *Acanthodes lundi*. Both a mentomandibular knob and a symphysal pit are absent unlike *Acanthodes lundi*. The suprascapula is well ossified in contrast to most *Acanthodes* species. The shape of the suprascapula is similar to that in *Acanthodes bronni*. The presence and/or absence of the suprascapula in different *Acanthodes* species is discussed at the end of chapter 2.2. The coracoid is fragmentarily preserved but probably occupied a larger space than in other *Acanthodes* species. The procoracoid is long and is orientated conspicuously dorsoventrally in contrast to *Acanthodes bronni* which has a markedly shorter and more or less antero-posteriorly orientated procoracoid. The dorsal fin spine is supported by only one basal plate in contrast to two more slender basal plates in *Acanthodes boyi* and *Acanthodes bridgei*. The open "pith" groove has already been figured (although not described) in *Acanthodes luedersensis* (DALQUEST, KOCURKO & GRIMES 1988). However, this structure extends in *Acanthodes luedersensis* at least up to two-thirds of the fin spine length in contrast to *Acanthodes fritschi* n. sp. where the "pith" groove extends to the first proximal quarter only. Dermotrichia of the anal fin are arranged in a rather long single row as in *Acanthodes bridgei*. This arrangement differs from the somewhat longer double row of the anal dermotrichia in *Acanthodes bourbonensis* (this species also shows a double row of the dorsal dermotrichia unlike the single row in *Acanthodes fritschi* n. sp.). The distal termination of the axial lobe is preserved but is somewhat less widened than in *Acanthodes bronni* and *Acanthodes bourbonensis*. Tesserae are not present on the head. The spiny posterior projection of the scale crown is very delicate and therefore usually broken. Similar projections were found in *Acanthodes luedersensis* (scales are more robust as the whole animals), in some of isolated scales often named as *Acanthodes* sp. (DERYCKE & CHANCOGNE-WEBER 1995, Pl. 1/1; SCHULTZE 1985, Fig. 5; TWAY 1979, Pl. 7 etc.) and in *Traquairichthys pygmaeus* and *Pseudacanthodes pinnatus*. Each posterior projection overlapped the following scale in the living animal. Scales of the trunk sensory lines are characteristically overlapped as in *Acanthodes gracilis* from the Krkonoše Piedmont Basin. The medioventral sensory line is the same nature as in *Acanthodes bridgei*. Despite the specific features, *Acanthodes fritschi* n. sp. seems to be most related to the North American Stephanian *Acanthodes bridgei* (from Kansas) and to the German Autunian *Acanthodes bronni* (from the Saar-Nahe Basin).

2.4. *Acanthodes* sp.

Acanthodes sp.

(Figures 52–78; Plates 18–22)

1875 *Acanthodes* sp.: A. Frič, Über die Fauna etc.; p. 77.
1877 *Acanthodes* sp.: A. Frič, Zur Fauna etc.; p. 47, 49.
1893 *Acanthodes Bronni?* (partim): A. Fritsch, Fauna der Gaskohle etc.; p. 61; Pl. 107/6.
1893 *Acanthodes punctatus*, Fr.: A. Fritsch, Fauna der Gaskohle etc.; p. 61–62; Fig. 205; Pls. 107/7–9.
1981 *Acanthodes* cf. *punctatus* Fritsch, 1893 (partim): J. Zajíc, Možnosti interpretace etc.; p. 13–24; Figs. 1, 2; Pls. 5, 6, 7/2–3, 8, 9.
1985 *Acanthodes* sp. indet. (partim): J. Zajíc, New finds etc.; p. 278–284; Figs. 1, 3, 5; Pls. II/1, III/2, IV.
1988 *Acanthodes* sp. indet. (partim): J. Zajíc, Acanthodian (Acanthodii) jaws etc.; p. 222; Fig. 1; Pl. II/3.

Material: The poorly preserved specimens from the Jelenice Member were registered in the boreholes Lib-1 (Liběchov), and Sa-21 (Slaný). These unnumbered specimens are not deposited in a collection. The numbered specimens are from the Mšec Member (M 1115, YA 1348, YA 1380, YA 2346, YA 2348-2355, YA 2357-2380, YA 2382-2383, YA 2385-2396, YA 2398-2405, YA 2407-2413, YA 2453-2455, YA 2457-2458), Kounov Member (JZ 1/20, M 818, M 826, M 1364, M 3627-3628, M 3631-3632, M 3634, M 3636-3645, P 30 677/ šv., P 30 679-30 690/ šv., P 30 692-30 693/ šv., P 30 695-698/ šv., P 30 701/šv., P 30 707/ šv., P 30 713/ šv., P 30 727/ šv., P 30 730/ šv., YA 2417-2418, YA 2462-2469, YA 2471-2490, and YA 2492), Zdětín Horizon (YA 2414-2416 and YA 2419-2422), Klobuky Horizon (JZ 1/1, JZ 2/32, and YA 2423-2424), Ploužnice Horizon (M 3646), and Štěpanice-Čikvásky Horizon (YA 2456).

Notes: Specimens named here as *Acanthodes* sp. are very uniform. In my opinion, they could therefore pertain to *Acanthodes fritschi* n. sp. in all probability. This assignment is, however, impossible because no critically diagnostic features are present. The hyoid gill rakers are quite different from those described so far in *Acanthodes* but they were not found as a component of a clearly determine specimen of *Acanthodes fritschi* n. sp. and their specific determination is therefore not possible. Homogeneity of the material is, however, not proven.

Description: The poorly preserved fragment of a quadrate was found in M 1115 which was described and figured by FRITSCH (1893, Pl. 107/6) as *Acanthodes Bronni?* Ag. FRITSCH's figure is, however, incomplete and rather confused. The complex of bones, identified by FRITSCH as "Kieferstück", consist of the quadrate jointed with the articular, the mandibular bones, and other elements (Pl. 18D). The second fragment of quadrate (Fig. 53; Pl. 19E) was found in YA 1348 which was described by ZAJÍC (1988b; Fig. 1; Pl. II/3) from the same layer of the Sa-2a borehole as the pair of lower jaws of *Acanthodes fritschi* n. sp. (YA 1347). It is not possible to decide whether both the above-mentioned specimens belong to one animal (both specimens were separated before of their examination) and whether therefore it is possible to assign the quadrate to *Acanthodes fritschi* n. sp. The quadrate bears a clearly visible prearticular process and the groove for the hyomandibula.

The shape and proportions of the meckelian cartilage (Fig. 54; Pls. 18B, 18D, 19A, 19G) and mandibular bones (Fig. 55; Pls. 19B–D) are similar to that of *Acanthodes fritschi* n. sp. Mandibular bones are often found isolated. They are distinctively shaped as in those of *Acanthodes fritschi* n. sp. A flat trianguloid process (Fig. 55) can often be seen (probably in mesial view) on the ventral boundary of the sigmoid bend in the middle part of the mandibular bone.

Branchial (posthyoid) gill rakers are mostly readily determined as *Acanthodes fritschi* n. sp. but some of them are not possible to identify specifically yet (Pls. 20F-G). The shape of the hyoid gill rakers are quite different (Fig. 52). They were found only twice and in both cases isolated. They are brush-pencil shaped without a distal termination which was probably cartilaginous. The body of this element is ornamented by longitudinal grooves which extend proximally. The basis is short and narrower than the body. Similarly shaped hyoid gill rakers have not been found in any *Acanthodes* species and these elements doubtless belong to a new species. However, they were not so far found in articulation with any certain specimen of *Acanthodes fritschi* n. sp.

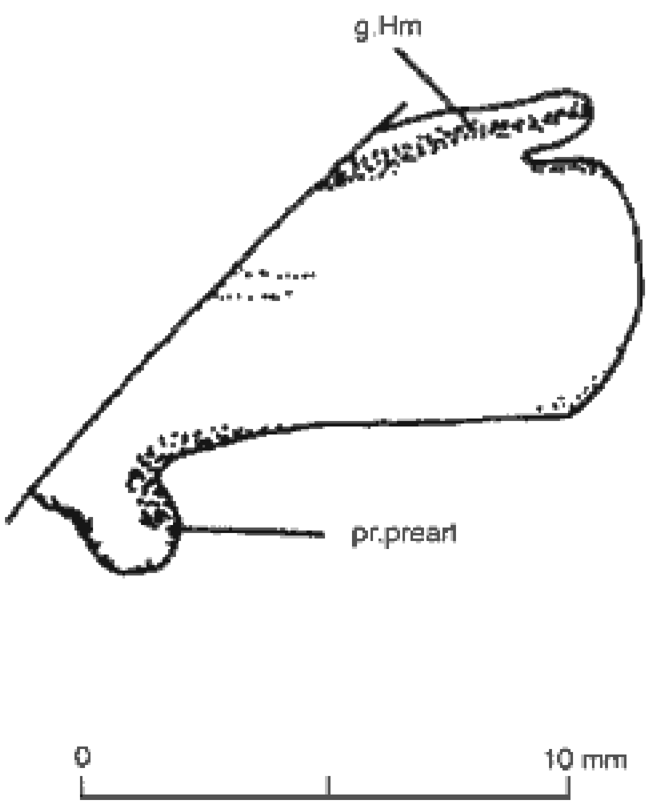


Fig. 53. *Acanthodes* sp.; the anteroventral part of the incomplete left quadrate, mesial view; YA 1348; Mšec Member; from ZAJÍC (1988b; Fig. 1).

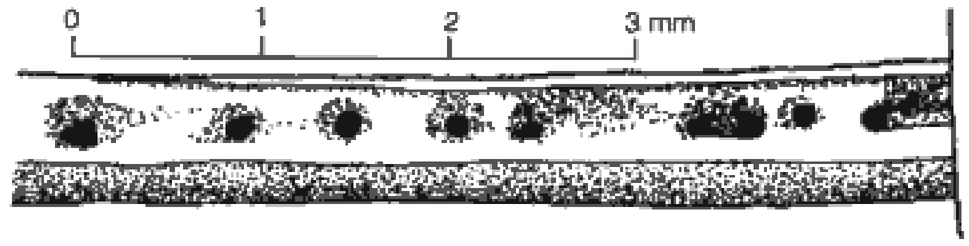


Fig. 57. *Acanthodes* sp.; posterior margin of the fin spine with the shallow groove and the row of pores; YA 2374; Mšec Member.

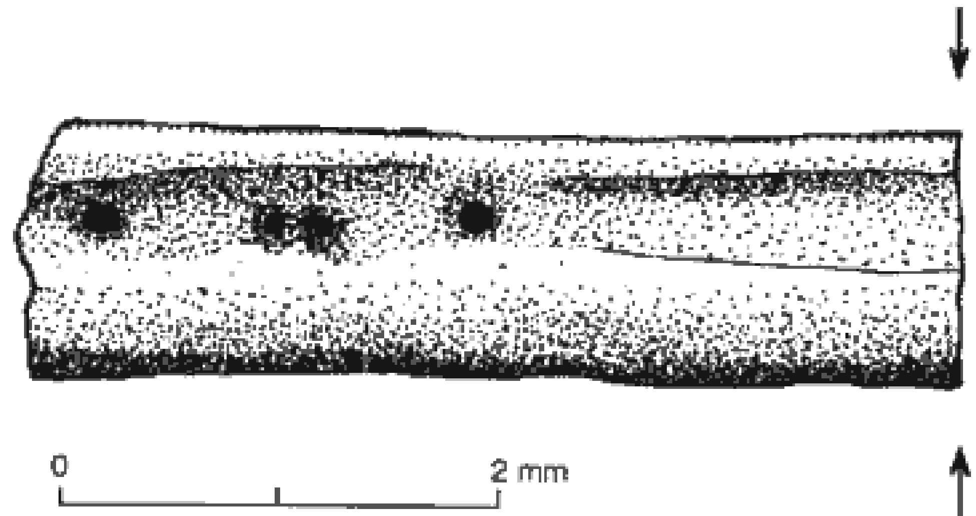


Fig. 58. *Acanthodes* sp.; posterior margin of the fin spine with the shallow groove and the row of pores, the localisation of the cross section illustrated in Fig. 65 is indicated by arrows; YA 2383; Mšec Member.

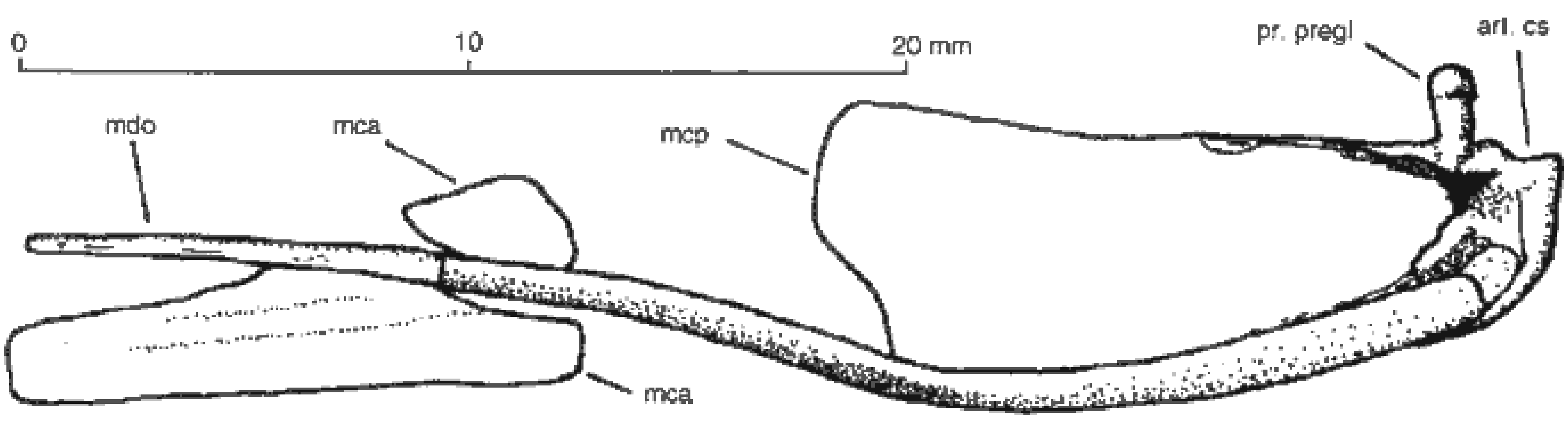


Fig. 54. *Acanthodes* sp.; the lower jaw, lateral view; YA 2354; Mšec Member.

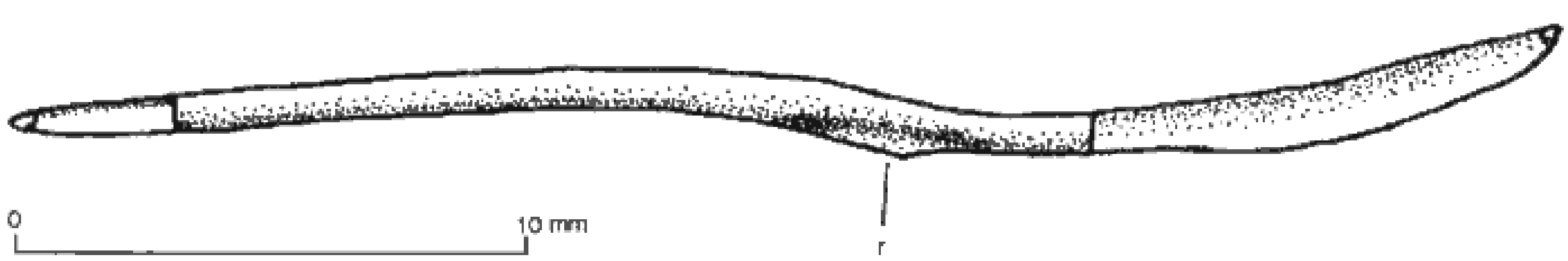


Fig. 55. *Acanthodes* sp.; the isolated mandibular bone, probably mesial view; YA 2355; Mšec Member.

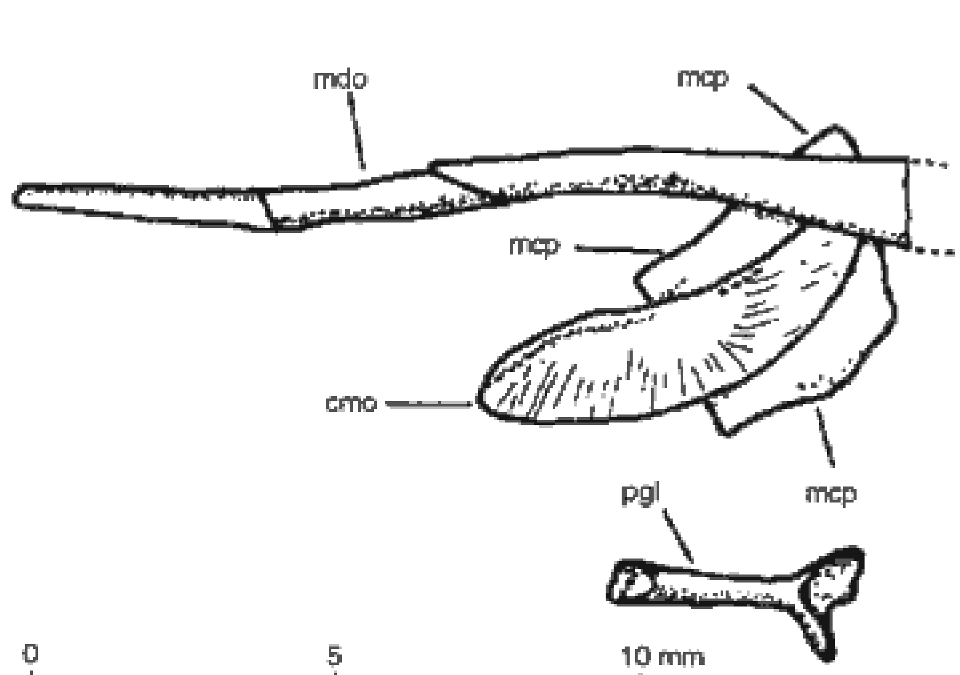


Fig. 56. *Acanthodes* sp.; young specimen, mandibular bone, articular, circumorbital plate, and pectoral girdle; YA 2380; Mšec Member.

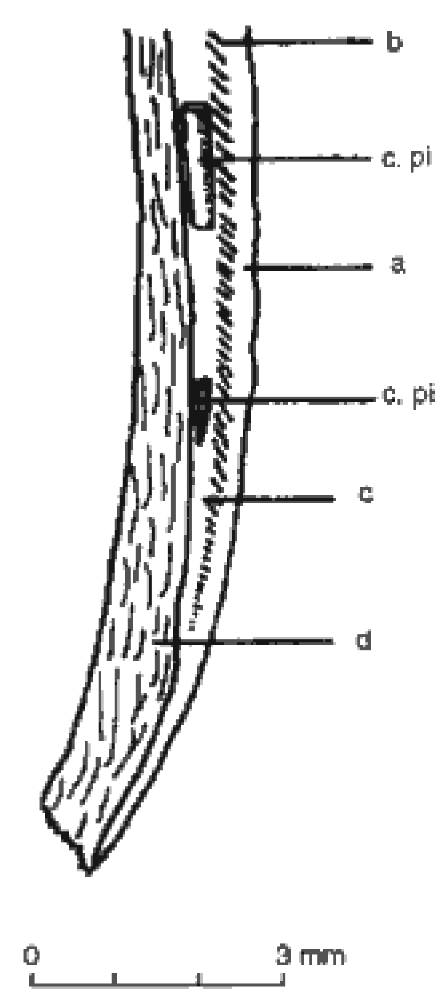


Fig. 59. *Acanthodes* sp.; inner structure of distal part of fin spine whose proximal part is in Pl. 20C, simplified; P 30 680/šv.; Kounov Member; from ZAJÍC (1985b, Fig. 5).

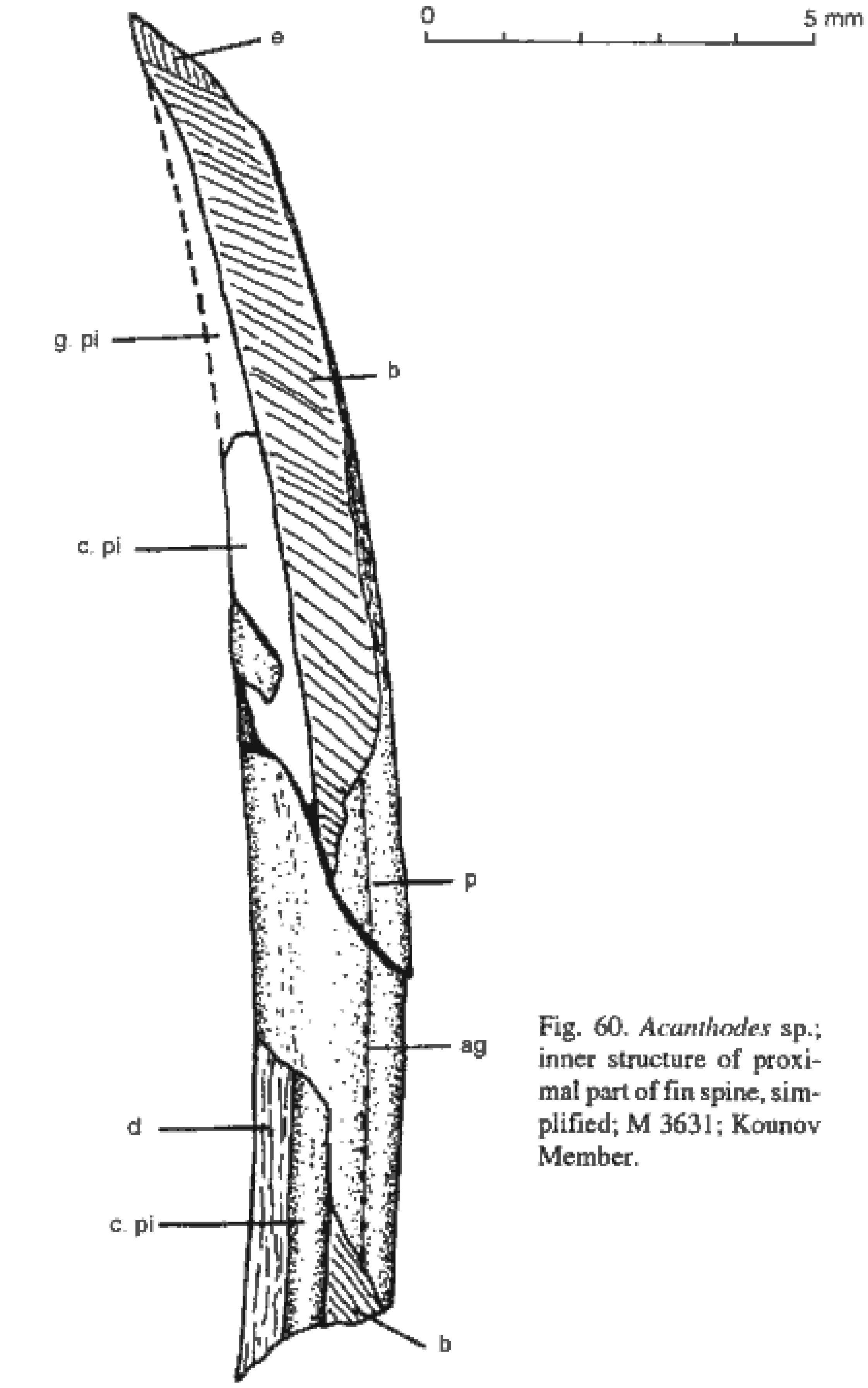


Fig. 60. *Acanthodes* sp.; inner structure of proximal part of fin spine, simplified; M 3631; Kounov Member.

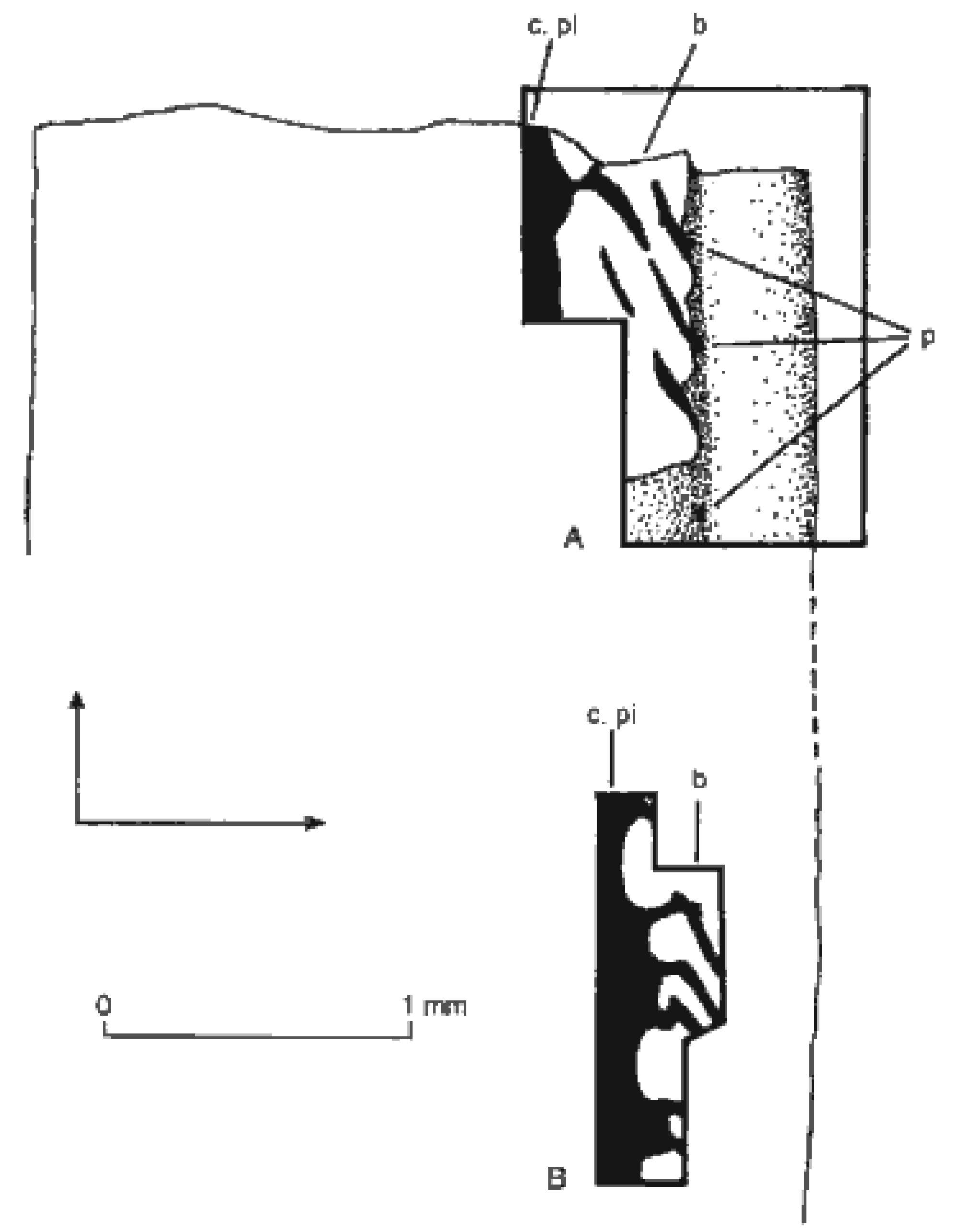


Fig. 62. *Acanthodes* sp.; distance between details A and B of inner structure of fin spine is 4.3 mm (reduced length of anterior margin is marked by dashed line), the detail A is placed 12 mm from the distal spine termination and the detail B only 7.7 mm, anterior and dorsal directions are marked by arrows; YA 2385; Mšec Member.

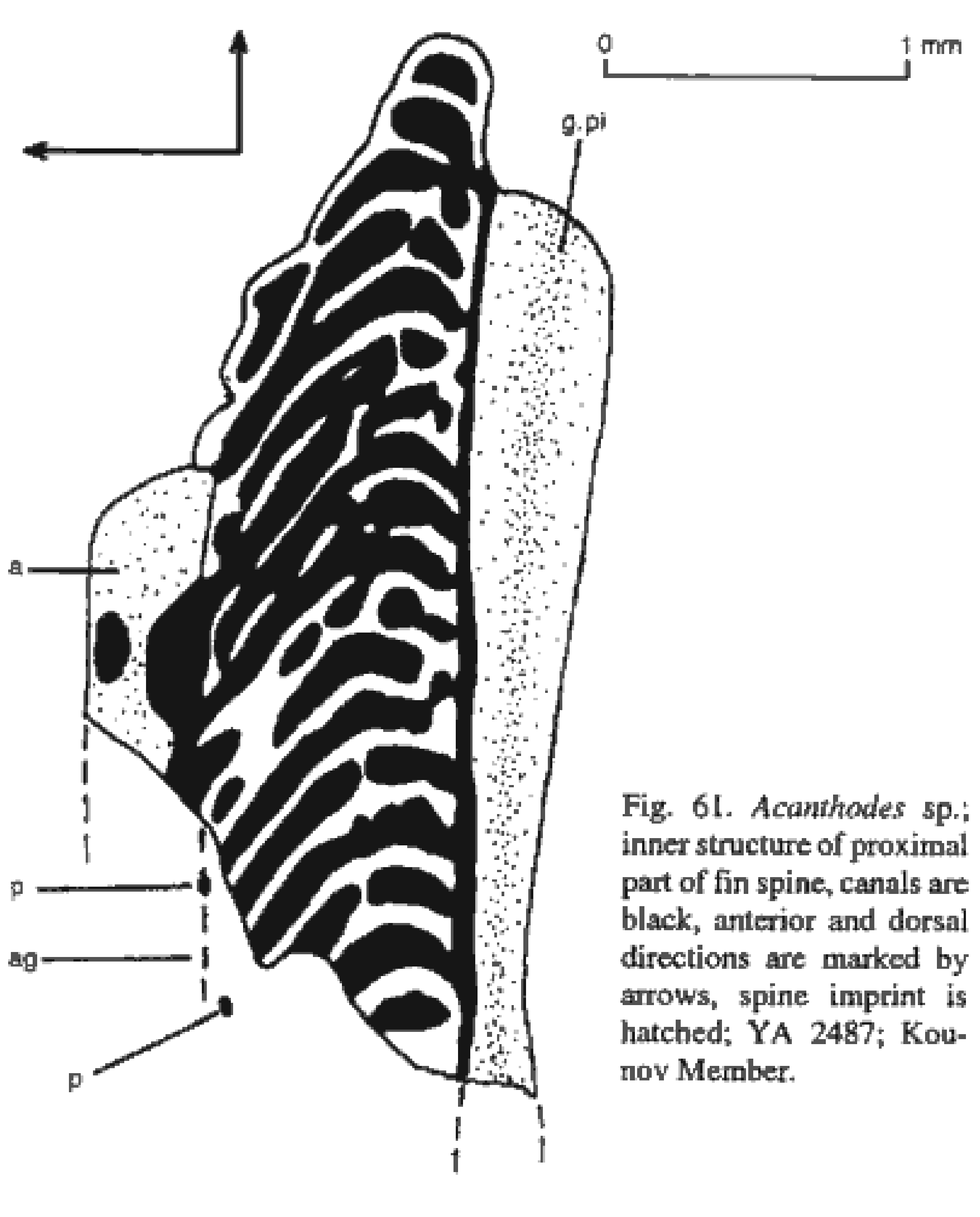


Fig. 61. *Acanthodes* sp.; inner structure of proximal part of fin spine, canals are black, anterior and dorsal directions are marked by arrows, spine imprint is hatched; YA 2487; Kounov Member.

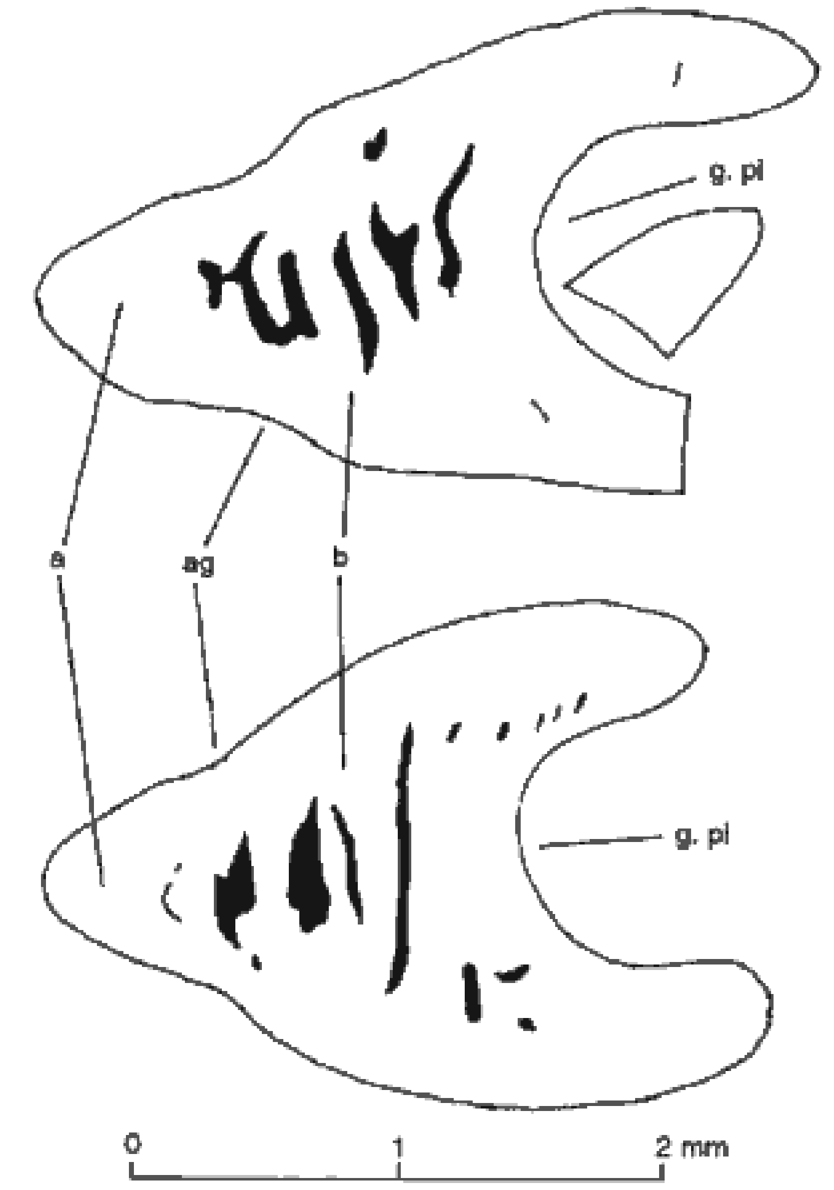


Fig. 63. *Acanthodes* sp.; cross sections of the proximal part of fin spine (distance between them is 3.6 mm); YA 2400; Mšec Member.

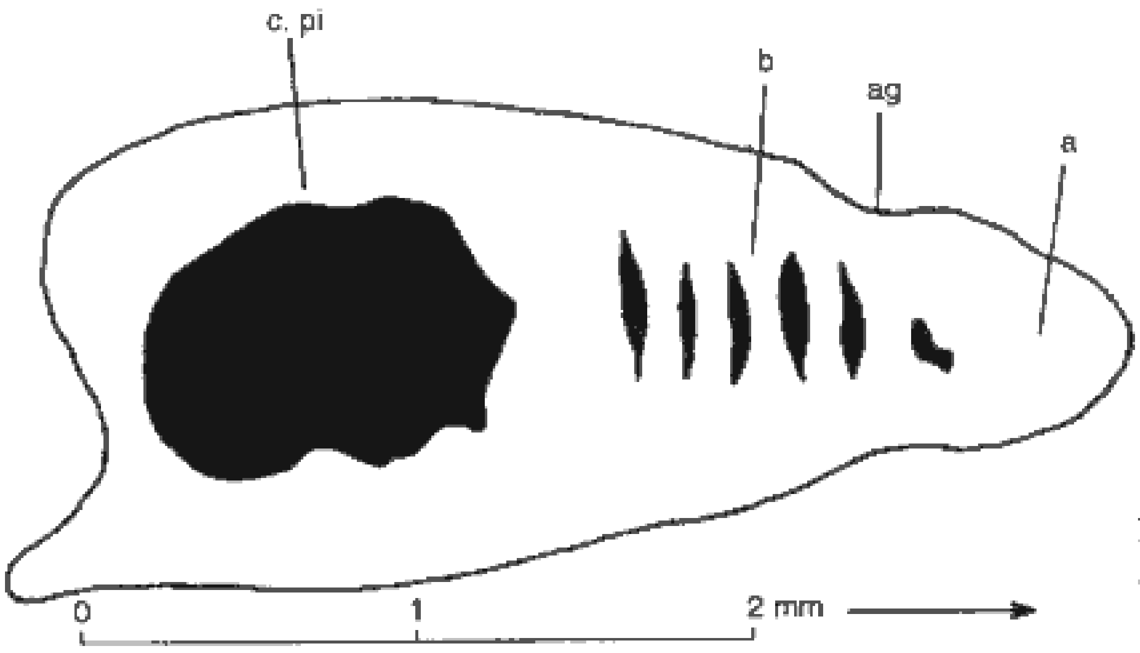


Fig. 64. *Acanthodes* sp.; cross section of the fin spine, distance from the distal spine termination is 40 mm, anterior direction is marked by an arrow; YA 2379; Mšec Member.

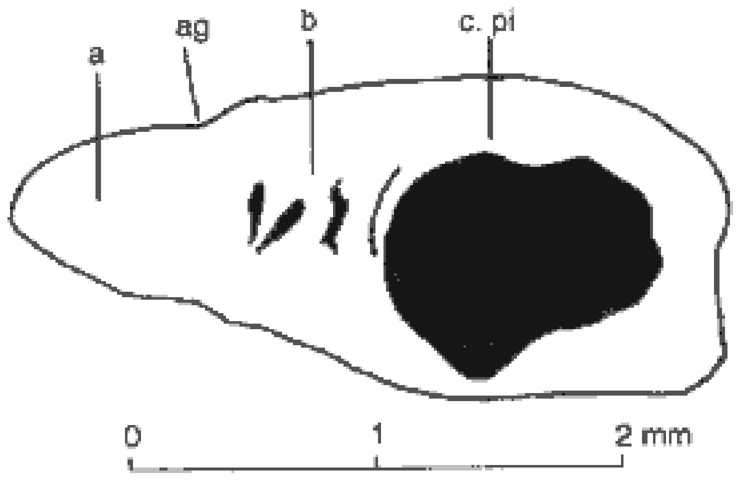


Fig. 65. *Acanthodes* sp.; cross section of the fin spine, distance from the proximal spine termination is 16.5 mm; YA 2383; Mšec Member.

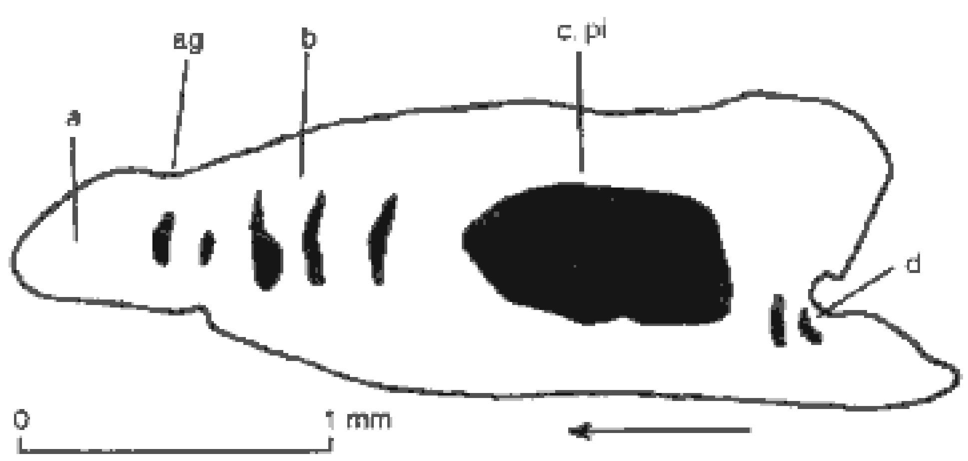


Fig. 66. *Acanthodes* sp.; cross section of the fin spine, anterior direction is marked by an arrow; YA 2371; Mšec Member.

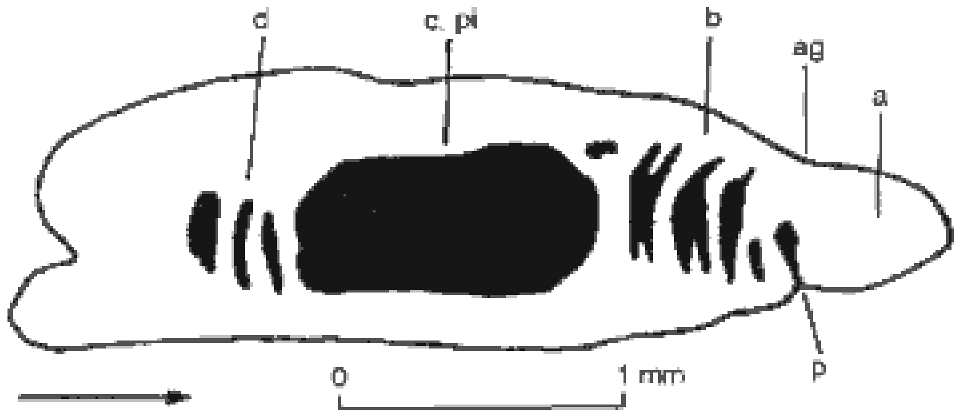


Fig. 67. *Acanthodes* sp.; cross section of the fin spine which is illustrated in Pl. 20, anterior direction is marked by an arrow; YA 2362; Mšec Member.

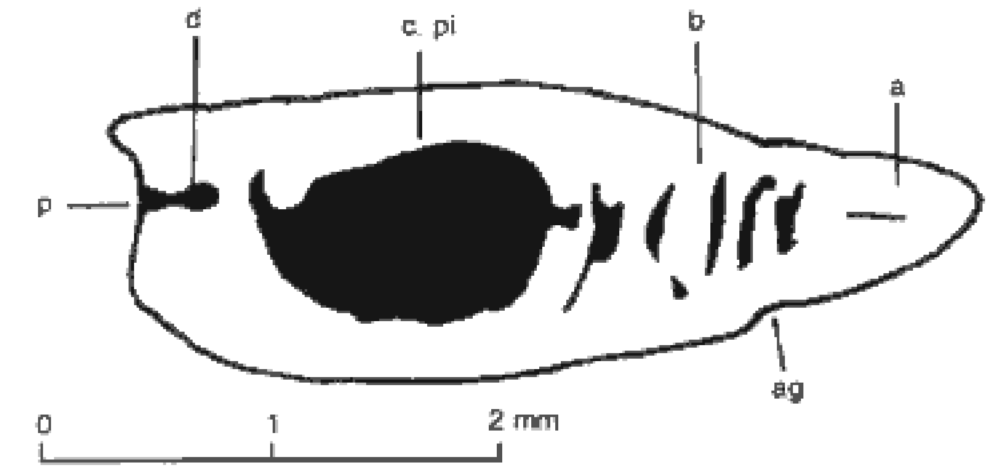


Fig. 68. *Acanthodes* sp.; cross section of the fin spine; YA 2382; Mšec Member.

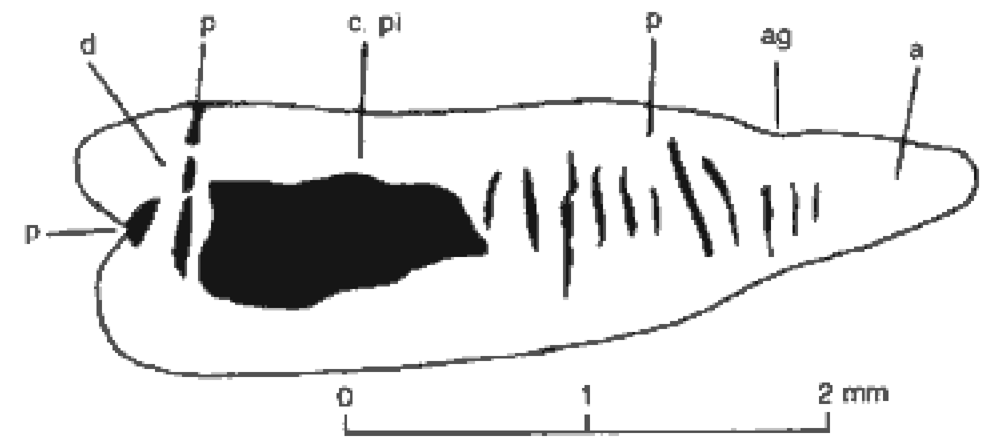


Fig. 69. *Acanthodes* sp.; cross section of the fin spine; YA 2393; Mšec Member.

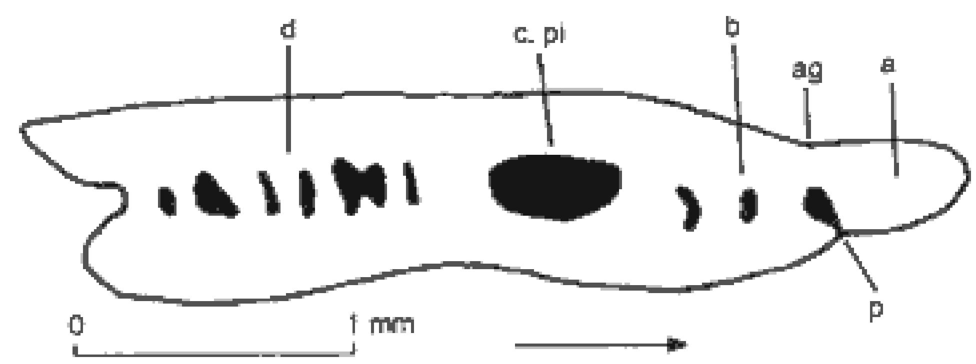


Fig. 70. *Acanthodes* sp.; cross section of the fin spine; YA 2368; Mšec Member.

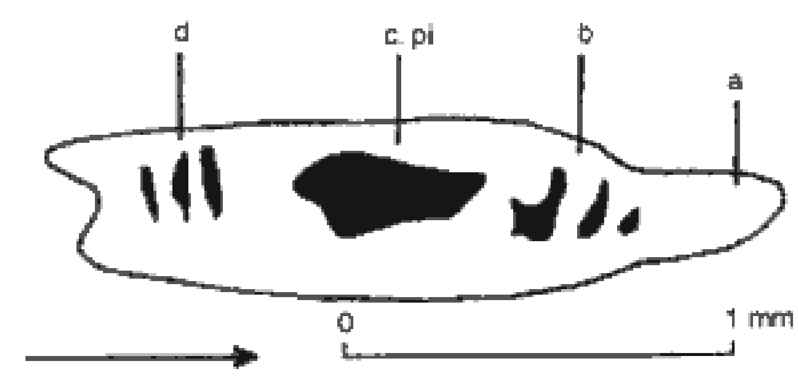


Fig. 71. *Acanthodes* sp.; cross section of the fin spine, distance from the distal spine termination is 11 mm, anterior direction is marked by an arrow; YA 3636; Kounov Member.

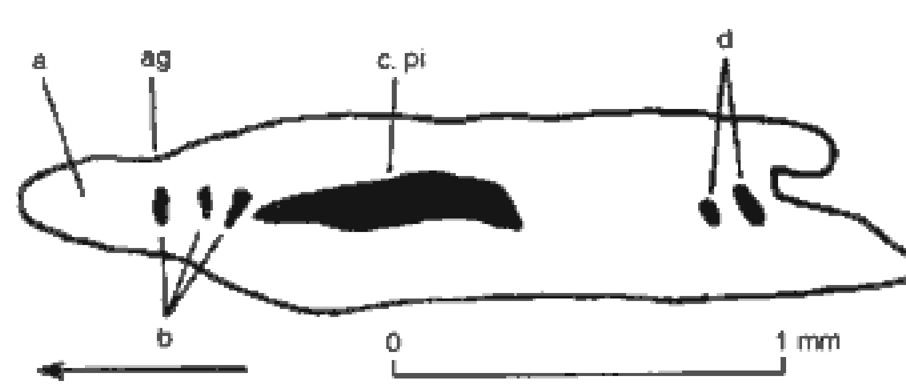


Fig. 72. *Acanthodes* sp.; cross section of the fin spine, anterior direction is marked by an arrow; YA 2360; Mšec Member.

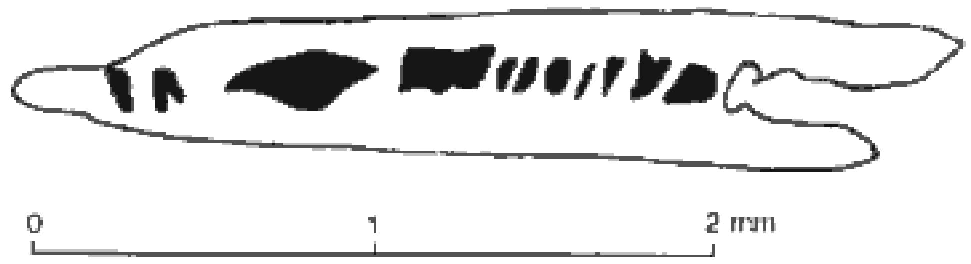


Fig. 73. *Acanthodes* sp.; cross section of the distal part of the fin spine, distance from the proximal spine termination is 44 mm; YA 2402; Mšec Member.

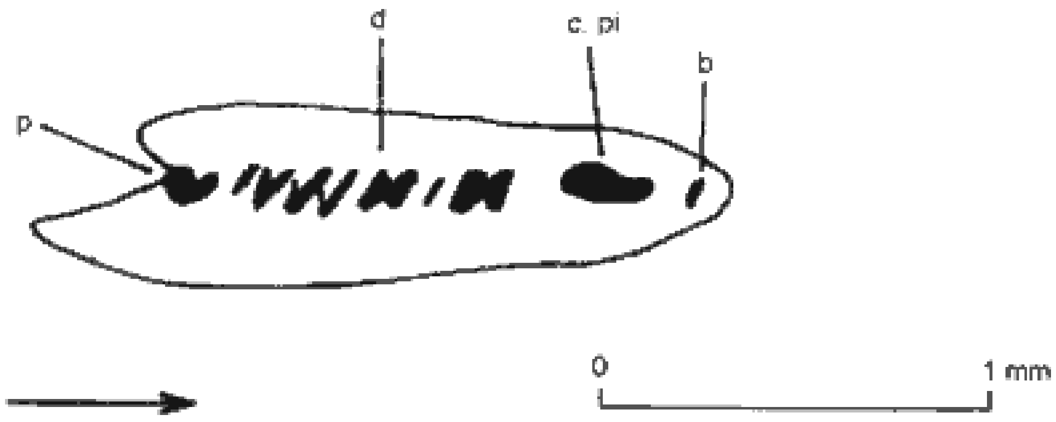


Fig. 74. *Acanthodes* sp.; cross section of the distal part of the fin spine which was figured by FRITSCH (1893, Fig. 256) as *Acanthodes punctatus*, anterior direction is marked by an arrow; M 826; Kounov Member.

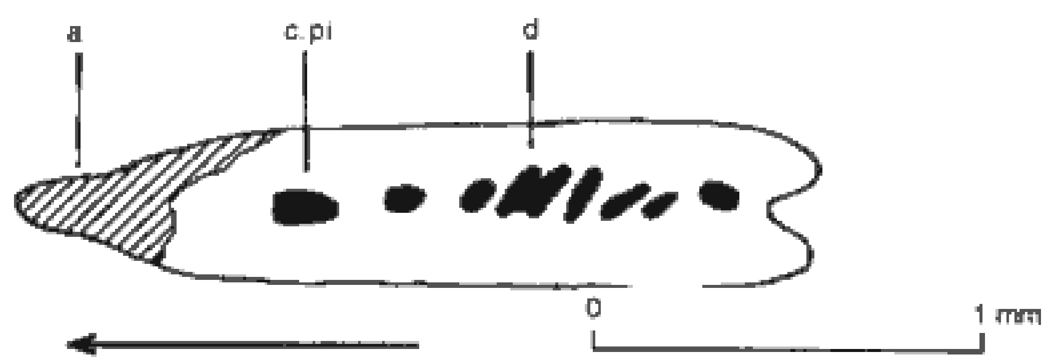


Fig. 75. *Acanthodes* sp.; cross section of the fin spine, distance from the distal spine termination is 7 mm, anterior direction is marked by an arrow, broken part is hatched; YA 2470; Kounov Member.

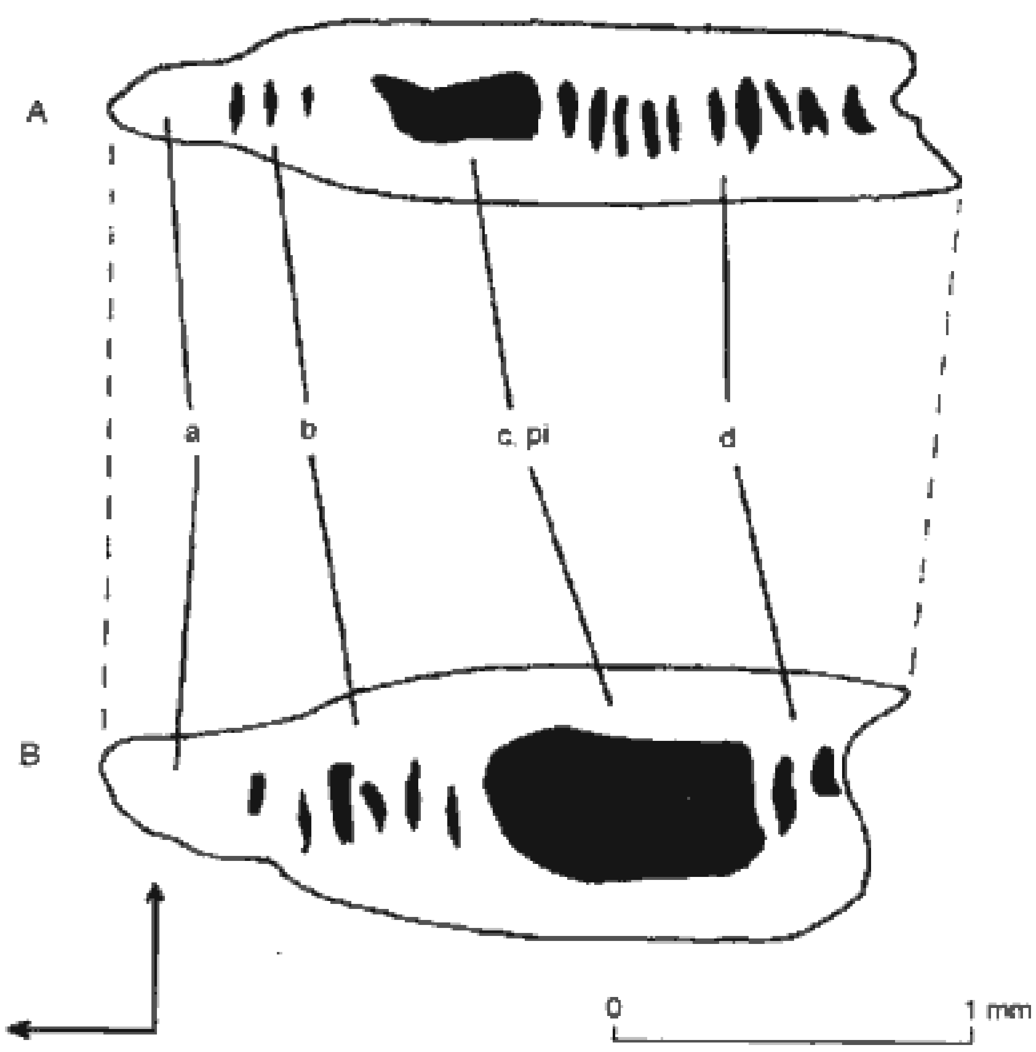


Fig. 76. *Acanthodes* sp.; two cross sections of the fin spine which was figured by FRITSCH (1893, Pl. 107/9) as *Acanthodes punctatus*, distance between the cross section A (natural broken) and B (original polished section of FRIČ) is 11 mm, anterior and distal directions are marked by arrows; M 1364; Kounov Member.

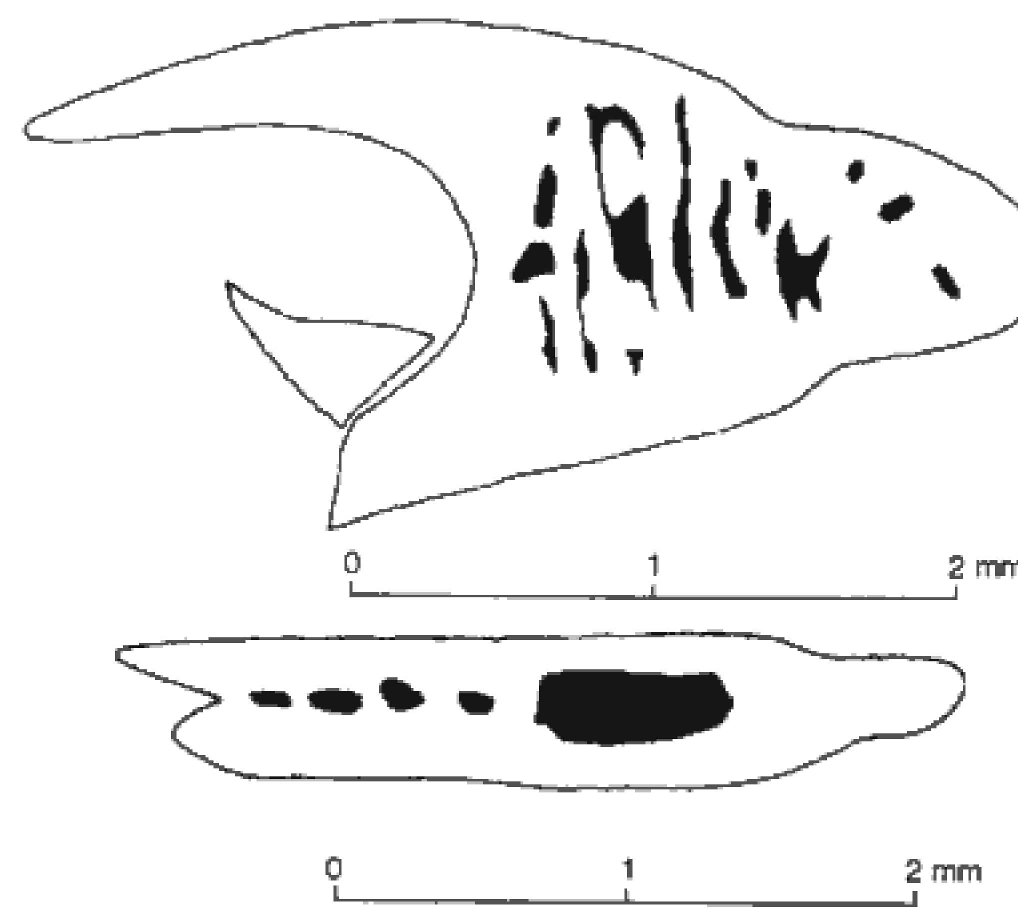


Fig. 77. *Acanthodes* sp., cross sections of the proximal and distal parts of fin spine, distance between them is 29 mm; YA 2419; Zdětín Horizon.

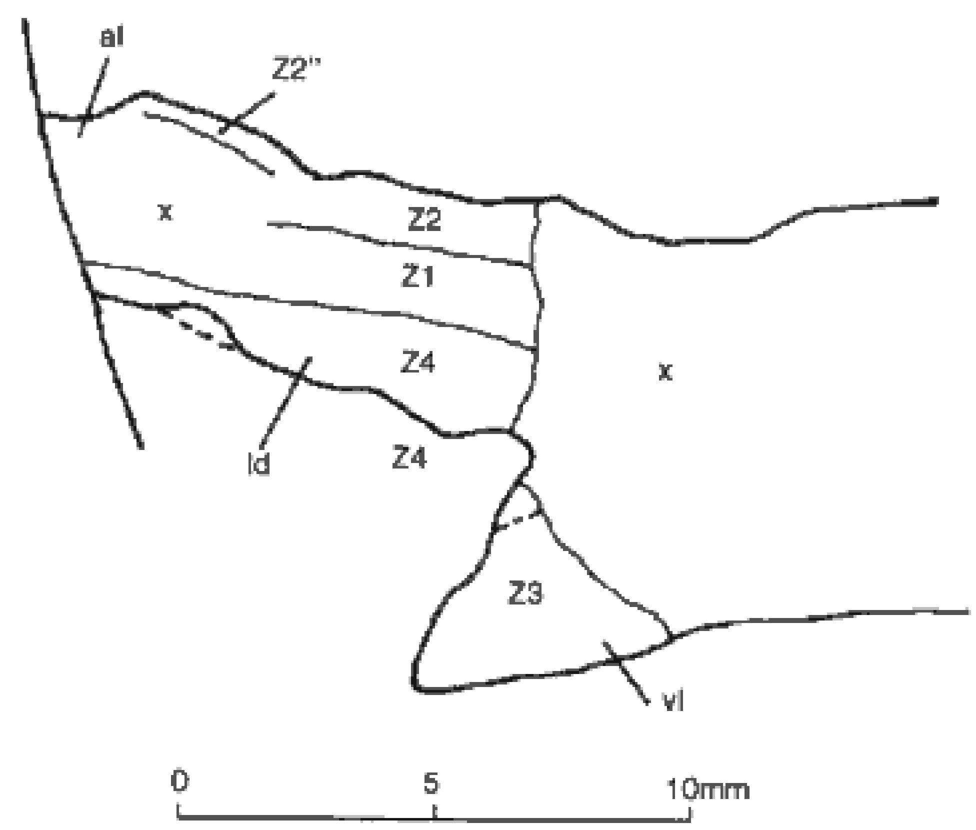


Fig. 78. *Acanthodes* sp., caudal fin of a small specimen; YA 2359; Mšec Member.

Isolated circumorbital plates (or segments) are common (Pls. 18C, 19H, 20A, 20B, 20D, and 20E). The style of their sculpture is the same as in *Acanthodes fritschi* n. sp. (see above), regardless of insignificant differences within the genus *Acanthodes*. Segments of various ontogenetic stages were found. Small plates show fine sculpture which is composed of prevailing striae and few minute tubercles (Fig. 56). Large plates show conspicuous sculpture with larger and more numerous tubercles which are often fuse into the short ridges.

The comparatively short branchiostegal rays are well preserved along the ventral margin of the meckelian cartilage of M 1115 (Pl. 18D). Their maximum width is 0.25 mm and the longest ones are at least 8.5 mm long. The FRITSCH's illustration (1893; Pl. 107/6) is incorrect.

Scapulocoracoids are the most frequently preserved parts of pectoral girdles. They are often articulated with suprascapulae (Pl. 18B). Procoracoids are mostly missing (probably as a result of postmortem processes) or imperfectly preserved. Their specific determination is therefore impossible.

The largest number of isolated findings represent scales and spines. Only the ventral spines may be distinguished among isolated spines on the basis of morphology. The pectoral fin spines are recognizable only when they are associated with the pectoral girdle. The great number of isolated spines allowed more detailed investigation of their inner structure on the basis of natural sections, especially the cross sections. The graph in Fig. 34 shows the dependence of the maximum spine width on the spine length. No differences between *Acanthodes fritschi* n. sp. and *Acanthodes* sp. are visible in this point. No significant differences among this material and spines of some other species of *Acanthodes* were observed. The largest spine found so far is the poorly preserved specimen M 3646 (Ploužnice Horizon) of estimated length about 71 mm. The outer spine morphology was described above under *Acanthodes fritschi* n. sp. Specimens YA 2374 (Fig. 57) and YA 2383 (Fig. 58) show a readily visible posterior groove which is deeper in the second specimen. The posterior groove can be deep with a U-shaped cross section or, by contrast, shallow to imperceptible. Pores of various size are situated in the groove. They are circular and irregularly placed. The inner canal system leads into these pores. The fin web was probably fixed to the fin spine along the anterior rib (further rows of oval pores are placed in the grooves between the anterior rib and the body of the spine). All pores doubtless served for innervation of and circulation within the fin web which thus was not limited to its base in this respect.

The inner structure of spines was already described by ZAJÍC (1985b; p. 282, Fig. 5). The "pith" cavity (main longitudinal canal) is circular in cross-section. Its proximal region opens into the posterior margin of the spine and forms a consequently deep and open "pith" groove with U-shaped cross section. The "pith" groove closes distally and successively shifts from the posterior to the anterior region of the spine body (its diameter simultaneously decreasing up to the spiny tip). The "pith" cavity is missing in the distal one fifth to one sixth of the spine. This structure therefore cannot be limited only to that part of the spine which was inserted between the myomeres as mentioned by WATSON (1937). An indicator of the depth of insertion could be the length of the "pith" groove. The canal system is present beside the "pith" cavity. HEYLER (1969a, b) was the first to describe the canal system as cavities which are separated one another by the flat septa and not as set of tube-shaped canals. ZAJÍC (1985b) described four zones of canals which it is possible to differentiate on the longitudinal section (Figs. 59 and 60). Zone a is represented by compact bone without canals in the anterior rib. Zone b is represented by a comparatively regularly arranged system of canals oblique to both longitudinal axis and spine surface. This zone communicates with the anterior groove by a row of pores. Zone c is mostly occupied by "pith" cavity which is circular or oval in cross-section. Zone d is represented by irregular anastomosing and moderately undulated canals (roughly parallel with the longitudinal spine axis). This zone gradually broadens from the posterior spine margin onward on the whole distal part of the spine. Another zone (e) was recognized during the recent investigation (Fig. 60) but its characteristics are not explicit (Fig. 61). The pattern of communication between inner canals and outer surroundings by means of pores is readily visible in Figs. 62, 67–70, and 73–74 and in Pls. 21D, E. The relationship of the changes of inner structure on the distance from both spine terminations is well shown on the spine cross-sections. The deep "pith" groove closes distally and forms the large "pith" cavity. The "pith" cavity successively diminishes (in the distal termination, it is entirely absent) and the spine flattens in the distal direction (Figs. 63–77).

The only one fragment of caudal fin of a small specimen was found (Fig. 78; Pl. 22C). Scales of adjacent part of the trunk are poorly preserved and determination of this specimen as *Acanthodes fritschi* n. sp. is therefore not possible.

Scales of specimens which are named here as *Acanthodes* sp. have crowns with poorly expressed posterior projections (Pls. 22E-G) or without them. These projections were, however, most probably originally present and their very delicate structure could be lost in various ways. Well preserved specimens of *Acanthodes fritschi* n. sp. show fewer complete preserved scales.

Ontogeny: The bone association of a young specimen (mandibular bone, articular, circumorbital bone, and pectoral girdle) is shown in Fig. 56 and Pl. 19F. The articular is short and the mentomandibular is not preserved. The sculpture of the circumorbital bone consists mostly of fine striae. The suprascapula is already developed in specimens of this size.

Stratigraphic occurrence: Stephanian B (Jelenice-Kounov Members)-Stephanian C (Zdětín, Klobuky, Ploužnice, and Štěpanice-Čikvásky Horizons).

Geographic occurrence: Czech Republic, Bohemia; Plzeň, Rakovník, Kladno, Roudnice, Mšeno, Mnichovo Hradiště, and Krkonoše Piedmont Basins.

Sites: Jedomělice, Klobuky, Kounov, Malesice, Nedvězí, Peruc, Ploužnice, Slaný, Záboř, Žilov, and boreholes Bc-1 (Brodce), Bš-1 (Byšice), Dch-3, 4 (Drchkov), Kbl-2 (Kbel), Ke-5, 7 (Kralovice), Krp-1 (Krpy), Lib-1 (Liběchov), Lo-6 (Lotouš), Mt-1 (Martiněves), MV-1, 2 (Mělnické Vtelno), Nb-5 (Neprobylice), Ob-5 (Otruby), Ři-22, 25, 26, 30 (Řisuty), Sa-2a, 21 (Slaný), Sč-1 (Semčice), Sš-1 (Sušno).

3. Taxonomy

3.1. Classification of Acanthodii

The following classification is based on that of ZIDEK (1993) and was first used by the author (ZAJÍC 1995):

Class Acanthodii OWEN, 1846

Order Ischnacanthiformes WOODWARD, 1891