the Czech Republic (GAČR 206/00/0942 – Permian acanthodians of the Czech Republic). Some of the new samples were collected with help of the previous project of the Grant Agency of the Czech Republic (GAČR 205/94/0692 – Environmental changes on the Carboniferous/Permian boundary and their impact on the assemblages of organisms in fossiliferous horizons in the Krkonoše Piedmont Basin) and with help of the Grant Agency of the Charles University, Prague (GAUK 227/200/B-GEO/PřF – Reconstruction of the environmental changes and the late Variscian development of the eastern part of the Bohemian Massif: Sedimentary and paleontological records of the Boskovice Basin). I thank to Zbyněk Šimůnek from the Czech Geological Survey, Prague for important help with collection of new acanthodian specimens. My thanks belong to Boris Ekrt from the National Museum, Prague for help during my study of older acanthodian specimens. Stanislav Štamberg from the Regional Museum of Eastern Bohemia, Hradec Králové helped me significantly during my study of his new acanthodian collection coming from Krkonoše Piedmont Basin and especially from the Boskovice Basin. I thank to Růžena Gregorová and Martin Ivanov from the Moravian Museum in Brno for help with my study of the older fossil material from the Boskovice Basin. Thanks to Miroslav Bařina, director of the Town Museum Nová Paka, I could study the sample with highest number of individuals, Ewa Swidnicka, curator of the Museum of the Department of Paleozoology of the Wroclaw University, allows me to study the original material of *Acanthodes gracilis* from the type locality and other comparative acanthodian material. My particular thanks go to my kind colleague Sally Young from the Department of Palaeontology of the Natural History Museum, London for help with my study of the large comparative collection of acanthodians and for important comments of my work.

2. Description

2.1. INDEX OF ABBREVIATIONS

alb – axial lobe of the caudal fin
as – anal fin scales
asp – anal fin spine
asq – anterior border of squamation
cmo – circumorbital bone
cs – semicircular canal
dmt – dermotrichia
d_O – outer diameter of circumorbital ring
dsp – dorsal fin spine
es – enlarged scales
gla – gill arch
glr – gill rakers
iosl – infraorbital sensory line
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_T – total specimen length
l_V – ventral spine length
lb – labyrinth infilling
m. add – surface for the dorsal adductor muscles
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
orb – orbit
oto – otolith
pgl – pectoral girdle
pop – preopercular sensory line
pr – procoracoid
psp – pectoral fin spine
qjsl – quadratojugal sensory line
qu – quadratum
rbr – branchiostegal ray(s)
rdl – radials
sc – scapular blade
scd – semicircular duct
scl – sacculus
sl – sensory line
sosl – supraorbital sensory line
ssc – suprascapula
ts – trunk scales
v – ventral sensory line (unpaired)
$v_{A\text{-}D}$ – anal-dorsal spine distance
$v_{D\text{-}Z}$ – distance from dorsal spine to caudal cleft
$v_{P\text{-}V}$ – pectoral-ventral spine distance
$v_{V\text{-}A}$ – ventral-anal spine distance
$v_{Z\text{-}O}$ – distance from caudal cleft to tip of axial lobe
vl – ventrolateral sensory line
vlb – ventral lobe of the caudal fin
vsp – ventral fin spine
vss – ventral scaly shield
Z1, Z2, Z2", Z3, Z4 – Heyler's scale zones of the caudal fin

2.2. METHODS

Methods of measurements and subsequent definition, calculation, and valuation of the ratios were exactly described in Zajíc (1998). There is highly important to assess grade of specimen deformation before a measurement. The postmortem body bents are not the main obstacle (see Zajíc 1998). Acanthodian trunk is frequently affected by a longitudinal deformation both compression and dilatation. The compression is accompanied by the skin wrinkles. The dilatation comes through the vertical skin gaps. Longitudinally deformed acanthodian bodies cannot be used for measurements of body proportions.

Digital photographs (large contrasting printouts) were successfully used as foundation of drawings. Cameras Nikon Coolpix 950 and Nikon Coolpix 4500 were used.

Specific types of sediment (marlstones, some limestones) allow chemical preparation and separation with help of acetic acid (for methods see Štamberg 2003, Zajíc 1997a, 1997c).

2.3. *Acanthodes gracilis* (BEYRICH, 1848)

Acanthodes gracilis (BEYRICH, 1848)
(Figures 3–25, 27–30; Plates 1A–6C, 9A–14B)
1848 *Holacanthodes gracilis*: E. Beyrich, Über *Xenacanthus decheni* und *Holacanthodes gracilis* etc.; p. 31–32.
1893 *Acanthodes gracilis* var. *Bendai*: A. Fritsch, Fauna der Gaskohle etc.; p. 64–67 (partim); Figs 261 and 265; Pl. 107/11.
1939 *Acanthodes gracilis* (BEYR.) var. *bendai* Fr.: J. Augusta, Acanthodes gracilis (BEYR.) var. bendai Fr. Etc.; p. 269–270.
1946 *Acanthodes gracilis bendai:* J. Augusta, Příspěvky k poznání moravského etc.; p. 80–81 (partim).
1947. *Acanthodes gracilis* (BEYRICH) ROEMER var. *bendai* Fr.: J. Augusta, Spodnopermská zvířena a května etc.; p. 196–197 (partim).
1989 *Acanthodes "gracilis bendai"*: J. Zajíc, Remains of Permo-Carboniferous etc.; p. 289–291 (partim – specimen YA 1360).

Notes: The synonymy (above) is not complete for the species because the planned redescription of *Acanthodes gracilis* by HEIDTKE and SCHNEIDER will come soon (HEIDTKE 1998, p. 6). The herein used synonymy includes both the first description and descriptions of important Bohemian and Moravian specimens (Czech Republic region). The references without description or pictures are not included. The diagnosis concerns just Bohemian and Moravian specimens by the same reason.

Age: Lower Permian: Asselian (Lower Autunian).

Material: Specimens from various localities and boreholes of the Rudník Horizon of the Krkonoše Piedmont Basin – M 1933, M 1937, M 4227, M 4228/1+2, M 4358–M 4360, M 4364–M 4365, M 4369–M 4371, M 4377/2, M 4383–M 4384, M 4389–M 4390, M 4394/1–M 4395, M 4401–M 4406, M 4413–M 4414, M 4418–M 4420/1, M 4423, M 4425, M 4433, M 4435–M 4436, M 4440, M 4442, M 4447/2, M 4453–M 4454, M 4461–M 4463, M 4465, M 4467–M 4470, M 4475, M 4477–M 4478, M 4481, M 4491–M 4493, M 4497–M 4499, M 4501, M 4514/2, YA 1360, No. 30895, Nos 63635–63636, Nos 63639–63640, Nos 63643–63645, No. 63647; Specimens from the Zbýšov Horizon of the Boskovice Basin (localities Padochov and Zbýšov) – M 4235–M 4236, M 4245, M 4247, M 4263, M 4270, M 4282, M 4307–M 4308, M 4311/1–M 4312, M 4321–M4322, M 4326–M 4327, M 4331, M 4343, M 4345–M 4347, M 4350–M 4351; Specimens from the Zbraslavec Horizon (Zbraslavec locality) – PUK 15, PUK 17, PUK 24-PUK 25; Specimens from the Zboněk-Svitávka Horizon (Černá Hora locality) – PUK 02-PUK03, PUK 05; Specimens from the Lubě Horizon (Kladoruby locality) – M 4286–M 4287, M 4291–M 4293, No. 63752/2–63753, No. 63756–63758, No. 63765, No. 63769, No. 63781, No. 63784, No. 63 786, No. 63789, No. 63794, No. 63796/A–63797, No. 63802–63803, No. 63809.

Diagnosis (Bohemian and Moravian specimens): Large-sized acanthodian (estimated length more than 567 mm). Completely squamated area starts in front of the pectoral girdle. Dorsal fin slightly more posterior than anal fin. Anal : pectoral spine length ratio (A^1) = 50–76%; dorsal : pectoral spine length ratio (A^2) = 50–68%; ventral : pectoral spine length ratio (B) = 15–62%; pectoral spine length: total specimen length (C) = 15%; anal spine length : total specimen length (D^1) = 10%; dorsal spine length : total specimen length (D^2) = 8%; ventral spine length : total specimen length (E) = 4%; distance between pectoral and anal spines : total specimen length (F) = 46%; distance between ventral and anal spines : total specimen length (G) = 32%; prepectoral : total specimen length (H) = 23%; distance from dorsal spine to caudal cleft : total specimen length (I) = 19%; distance from caudal cleft to tip of axial lobe : total specimen length (J) = 10%; outer diameter of circumorbital ring : prepectoral length (K) = 24–30%; mandibular bone : pectoral spine length (L) = 49–88%; distance between pectoral and ventral spines : distance between ventral and anal spines (M) = 29–88%; mandibular bone : prepectoral length (N) = 45–95%; mandibular bone : total specimen length (O) = 11%. Circumorbital ring with 5 segments. Wide scapulocoracoid plate: suprascapula co-ossified with scapular blade. Pectoral fin supported by short dermotrichia. The caudal fin contains five short radialia. Delicately pitted scale crown with very thin pointed posterior projection.

Description: The body of younger specimens is rather fusiform (see Fig. 21), the longer ones are slenderer but not quite eel-like. The body shape of the young specimens is therefore similar as in *Acanthodes bridgei* (ZIDEK 1976, Fig. 15). Older specimens are more elongated, similarly as in *Acanthodes bronni* (HEIDTKE 1990a, Fig. 39). The total length were estimated with the aid of the ratio C (15) which were computed from the data measured in specimen M 4413 + M 4414. In the event of incomplete pectoral fin spines is possible to use the pectoral fin spines maximum width/length diagram (Fig. 15). The estimated total length ranges from 61 to 567 mm. However, computed total specimen lengths could be underestimated in some larger specimens. Measurement of distances is often problematic. Acanthodian soft body is frequently affected by a deformation (see chapter 2.2). Three clusters of measured values were used for computing of the body ratios (see Fig. 3). Body proportions (in %) are following: anal : pectoral spine length ratio (A^1) = 50–76 (total average is 63); dorsal : pectoral spine length ratio (A^2) = 50–68 (total average is 57); ventral : pectoral spine length ratio (B) = 15–62 (total average is 18); pectoral spine length : total specimen length (C) = 15; anal spine length : total specimen length (D^1) = 10; dorsal spine length : total specimen length (D^2) = 8; ventral spine length : total specimen length (E) = 4; distance between pectoral and anal spines : total specimen length (F) = 46; distance between ventral and anal spines : total specimen length (G) = 32; prepectoral : total specimen length (H) = 23; distance from dorsal spine to caudal cleft : total specimen length (I) = 19; distance from caudal cleft to tip of axial lobe : total specimen length (J) = 10; outer diameter of circumorbital ring : prepectoral length (K) = 24–30 (total average is 26); mandibular bone : pectoral spine length (L) = 49–88 (total average is 67); distance between pectoral

Measurements quality class	A^1	A^2	B	C	D^1	D^2	E	F	G	H	I	J	K	L	M	N	O	y	Estimated l_T
Exact (average)	50–73 (63)	59	25–29 (27)										30	62–84 (71)	62				
Fairly good (average)	55–76 (65)	50–68 (57)	22–62 (29)												40–59 (49)	82			
Worse but usable (average)	50–72 (61)	57	15–43 (27)	15	10	8	4	46	32	23	19	10	24–26 (25)	49–88 (66)	29–88 (52)	45–95 (64)	11	3–14	63–340
Average in total	63	57	28	15	10	8	4	46	32	23	19	10	26	67	51	68	11		

Fig. 3. *Acanthodes gracilis*, proportions and measurements based on 38 specimens from the Czech Republic. Ratios are given in percent.

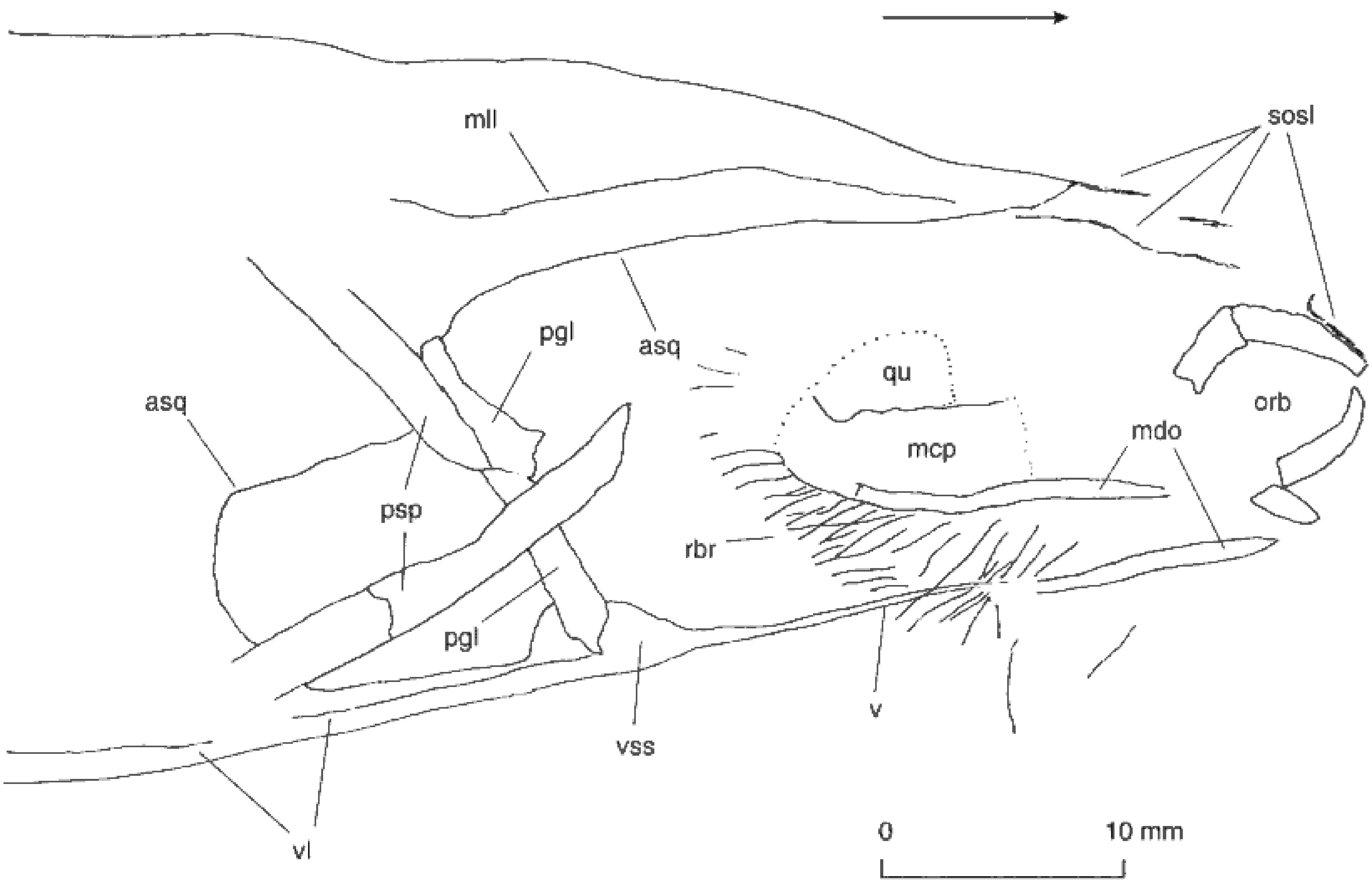

Fig. 4. *Acanthodes gracilis*, anterior part of the body in front of the ventral fin spine in lateral view; MHK 63 797; Kladoruby, Dolní pepřík; Lubě Horizon.

and ventral spines : distance between ventral and anal spines (M) = 29–88 (total average is 51); mandibular bone : prepectoral length (N) = 45–95 (total average is 68); mandibular bone : total specimen length (O) = 11. Some of extreme values (as in B, L, M, and N) come from poorly preserved specimens and total averages are therefore more applicable. The only specimen (M 4413 + M 4414) yielded the values needed for the computation of all ratios.

All elements of the neural and visceral endocrania are poorly preserved (or missing) contrary to Stephanian *Acanthodes fritschi* or Lower Permian *Acanthodes bronni*. The dermal elements (the circumorbitals, mandibular bones, branchiostegals, gill rakers, tesserae, and segments of sensory lines) are, however, rather well preserved.

Components of the neural endocranium were not recognized yet. Some fragments can, however, be admixed in hotchpotches of indeterminable viscerocranial fragments of some specimens.

Upper jaws are represented by poorly preserved quadrates that are practically always tightly connected with articulars (Fig. 4; Pl. 9A). The exact articulation and boundary of both elements are often unrecognizable. The outlines of quadrates are mostly indistinct.

The meckelian cartilage consists of two separated ossifications (Pl. 1A) – the anterior (mentomandibular) and the posterior (articular). Specimen M 4402 + M 4403 shows the best-preserved elements of the lower jaw (Fig. 5; Pls 1B and 1C). The mentomandibular is about 9.6 mm long and at most 3 mm high. The articular is around 13.5 mm long and

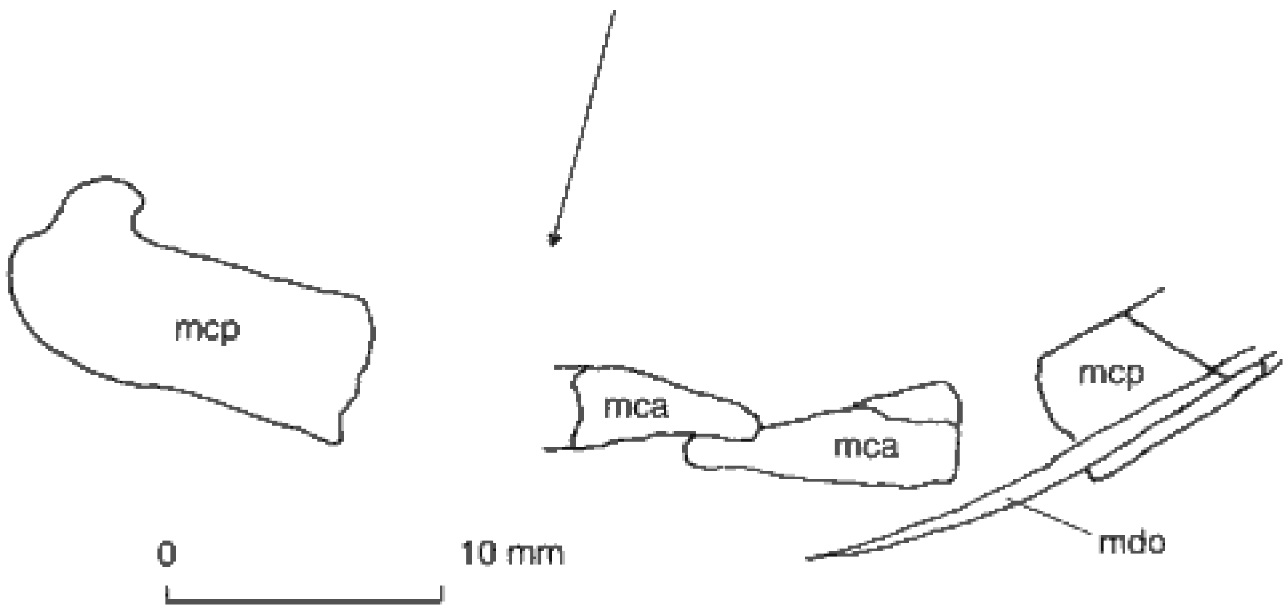

Fig. 5. *Acanthodes gracilis*; incomplete lower jaws; anterior direction is marked by an arrow; M 4402; Košťálov; Rudník Horizon.

no more than 5.4 mm high. The preglenoid process seems to be somewhat broader than in *Acanthodes fritschi* and tends anteriorly. The articular cotylus is poorly developed. The gap between the two "ossifications" of the meckelian cartilage is ca 3.5 mm. The anterior terminations of both mentomandibulars are damaged. Specimen M 4435 + M 4436 with estimated length 373 mm has the articular 12 mm long and 5 mm high. No specimen with co-ossified articular and mentomandibular was found.

Very poorly preserved fragments of hyoid and posthyoid arches are present in some specimens. They are, however, too fragmentary for a determination. They are mostly part of hotchpotches. The gill arches in natural position are not preserved but articulated gill rakers trace in varied degree their course on some specimens (Figs 6–7; Pls 4A, 9B–10A, 12D). No more than five gill rakers traces were found on one specimen. The hyoid arch or the most posterior gill one is either not present or visible. Gill rakers are larger and solider on the anterior gill arch and decrease posteriorly. Special shaped hyoid gill rakers as in *Acanthodes lundi* or *Acanthodes* sp. from Stephanian B of the Central and Western Bohemian Basins (see Zidek 1992, Fig. 12) were not found. The gill rakers are tightly articulated, sometimes create rigid blocks and look like baked together. The individual gill rakers are sabre-shaped (more or less curved). Their bases are always poorly preserved (primarily weak "ossification"?) with indistinct shape. Maximal measured lengths oscillate between 0.4 and 3.0 mm yet. The surface of the gill rakers is not covered by striae or tiny ridges as in *Acanthodes fritschi*.

The dermal bones of the neurocranium (neural exocranium) are represented by five circumorbital bones arranged around the orbit as the circumorbital ring (Figs 4, 6–8; Pls 1A, 2A, 3B, 9A, 10B, 11B). The relationship between the outer diameter of the orbit and the estimated total specimen length is shown on the Fig. 9. The larger spread of the points is caused by difficult estimation of the outer diameter of the orbit in particular. The individual segments are numbered (in parentheses) according to Heidtke (1990a; Fig. 15) on the Fig. 7. The inner surface is smooth and concave. The outer surface is convex and covered by sculpture. The individual segments are irregularly crescent-shaped, each with an elevated rim along the inner margin. The density and nature of the sculpture depend particularly on the specimen length. Circumorbitals of the very young specimens (like M 4282; Pl. 10B) are almost smooth. The inner borders of the segments are markedly thicker (rim) and their boundaries are shaped like set of little bows. Height of the inner border increases during ontogeny up to the conspicuous concentrical rim. The ornament becomes more robust during ontogeny because the tubercles grow and become fused into ridges, and the number of radial striae increases. The rim of larger specimens is also covered by abundance of the largest tubercles which connect into short concentric ridges near the inner border of segments. The ridges become longer during ontogeny and could be slightly undulated. The radially arranged rows of smaller rounded tubercles alternated with radial striae. The radial sculpture covers the rest of surface of the larger specimens. The arrangement of this sculpture is, however, fan-shaped on the region of the shorter end of segments. The tubercles and ridges are sometimes (as in M 4394/1) high and pointed. The longest measured segment is 13.9 mm long. The whole sculpture is not so robust like in *Acanthodes fritschi* (see Zajíc 1989; Fig. 2).

The mandibular bone (or splint) is the only dermal bone of the jaws. The characteristic shaped slender bone (see Figs 4–6, 10; Pls 1A, 1C, 2C, 2B, 2D–3B) is thin and bent along about half its length. A shallow longitudinal groove is situated on the posterior half of the bone. The central bone curve lies under the gap between the mentomandibular and articular. Both (anterior and posterior) parts of the mandibular bone are almost horizontally situated in the lower jaw, although the anterior one lies somewhat higher. The curve is slightly gentler in younger specimens like in M 4413 (Pl. 2C). The most similar situation is shown by *Acanthodes fritschi* (Zajíc 1998, Figs 8, 16), *Acanthodes* sp. (Zajíc 1998, Fig. 54), *Acanthodes bourbonensis* (see Heyler 1969, Fig. 2B), and *Acanthodes lundi* (Zidek 1980, Fig. 4A) in the curve of the mandibular bone. *Westrichus kraetschmeri* shows similarly curved mandibular bone (Heidtke 2003; Fig. 3b) as well. The central curvature is not present in *Acanthodes bronni* (Heidtke 1990a, Fig. 18B; Miles 1973, Fig. 12 etc.) and still known in *Acanthodes boyi* and *Acanthodes tholeyi*. The mandibular bones in *Acanthodes gracilis* are pointed in the front and extended and flattened at the back. The posterior extension is, however, somewhat shorter than in *Acanthodes fritschi*.

The gill covers are represented by very thin branchiostegal rays (Figs 4, 6; Pls 1A, 2B, 2D, 9A, 9B, 10B, 11A, 11B) of different length. Their various shapes (from straight to variously curved) are probably caused by postmortem deformation of the relatively soft tissue. The original shape, arrangement, and body position are shown in

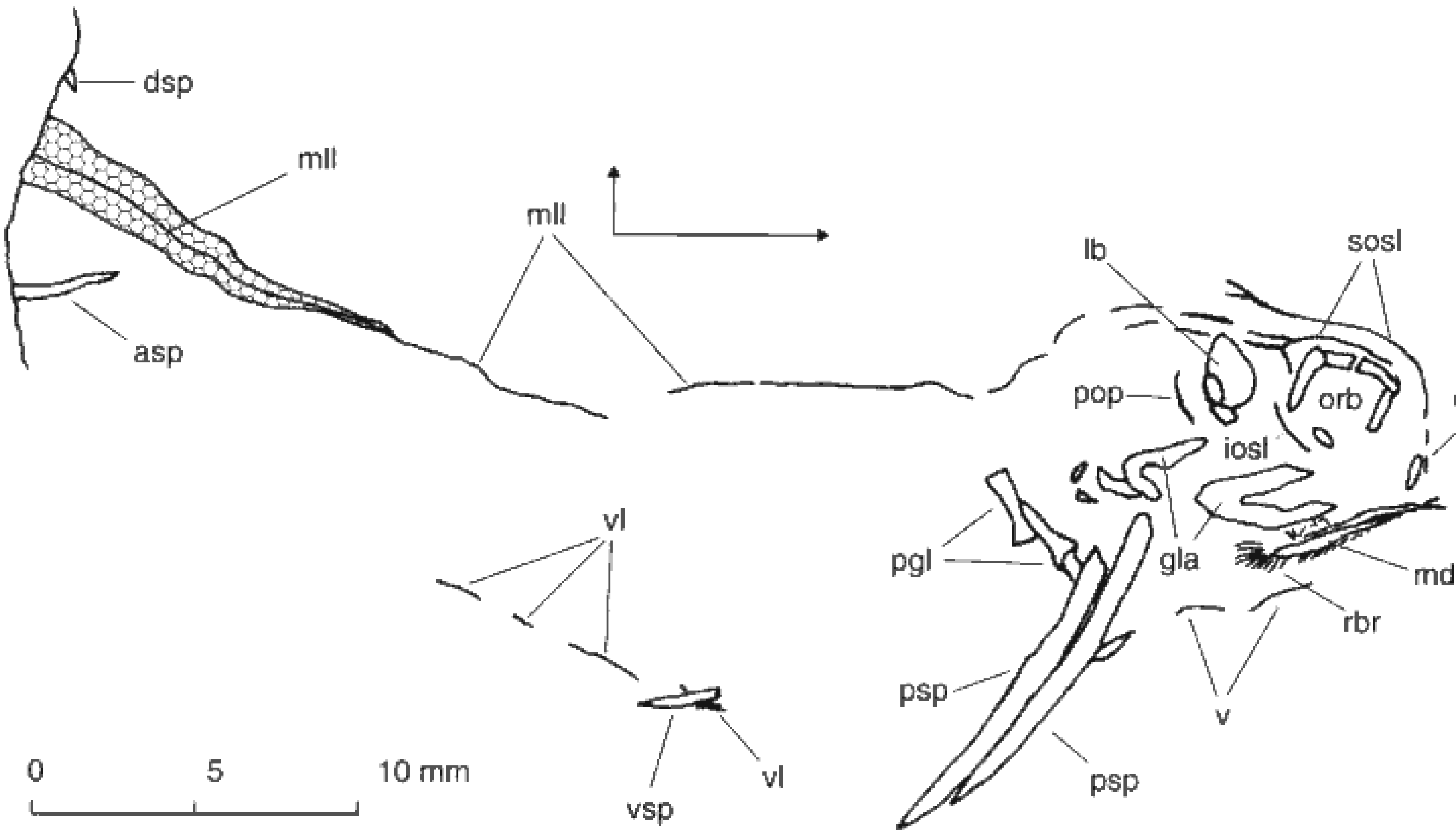

Fig. 6. *Acanthodes gracilis*; juvenile specimen, posterior part is broken off; squamation is indicated by hexagonal fill; for the detail of the pectoral region see Fig. 13; anterior and dorsal directions are marked by arrows; M 4282; Padochov; Zbýšov Horizon.

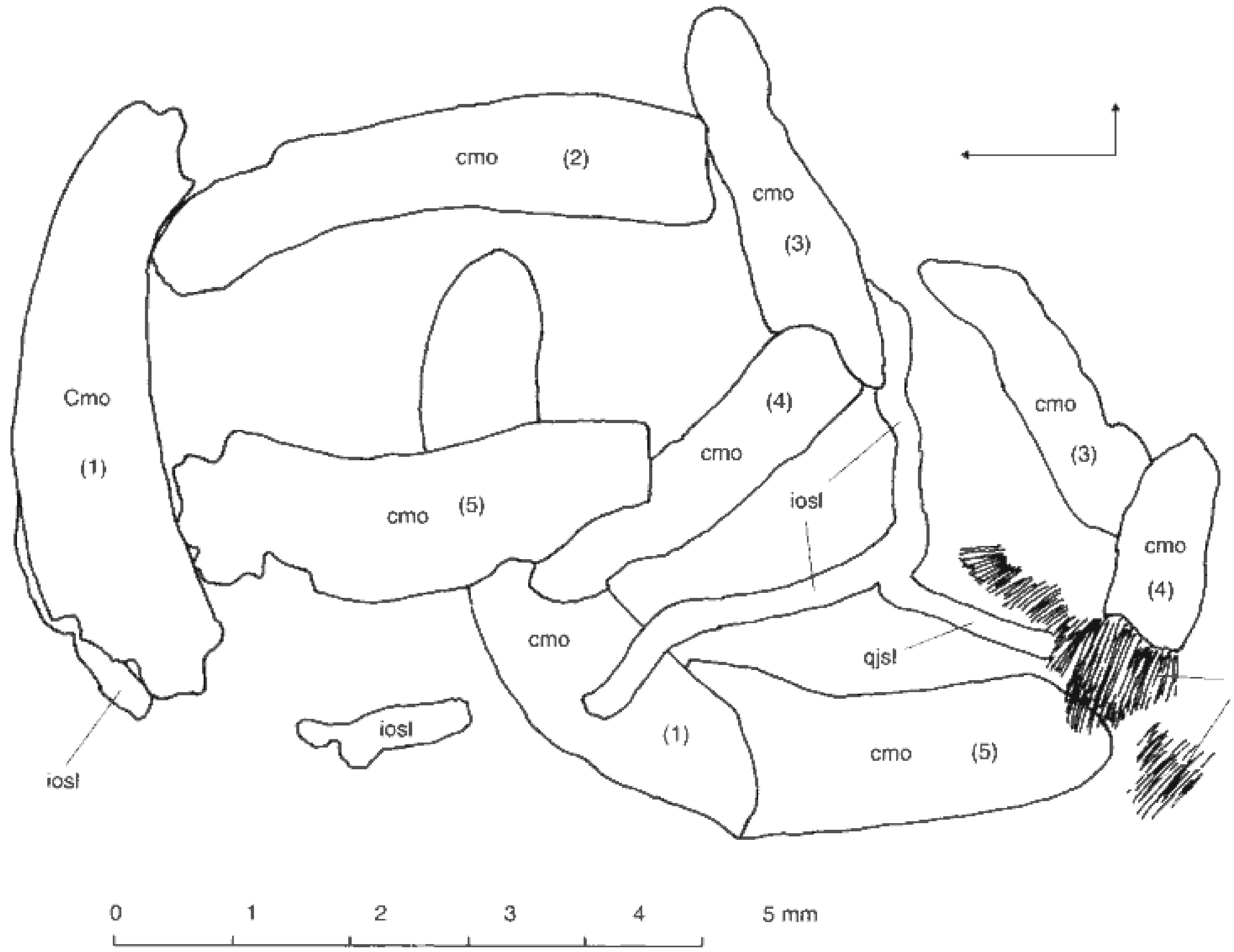

Fig. 7. *Acanthodes gracilis*; both orbits and the principal sensory lines of the head; short sections of sensory lines and disarticulated elements like sensory line segments or gill rakers are not drawn; the individual circumorbitals are numbered according to HEIDTKE 1990a (numbers in parentheses); anterior and dorsal directions are marked by arrows; M 4307; Padochov; Zbýšov Horizon.

Acanthodes sp. specimens M 4344 (Fig. 36) and M 4274 + M 4275 (Pl. 15B).

The labyrinth and otoliths are known in not many acanthodian species. For the situation within the orders

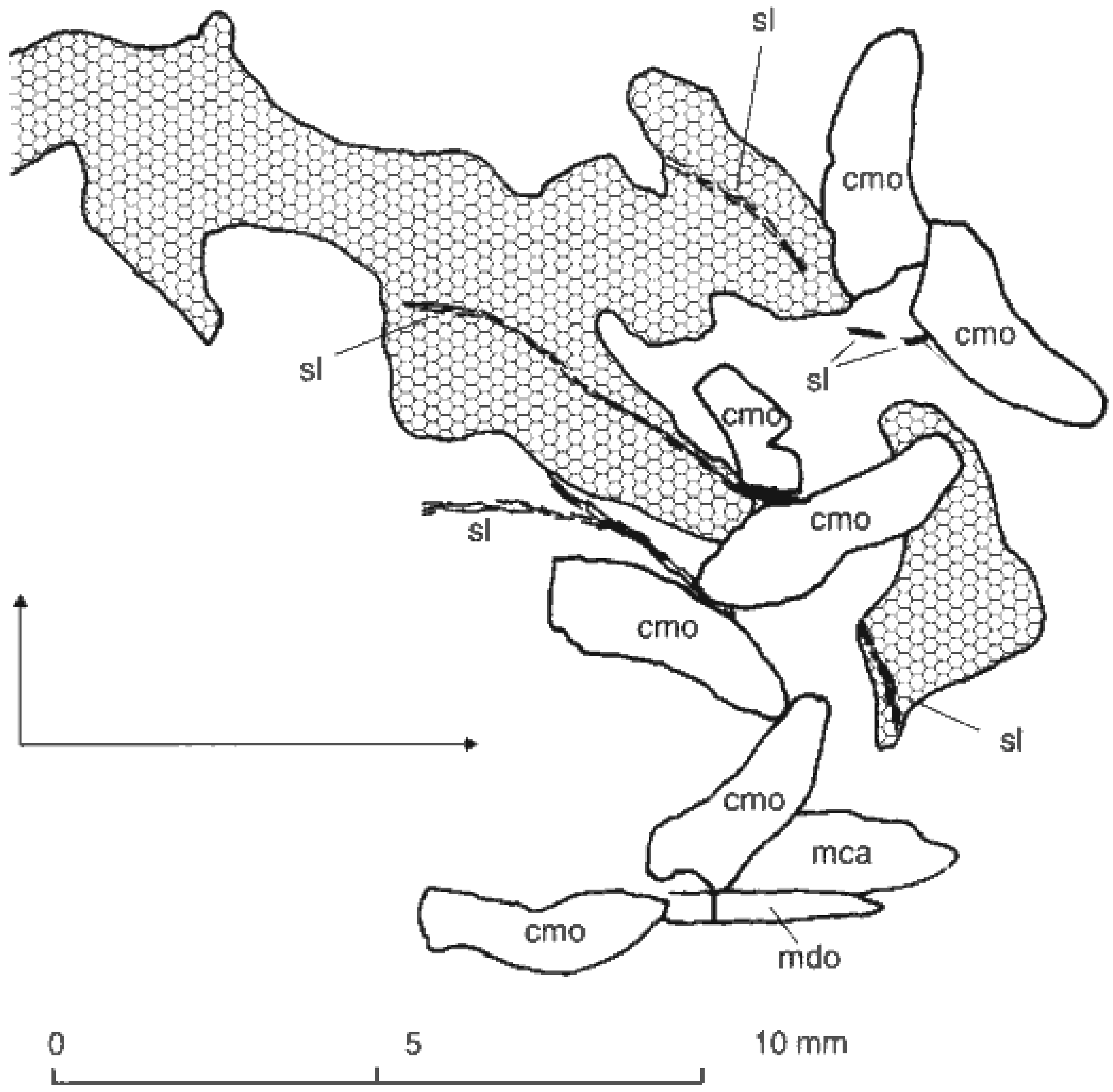

Fig. 8. *Acanthodes gracilis*; anterodorsal part of the head with circumorbitals of the both orbits, rostral part of the lower jaw, sensory lines of the head, and dorsally situated tesserae (hexagonal fill); anterior and dorsal directions are marked by arrows; M 1937; Košťálov; Rudník Horizon.

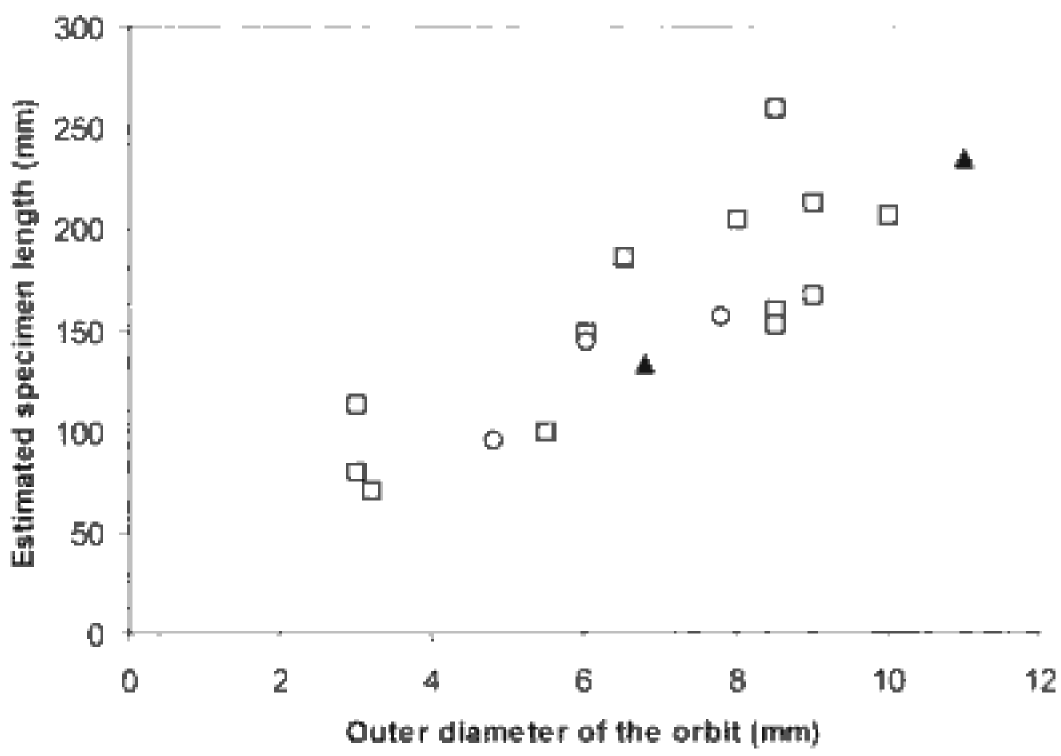

Fig. 9. Relationship between the outer diameter of the orbit and the estimated total specimen length. The values of *Acanthodes gracilis* are shown by open squares, the values of *Acanthodes stambergi* n. sp. (questionable) by solid triangles, and the values of *Acanthodes* sp. by circles. The upper trend line belongs to the *Acanthodes* sp. values and the lower one to the *Acanthodes gracilis* values.

Ischnacanthiformes and Climatiiformes see SAHNEY & WILSON (2001). The otoliths and/or labyrinths of representatives of the order Acanthodiformes were described in *Acanthodes bourbonensis* (see HEYLER 1969), *Acanthodes bridgei* (see ZIDEK 1976), *Acanthodes bronni* (see HEIDTKE 1990a, MILES 1973), *Acanthodes ovensi* (see FOREY & YOUNG 1985), *Carycinacanthus lopatini* (see MILES 1973), *Mesacanthus mitchelli* (see WATSON 1937), *Traquairichthys pygmaeus* (see FRITSCH 1893), *Triazeugacanthus affinis* (see BÉLAND & ARSENAULT 1985), and *Utahacanthus guntheri* (see SCHULTZE 1990). Otoliths and fragments of labyrinth infillings were found in all Permian taxa from the Czech Republic (Fig. 12; for *Acanthodes gracilis* see Fig. 6, 11, and Pls 10A, 10B). The labyrinth infillings are composed by fine sand-sized grains (as was shown by SAHNEY & WILSON 2001). The colour and grain size differ from that of the sediment matrix. The origin, chemical composition, and appearance (colour and absence of discernible granularity) of the inserted otoliths are different from the labyrinth infillings. The sediment matrix is greyish yellow or yellowish grey or yellowish pink, the labyrinth infillings are grey, and the otoliths are black or greyish black (as the other skeletal elements) in the Padochov locality. The rock matrix is blackish grey or greyish black, the labyrinth infillings are lighter than the matrix, and the otoliths are mostly darker than the matrix in the localities of the Rudník Horizon. Some otoliths that are embedded in the sacculus are covered by the sacculus wall. The otoliths are of similar shape as lagenar one in *Utahacanthus guntheri* (SCHULTZE 1990; Fig. 3) or otolith in *Acanthodes bridgei* (ZIDEK 1976; Fig. 2C). The bean-shaped otoliths have high relief. The outline of the mostly flat labyrinth infillings is not regular. All combinations (otoliths, labyrinth infillings, otoliths + labyrinth infillings) were discovered. Common number of the otoliths is one pair. Two pairs of otoliths were found in one case (uncertain; Rudník Horizon). The labyrinth infillings and otoliths were placed behind the orbits and over the posterior part of the jaws.

The pectoral girdle (Figs 4, 6, 10, and 13; Pls 4A, 4B, 12D, 12E) is composed of the central scapulocoracoid, dor-

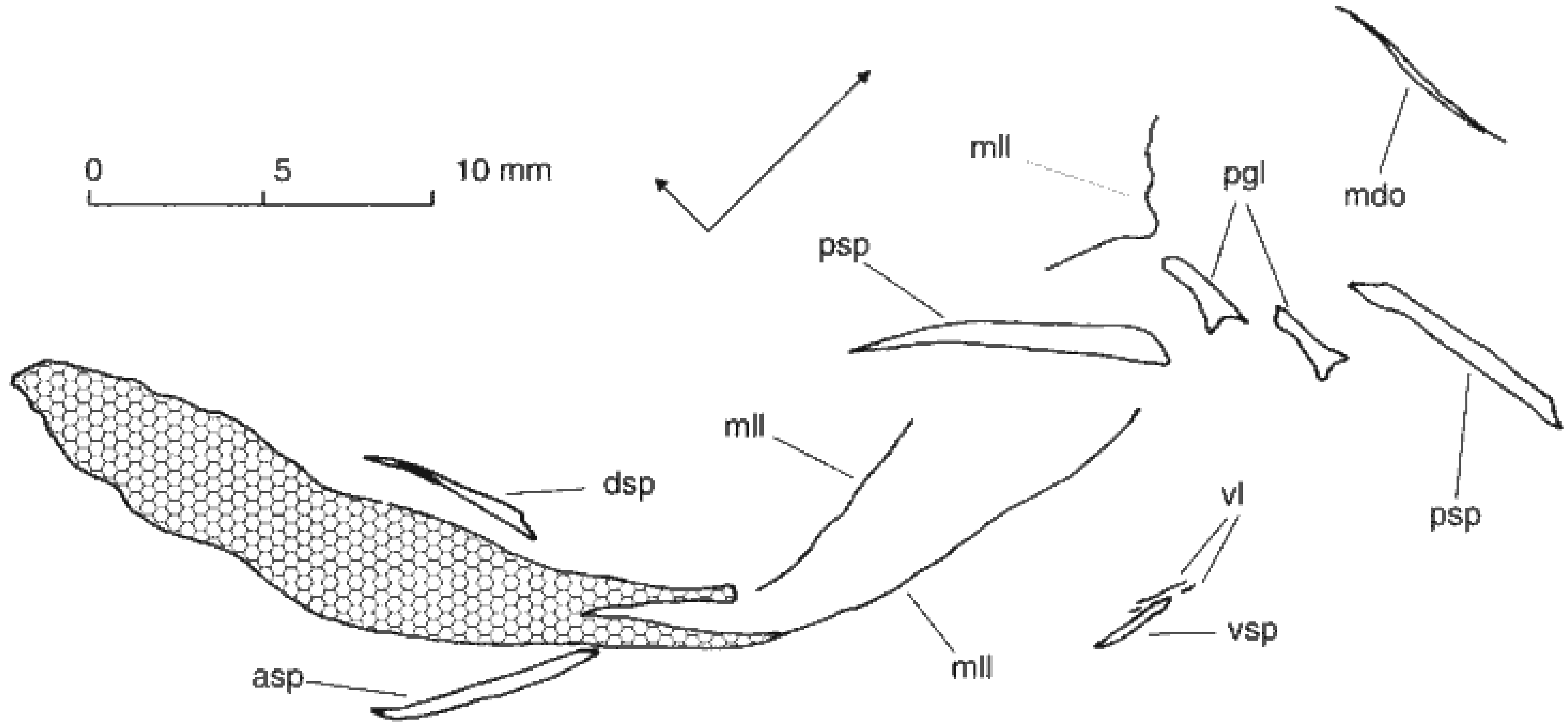

Fig. 10. *Acanthodes gracilis*; juvenile specimen without caudal fin; squamation is indicated by hexagonal fill; branchiostegals and partially articulated gill arches are not drawn; anterior and dorsal directions of the anterior half of body are marked by arrows; M 4343; Padochov; Zbýšov Horizon.

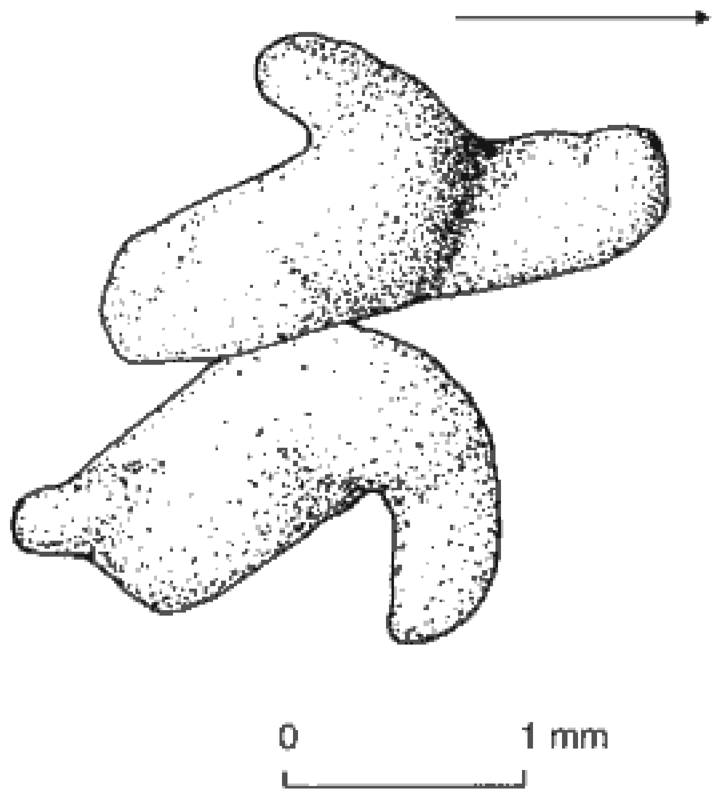

Fig. 11. *Acanthodes gracilis*; paired labyrinth infillings; anterior direction is marked by an arrow; M 4351; Padochov; Zbýšov Horizon.

sal suprascapula, and ventral procoracoid. The procoracoid is co-ossified with the slender dorsal scapular blade and the wide ventral coracoid. No complete pectoral girdle has been found yet. The best preserved elements are regularly scapular blades. The generally poorly preserved part of the pectoral girdle is coracoid plate. However, morphology of the ventral bone association seems to be very similar as in Stephanian *Acanthodes fritschi*. The opening for articulation with the pectoral fin spine (pectoral fossa) is thus bordered by the scapular blade, coracoid, and procoracoid. The procoracoid is long and rather well ossified even if not so well as in *Acanthodes fritschi*. The massive plate with surface for the dorsal adductor muscles is preserved in specimen M 4435 + M 4436 from the Rybnice, Hrádecký potok locality (Pl. 4B). The scapular blade is a slender bone and its most narrow 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 rather well ossified suprascapula is jointed to the above-mentioned dorsal termination of the scapular blade. This relatively long bone is somewhat wider than the dorsal termination of the suprascapula. Their degree of ossification is, however, clearly lower 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 pectoral fin spines (Figs 13, 15; Pls 3A, 4A, 4B, 9A, 9B, 10C, 11B, 11C, 12D, 12E) are both the longest and the only paired fin spines of the genus *Acanthodes*. They are moderately sabre-shaped and distally pointed as is usual in *Acanthodes*. Their widest part is situated near the proximal termination. All the fin spines have a prominent rib on the anterior margin. The rib is separated from the lateral and mesial sides of the spine by longitudinal grooves containing mostly inconspicuous (contrary to *Acanthodes fritschi*) irregularly spaced pores. Spine thickness diminishes distally. A less clear rib is situated along the posterior margin with poorly defined bordering longitudinal grooves. The posterior groove (as well as the posterior margin) extends proximally 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 (analogically with pectoral spines of *Acanthodes fritschi*) the pith cavity. The lateral and mesial sides of the pectoral fin spines bear, from front to rear, the above mentioned anterior rib which proportionally narrows to the distal tip, the medial rib, and the posterior rib. The flat or slightly convex medial rib occupies more than one third of the spine width in the proximal fourth of the spine. Distally, the medial rib rapidly narrows and almost disappears (transforms into the narrow ridge). The posterior rib becomes flat distally and spreads on the majority of the lateral and mesial spine sides in their distal quarter. The lateral and mesial surfaces of the distal termination of the spine occasionally bear striae which are quasiparallel to the longitudinal spine axis (Pl. 4C) and

Taxon	Label	Otoliths (mm)	Labyrinth infillings (mm)	Estimated total specimen length	Locality
Acanthodes gracilis	M 4491 + M 4492	two pairs (?)	–	63 mm	Kundratice, Doly
	M 4282	0.8 × 0.4 0.8 × 0.4	2.6 × 1.2	71 mm	Padochov
	M 4350 + M 4351	0.4 × 0.3 0.4 × 0.3	1.9 × 1.3 1.7 × 1.1	77 mm	Padochov
	M 4321 + M 4322	–	1.7 × 1.5 1.7 × 1.5	91 mm	Padochov
	M 4413 + M 4414	0.75 × 0.55 0.75 × 0.4	–	99 mm	Košťálov, za hospodou
	M 4383 + M 4384	0.7 × 0.4	1.9 × 1.3 1.7 × 1.1	160 mm	Košťálov, Kovářův mlýn
	M 4270	one pair	–	163 mm	Padochov
	M 4442	0.45 × 0.25 0.45 × 0.25	–	?	Košťálov, za hospodou
Acanthodes stambergi n. sp.	MHK 63 762/1	one pair	–	133 mm	Kladoruby, Dolní pepřík
Acanthodes sp.	M 4388	0.6 × 0.3 0.6 × 0.3	–	213 mm	Košťálov, za hospodou
	M 4254	0.45 × 0.25	1.75 × 1.1 1.4 × 1.1	?	Padochov
	M 4259 + M 4260	0.7 × 0.5 0.65 × 0.45	one with duct (fragments)	?	Padochov
	M 4274 + M 4275	–	2.1 × 0.9 1.8 × 1.2	?	Padochov
	M 4285	0.75 × 0.3 (?)	–	?	Padochov
	M 4316	0.6 × 0.4	2.0 × 1.2	?	Padochov
	M 4324	0.8 × 0.5	2.2 × 1.4	?	Padochov
	M 4325	1.0 × 0.45	one fragment	?	Padochov
	M 4333	one	two agglutinated	?	Padochov
	M 4344	–	1.9 × 1.7	?	Padochov
	M 4352	0.7 × 0.3 0.5 × 0.3	1.9 × 1.2 1.6 × 1.3	?	Padochov
	M 4353	0.9 × 0.3	one	?	Padochov

Fig. 12. Otoliths and the labyrinth infillings of the Czech Permian acanthodians.

sometimes also irregularly spaced pores. The pectoral fin spines of the juvenile specimens somewhat differ from the spines of the subadult and adult specimens. The proximal extremities are straight and oblique to the longitudinal axis, the distal terminations are very sharp, and the whole spines look generally less ossified (Fig. 13; Pls 3A, 11C). The inner structure of the fin spines corresponds to the description in *Acanthodes* sp. (see Zajíc 1998). The spine maximum width : length ratio (Fig. 15) has no taxonomical significance (compare with values of *Acanthodes* sp. in Fig. 34).

The ventral spine (Figs 6, 10, 14, 16; Pls 12A, 13A) differs from other fin spines not only in its length (the ventral spines are considerably shorter) but also in morphology. The ventral spine is only slightly sabre-shaped with the relatively widest proximal termination among all fin spines. This dissimilarity is clearly visible already in juvenile specimens of the estimated total specimen length 71mm (M 4282). The proximal terminations are not pointed, unlike in *Acanthodes fritschi*. The values of the spine maximum width : length ratio (Fig. 16) show the main trend. Some extreme values correspond rather to postmortem deformations than to a variability of the species.

The anal (Figs 17, 18; Pls 4D, 13B) and dorsal (Fig. 19) fin spines are about the same lengths. Their exact differentiation is possible only through the position on the body. The dorsal fin is situated slightly posteriorly. Both fin spines are shorter and straighter than the pectoral one. The outer morphology and the inner structure are very similar or almost the same as in *Acanthodes fritschi* (see Zajíc 1998). However, only ventral spines are safely distinguishable among isolated spines.

No radialia of the pectoral fins were found. Four radialia of the caudal fin were found in specimen M 2180 (Fig. 20;

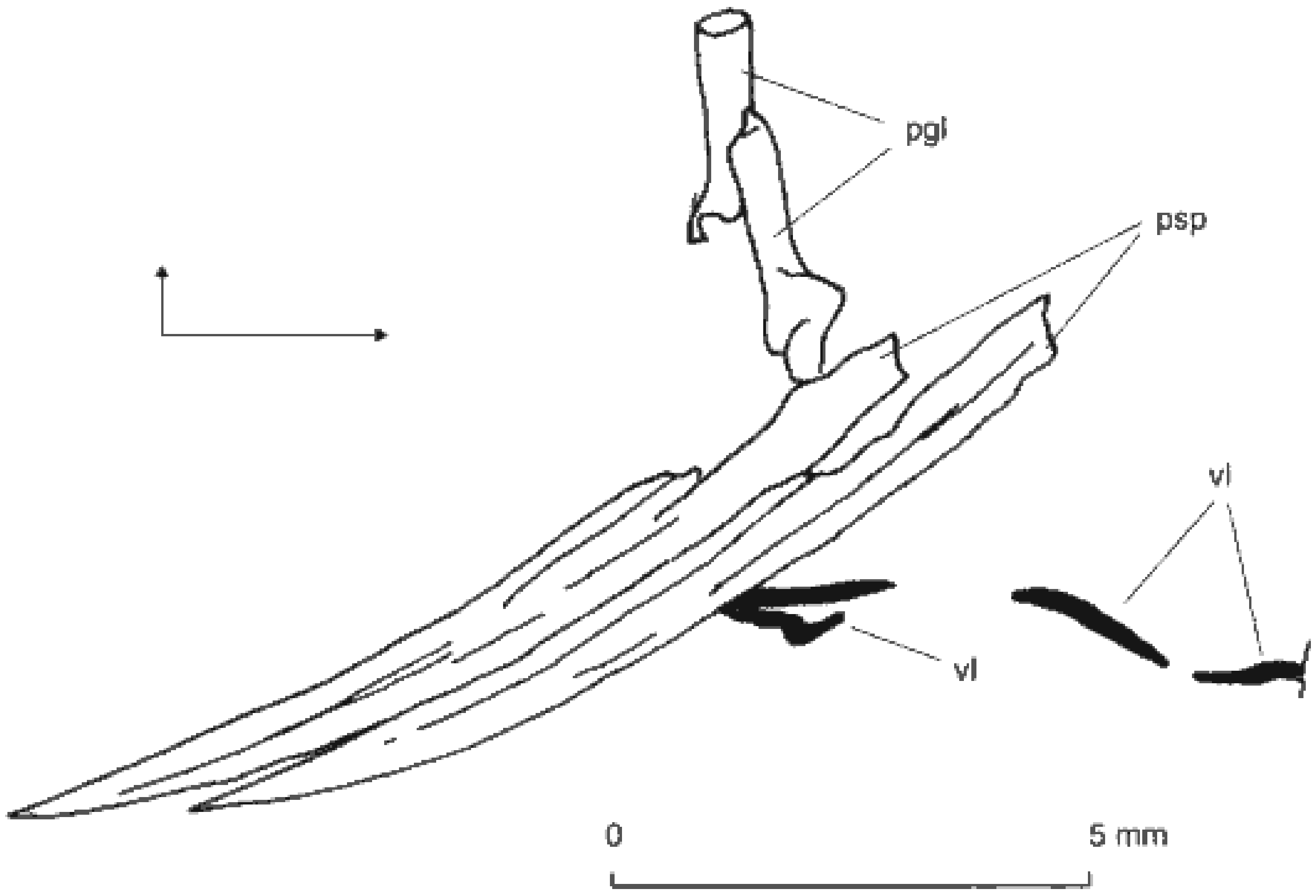

Fig. 13. *Acanthodes gracilis*; pectoral region of the juvenile specimen from Fig. 6; anterior and dorsal directions are marked by arrows; M 4282; Padochov; Zbýšov Horizon.

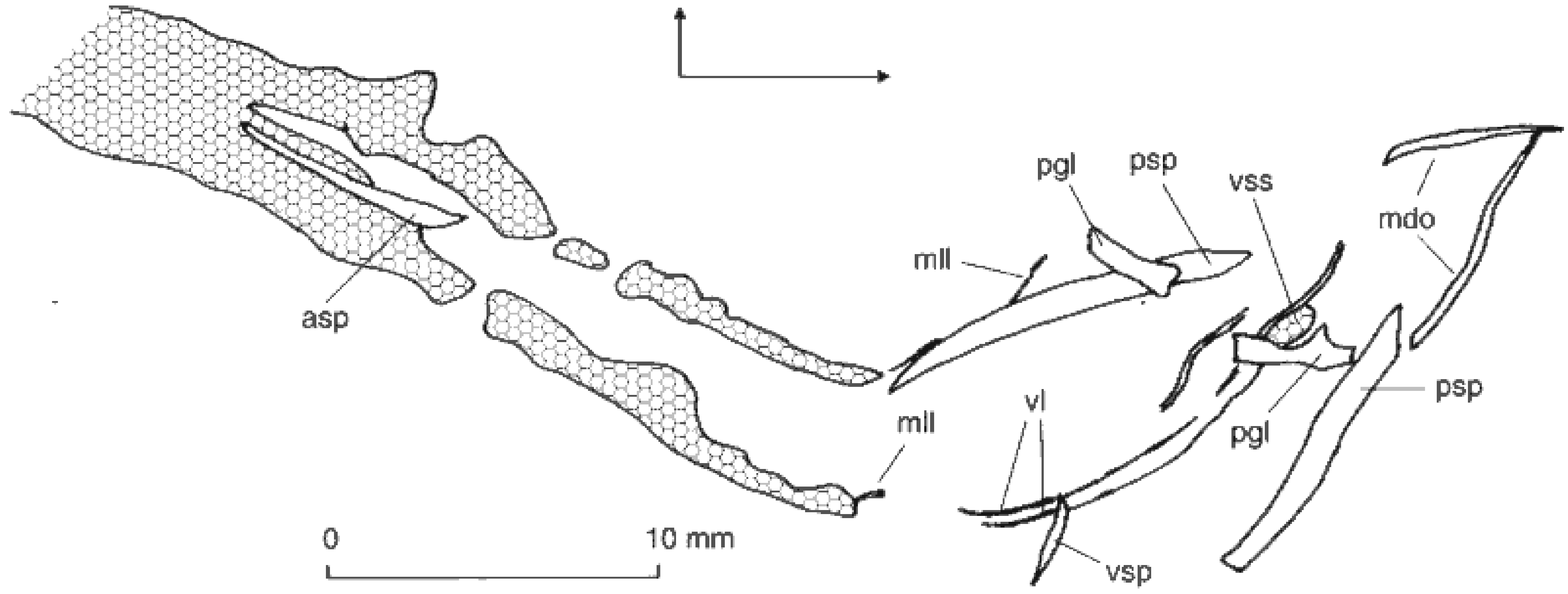

Fig. 14. *Acanthodes gracilis*; juvenile specimen without a caudal fin; squamation is indicated by hexagonal fill; hotch-potch of the cephalic and branchial elements is not drawn; anterior and dorsal directions are marked by arrows; M 4350; Padochov; Zbýšov Horizon.

Pl. 5A). The caudal radialia are formed by short rods with rectangular outlines. The four or five not clear imprints were found also in the same place (near base of the hypochordal lobe) on specimen M 1937.

Dermotrichia of the pectoral fin (Pls 4A, 5A, 9B) are narrow and long but not so extremely long as in *Acanthodes stambergi* n. sp. They are arranged in the row parallel to the pectoral fin spine and placed distally from the scapulocoracoid in the pectoral fin. The longest dermotrichia in the row are situated in the middle or slightly anteriorly. Posteriorly, dermotrichia become shorter and weakly ossified. All dermotrichia are represented by the non-articulating rods with oval cross section as in *Acanthodes fritschi*. The maximum measured lengths range from 1.9 mm in specimen M 4245/1 (estimated total specimen length is 165 mm) to 9.0 mm in specimen MHK 63 639 (estimated total specimen length is 567 mm). The narrower side (thickness) is usually visible. The true width is about three to four times wider than the thickness and is only seldom measurable. The maximum measured thicknesses (mostly the inclined ones) range from 0.1 mm in specimen M 4286 + M 4287 (estimated total specimen length is 140 mm) to the true width more than 0.6 mm and true thickness 0.2 mm in specimen MHK 63 639 (estimated total specimen length is 567 mm). The longest row of the dermotrichia (12.5 mm) was measured in the latter specimen. The highest number of dermotrichia in one row (about 60) was counted in specimen M 4245/2. Dermotrichia of the anal fin were found in two specimens only. Small anal fin with somewhat dislocated row of short dermotrichia occurs in specimen M 4394. The very long row (around 1.7 mm) was found in the deformed larger specimen PUK-25. The dermotrichia of the dorsal fin are visible on the latter specimen as a short fragment of the row.

The caudal fins (Fig. 20; Pl. 5A) were found in nine specimens. The best preserved caudal fin (specimen M 2180) shows all Heyler's zones and four radialia (see above) but the terminations of both (axial and hypochordal) lobes are missing. The Heyler's zone Z2 extends extraordinarily far to the body. The proximally widened termination of the axial lobe is missing or poor contrary to

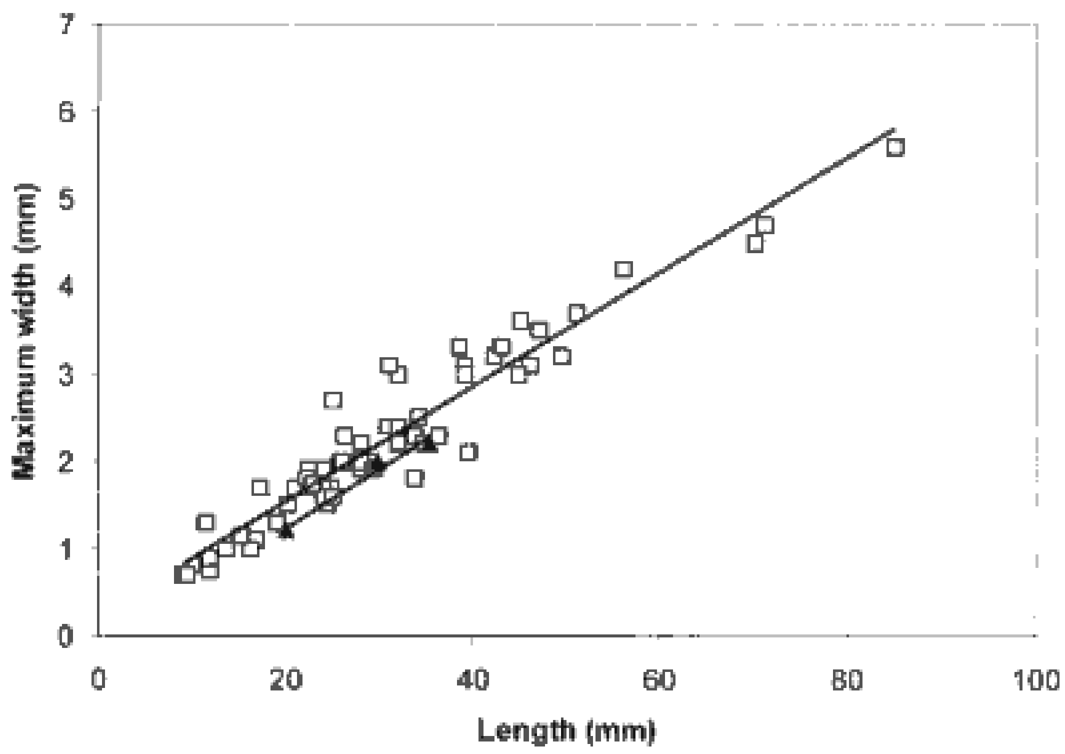

Fig. 15. Relationship between the length and the maximum width of pectoral fin spines. The values of *Acanthodes gracilis* are shown by open squares and the values of *Acanthodes stambergi* n. sp. by solid triangles. The trend line of the *Acanthodes gracilis* values (longer, above) is parallel to the trend line of the *Acanthodes stambergi* n. sp. ones. The trend line of the *Acanthodes* sp. values (Fig. 34) occupies almost the same direction and position.

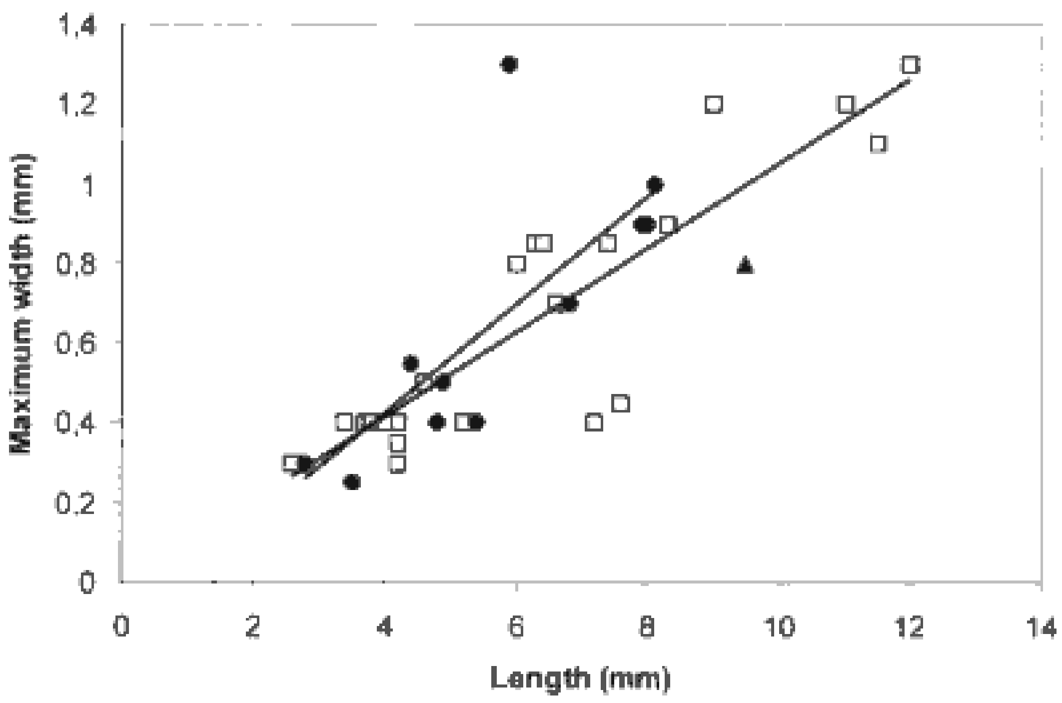

Fig. 16. Relationship between the length and the maximum width of ventral fin spines. The values of *Acanthodes gracilis* are shown by open squares, the values of *Acanthodes stambergi* n. sp. (questionable) by solid triangles, and the values of *Acanthodes* sp. by solid circles. The upper trend line belongs to the *Acanthodes* sp. values and the lower one to the *Acanthodes gracilis* values.

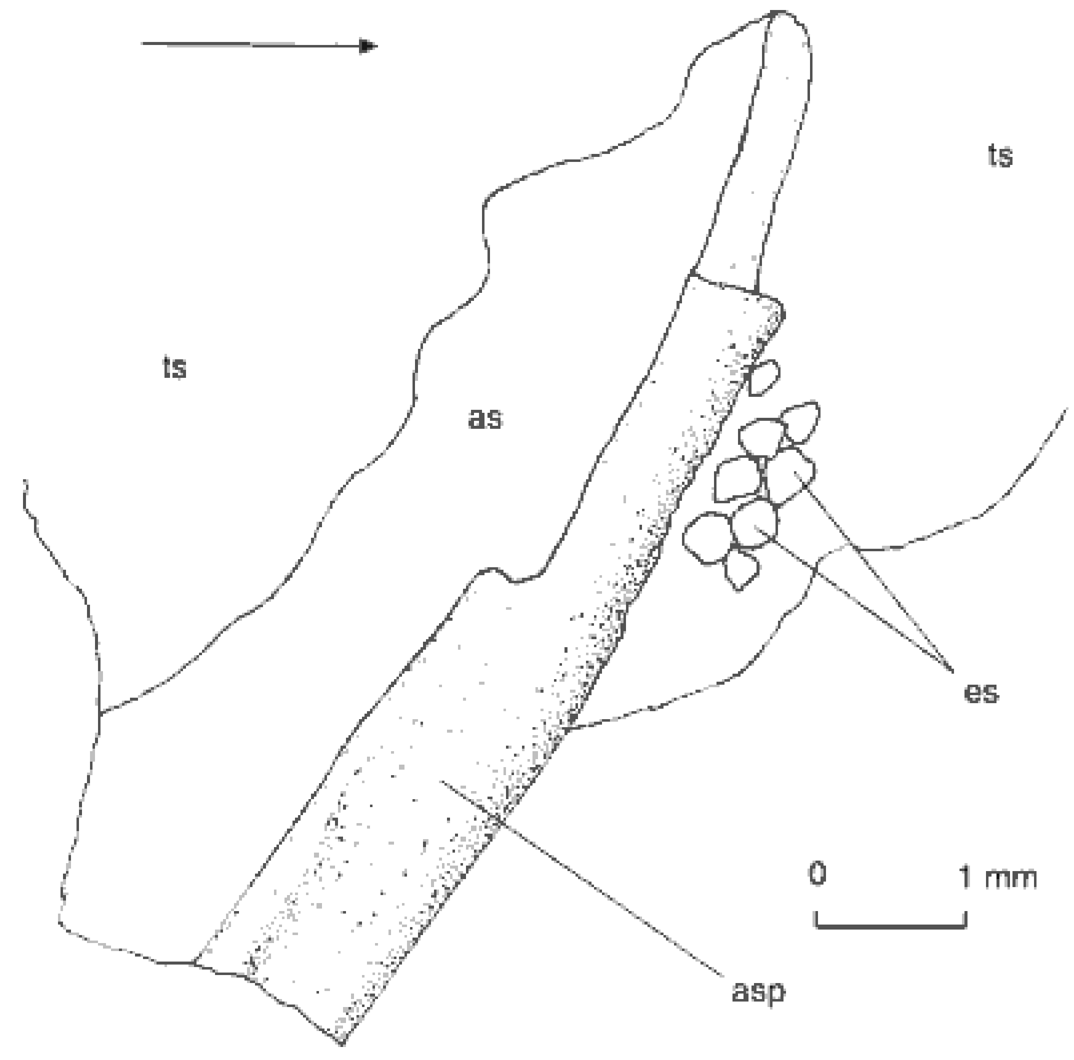

Fig. 17. *Acanthodes gracilis*; fragment of the anal fin spine with anterior part of the anal fin; the finest scales cover the anal fin web; eight enlarged scales are situated in front of the proximal part of the anal fin spine; anterior direction is marked by an arrow; MHK 63 784; Kladoruby, Dolní pepřík.

Acanthodes bourbonensis (Heyler 1969b, Pl. 7; Heidtke 1996, Figs 1A, 1B, 6) or *Acanthodes fritschi* (Zajíc 1998, Fig. 37).

The *Acanthodes*-type scales (sensu Gross 1973) have delicately pitted scale crowns which terminate in posteriorly orientated spiny projections. Posterior projections were within the family Acanthodidae described in *Acanthodes fritschi*, *Acanthodes luedersensis*, various isolated scales of *Acanthodes* sp., *Traquairichthys pygmaeus*, and *Pseudacanthodes pinnatus* (for details see Zajíc 1998). 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. Specimen M 4435 + M 4436 (Pls 12B, 12C) shows scales with secondarily rounded posterior projections. Overlapping of scales is arranged with help of tiny roof that is formed by the expanded scale crown transcending over one posterior scale side. Scales overlapping (in the lateral sensory line in this case) was already pictured by Zajíc (1989; Fig. 3) from the Krkonoše Piedmont Basin. The sculpture of the scale crown is formed by very fine holes and sometimes is not easily visible. Size of the trunk scales varies from 0.1 mm to 0.5 mm (M 4435 + M 4436). The scales covering the pectoral, anal (Pls 4D, 13B), and dorsal fins are very small and rounded. Shapes of the fins are marked by scale covers (the inner reinforcement is formed by dermotrichia). The anal fin of specimen M 2180 (Pl. 4D; estimated total specimen length is 299 mm) is almost as long (26 mm) as the anal fin spine (27 mm). Eight unusually enlarged scales (0.3 mm) are placed close in front the anal fin spine (Fig. 17) on specimen MHK 63 784. A low rim formed by the tiny scales of the same type as in the anal and dorsal fin webs were found anteriorly from the ventral fin spine on specimen M 4493 (Pl. 13B). The scales of the trunk sensory lines are markedly larger than the surrounding ones (0.13 mm versus 0.3. mm in M 4245 or 0.35 mm versus 0.75 mm in MHK 63 639).

The dorsal scales (over the gill region) continuously transform to the tesserae (over the head). Tesserae cover the head dorsally and frontally (Fig. 8). The main concentration of tesserae is between the orbits and behind them. The tightly crowded tesserae form a roof or shield there in larger specimens. The sensory lines of the head (particularly the supraorbital canal) cross the roof (Pl. 5B). Tesserae have pentagonal, hexagonal, irregular or rounded (the smallest ones) outlines. The rounded tubercle of various size is placed centrally or slightly eccentrically. The

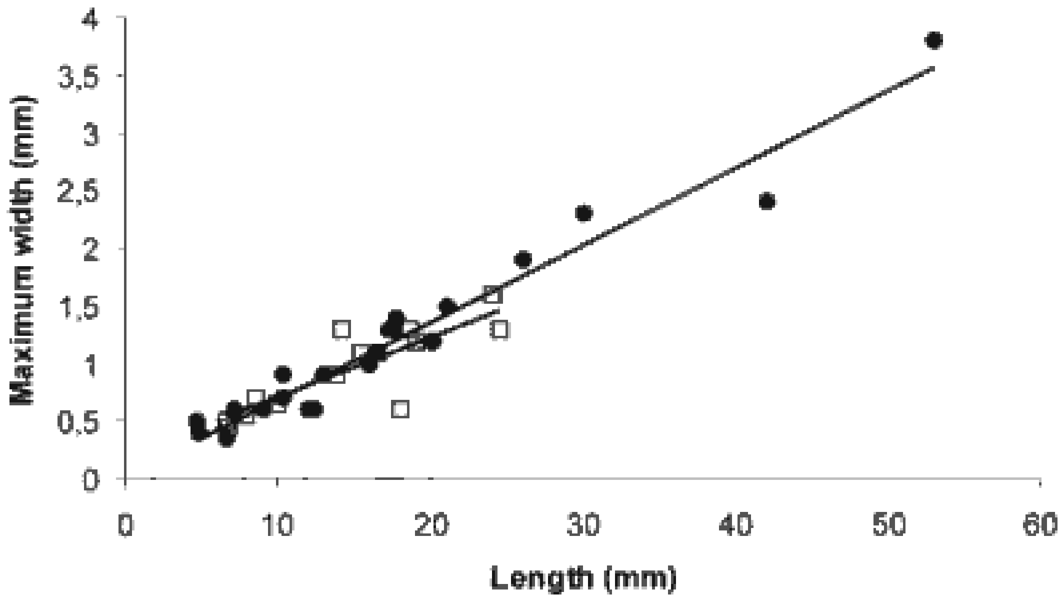

Fig. 18. Relationship between the length and the maximum width of anal fin spines. The values of *Acanthodes gracilis* are shown by open squares and the values of *Acanthodes* sp. by solid circles. The longer trend line belongs to the *Acanthodes* sp. values and the shorter one to the *Acanthodes gracilis* values.

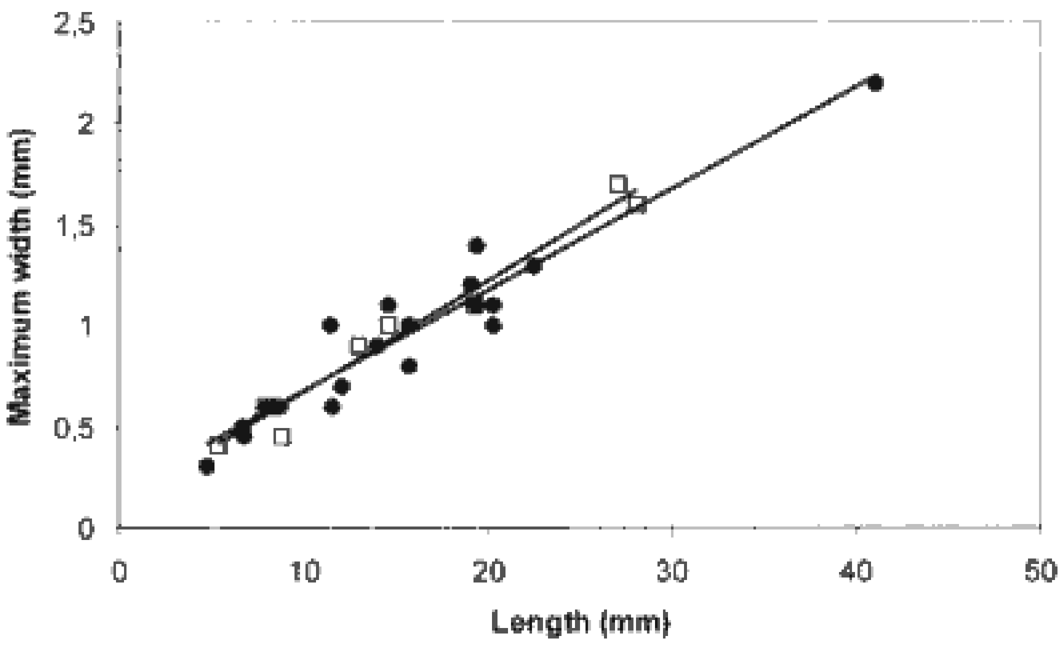

Fig. 19. Relationship between the length and the maximum width of dorsal fin spines. The values of *Acanthodes gracilis* are shown by open squares and the values of *Acanthodes* sp. by solid circles. Both trend lines have the same direction.

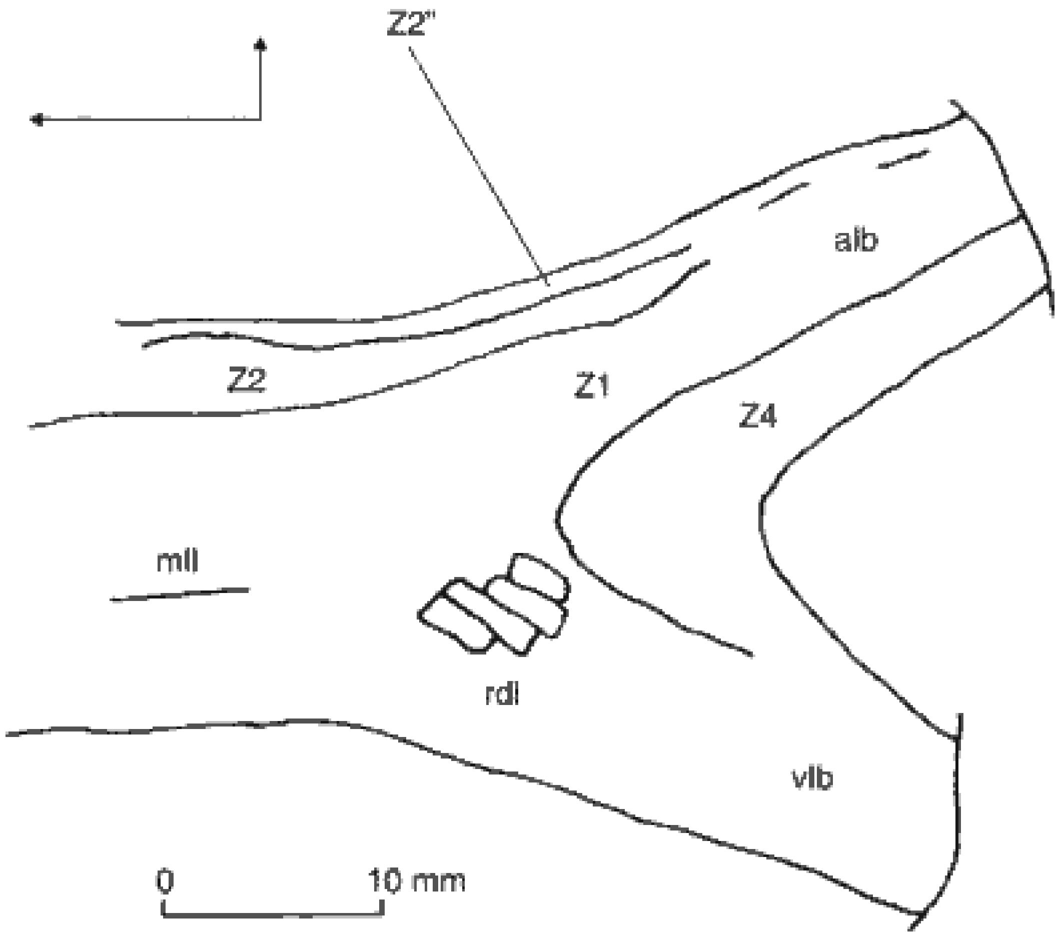

Fig. 20. *Acanthodes gracilis*; caudal fin without distal tips of both lobes and with four well preserved short radialia; anterior and dorsal directions are marked by arrows; M 2180; Košťálov; Rudník Horizon.

central tubercles are unlike *Acanthodes bronni* (see Heidtke 1900; Fig. 45b) conical with circular base. The tubercle can be absent especially in case of small tesserae. The largest discovered tesserae measure 0.35 mm and was detected in specimen M 1937 (Pl. 5B) of the estimated total specimen length 340 mm.

The sensory lines of the head (Figs 4, 6–8; Pls 1A, 3B, 5B, 9A, 10C) are often preserved as shorter parts but longer segments were also found. These sensory lines are composed of individual segments (modified scales) whose morphology is similar to those in *Acanthodes fritschi* (Zajíc 1998; Figs. 45) or in *Acanthodes bridgei* (Zidek 1976; Fig. 5). The unbroken segments are formed by two unified enlarged scales as is visible on specimen MHK 63 758 (size of the segments is about 0.5 × 0.45 mm). The preopercular sensory line (Fig. 6) is situated behind the jaws and is oriented vertically (parallelly with the postorbital branch of the infraorbital sensory line). The quadratojugal sensory line (Fig. 7 shows the connection with the infraorbital sensory line) is oriented horizontally and connects the postorbital and the infraorbital sensory lines. The connection with the quadratojugal sensory line divides the suborbital branch of the infraorbital sensory line (Fig. 7) from the postorbital one (Figs 6, 7; Pls 1A, 3B). The Preorbital branch of the infraorbital sensory line (Fig. 7) is placed in front of the orbit. The supraorbital sensory line is the most frequently found sensory line of the head (Figs 4, 6, 8; Pls 1A, 3B, 5B, 9A, 10C). Pair of the supraorbital sensory lines runs through the shield of tesserae between the orbits. The sensory lines of the head are best preserved on the juvenile specimen M 4282 (estimated total length = 71 mm; Figs 6 and 13; Pls 10C, 11C–12A).

The trunk sensory lines are represented by the paired lateral (main) sensory line (with derived vertical sensory lines) and by the paired ventrolateral sensory line. The lateral sensory line (Figs 4, 6, 10, 14, and 20; Pls 3A, 3B, 9A, 9B, 10C, 12D, 12E) begins near the caudal fin (Fig. 20) and runs up to the head. The substantial (posterior) part from the caudal peduncle up to the pectoral region goes at the middle of the trunk height. The sensory line then steeply ascends in the gill region and so on the head already occupies dorsal or dorsolateral position. The sensory line is formed by two rows of the enlarged scales up to the posterior part of the head. The most anterior part of the line (between the orbits) is formed by united segments. The main lateral sensory line represents the most heavily "ossified" sensory line of the head region of the juvenile specimen M 4282 (estimated total specimen length is 71 mm; Fig. 6; Pl. 10C). The only supraorbital sensory line is similarly "ossified". The main lateral sensory line of the same specimen gets thinner caudally (notably behind the ventral spine region) and starts to be thicker when begins be surrounded by trunk scales. The scales of the sensory line are slightly above two times larger than surrounding trunk scales. The squamation of the juvenile and younger subadult specimens starts anteriorly along the sensory lines. Specimen M 4461 (estimated total specimen length is 160 mm; Pl. 6B) shows the vertical secondary sensory line derived from the main lateral sensory line (5.4 mm posteriorly from the pec-

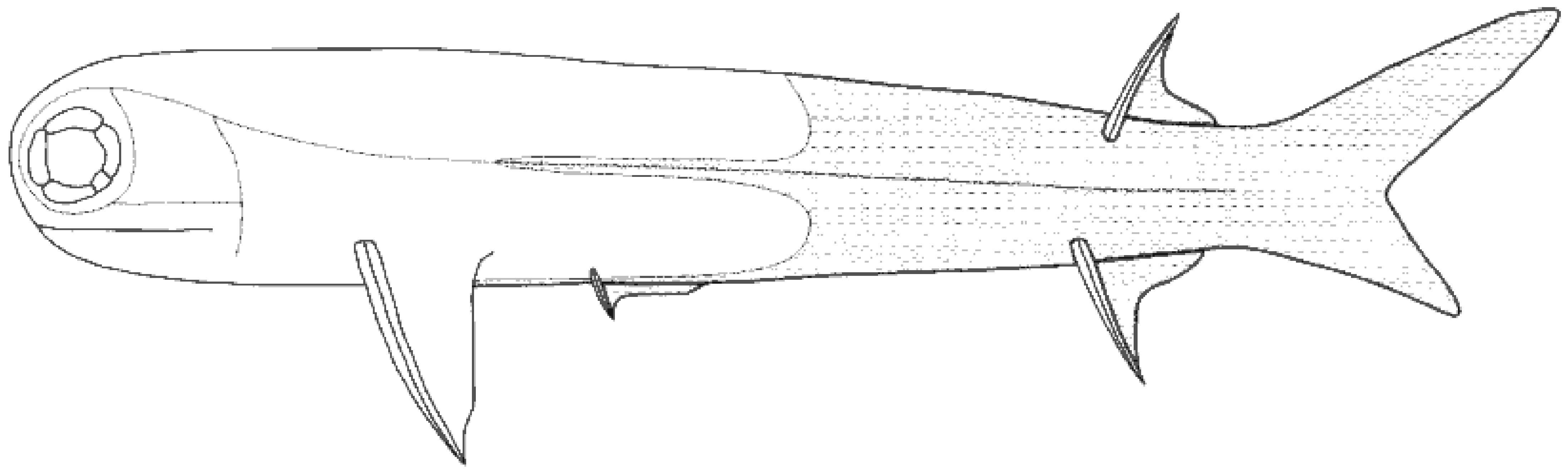

Fig. 21. *Acanthodes gracilis*; restoration with the scale cover after the younger but most complete specimen M 4413 + M 4414, shape of sensory lines and fins were compiled with the help of various specimens, scales of the dorsal and anterodorsal region of the head are represented by tesserae.

toral fin spines). There was probably not only one vertical secondary sensory line like in *Acanthodes bridgei* (Zidek 1976; Fig. 15). The found vertical sensory line is, however, considerably shorter. Ventrolateral sensory lines (Figs 4, 6, 10, 13, 14; Pls 6A, 9A, 9B, 10C, 11C–12A, 12D–14B) are formed by two rows of noticeably larger scales than surrounding ones. Both ventrolateral sensory lines (left and right) are united into the unpaired and anteriorly orientated ventral sensory line (Figs 4 and 6; Pls 9A, 9B, 12D). The ventral scale shield (Fig. 4; Pls 9A, 9B, 12D–F) covers the connection on the ventral part of body under the pectoral region. This structure somewhat differs from that in *Acanthodes bridgei* (Zidek 1976, Fig. 4C) and in *Acanthodes fritschi* in shape. However, the posterior notch was found in specimen M 4477 (Pl. 14B) only. The shield is usually affected by a deformation. The original shape was, however, probably orthorhombic or longwise oval. Surrounding by trunk scales is similar as in lateral sensory line.

Ontogeny: The term "ossification" is used throughout and no distinction is made between ossification and globular calcification of cartilage in agreement with Zidek (1985). All measurements of lengths and distances (for both ontogenetic and taxonomic purposes) are complicated by remarkable extent of deformation (in contrast to other fish remains). Acanthodian body was probably very pliable and therefore susceptible to a postmortem deformation both before fossilisation (particularly body distortions and dismembers) and during fossilisation (particularly compression or extension up to fragmentation of bodies or skeletal elements). Results of measurements are inapplicable in sediments evidently affected by pressure like in the Vrchlabí, road cut locality. All abundant acanthodian remains of this locality are therefore marked as *Acanthodes* sp.

Various lengths, widths, and body proportions were measured in 93 specimens of *Acanthodes gracilis* and 38 of them were used for the computing of ratios (Fig. 3).

The body restoration (Fig. 21) were drawn on the basis of the younger specimen M 4413 + M 4414 (the only complete and reliably measurable specimen) together with various data of numerous specimens concerning sensory lines and fins. The body of younger specimens is higher and shorter than in *Acanthodes bronni* (Heidtke 1990a, Fig. 39)

Specimen	Estimated specimen length	Length : width ratio
M 4270	163	4.63
M 4307 + M 4308	186	4.42; 4.55; 3.40; 4.11
MHK 30 895	281	2.80; 2.87; 2.78

Fig. 22. *Acanthodes gracilis*; length : width ratio of the circumorbitals computed from the maximum measured values.

and is more similar to the fusiform body of *Acanthodes bridgei* (Zidek 1976, Fig. 15). Body of older specimens tends to be more elongated and slender somewhat similarly as in *Acanthodes bronni*. Scales of the dorsal and anterodorsal region of the head are represented by tesserae. Body scales continuously segue into tesserae over the gill region. The smallest specimen M 4343 (61 mm) has developed mandibular bones. The poorly preserved elements of jaws (articulars, mentomandibulars, and quadrates) were firstly found in specimen M 4468 + M 4469 of the estimated length167 mm. The gradual loss of gill rakers was detected in accord with Zidek (1985). Five gill arches were discovered on the specimens of estimated length up to 100 mm with help of the articulated gill rakers. Sensory lines of the head, otoliths (two pairs unlike all other larger specimens with one pair), scapulocoracoids, and all fin spines are presented in the smallest specimens. Orbits were already detected in specimen M 4475 of estimated length 80 mm. The length : width ratio of the circumorbitals decreases during individual growth and become broader (see Fig. 22) in agreement with Zidek (1985, p. 152). The completely squamated area (scales cover the entire circumference of the cross section of the trunk) moves from behind anteriorly during growth. The paired narrowly triangular squamated areas reach far ahead along the main lateral sensory lines. Similar but fused areas surround the ventrolateral sensory lines. The unpaired ventral scale shield (see above) is developed slightly anteriorly of this area or at their termination. Both ventrolateral sensory lines fuse in the ventral scale shield into the unpaired ventral sensory line. The development of squamation during ontogeny is illustrated on Fig. 23. The largest body scales are situated near the lateral sensory line behind the posterior fin spines

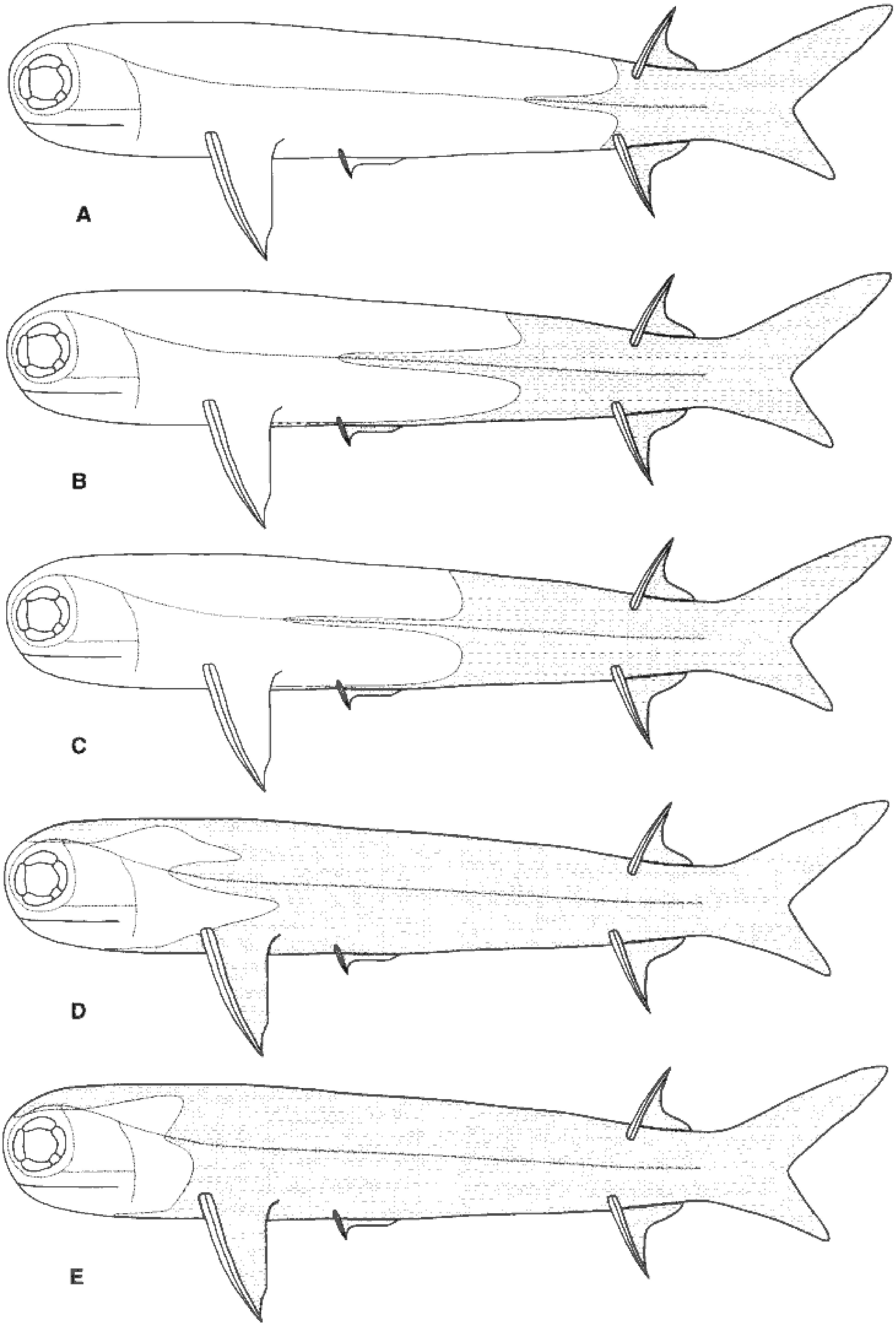

Fig. 23. *Acanthodes gracilis*: development of squamation; A – specimen M 4343 (estimated total specimen length is 61 mm); B – specimen M 4475 (estimated total specimen length is 80 mm); C – specimen M 4413 + M 4414 (estimated total specimen length is 113 mm); D – specimen MHK 63 797 (estimated total specimen length is 205 mm); E – specimen M 1933 (estimated total specimen length is 300 mm).

(anal and dorsal). Dependence of the total specimen length on number of scales per mm in a row is demonstrated on the Fig. 24. Prepectoral length is rarely measurable. The ratio K was computed only in three events considering the difficultly measurable prepectoral length. The values generally decrease from 30% (in the specimen of the estimated length 71 mm) to 25% (in the specimen of the estimated length 181 mm). This value range is, however, not significant. Values of the ratio L oscillate around the 70% during growth. The great oscillation of the computed values is probably caused by poorly preserved and deformed mandibular bones. The values of the ratio N are quite inapplicable because of combination of both seldom reliable measurements (prepectoral lengths and mandibular bones). Body proportions are best visible on the Zidek's diagrams. For explanation of the diagrams see Fig. 26. Six specimen of different growth stages is presented on the Fig. 27. The four longer specimens suggest an undervaluation of the estimated total specimen lengths. The body thus becomes more elongated and slenderer during the individual growth. Three growth stages are recognized. This separation is conventional but based on the natural fundamentals.

The juvenile stage includes specimens of the total length up to 100 millimetres (Figs 23A, 23B, 27A, 27B). The mandibular bones and circumorbitals are developed. The gill rakers cover all gill arches. Two pairs of otoliths were found on the second smallest specimen of the estimated length 63 millimetres. All longer specimens have one pair of otoliths. Fragments of sensory lines of the head are preserved. The completely squamated area covers trunk behind up to 55% of the distance between the ventral and anal fin spines ($v_{V\text{-}A}$). The squamation surrounding the lateral and ventrolateral sensory lines reaches approximately up to 50% of the distance between the pectoral and ventral fin spines ($v_{P\text{-}V}$). The ventral scale shield is not developed yet.

The subadult stage contains specimens of the total length from 101 to 220 millimetres (Figs 23C, 23D, 27C, 27D). The mentomandibular, articular, and quadrate are developed but poorly preserved. Preservation of the other skull elements is poor and they are mostly unidentifiable. On the contrary, the elements of the gill cover (branchiostegals) are usually well preserved. The way of preservation suggests a primary poor "ossification" because specimens coming from localities with various way of fossilization. The completely squamated area can reach closely behind the pectoral girdle. The squamation surrounding the lateral, ventrolateral, and possibly ventral sensory lines continues to the area in front of the pectoral girdle. The ventral scale shield is developed. Tiny scales continuously convert into the tesserae dorsally from the gill region of the longer specimens of the estimated length 160 millimetres minimally. This length could therefore be a boundary between the younger subadult substage and the older one. Number the gill arches which can be identifiable according to the articulated gill rakers diminishes.

The adult stage includes specimens longer than 220 millimetres (Figs 23E, 27E, 27F). Skeletal elements of the head (except of the mandibular bones, circumorbitals, and branchiostegals) are still poorly preserved. The completely squamated area starts in front of the pectoral girdle. Former ventral scale shield is incorporated in the ventral squamation. The central part of the anterodorsal tesserae is tightly agglomerated and forms an armour.

The complete distribution of the growth stages is demonstrated on the Fig. 28. Figure 29 shows a finer distribution based on the size categories.

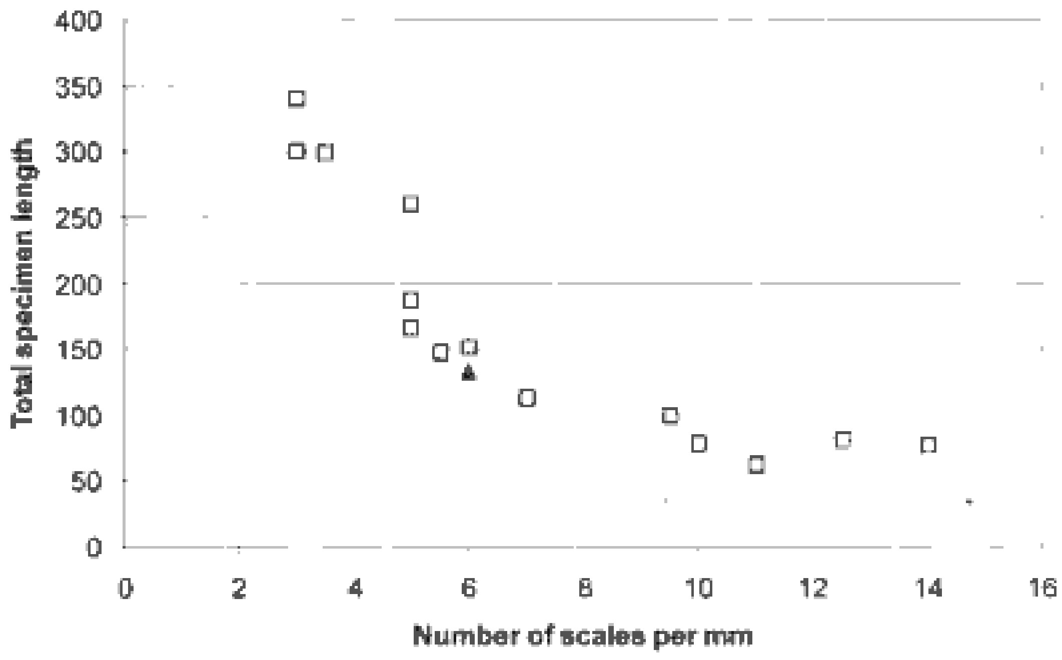

Fig. 24. Dependence of the total specimen length on number of scales per millimetre in an actual row. The values of *Acanthodes gracilis* are shown by open squares and the value of *Acanthodes stambergi* n. sp. by solid triangles.

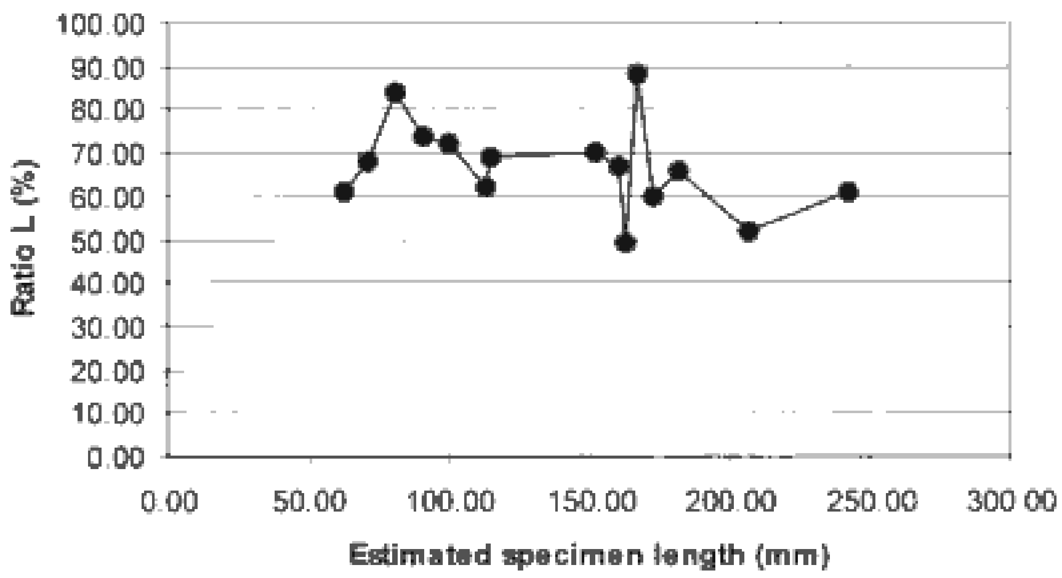

Fig. 25. *Acanthodes gracilis*: oscillation of the ratio L during growth.

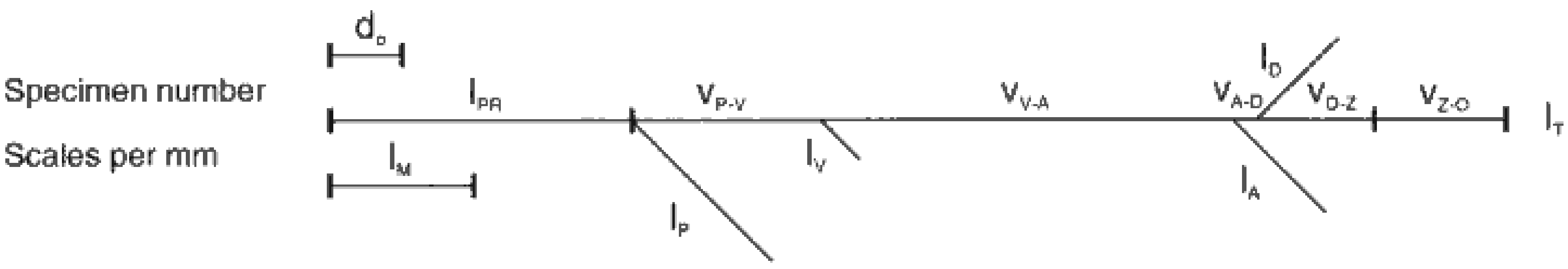

Fig. 26. Zidek's diagram; d_O – outer diameter of circumorbital ring; l_A – anal spine length; l_D – dorsal spine length; l_M – mandibular bone length; l_P – pectoral spine length; l_{PR} – prepectoral distance; l_T – total specimen length; l_V – ventral spine length; $v_{A\text{-}D}$ – anal-dorsal spine distance; $v_{D\text{-}Z}$ – distance from dorsal spine to caudal cleft; $v_{P\text{-}V}$ – pectoral-ventral spine distance; $v_{V\text{-}A}$ – ventral-anal spine distance; $v_{Z\text{-}O}$ – distance from caudal cleft to tip of axial lobe.

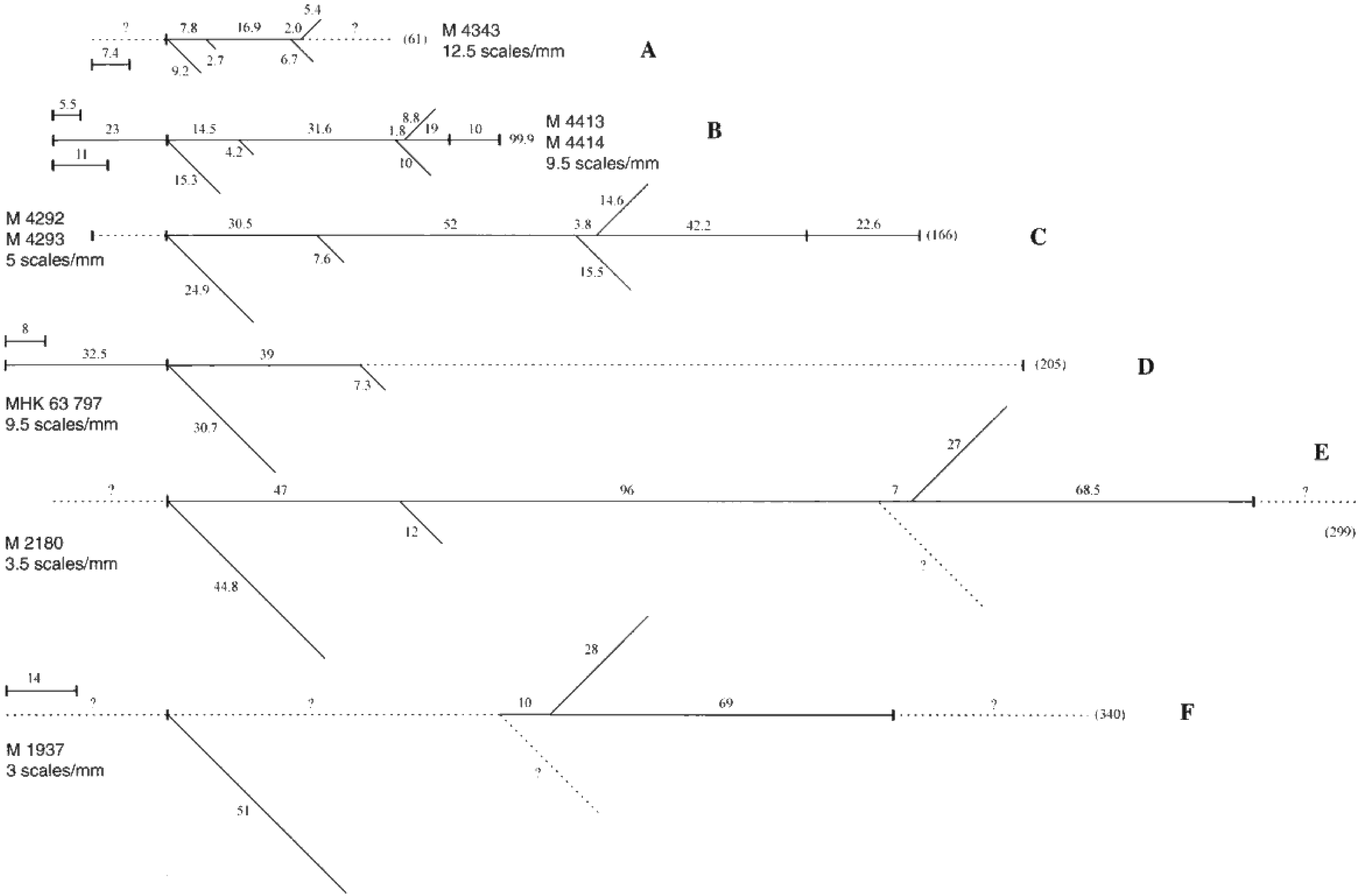

Fig. 27. *Acanthodes gracilis*; Zidek's diagrams of the six specimens (two juvenile, two subadult, and two adult stages); values in parentheses means the estimated total specimen length unlike the measured values.

Geographic distribution: Occurrence of the *Acanthodes gracilis* is probably restricted to the basins of the Bohemian Massif *sensu lato*. The original fossil material comes from the type locality of Wolbromów (the old German name is Klein Neudorf) in the North Sudetic Basin (Poland). The fossiliferous Upper Anthracosia Shale at the top of the Świerzawa Formation in the North Sudetic Basin (see Mastalerz 1990) is very similar to the Rudník Horizon in the Krkonoše Piedmont Basin. The fossil content, taphonomy, type of fossilization, and type of sediment are very close in both basins. The Rudník Horizon is the traditional term but this unit has a real character of a Member. However, the redefinition of this unit was not done yet. Specimens from the Krkonoše Piedmont and Boskovice basins are described above. Asselian sediments of the Saxothuringian basins (Germany) yielded remains of the genus *Acanthodes* but their redescription is not done yet. Occurrence of *Acanthodes gracilis* is, however, expected.

Sites (investigated specimens): Černá Hora (3 specimens), Kladoruby (17 specimens), Košťálov (28 specimens), Kundratice (4 specimens), Padochov (15 specimens), Prostřední Lánov (4 specimens), Rudník (1 specimen), Rybnice (16 specimens), Zbraslavec (3 specimens), Zbýšov (1 specimen). The specimens deposited in the Moravian Museum in Brno (particularly from the Malá Lhota locality but also from the Hluboké Dvory, Moravský Krumlov, and Svitávka localities) were temporarily inaccessible. They will be investigated subsequently.

Remarks and relationship: The close relationship between *Acanthodes gracilis* and *Acanthodes stambergi* n. sp. (e. g. the identical morphology and sculpture of scales) as well as small number of measurements of the latter species (three specimens are known till now) make unable to determine great number of specimen. The acanthodians without preserved significant pectoral dermotrichia must therefore be classified as *Acanthodes* sp. All these acanthodian remains are, however, very similar and their attribution either to *Acanthodes gracilis* (noticeably frequenter species) or to *Acanthodes stambergi* n. sp. is therefore very probable. Occurrence of the *Acanthodes stambergi* n. sp. has been reported only from the upper part of the *Acanthodes gracilis* biozone i.e. from the Middle Letovice Formation so far. *Acanthodes stambergi* n. sp. was probably recently detached from the *Acanthodes gracilis* but at the end of the biozone both taxa became extinct in the basins of the Bohemian Massif (in the area of the Czech Republic and Poland at least). All calculated ratios of the *Acanthodes gracilis* are shown in Fig. 3. Figure 30 presents a comparison of individual ratios of various *Acanthodes* species. The table is based on the Zajíc (1998, Fig. 51) and filled in by new measurements. The values of the ratios A^1 and A^2 are closest to these in *Acanthodes bourbonensis*, *Acanthodes bronni*, and *Acanthodes wardi*. The values of majority ratios (C, D1, D2, E, F, G, H, I, J, K, and O) are close in most of species. The large span of values of the ratios B, L M, and N do not permit a valid comparison of the Czech and Moravian specimens of *Acanthodes gracilis* with other species. All adequately measurable Lower Permian representatives of the genus (*Acanthodes*

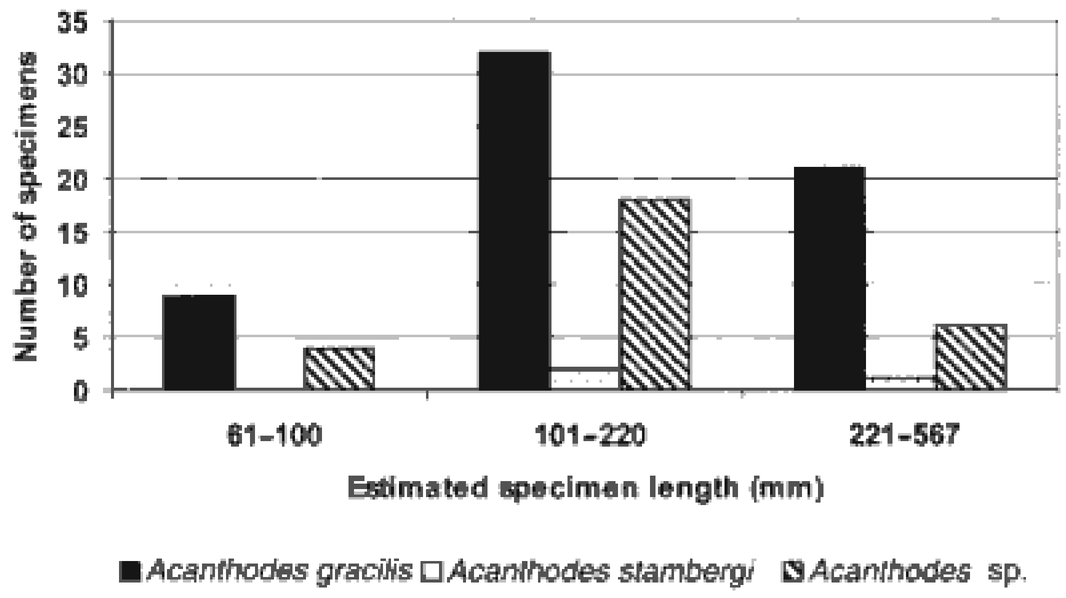

Fig. 28. Distribution of the growth stages – the juvenile stage (61–100 millimetres), the subadult stage (101–220 millimetres), and the adult stage (221–567 millimetres). The spans of the growth stages are based on *Acanthodes gracilis*.

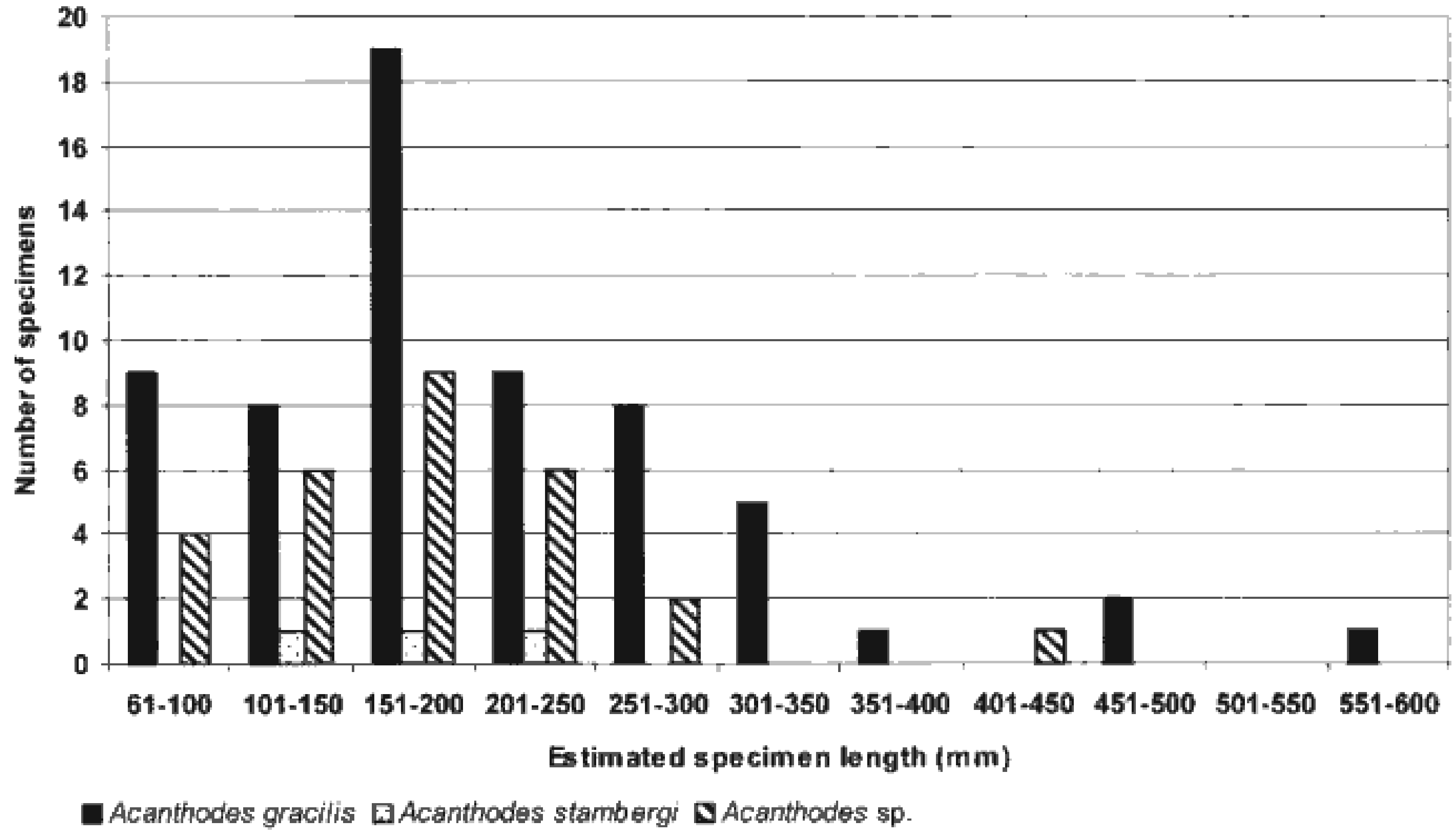

Fig. 29. Distribution of the size categories.

	A^1	A^2	B	C	D^1	D^2	E	F	G	H	I	J
Acanthodes *"beecheri"*	– –	– –	– –	– –	8–12 –	11–12 –	4 –	35 –	24 –	– –	– –	– –
Acanthodes bourbonensis	59–88 –	50–69 –	29–43 –	17–20 –	11–18 –	9–13 –	6–9 –	– –	35 –	19 –	– –	– –
Acanthodes bridgei	64–74 –		37–45 –	16–20 –	12–14 –		7–8 –	42–58 –	28–41 –	16–24 –	15–20 –	8–13 –
Acanthodes bronni	58–65 (95) 52–69		(32–47) 26	10–22 –	6–12 –		(9) –	(44–46) –	(36) –	(18–24) –	– –	– –
Acanthodes fritschi	70 –	– –	31–33 –	– –	– –	– –	– –	– –	– –	– –	– –	– –
Acanthodes gracilis (P)	58–73	48–59	25–30	–	–	–	–	–	–	–	–	–
Acanthodes gracilis (CR)	60 50–(76)	50 (50–68)	36 (15–62)	16–17 (15)	9–10 (10)	8 (8)	6 (4)	– (46)	– (32)	– (23)	– (19)	– (10)
Acanthodes kinneyi	42	42–55	26	18–21	9	9–10	5	52–55	36	–	–	–
Acanthodes lundi	72–77	64–74	27–35	15–21	11–16	11–13	5–6	46–52	38	21–29	?13	?12
Acanthodes nitidus	78	–	40	–	–	–	–	–	–	–	–	–
Acanthodes ovensi	90 73		50 55	– –	– –		– –	– –	– –	– –	– –	– –
Acanthodes sippeli	57	–	–	17	–	–	–	–	–	–	–	–
Acanthodes stambergi n. sp.	–	–	32	–	–	–	–	–	–	–	–	–
Acanthodes sulcatus	20 60–83		29 23–29	17 –	– –		– –	– –	– –	41 –	– –	– –
Acanthodes wardi	65 –	60 –	– –	20 –	10–13 –	7–12 –	5 –	41–48 –	29 –	18–29 –	– –	– –
Acanthodes sp. Kansas (HQ)	67		35	20	14		7	51	37	16	21	9
Acanthodes sp. Oklahoma, Texas	75		–	–	–		–	–	–	–	–	–
Acanthodes sp. Spain	50 –	– 79	– 32	20 –	10 –	– –	– –	44 –	32 –	24 –	– –	– –

bourbonensis, *Acanthodes bronni*, and *Acanthodes gracilis*) show similar values of the body ratios. The relationship among the others species is described in Zajíc (1998). The body is rather fusiform (as in *Acanthodes bridgei*) in juvenile and subadult stages. The body of adults tends to become longer somewhat as in *Acanthodes bronni*. The neural and visceral endocranium are poorly preserved (or missing) contrary to the Stephanian *Acanthodes fritschi* or particularly to Lower Permian *Acanthodes bronni*. Bases of the gill rakers are not preserved as much as necessary for comparison with other species. No striae on the surfaces of the branchial gill rakers were detected unlike *Acanthodes bridgei* or *Acanthodes fritschi*. No differently shaped hyoid gill rakers were found contrary to *Acanthodes lundi* or *Acanthodes* sp. from the Stephanian of the Czech Republic (Zajíc 1998, Fig. 52). Ornamentation of the circumorbitals looks somewhat more delicate than in *Acanthodes fritschi* or *Acanthodes bronni*. For the discussion concerning labyrinths and otoliths see the descriptive part. The long procoracoid and presence of the suprascapula are similar to Stephanian *Acanthodes fritschi*. However, absence of the both features in the overall majority of other species could be simply seeming (depending on the insufficient preparation). The dermotrichia of the pectoral fin are comparatively short as is common in the genus *Acanthodes* unlike *Acanthodes tholeyi* and *Acanthodes stambergi* n. sp. The delicately pitted scale crowns were within the genus *Acanthodes* so far described only in *Acanthodes gracilis*. The second feature – the posteriorly oriented spiny projections of the scale crowns were found also in *Acanthodes fritschi*, *Acanthodes luedersensis*, and various isolated scales of *Acanthodes* sp. (see Zajíc 1998, p. 23). This feature thus cannot be understanding as specific for *Acanthodes fritschi*. The posterior projections are very tiny and fragile (unlike the robust ones in *Acanthodes luedersensis*). They are mostly broken off and detailed observation is thus essential. The posterior spiny projections of *Traquairichthys pygmaeus* and *Pseudacanthodes pinnatus* thus cannot be considered as a generic feature. Reclassification of both taxa as species of the genus

K	L	M	N	O
– –	– –	46 –	– –	9–11 –
– –	50 –	36–42 –	43–48 –	9 –
20–35 –	53–75 –	29–52 –	43–58 –	10–14
18–(24) 27	(61–85) 47–69	(35–44) 36	(56–60) –	(11) –
21–23 –	73–78 –	– –	52–60 –	– –
18	51–68	36–43	44	–
– 30	49–54 (49–88)	– (29–88)	50 (45–95)	– (11)
30	49–50	–	–	9–10
27	63–86	33–35	48–53	11–14
27–34	75	78–120	53–70	–
– 43	– –	– 66	– 50	– –
–	–	–	–	15
28	–	–	–	–
– 27–35	– 92–102	100 71–105	– 55–63	– –
24 –	– –	67 57–66	54 –	– –
44	74	38	44	15
–	–	–	–	–
– –	– –	40 37–52	– –	– –

Fig. 30. Comparison of the values of individual ratios in *Acanthodes*; the upper line of values was compiled on the base of data in Zajíc (1998, Fig. 51); the lower line of values was newly measured by the author; *Acanthodes "beecheri"* – the numerical values was computed from data in Zidek (1976, p. 37); *Acanthodes bourbonensis* – the numerical values was computed according to measurements and photographs of Heyler (1969, p. 40, Pls III/1–2, IV/1); *Acanthodes bridgei* – the numerical values combine the data of Zidek (1976, 1988); *Acanthodes bronni* – the upper line of values was computed according to Heidtke (1990a), the values based on the illustrations of Boy (1976, Fig. 12), Dean (1907, Fig. 28), Heidtke (1990a, Figs 2C, 30, 39, 47, 49, 53, 54), Kner (1868, Pl. 5/1), and Reis (1895, Pl. I/4) are in the brackets, the lower one was measured in the collections of the Natural History Museum in London; *Acanthodes fritschi* – the numerical values come from Zajíc (1998); *Acanthodes gracilis* (P) – specimens from Poland measured by the author in the collections of the Natural History Museum in London; *Acanthodes gracilis* (CR) – specimens from the Czech Republic, the upper line of values was computed according to the figure of Fritsch (1893, Fig. 265) and the data of Augusta (1939), the lower one represents here described specimens; *Acanthodes kinneyi* – from Zidek (1992); *Acanthodes lundi* – from Zidek (1980); *Acanthodes nitidus* – specimens measured by the author in the collections of the Natural History Museum in London, the less reliable values are in parentheses; *Acanthodes ovensis* – the upper line of values is based on the data of Forey & Young (1985), the lower line of values was measured in the collections of the Natural History Museum in London; *Acanthodes stambergi* n. sp. – the values are based on specimen MHK 63 762/A; *Acanthodes sippeli* – the numerical values combine the data obtained and computed from Heidtke (1995); *Acanthodes sulcatus* – the upper line of values is based on Zidek (1980, p. 67), the lower one was measured in the collections of the Natural History Museum in London; *Acanthodes wardi* – the upper line of values was computed according to Davis (1894, Pls 27/1, 28/1, 29/2), the lower one was measured in the collections of the Natural History Museum in London; *Acanthodes* sp. from Kansas (Hamilton Quarry) – see Zidek (1976); *Acanthodes* sp. from Oklahoma and Texas – see Zidek (1975); *Acanthodes* sp. from Spain – the upper line of values were measured from an unpublished photograph supplied by Soler-Gijón, the lower one was measured in the collections of the Natural History Museum in London.

Acanthodes is therefore even more presumable. Tesserae can be within the genus *Acanthodes* either absent as in *Acanthodes fritschi* or present. The convexly sculptured tesserae of *Acanthodes gracilis* are quite different from the tesserae of *Acanthodes lundi* Zidek 1980, Fig. 3). The most similar sculpture of tesserae was found in *Acanthodes bronni*. Differences between both species are, however, distinct. Morphology of the individual segments of the head sensory lines is similar to those in *Acanthodes fritschi* or in *Acanthodes bridgei*. The fusion of the paired ventrolateral sensory lines into the anteriorly headed unpaired lateral one were also described in *Acanthodes bridgei*. The latter species have also developed the ventral scale shield around the sensory lines fusion. The squamation pattern is, generally, similar in juvenile stages of the various *Acanthodes* species. The subsequent ontogenetic stages, however, start to differ. The anteriorly advanced ventral squamation starts as in *Acanthodes bridgei* (Zidek 1976, Fig. 13) early in ontogeny (juvenile stage). The anteriorly advanced dorsal squamation is in the early subadult stages similar as in *Acanthodes bronni* (Heidtke 1990a, Fig. 52). The squamation pattern of *Acanthodes ovensi* is in the Fig 1f (Forey & Young 1985) somewhat schematized. The advanced dorsal squamation of the oldest specimen (probably a late subadult stage) is, however, well documented. Tiny parts of the cranium (mainly the most anterior ones) of some specimens from the Rudník Horizon of the Krkonoše Piedmont Basin show signs of a "scaumenellisation" (see Béland & Arsenault 1985) – a chemical (?) degradation of the skeletal elements during fossilization.

2.4. ***Acanthodes stambergi* n. sp.**

Acanthodes stambergi n. sp.
(Figs 9, 12, 15, 16, 24, 28–33; Pls 8C, 14C, 14D)

Etymology: Named in honour of the Czech palaeontologist S. Štamberg who collected the herein described specimens.

Measurements quality class	A^1	A^2	B	C	D^1	D^2	E	F	G	H	I	J	K	L	M	N	O	y	Estimated l_T
Exact			32										28					6	133–198

Fig. 31. *Acanthodes stambergi* n. sp., ratios and measurements based on 3 specimens. Ratios are given in percent.

Holotype: Specimen MHK 63 762/A (Regional Museum of Eastern Bohemia, Hradec Králové)

Type locality: Kladoruby, Dolní pepřík; Boskovice Basin; part of the municipality Letovice; Blansko district; South Moravian region; Czech Republic.

Horizon: Lower Letovice Formation

Age: Lower Permian; Upper Asselian (Lower Autunian).

Paratypes: MHK 63 762/B, MHK 63 796/C

Diagnosis: Medium-sized acanthodian (estimated length up to 250 mm). Completely squamated area starts in front of the pectoral girdle. Dorsal fin slightly more posterior than anal fin. Ventral : pectoral spine length ratio (B) = 32%; outer diameter of circumorbital ring : prepectoral length ratio (K) = 28%. Circumorbital ring with 5 segments. Wide scapulocoracoid plate; suprascapula co-ossified with scapular blade. Pectoral fin supported by extremely long dermotrichia (along whole length of the pectoral fin). Delicately pitted scale crown with very thin pointed posterior projection.

Description: The body form is probably fusiform as in *Acanthodes gracilis* (see Fig. 21). The total length was estimated with the aid of ratio C (15) analogically to *Acanthodes bronni* (see chapter 2.3). In the event of incomplete pectoral fin spines, it is possible to use the pectoral fin spines maximum width/length diagram (Fig. 15). The estimated total length ranges from 133 to 235 mm in the three specimens so far known. All computed body ratios and measured numbers of scales per millimetre in a row are presented on Fig. 31. Body ratios are as follows: ventral : pectoral spine length ratio (B) = 32; outer diameter of circumorbital ring : prepectoral length (K) = 28.

All elements of the neural and visceral endocranium are poorly preserved or missing as in *Acanthodes gracilis* and contrary to Stephanian *Acanthodes fritschi* or Lower Permian *Acanthodes bronni*.

Fragment of one posterior jaw element (articular or quadrate) is present in specimen MHK 63 796/C.

Cluster of the poorly preserved gill rakers of the holotype looks as baked together with no visible details.

The dermal bones of the neurocranium are represented by five circumorbital bones arranged around the orbit as the circumorbital ring (Pls 8C, 14D). The relationship between the outer diameter of the orbit and the estimated total specimen length is shown on the Fig. 9. The inner surface is smooth and concave. The outer surface is not visible. The individual segments are irregularly crescent-shaped.

The mandibular bones (Pls 8C, 14D) are imperfectly preserved on all three specimens. All visible features are undistinguishable from those in *Acanthodes gracilis*.

The gill covers are represented by two series of very thin branchiostegals rays (Pls 8C, 14D). Each consist of 15 rays at least. They were arranged almost parallelly each other, backwards from the inner ventral borders of the lower jaws.

Both labyrinth infillings are preserved on the holotype (Fig. 12; Pls 8C, 14D). They are composed by fine sand-sized grains as in *Acanthodes gracilis*. Their shape is shortly bean-shaped. No otoliths were found.

The pectoral girdle (Fig. 32; Pls 8C, 14C, 14D) is composed of the same elements as in *Acanthodes gracilis* (see chapter 2.3 Scapulocoracoids seem to be somewhat weakly preserved than in *Acanthodes gracilis*. The coracoid plates are wide The suprascapula is co-ossified with the scapular blade.

The pectoral fin spines (Fig. 32; Pls 8C, 14C, 14D) are moderately sabre-shaped and distally pointed as is usual in *Acanthodes*. The better preserved spine of the holotype shows following features. The groove between the medial and posterior ribs bears infrequent but conspicuous pores. The posterior rib passes distally to absolute majority of the lateral and mesial surfaces of the spine. Other features are similar or the same as in *Acanthodes gracilis*. The spine maximum width : length ratio (Fig. 15) has no taxonomical significance (compare with values of *Acanthodes* sp. in Fig. 34). The trend line is parallel and close to the trend line of *Acanthodes gracilis* and *Acanthodes* sp. The measurements (length x maximal width) of all specimens are 20.0 mm × 1.2 mm; 29.7 mm × 2.0 mm; 35.3 mm × 2.2 mm.

The ventral spine was not found in the holotype. The best preserved one (MHK 63 762/B) is around 9.5 mm long and 0.8 mm in maximum width. The value of the spine maximum width : length ratio (Fig. 16) is about 8.5%. This value fit in the wide variational span of *Acanthodes gracilis* and *Acanthodes* sp.

The anal and dorsal fin spines are preserved only in the holotype as small proximal fragments (close to the posterior end of the specimen on Pl. 8C).

No radialia were found.

Dermotrichia of the pectoral fin (Fig. 32; Pls 8C, 14C, 14D) are narrow and extremely long. They are arranged in the row parallel to the pectoral fin spine. The dermotrichia placed close the pectoral fin spine run distally from the scapulocoracoid up to the tip of the fin spine. The maximum measured lengths of pectoral dermotrichia are in *Acanthodes stambergi* n. sp. about nine to ten times longer than in *Acanthodes gracilis*. Dermotrichia probably filled majority of the pectoral fins during animal's lifetime. Dermotrichia are represented by the flattened non-articulating rods with oval cross section as in *Acanthodes gracilis* or *Acanthodes fritschi*. The common occurrence of the predominant acanthodian species *Acanthodes gracilis* with short pectoral dermotrichia and the rare species

Acanthodes stambergi n. sp. with extremely long pectoral dermotrichia in the Boskovice Basin has remarkable analogue in the Lower Permian sediments of the Saar-Nahe Basin. The predominant acanthodian species with short pectoral dermotrichia is there represented by long time known *Acanthodes bronni*. Another three rare species were recently described by HEIDTKE (1990b, 1993, 2003). They are represented by *Acanthodes tholeyi* with extremely long pectoral dermotrichia, *Acanthodes boyi*, and *Westrichus kraetschmeri*. Dermotrichia of the other fins were not found.

No caudal fin has been found yet.

The delicately pitted scale crowns are terminated in posteriorly orientated and fragile spiny projections. The sculpture and shape of the body scales cannot be distinguished from those of *Acanthodes gracilis*. For the detailed description see chapter 2.3. For the time being, *Acanthodes gracilis* and *Acanthodes stambergi* n. sp. are therefore distinguishable only by the length of the pectoral dermotrichia. Six scales per millimetre in the natural row (measured behind the anal fin spine and near the lateral sensory line) were found in the holotype.

Tesserae were not recognized but this may be a result of imperfect preservation.

Fragments of the sensory lines of the head (Pls 8C, 14D) are relatively numerous but unidentifiable. They are formed by cracked segments of no taxonomic significance.

The poorly preserved trunk sensory lines are represented by the paired lateral (main) sensory line (with derived vertical sensory lines) and by the paired ventrolateral sensory line. They look undistinguishable from those of *Acanthodes gracilis*. No ventral scale shield was found, probably due to way of preservation.

Ontogeny: Three incomplete specimens do not allow to compile an ontogenetic series. Figure 31 shows all computed body proportions, some measurements, and estimated total specimen lengths. The completely squamated area of the holotype (scales cover the entire circumference of the cross section of the trunk) reaches close behind the pectoral region. Such extent of the completely squamated area corresponds (analogically with *Acanthodes gracilis*) to the older subadult stage. The complete distribution of the growth stages of all three acanthodian taxa is demonstrated in Fig. 28. Figure 29 shows a finer distribution based on the size categories. Dependence of the total specimen length on the number of scales per mm in a row is demonstrated in Fig. 24. For measurements and body proportions of the holotype see the Zidek's diagram in Fig. 33. For explanation of the diagrams see Fig. 26.

Geographic distribution: Occurrence of the *Acanthodes stambergi* n. sp. is so far restricted to the Kladoruby, Dolní pepřík locality in the Boskovice Basin. The age of the locality corresponds to the upper part of the *Acanthodes gracilis* biozone. Fossiliferous sediments of this stratigraphic level are developed only in the Boskovice Basin. Other basins of the Czech Republic (particularly the Krkonoše Piedmont Basin) did not yield determinable vertebrate remains yet.

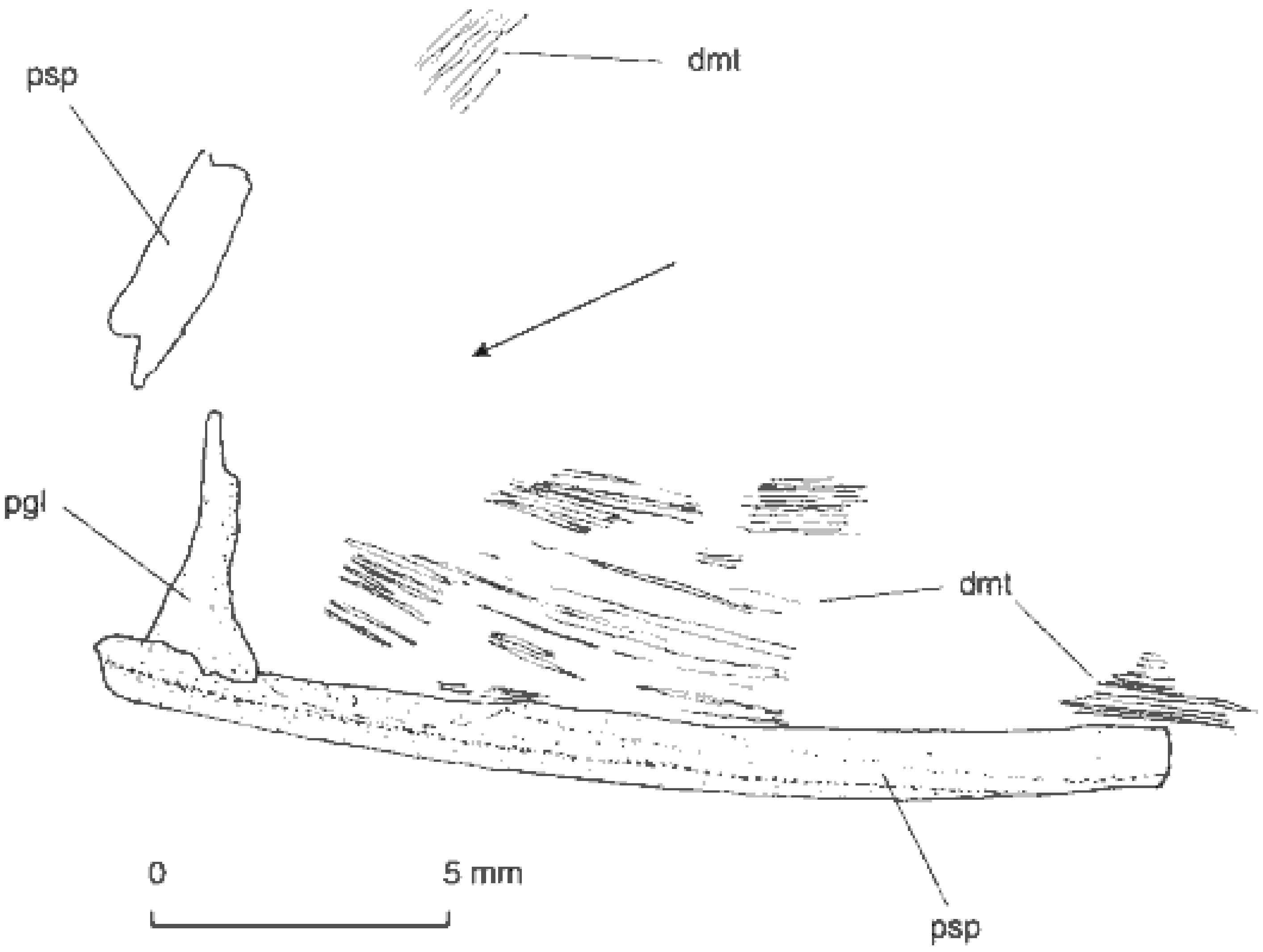

Fig. 32. *Acanthodes stambergi* n. sp.; fragments of scapulocoracoid and pectoral spines with long dermotrichia; anterior direction is marked by an arrow; MHK 63 762 (holotype); Kladoruby, Dolní pepřík.

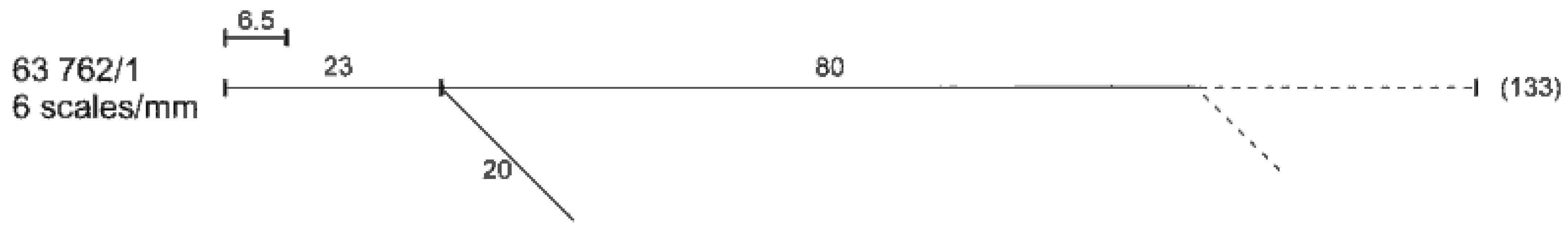

Fig. 33. *Acanthodes stambergi* n. sp.; Zidek's diagram of the holotype; MHK 63 762; Kladoruby, Dolní pepřík.

Sites: Kladoruby, Dolní pepřík (3 specimens).

Remarks and relationship: *Acanthodes stambergi* n. sp. is closely related to the predominant *Acanthodes gracilis*. Three incomplete specimens do not allow to compile an ontogenetic series. The two species have identical morphology and ornamentation of the scale crowns. *Acanthodes stambergi* n. sp. differs from the *Acanthodes gracilis* in extremely long pectoral dermotrichia, somewhat weakly developed scapulocoracoids (but with the wide coracoid plates), and absence of tesserae. The latter feature, however, may be caused by an imperfect preservation of the specimens. The acanthodians without preserved pectoral dermotrichia must therefore be classified as *Acanthodes* sp. yet. The occurrence of the *Acanthodes stambergi* n. sp. has been reported only from the upper part of the *Acanthodes gracilis* biozone, i.e., from the Middle Letovice Formation. *Acanthodes stambergi* n. sp. probably evolved from the *Acanthodes gracilis* short time ago. Both taxa, however, became extinct in the basins of the Bohemian Massif (in the area of the Czech Republic and Poland at least) at the end of the *Acanthodes gracilis* biozone. All calculated ratios of the *Acanthodes stambergi* n. sp. are shown in Fig. 31. Figure 30 presents a comparison of individual ratios of various *Acanthodes* species. The table is based on the Zajíc (1998, Fig. 51) and complemented by new measurements. The values of the ratio K are close in most of species. The large span of values of the ratio B does not permit a valid comparison of *Acanthodes stambergi* n. sp. with other species. The long procoracoid and the presence of the suprascapula are similar to *Acanthodes gracilis* and to the Stephanian *Acanthodes fritschi*. The dermotrichia of the pectoral fins are extremely long as in the Lower Permian (Asselian) *Acanthodes tholeyi* from the Saar-Nahe Basin (Germany). The delicately pitted scale crowns are within the genus *Acanthodes* known only in *Acanthodes gracilis* and *Acanthodes stambergi* n. sp. The posteriorly oriented spiny projections of the scale crowns were found in *Acanthodes fritschi, Acanthodes gracilis, Acanthodes luedersensis, Acanthodes stambergi* n. sp., and various isolated scales of *Acanthodes* sp. (see Zajíc 1998, p. 23).

2.5. *Acanthodes* sp.

Acanthodes sp.

(Figs 9, 12, 15, 16, 18, 19, 28, 29, 34–44; Pls 6D–8B, 15A–16D)

1893 *Acanthodes gracilis* var. *Bendai*: A. Fritsch, Fauna der Gaskohle etc.; p. 64–67 (partim); Figs 260, 262–264; Pl. 107/10

1946 *Acanthodes gracilis bendai*: J. Augusta, Příspěvky k poznání moravského etc.; p. 80–81 (partim).

1947 *Acanthodes gracilis* (Beyrich) Roemer var. *bendai* Fr.: J. Augusta, Spodnopermská zvířena a květena etc.; p. 196–197 (partim).

1989 *Acanthodes "gracilis bendai"*: J. Zajíc, Remains of Permo-Carboniferous etc.; p. 289–291 (partim); Figs 2, 3; Pls 1, 2.

Notes: All specimens without presence of the distinguishable key feature (length of the pectoral dermotrichia) are here provisionally labelled as *Acanthodes* sp. The redescription of the Polish type material of *Acanthodes gracilis* (see notes in the chapter 2.3) and research of any new better preserved specimens of *Acanthodes stambergi* n. sp. is needed in the future.

Age: Lower Permian; Asselian (Lower Autunian).

Material: Specimens from various localities and boreholes of the Rudník Horizon of the Krkonoše Piedmont Basin – M 2180–M 2181, M 2183, M 2188, M 3648–M 3651, M 3653, M 4357, M 4361–M 4363, M 4366–M 4368, M 4372–M 4376, M 4377/1+3+4–M 4382, M 4385–M 4388, M 4391–M 4394/2, M 4396–M 4400, M 4407–M 4412, M 4415–M 4417, M 4420/2–M 4422, M 4424, M 4426–M 4432, M 4434, M 4443–M 4447/1+3, M 4448–M 4452, M 4455–M 4460, M 4464, M 4466, M 4471–M 4474, M 4476, M 4479–M 4480, M 4482–M 4490, M 4494–M 4496, M 4500, M 4502–M 4514/1, M 4515–M 4521, M 4522–M 4701, M 4704–M 4745, YA 1359, YA 1361–YA 1364, A 1213, I 1919–I 1922, I 1998, PUK 01, PUK 07–PUK 09, No. 63633–63634, No. 63637–63638, No. 63641–63642, No. 63646, No. 63648–63650, Unnumbered carbonate plate from the Town Museum Nová Paka; Specimens from the Zbýšov Horizon of the Boskovice Basin (Padochov and Zbýšov localities) – M 4230–M 4234, M 4237–M 4241, M 4244, M 4246, M 4248–M 4262, M 4264–M 4269, M 4271–M 4281, M 4283–M 4306, M 4309–M 4311/2, M 4313–M 4320, M 4323–M4325, M 4328–M 4330, M 4332–M 4342, M 4344, M 4348–M 4349, M 4352–M 4356; Specimens from the Zbraslavec Horizon (Zbraslavec locality) – PUK 11–PUK 14, PUK 16, PUK 18–PUK 23; Specimens from the Zboněk-Svitávka Horizon (Černá Hora locality) – PUK 04, PUK 06; Specimens from the Lubě Horizon (Kladoruby locality) – M 4288–M 4290, M 4294–M4301, No. 63752/1–63755, No. 63759–63761, No. 63763–63764, No. 63766–63768, No. 63770–63780, No. 63782–63783, No. 63785, No. 63787–63788, No. 63790–63793, No. 63795–63796/B, No. 63798–63801, No. 63804–63808.

Note: The only known acanthodian specimen from the Blanice Basin is now missing. The unnumbered specimen (skin fragment) of the National Museum, Prague came from the Český Brod, Na skalce locality. Specimens from the Moravian Museum, Brno were not studied in detail yet. The following specimens are provisionally labelled as *Acanthodes* sp., and will be determined in a subsequent paper. Most of the specimens come from the Malá Lhota locality (without exact localisation) – MZM 21289, MZM 21291, MZM 21294, MZM 21300, MZM 21308, MZM 21374, MZM 21376, MZM 21378–MZM 21379, MZM 21381, MZM 21385–MZM 21387, MZM 21391, MZM 21415, MZM 21418–MZM 21419, MZM 21433, MZM 21441–MZM 21442, MZM 21451–MZM 21454, MZM 21509, and several unnumbered fragments. The Malá Lhota, Příčná zmola locality is represented by MZM 21212 and MZM 21304; the Malá Lhota, Podhájí locality by five unnumbered fragments. The last three specimens come from the Hluboké Dvory (MZM 22363), Moravský

Krumlov (MZM 21544), and Svitávka (MZM 22123) localities.

Description: The body form looks similar to *Acanthodes gracilis* (see chapter 2.3. and Fig. 21). The total length were estimated with the aid of the ratio C = 15 (according to *Acanthodes gracilis*). In the event of incomplete pectoral fin spines is possible to use the pectoral fin spines maximum width/length diagram (Fig. 34). The estimated total length ranges from 83 to 480 mm. However, computed total specimen lengths could be underestimated in some larger specimens. Deformations of the bodies are of the same type as in *Acanthodes gracilis* or *Acanthodes stambergi* n. sp. Measurements of distances are therefore often problematic. Two clusters of measured values were used for computing of the body ratios (see Fig. 35). Computed body proportions are following: dorsal : pectoral spine length ratio (A^2) = 60; ventral : pectoral spine length ratio (B) = 19–29 (total average is 25); outer diameter of circumorbital ring : prepectoral length (K) = 13; mandibular bone : pectoral spine length (L) = 52; distance between pectoral and ventral spines : distance between ventral and anal spines (M) = 49–58 (total average is 54); mandibular bone : prepectoral length (N) = 33–55 (total average is 44).

Elements of the neural endocranium are missing or unrecognizable due to poor preservation as in *Acanthodes gracilis* or *Acanthodes stambergi* n. sp. and contrary to Stephanian *Acanthodes fritschi* or Lower Permian *Acanthodes bronni*. A weak "ossification" is probably the reason. The dermal elements (the circumorbitals, mandibular bones, branchiostegals, gill rakers, tesserae, and segments of sensory lines) are, however, rather well preserved. Components of the neural endocranium were not recognized yet but some hotchpotches of indeterminable viscerocranial fragments can contain them. Two specimens (M 4673/B and M 4696/A) from the Vrchlabí locality, however, yielded poorly preserved and deformed basisphenoids (visible from the ventral side). The way of the preservation of the Vrchlabí locality specimens do not allow detailed description (see chapter 3).

Upper jaws are represented by two poorly preserved quadrates. The poorly preserved pterygoid or autopalatine were found in specimen M 4582 from the Vrchlabí locality.

The meckelian cartilage consists of two separated "ossifications". They are usually poorly preserved. Slender mentomandibulars show no details. The articular of specimen MHK 63 752 (Pl. 16A) reaches anteriorly up to the rostral half of the sigmoid bend of the mandibular bone. The sigmoid bend is poorly visible but its presence is possible to identify according to position of the flat triangular process on the ventral boundary of the anterior half of the sigmoid bend by analogy with Stephanian *Acanthodes* sp. (see Zajíc 1998, Fig. 55, r). The preglenoid process is rarely preserved as in M 4363 (maximum extents of articular are 11.7 × 4.1 mm) but without visible details. No specimen with co-ossified articular and mentomandibular was found. The jointed articulars and quadrates are common particularly in specimens from the Vrchlabí locality. Both left and right articulated mentomandibulars are also common there.

Remains of the visceral skeleton are comparatively common but they are mostly poorly preserved. They are often part of hotchpotches. The undeterminable elements of the viscerocranium come from the Vrchlabí locality. The hyoid arch of specimen PUK-12 is detectable due to articulated gill rakers. The hyoid gill rakers do not differ from the posthyoid ones contrary to hyoid gill rakers in *Acanthodes lundi* or *Acanthodes* sp. from Stephanian B of the Central and Western Bohemian Basins (see Zidek 1992, Fig. 12). The articulated posthyoid gill rakers trace course of the missing gill arches of some specimens. No more than five gill rakers traces were found on one specimen. Gill rakers are larger and solider on the anterior gill arch and decrease

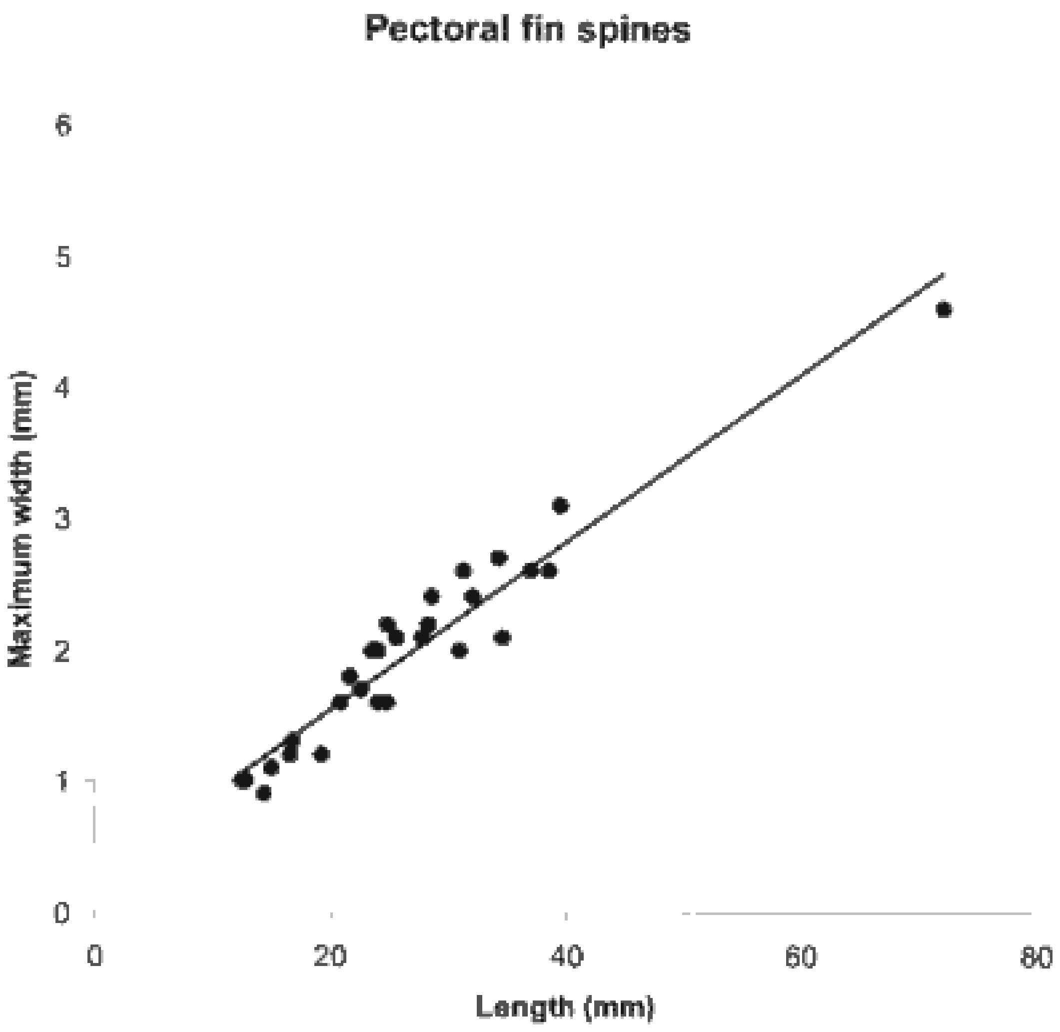

Fig. 34. *Acanthodes* sp.: Relationship between the length and the maximum width of pectoral fin spines with their trend line. The position and direction of the trend line is almost the same as in *Acanthodes gracilis* (see Fig. 15).

Measurements quality class	A^1	A^2	B	C	D^1	D^2	E	F	G	H	I	J	K	L	M	N	O	y	Estimated l_T
Exact (average)			27–29 (28)												49–54 (52)				
Worse but usable (average)		60	19										13	52	58	33–55 (44)		3.5–9	157–299
Average in total		60	25										13	52	54	44			

Fig. 35. *Acanthodes* sp.; proportions and measurements based on 6 specimens. Ratios are given in percent.

posteriorly. The gill rakers (Fig. 36; Pls 6D, 7A) are tightly articulated, sometimes create rigid blocks and look like baked together. The individual gill rakers are sabre-shaped (more or less curved). Their bases are always poorly preserved with indistinct shape. Maximal measured lengths oscillate between 0.7 and 1.3 mm yet. The surface of the gill rakers is not covered by striae or tiny ridges as in *Acanthodes fritschi*.

Five circumorbital bones are arranged around the orbit as the circumorbital ring (Fig. 36; Pls 7A, 15B). The relationship between the outer diameter of the orbit and the estimated total specimen length is shown in Fig. 9. The maximal measured diameter is 9 mm. The inner surface of all segments is smooth and concave. The outer surface is convex and covered by sculpture. The individual segments are irregularly crescent-shaped, each with an elevated rim along the inner margin. The density and nature of the sculpture depend particularly on the specimen length. The principal arrangement of the ornamentation of circumorbitals is the same as in *Acanthodes gracilis*. Ornamentation is fine in younger specimens as in M 4473. Small tubercles are arranged particularly along the inner border of the ring there. Ornamentation is, however, formed mainly by the radial striae. Circumorbitals of older specimens (as in MHK 63 633) are markedly sculptured. The almost continuous row of fused elongated tubercles form distinct ridge along the inner border. The radially arranged rows of tubercles are separated from each other by groves. These groves define the undulation of the outer circumorbital borders. The longest measured segment is 6.5 mm long. The sculpture is similar to *Acanthodes gracilis* and not so robust as in *Acanthodes fritschi* (see Zajíc 1989; Fig. 2) on the whole. Indication of a sculpture is rare in the case of specimens from the Vrchlabí locality.

The mandibular bone (Figs 36, 37; Pls 7A, 7B, 15B, 16A) is the only dermal bone of the jaws. Isolated mandibular bones are rather rare in contrast to *Acanthodes* sp. from the Bohemian Stephanian. The characteristic shaped slender bone is thin and bent along about half its length. The shallow longitudinal groove (well visible on Pl. 7B) is situated on the posterior half of the bone. The central bone bend lies under the gap between the mentomandibular and articular. Both (anterior and posterior) parts of the mandibular bone are almost horizontally situated in the lower jaw, although the anterior one lies somewhat higher. The curve is slightly gentler in younger specimens like in M 4316. The mandibular bones of the older specimens bear more conspicuous longitudinal grooves and sometimes slightly horizontally wrinkled posterior extensions. The most similar situation is shown by *Acanthodes gracilis*. The inner rostral (symphyseal) terminations of both (left and right) mandibular bones are shaped as very small round articular surfaces. Length of the complete bones range from 6.1 mm to 21.0 mm. The maximum measured height of the flat posterior extension is 0.9 mm.

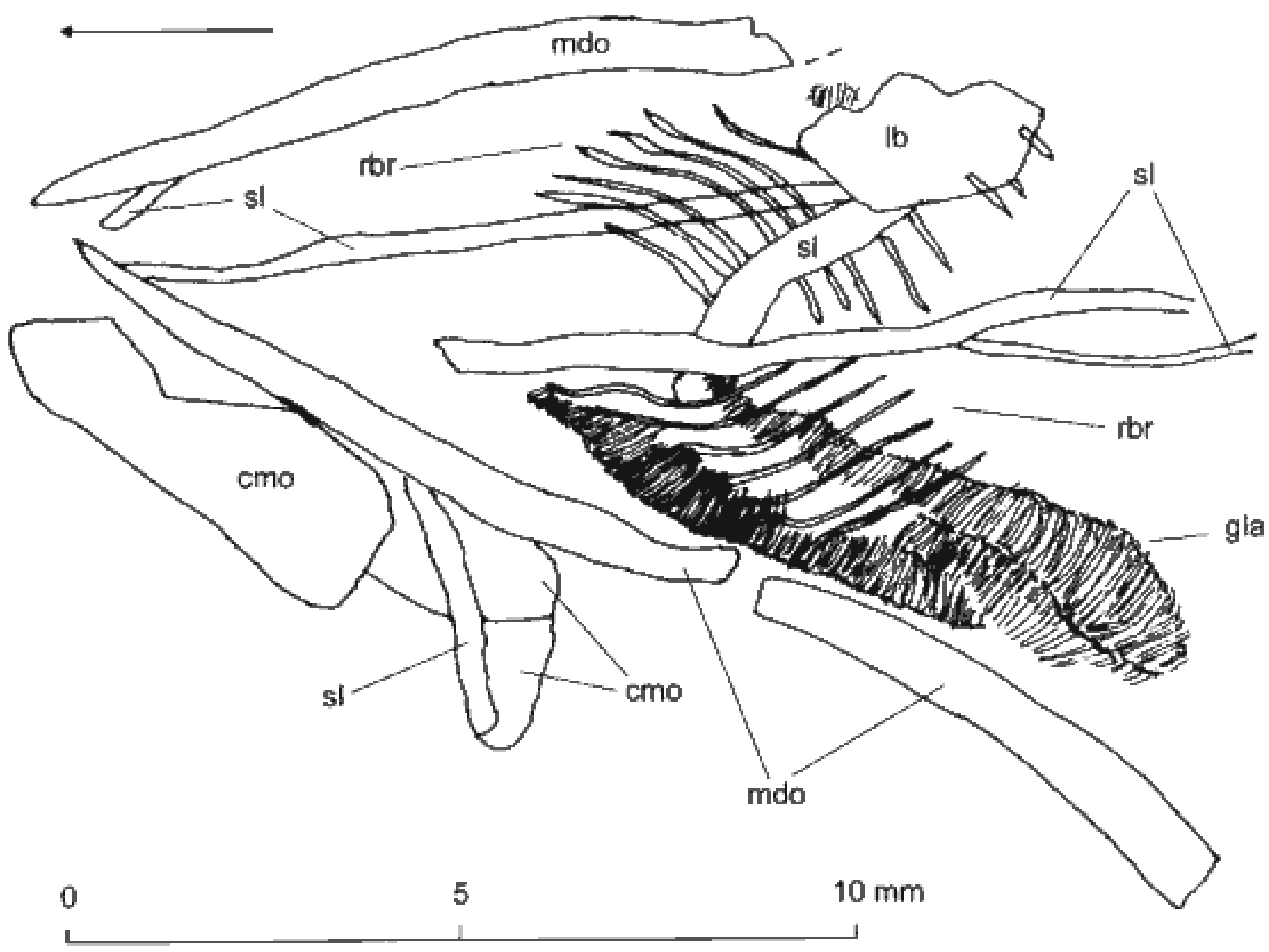

Fig. 36. *Acanthodes* sp.; incomplete head from the ventral view with circumorbitals, mandibular bones, branchiostegal rays, labyrinth infilling, articulated gill rakers of the gill arches, sensory lines of the head; anterior direction is marked by an arrow; M 4344; Padochov; Zbýšov Horizon.

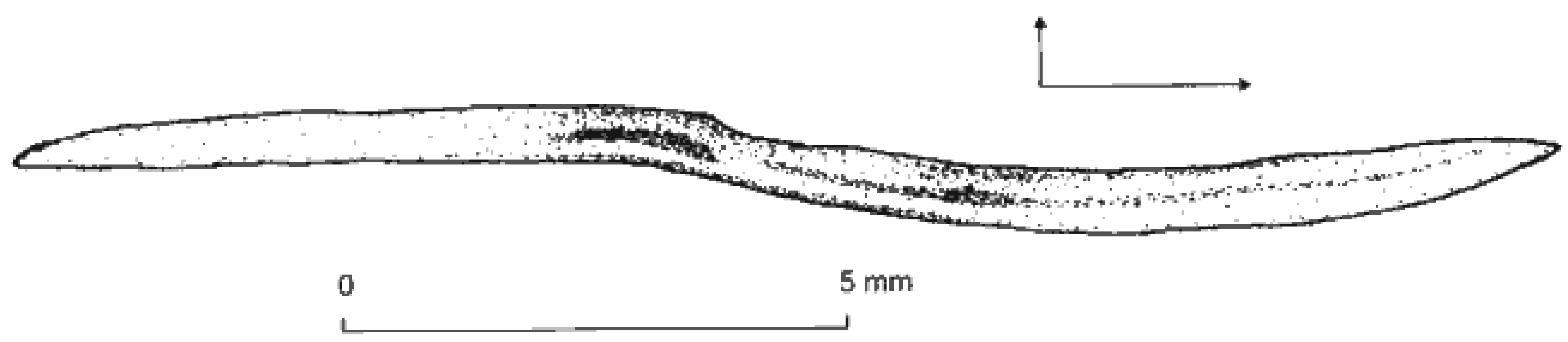

Fig. 37. *Acanthodes* sp.; mandibular bone in lateral view; anterior and dorsal directions are marked by arrows; M 4302; Padochov; Zbýšov Horizon.

The gill cover is formed by numerous very thin branchiostegal rays (Fig. 36; Pl. 8C) of different length. More than 22 pairs were found in specimen M 4353. Their various shape (from straight to variously curved) is probably caused by postmortem deformation of the relatively soft tissue. The maximum measured length is 3.5 mm in specimen M 4274 + M 4275 (Pl. 8C). The measured widths range from 0.04 mm to 0.2 mm. The original shape, arrangement, and body position are shown in specimen M 4344 (Fig. 36) and M 4274 + M 4275 (Pl. 8C).

The labyrinth infillings (Figs 38–40) are composed by fine sand-sized grains as in *Acanthodes gracilis* or *Acanthodes stambergi* n. sp. The colour and grain size differ from that of the sediment matrix. The colour also differs from the colour of the skeletal remains. The origin, chemical composition, and appearance (colour and absence of discernible granularity) of the inserted otoliths are different from the labyrinth infillings. For the detailed description see the chapter 2.3. Some otoliths that are embedded in the sacculus are covered by the sacculus wall as in specimen M 4254 (Fig. 38). Specimen M 4259 shows not only the sacculus with embedded otolith but also fragment of the semicircular duct (Fig. 40). The bean-shaped otoliths have high relief. The outline of the mostly flat labyrinth infillings is not regular. Summary of the labyrinth infillings and otoliths of the Lower Permian acanthodians of the Czech Republic is presented on the Fig. 12. One pair of the otoliths was found. The labyrinth infillings and otoliths were placed behind the orbits and over the posterior part of the jaws.

The structure and description of the pectoral girdle is described in the chapter 2.3. Absolute majority of specimens with preserved pectoral girdles can be classify as *Acanthodes gracilis* or *Acanthodes stambergi* n. sp. One of the four known indeterminable specimens is M 4266 (Pl. 41). The scapulocoracoid of the specimen is 2.7 mm high (including the suprascapula) with the scapular blade of minimal width 0.25 mm. These measurements correspond to juvenile stages. Three specimens of *Acanthodes gracilis* (M 4343, M 4491 + M 4492, MHK 63 796/A) and one specimen of *Acanthodes* sp. (MHK 63 806) have values of the minimal width of the scapular blade from 0.2 to 0.3 mm. Their estimated total lengths are 61, 63, 80, and 83 mm.

The pectoral fin spines (Fig. 41; Pl. 7A) are both the longest and the only paired fin spines of the genus *Acanthodes*. Most of the well preserved pectoral fin spines are (similarly as pectoral girdles) determinable as *Acanthodes gracilis* or *Acanthodes stambergi* n. sp. For the detailed description see chapter 2.3. The distal end can be longitudinally grooved (MHK 63 633/1,2) or covered by common pores (MHK 63 646). The estimated total specimen length ranges from 83 to 480 mm. The longest known pectoral fin spine (MHK 63 638) is 72 mm long. The inner structure of the fin spines correspond to description in *Acanthodes* sp. (see Zajíc 1998). The spine maximum width : length ratio (Fig. 34) has no taxonomical significance (compare with values of *Acanthodes gracilis* and *Acanthodes stambergi* n. sp. in Fig. 15).

The ventral spines (Pl. 7A) were found in two specimens. For the description see chapter 2.3. The comparison

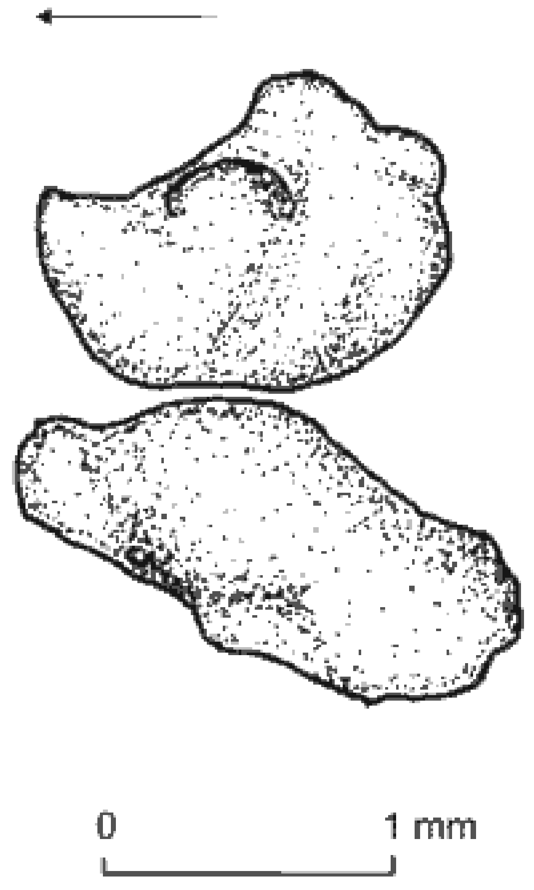

Fig. 38. *Acanthodes* sp.; both labyrinth infillings, the upper one with embedded otolith; anterior direction is marked by an arrow; M 4254; Padochov; Zbýšov Horizon.

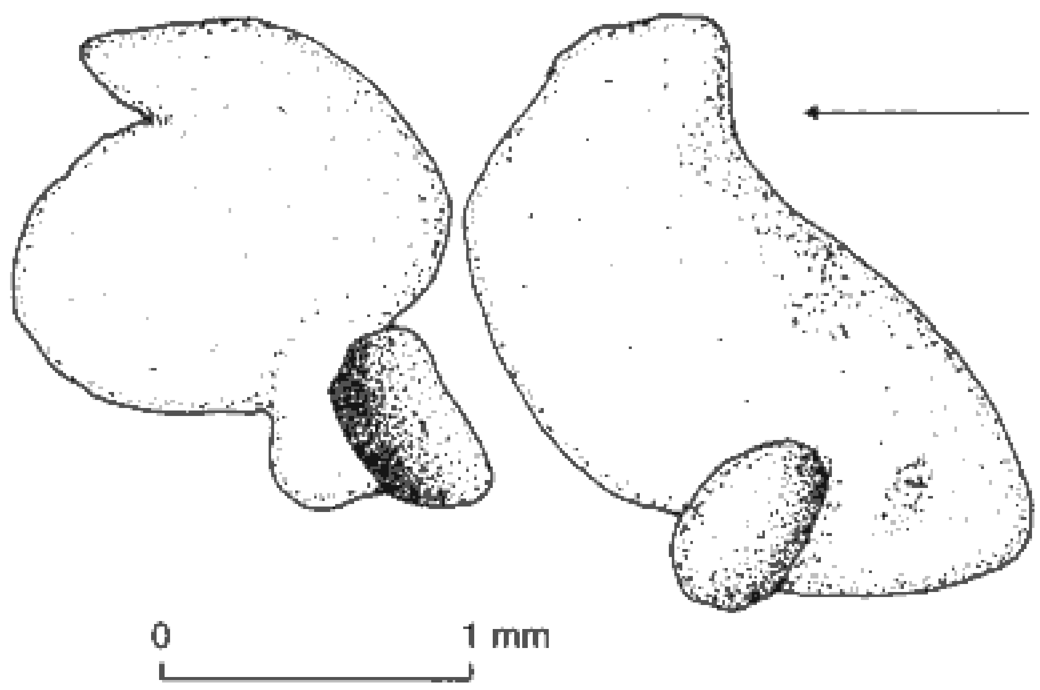

Fig. 39. *Acanthodes* sp.; paired labyrinth infillings with otoliths; anterior direction is marked by an arrow; M 4352; Padochov; Zbýšov Horizon.

of the spine maximum width : length ratios of all Lower Permian taxa from the Czech Republic is shown in Fig. 16.

The anal and dorsal (Pl. 16B) fin spines are about the same lengths. The dorsal fin is situated slightly posteriorly. Both fin spines are shorter and straighter than the pectoral one. The ribs of the anal fin spine of specimen PUK-18 are rather arched proximally and become flat distally. The pores are infrequent in the anterior growth between the ribs and missing in the posterior one. The pores of the distal part of the spine occur on the flat rib surfaces. The anal fins are up to 52.0 mm long (PUK-19) and 18.0 mm high (M 4464). The small patch of the enlarged scales is often situated close in front of the spine insertion. The anal fin of specimen MHK 63 775 shows following maximum sizes: the enlarged scales = 0.4 mm, the scales on the fin spine = 0.25 mm, scales behind the spine = 0.15 to 0.075 mm. The deformed posterior part of the anal fin of specimen M 4443 shows two scale zones. The zone with scales arranged parallelly with the longitudinal axis of the body is situated close the body scales. The obliquely arranged scale rows

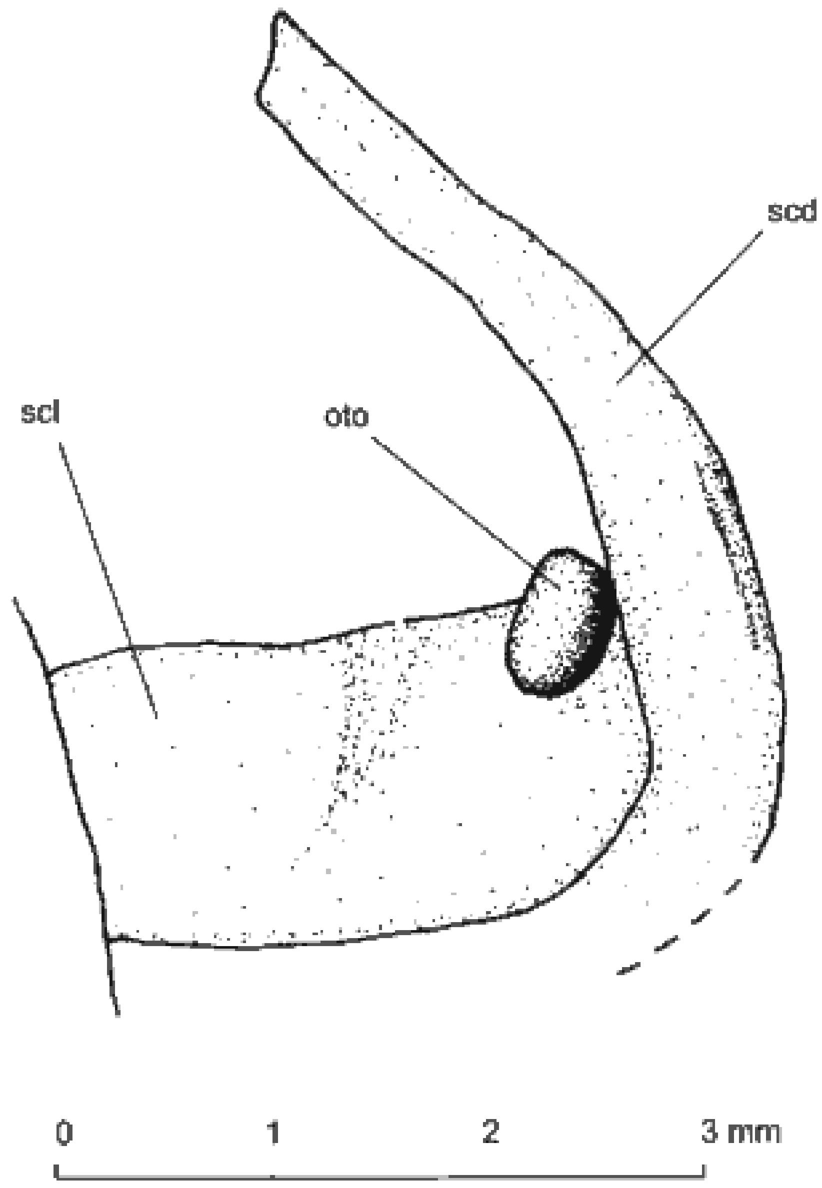

Fig. 40. *Acanthodes* sp.; partially preserved labyrinth (labyrinth infilling) with incomplete semicircular duct, sacculus, and otolith; M 4259; Padochov; Zbýšov Horizon.

(as in the body) are situated on the rest of the fin. The anal fin of specimen PUK-19 is formed by small scales with central hollows (see remarks). The scales decrease towards the fin margin. The hollows decrease as well up to disappearance. Rows of the short (up to 1.6 mm) dermotrichia were preserved as short fragments (up to 3.1 mm). The anterior rib of the dorsal fin spine of specimen PUK-19 is forms more than half of the proximal spine width. The middle rib moves forward in the distal direction. The posterior rib is missing in the proximal part of the spine that was inserted in the body during the animal life. The insertion of the dorsal fin spine was deep (28% of the total spine length) in the body of specimen M 4392. The robust dermotrichia (4.0 mm long and 0.2 mm thick) were found in specimen MHK 63 799 (Pl. 16B). Length of their row fragment was, however, only 1.8 mm. The most complete 34.0 mm long dorsal fin was found in specimen M 4443.

The outer morphology and the inner structure are very similar or almost the same as in *Acanthodes fritschi* (see Zajíc 1998). However, only ventral spines are safely distinguishable among isolated spines. Measurements of the unidentified isolated fin spines (Fig. 42) show evident trend. The values are accumulated near the trend line and show only low spread.

No radialia of the pectoral or caudal fins were found.

Dermotrichia of the pectoral fins were not preserved as much as necessary for the specific determination.

The caudal fins (Pls 7C, 16D) were found in fifteen specimens. The proximally widened termination of the axial lobe is preserved in some specimens as in M 3653 and M 4323. This swelling is similar as in *Acanthodes fritschi* (Zajíc 1998, Fig. 37) and therefore not so prominent as in *Acanthodes bourbonensis*. All Heyler's zones were found in various specimens. The hypochordal lobe of specimen M 4368 shows indication of a zone formed by tiny scales (similar to zone Z2") with not so clear orientation of the rows. The incomplete caudal fin of the very young specimen M 4375 is partially covered by tiny scales with the central hollows (see remarks).

The *Acanthodes*-type scales (sensu Gross 1973) have delicately pitted scale crowns as in *Acanthodes gracilis* or *Acanthodes stambergi* n. sp. Scales (Pl. 8A) terminate in posteriorly orientated spiny projections. Posterior projections were within the family Acanthodidae described in *Acanthodes fritschi*, *Acanthodes gracilis*, *Acanthodes luedersensis*, *Acanthodes stambergi* n. sp., various isolated scales of *Acanthodes* sp., *Traquairichthys pygmaeus*, and *Pseudacanthodes pinnatus* (for details see Zajíc 1998). The very thin spiny posterior projections which overlapped the back scales are well visible on specimen M 4464. The projections were broken in the majority of cases (see chapter 2.3.). The scales of the lateral or ventrolateral sensory lines are markedly larger than the surrounding ones. Measured maximum scale sizes (sensory line scales versus surrounding ones) are 0.25 versus 0.15 mm in specimen M 4280, 0.7 versus 0.26 mm in specimen M 4289 + M 4290, and 1.8 versus 1.3 mm in specimen M 4277 + M 4278. The scales covering the fins are very small and rounded. Maximum scale size in a posterior fin of specimen M 4280 is 0.08 mm. Shapes of the fins are marked by scale covers. The enlarged scales are often found close in front of the anal and dorsal fin spines. No sculpture is preserved on the scale crowns from the Vrchlabí locality.

Scales with central hollows were found in six specimens. The most distinct hollows appear on the smallest scales (including scales of the caudal fin) of the juvenile specimen M 4375. No hollows were found on the scales of sensory lines. Rather small scales bear hollows also in the larger specimens M 4393 and M 4485/C (Pl. 8B). For discussion see the paragraph remarks and relationships.

Tesserae cover the head dorsally and frontally. The main concentration of tesserae is between the orbits and behind them. The tightly crowded tesserae form a shield surrounding two weak sensory lines of the head of specimen M 4259 + M 4260. The tesserae are tiny (0.04 to 0.08 mm) there. They are of various shape – rounded, oval, or polygonal. The large polygonal tesserae (up to 0.16 mm) occur out of the above mentioned area. The irregularly shaped tesserae of specimen M 4297 + M 4298 are situated above the orbits. Their maximum size is 0.2 mm. The circular tesserae near the sensory line of the head (specimen PUK-12; Fig. 43) resemble continuous transition from dorsal scales to tesserae.

The sensory lines of the head (Fig 43; Pl. 7A) are often preserved as shorter parts. Longer segments were, however, also found. These sensory lines are composed of individual segments (see Fig. 43) whose morphology is similar to those in *Acanthodes gracilis*, *Acanthodes fritschi* (Zajíc 1998; Fig. 45) or in *Acanthodes bridgei* (Zidek 1976; Fig. 5). The broken segments are of rectangular shape that is disturbed by the central (longitudinally oriented) semicircular canal (Fig. 43). The maximum measurable size of the broken segments of specimen M 4274 + M 4275 is

0.28 × 0.19 mm. Specimen M 4309 yielded the widest segment of the supraorbital canal (0.3 mm). The dorsolaterally situated anterior part of the lateral sensory lines are surrounded by tiny posterior tesserae of irregularly rounded shape in specimen M 4259 + M 4260. The paired supraorbital, quadratojugal, and fragmental infraorbital sensory lines are identifiable in specimen MHK 63 800. The supraorbital canals are the most frequently determinable sensory lines of the head at all.

The trunk sensory lines are represented by the paired lateral and ventrolateral sensory lines The lateral sensory line (Pls 7A, 7C) begins near the caudal cleft of the caudal fin (Pl. 7C) and runs up to the head. The maximum scale size of the lateral sensory line is 0.3 mm in the area behind the posterior (dorsal and anal) fin spines of specimen MHK 63 641. The surrounding scales measure up to 0.22 mm. Ventrolateral sensory lines (Pls 7A, 16C) are formed by two rows of noticeably larger scales than surrounding ones. Difference between scales of the sensory line and the surrounding scales is here bigger than in case of the lateral sensory line. Both ventrolateral sensory lines (left and right) are united into the unpaired and anteriorly orientated ventral sensory line that is well visible e. g. in specimen M 4344. The ventral scale shield covers the connection on the ventral part of body under the pectoral region or slightly behind them. The shield is usually affected by a deformation. The irregular and triangular shields of the measurements from 1.3 × 0.9 mm up to 9.8 × 3.7 mm were found. The scaly shields were also found in the specimens from the Vrchlabí locality. Both ventrolateral (Pl. 16C) and lateral sensory lines are surrounded by scales which form slender hornlike protrusions of the squamation. They project anteriorly from the completely squamated trunk cover. The large scales (1.5 mm) of the ventrolateral sensory line on the hornlike protrusion of specimen M 4249 (Pl. 16C) are surrounded by tiny body scales of the size from 0.04 up to 0.1 mm.

Ontogeny: Neither Meckelian cartilage nor palatoquadrate were detected in juvenile specimens M 4274 + M 4275 (Pl. 15B) and M 4344 of unknown total specimen lengths. However, mandibular bones, circumorbitals, branchiostegals, labyrinth infillings (one pair), articulated gill rakers, and sensory lines of the head were already developed. Various lengths, widths, and body proportions were measured in 141 specimens of and 6 of them were used for the computing of ratios (Fig. 35). Numerous specimens (360) coming from the Vrchlabí, zářez silnice locality (Pl. 15A) were not measured with respect to considerable pressure struck.

Scales of the dorsal and anterodorsal region of the head are represented by tesserae. Specimen M 4250 + M 4251 is unquestionably the smallest measured Permian acanthodian from the Czech Republic till now. Its completely squamated area starts 9 mm behind the anal fin spine. The total specimen length of this specimen cannot be estimated with help of the value C because a length of the pectoral fin spine is not known. The smallest known specimen of *Acanthodes gracilis* (M 4343) is 61 mm long and its completely squamated area starts at the same level as the anal

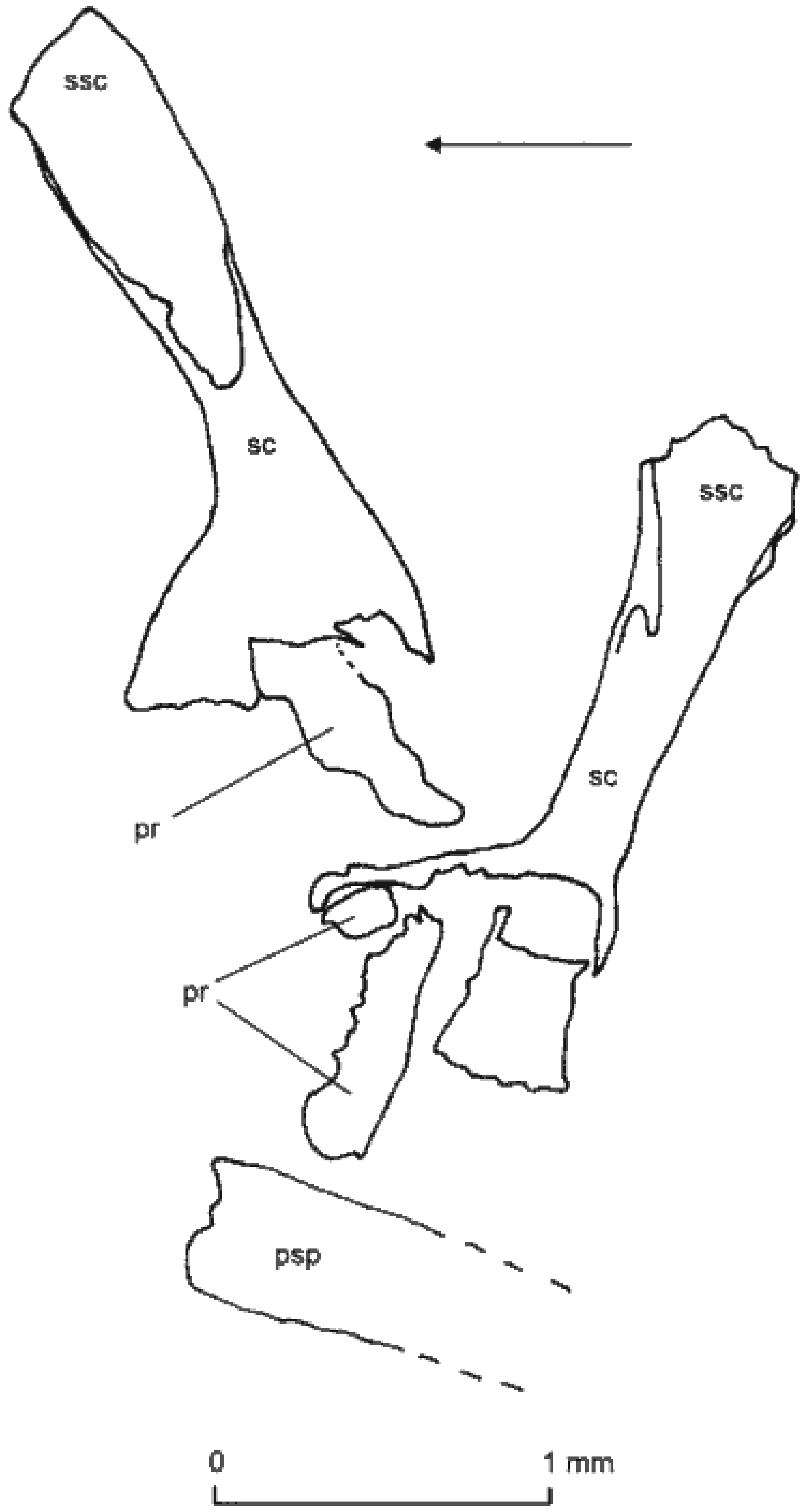

Fig. 41. *Acanthodes* sp.; both scapulocoracoids of a juvenile specimen; anterior direction is marked by an arrow; M 4266; Padochov; Zbýšov Horizon.

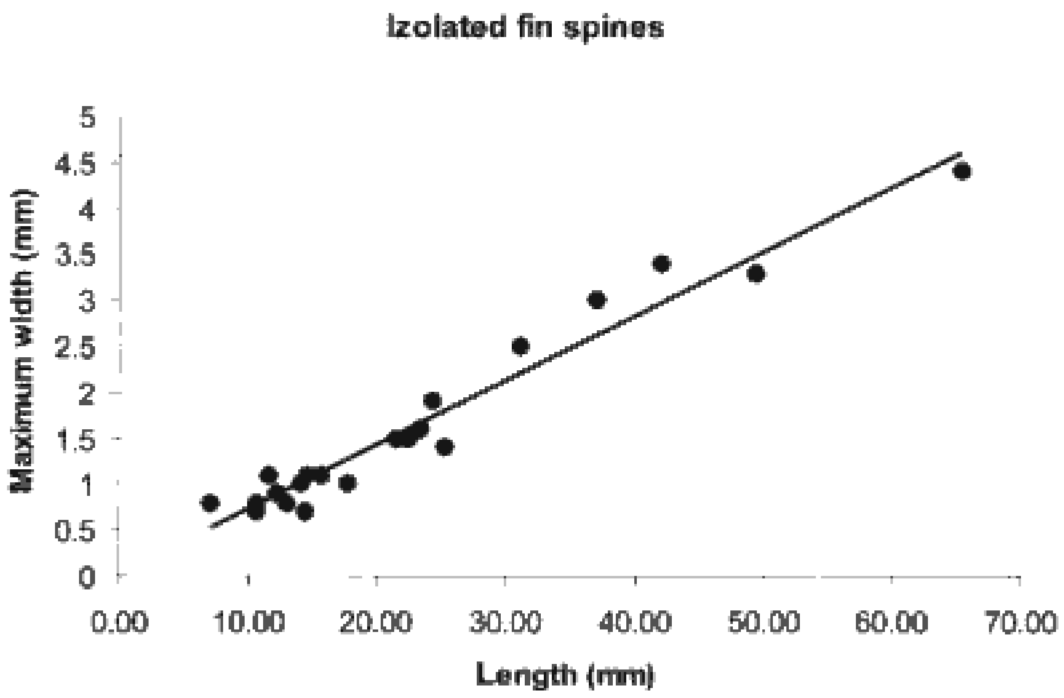

Fig. 42. *Acanthodes* sp.; relationship between the length and the maximum width of isolated fin spines with their trend line.

fin spine. Specimen M 4250 + M 4251 could therefore be around 50 mm long. The development of squamation during ontogeny is probably very similar to that in *Acanthodes*

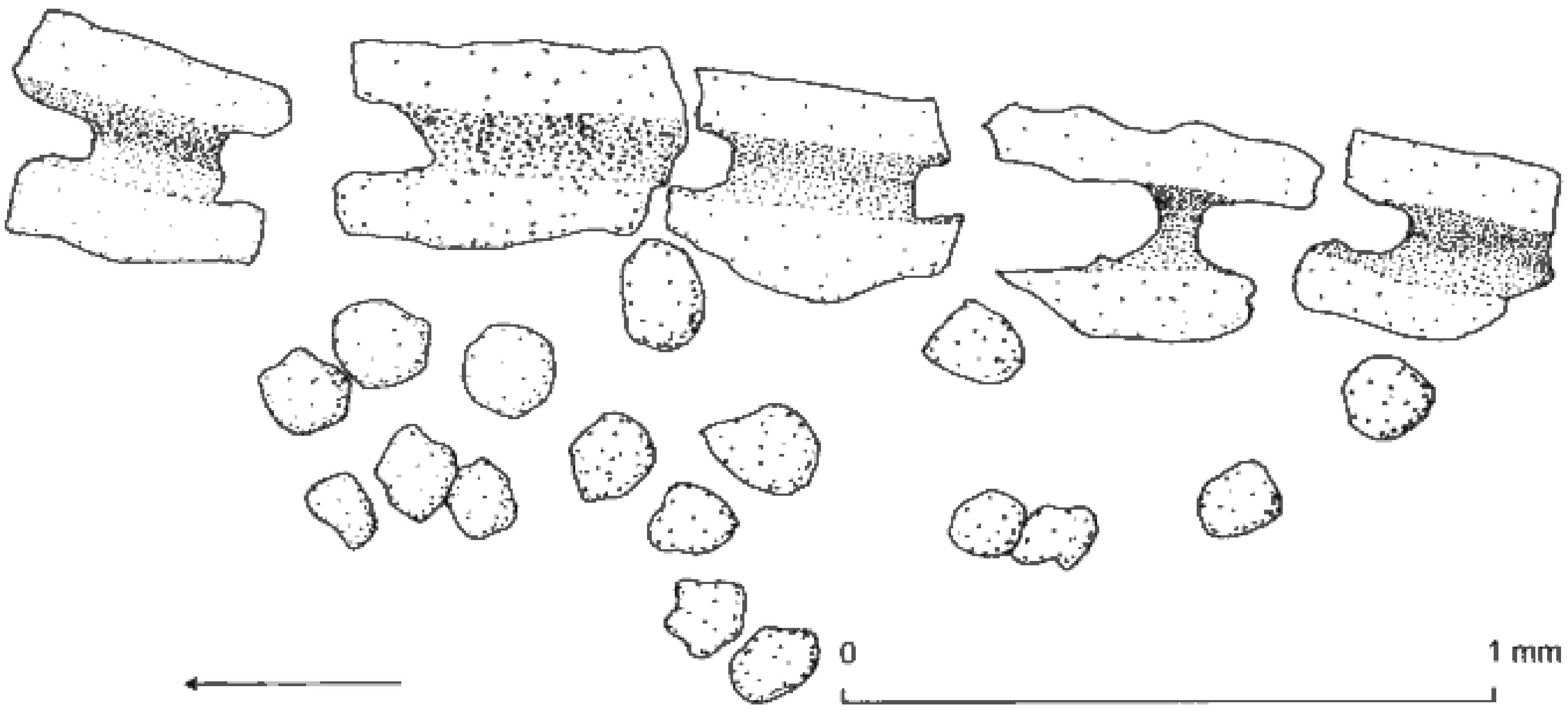

Fig. 43. *Acanthodes* sp.; five segments of a sensory line of the head with obvious longitudinal canal (on top) and attendant circular tesserae (below); anterior direction is marked by an arrow; PUK-12; Zbraslavec; Zbraslavec Horizon.

Fig. 44. *Acanthodes* sp.; Zidek's diagrams of two specimens; values in parentheses mean the estimated total specimen length unlike the measured values.

gracilis (Fig. 23). Body ratios of the juvenile (M 4444) and early subadult (M 4287) specimens are compared in the Zidek's diagrams (Fig. 44). Three growth stages are recognized analogically as in *Acanthodes gracilis* (see chapter 2.3).

The complete distribution of the growth stages of the all taxa is demonstrated in Fig. 28. Figure 29 shows a finer distribution based on the size categories. The size distribution of the all taxa is graphically demonstrated in Fig. 45.

Geographic distribution: Almost all fossiliferous strata of the *Acanthodes gracilis* biozone (Asselian) of the Czech Republic (see Fig. 1).

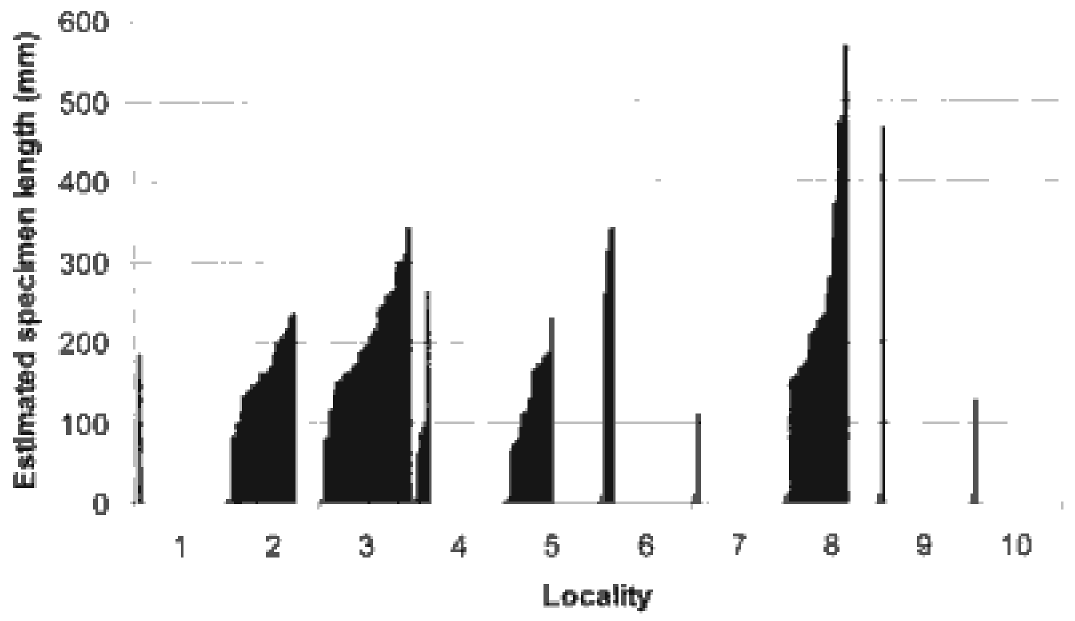

Fig. 45. Size distribution of all acanthodian taxa at the localities Černá Hora (1), Kladoruby (2), Košťálov (3), Kundratice (4), Padochov (5), Prostřední Lánov (6), Rudník (7), Rybnice (8), Zbraslavec (9), Zbýšov (10).

Sites (investigated specimens): Černá Hora (2 specimens), F-2 borehole (Fořt; 1 specimen), F-3 borehole (Fořt; 1 specimen), HK-1 borehole (Horní Kalná; 6 specimens), Janovice (2 specimens), Jk-6 borehole (Javorník; 3 specimens), Kladoruby (48 specimens), Košťálov (73 specimens), Kundratice (21 specimens), Neslovice (1 specimen), Padochov (65 specimens), Prostřední Lánov (9 specimens), Rk-9a borehole (Rudník; 2 specimens), Rybnice (22 specimens), Víchová (1 specimen), Vrchlabí (358 specimens), Zbraslavec (12 specimens). The specimens deposited in the Moravian Museum in Brno (particularly from the Malá Lhota locality but also from the localities Hluboké Dvory, Moravský Krumlov, and Svitávka) were temporarily inaccessible. They will be investigated subsequently.

Remarks and relationship: The term "ossification" is used throughout and no distinction is made between ossification and globular calcification of cartilage in agreement with Zidek (1985). All measurements of lengths and distances (for both ontogenetic and taxonomic purposes) are complicated by remarkable extent of deformation (in contrast to other fish remains). Acanthodian body was probably very pliable and therefore susceptible to a postmortem deformation both before fossilisation (particularly body distortions and dismembers) and during fossilisation (particularly compression or extension up to fragmentation of bodies or skeletal elements). Results of measurements are inapplicable in sediments evidently affected by pressure like in the Vrchlabí, zářez silnice locality. For the time being all abundant acanthodian remains of this locality are therefore marked as *Acanthodes* sp. The mass occurrence of specimens on bedding surfaces is common there. Around 45 specimens of the various degree of preservation were detected on the unnumbered flag of carbonate in the Town Museum Nová Paka (Pl. 15A). Permian acanthodian specimens termed here as *Acanthodes* sp. pertain most likely to *Acanthodes gracilis*. Occurrence of *Acanthodes stambergi* n. sp. is questionable because this species is known from the uppermost part of the *Acanthodes gracilis* biozone for the time being. The Rudník Horizon is, however, of the lowermost *Acanthodes gracilis* biozone age. No indication of a third species was found out till now. Specimens from the Vrchlabí locality are both intensively deformed and carbonized. No measurements are therefore reliable. Various types of deformation (compression, dilatation, and shear) are notably well visible on the long elements as fin spines or mandibular bones. Both superficial and inner structures are missing due to carbonisation. Some specimens from the Rudník Horizon of the Krkonoše Piedmont Basin show signs of a chemical (?) degradation of the skeletal elements during fossilization (similar to scaumenellisation in sense of BÉLAND & ARSENAULT 1985). All skeletal elements known in *Acanthodes gracilis* and moreover basisphenoids were detected but their poor preservation do not allows a specific determination. Six specimens of *Acanthodes* sp. from diverse localities of the Rudník Horizon (except for Vrchlabí) yielded a strange sort of scales with central hollow in the crown (Pl. 8B). The circular hollow have rounded margin and bottom. Depth of the hollows varies. This sort of scales was found on the anal fin with surroundings (M 4485/C), caudal fins (M 4375, PUK-19), and on the trunk (M 4375, M 4393, M 4458, M 4485/B, M 4485/C). No hollows were found on the scales of sensory lines.

The scales with the central hollow were located in variously located foci on the body. The scales were therefore deformed by a disease with a high probability. The disease affects the inner tissue of the scale (like a caries) because the microsculpture of the outer vitrodentine layer is not eroded.

3. Paleogeography and important localities

Taxon *Acanthodes gracilis* is probably confined to the Asselian (Lowermost Permian) basins of the Bohemian Massif. This species was originally described by BEYRICH (1848) from the North Sudetic Basin in Poland (north border of the Bohemian Massif). The other presumable (and often mentioned) occurrences of the *Acanthodes gracilis* comes from the Austrian southernmost segment of the Boskovice Basin near Zöbing (VASICEK & STEININGER 1996), from the Saxo-Thuringian basins (e. g. the Thuringian Forest, the Saale Basin, the Weissig Basin, and the Saalhausen Basin) in Germany (north-western border of the Bohemian Massif). Redescription of the German and Polish specimens and taxonomic revision of the species *Acanthodes gracilis* is now being prepared by HEIDTKE and SCHNEIDER.

Other Asselian (and possibly also Sakmarian) species come from the Saar-Nahe Basin in Germany (*Acanthodes bronni*, *Acanthodes boyi*, *Acanthodes tholeyi*, *Westrichus kraetschmeri*) and the basins of the Massif Central in France (*Acanthodes bourbonensis*). The Asselian specimens named *Acanthodes* sp. are mentioned from New Mexico, Kansas, Oklahoma, and Texas (FOREMAN & MARTIN 1988, VAUGHN 1969). The youngest still known acanthodian is probably *Acanthodes luedersensis* from the Artinskian marine sediments (with continental fauna components as rare amphibian and reptilian remains) of Texas (DALQUEST, KOCURKO & GRIMES 1988).

Ten localities (Fig. 45) of the Bohemian and Moravian part of the Bohemian Massif yielded acanthodian specimens of all taxa capable of an approximation of the total specimen length:

Černá Hora locality – 1 subadult specimen

Kladoruby locality – 3 juveniles (14%), 16 subadults (76%), 2 adults (10%)

Košťálov localities – 2 juveniles (7%), 16 subadults (57%), 10 adults (36%)

Kundratice locality – 3 juveniles (75%), 1 adult (25%)

Padochov locality – 4 juveniles (29%), 9 subadults (64%), 1 adult (7%)

Prostřední Lánov locality – 3 adult specimens

Rudník locality – 1 subadult specimen

Rybnice localities – 9 subadults (47%), 10 adults (53%)

Zbraslavec locality – 1 adult specimen

Zbýšov locality – 1 subadult specimen.

Proportions among the growth stages are rather close in the above mentioned localities. However, the Padochov locality shows a more substantial shift to younger stages and the localities Rybnice on the contrary to older stages. Data are, however, unquestionably distorted, particularly in older collections. Fully developed adult specimens were preferred there. Juvenile specimens with their weak squamation passed unnoticed or they were assumed to be a mere body fragments. Distribution of the computed ratios sorted on the basis of the localities is documented in the Fig. 46. All three taxa (including the indeterminable specimens labelled here as *Acanthodes* sp.) were found together only at the Kladoruby locality.

4. Conclusions

Bohemian and Moravian specimens of *Acanthodes gracilis* were investigated. A closely related species *Acanthodes stambergi* n. sp. was described. The new species differs from *Acanthodes gracilis* particularly in its extremely long dermotrichia of the pectoral fins. A similar couple of species (the dominant *Acanthodes bronni* and rare *Acanthodes tholeyi* with extraordinarily long pectoral dermotrichia) has been reported from the Saar-Nahe Basin in Germany (HEIDTKE 1990a, 1990b). Additional two rare species (*Acanthodes boyi* and *Westrichus kraetschmeri*) were described from the Saar-Nahe Basin later (HEIDTKE 1993, 2003).

Labyrinth infillings and otoliths were found in all three taxa. Overlapping of body scales and microsculptures of scale crowns were detected unlike ZIDEK's statement