

A new species of the genus *Besania* BROUGH 1939 from the Middle Triassic of Canton Grisons (Switzerland) with a discussion of the phylogenetic status of the taxon

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Key words: *Besania schaufelbergi* sp. nov., morphology, phylogeny, Ladinian, Prosanto Formation, Switzerland

ZUSAMMENFASSUNG

Bei Ausgrabungen in der Mittleren Trias der Prosanto-Formation (Ladin, Kanton Graubünden, Schweiz) wurde u.a. neues Fossilmaterial der Gattung *Besania* BROUGH 1939 zu Tage gefördert. Bei den neuen Exemplaren konnten morphologische Merkmale identifiziert werden, die eine deutliche Abgrenzung zur Typusart *Besania micrognathus* BROUGH 1939 darstellen und die Errichtung einer neuen Art, *Besania schaufelbergi* nov. sp., erlauben. Die Identifizierung einiger morphologischer Details macht zudem eine Überarbeitung der systematischen Stellung der Gattung *Besania* notwendig. Die Gattung wird nunmehr an die Basis der Halecostomi (*sensu* Patterson 1973) gestellt.

ABSTRACT

Recent excavations in the Middle Triassic Prosanto Formation (Ladinian, Ct. Grisons, Switzerland) have produced new material of the genus *Besania* BROUGH 1939. These specimens show many previously unrecorded details. Some features differ from those of the type species *Besania micrognathus*, and we therefore erect a new species, *Besania schaufelbergi* sp. nov. This new material has prompted a re-evaluation of the phylogenetic interrelationships of the genus. The taxon seems to be closely related to basal Halecostomi.

1. Introduction

In the 1930s, the Natural History Museum in London acquired a large collection of Middle Triassic fishes from Besano and neighbouring localities in northern Italy and adjacent parts of Switzerland. This material formed the basis of Brough's (1939) monograph, in which he described a number of new lower actinopterygian genera and species. These new taxa included *Besania*, a small, elongated fish with a prominent opercle, a row of deepened flank-scales, three pairs of extrascapulars, a fused skull-roof, and relatively weakly developed jaws (Brough 1939: 49). *Besania micrognathus* was described and named on the basis of a single, incomplete specimen. The holotype BMNH P. 19383 does not show many details of the skull and body, and all of the fins are missing (Brough 1939: 51, text-fig. 20; plate VI fig. 4).

Besania was placed by Brough (1939: 39) in its new family Luganoiidae together with the genus *Luganoia*. Typical characters of luganoiid fishes include the fusion of skullroofing elements, and a large preopercle covering much of the cheek region, with an '...antero-ventral projection supporting small

and very forwardly situated jaws (Brough 1939: 39).' In addition, these fishes have a row of deep flank-scales on the anterior part of body, and the outline of the caudal fin is slightly rounded. The family Luganoiidae is a member of Brough's order Subholostei (Brough 1939: 109). Brough (1939: 109–110) classified the Actinopterygii into four orders: Palaeoniscoidea, Subholostei, Holostei, and Teleostei, and he noted that each of these orders are well-represented in the fossil record, with subholosteans typical of the Triassic period, Palaeoniscoidea in earlier geologic periods, and Holostei and Teleostei post-Triassic. In 1945 Romer placed all subholosteans within the Suborder Chondrostei, together with the Palaeoniscoidea, Polypterini and Acipenseroidea. Recently, the Family Luganoiidae has been considered to be part of a Triassic grade-level group, the Perleidiformes BERG 1937 (Bürgin 1992).

Recent excavations by the Palaeontological Institute and Museum, University of Zürich in the Prosanto Formation (Alpine Middle Triassic, Ladinian, Canton Grisons, Switzerland) have produced new specimens of *Besania* that allow for

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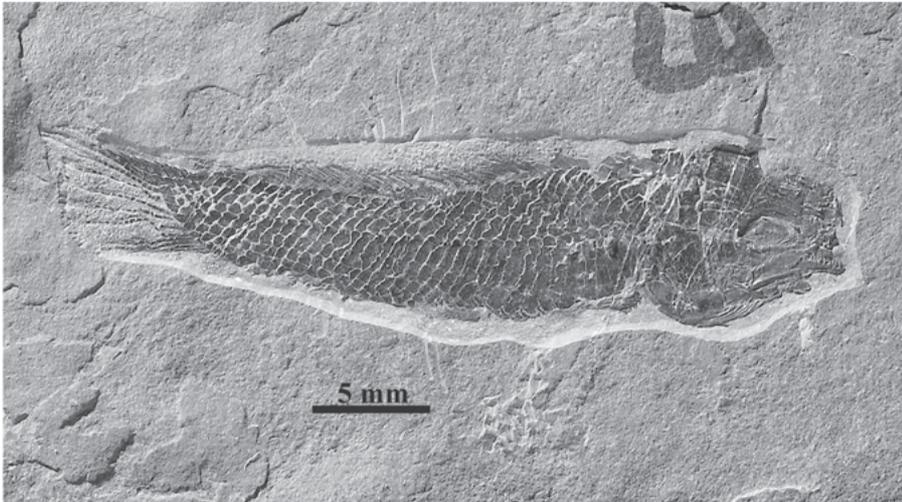


Fig. 1. *Besania schaufelbergi* sp. nov. PIMUZ A/I 3601, holotype in lateral view.

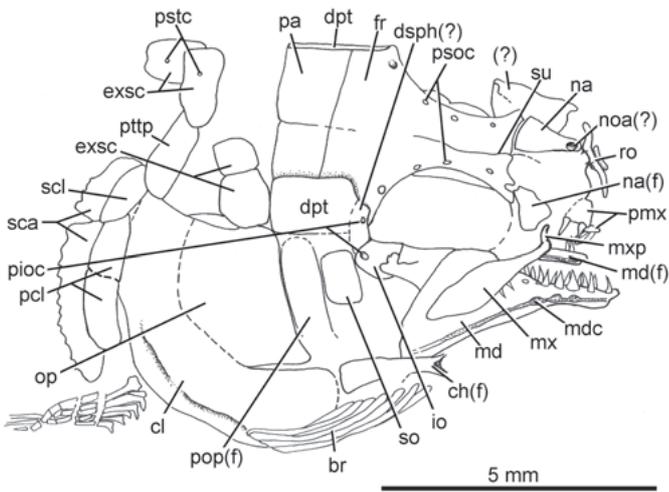


Fig. 2. *Besania schaufelbergi* sp. nov. PIMUZ A/I 3601, camera lucida drawing of the skull of the holotype in lateral view.

Abbreviations

apl, anterior pit line of skull-roof; bnc, bone of neurocranium; br, branchiostegals; ch, ceratohyal; cl, cleithrum; dpop, dorsal part of preopercle; dpt, dermopterotic; exsc, extrascapular; fr, frontal (= parietal, see Grande & Bemis 1998: 24); hp, posterior process of hyomandibula; hym, hyomandibula; io, infraorbital; ioc, infraorbital sensory canal; md, lower jaw; mdc, mandibular sensory canal; mx, maxilla; mxp, anterior articular process of maxilla; na, nasal; nappmx, nasal process of premaxilla; noa, opening for the external naris; op, opercle; opf, opercular facet; pa, parietal (= postparietal, see Grande & Bemis 1998: 27); pioc, openings to the infraorbital sensory canal; pmx, premaxilla; pop, preopercle; popc, preopercular sensory canal; ppopc, openings for the preopercular sensory canal; psp, parasphenoid; psc, openings for the supratemporal commissural canal; ro, rostral; sca, scales; scl, supracleithrum; so, suborbital; soc, supraorbital sensory canal; sop, subopercle; su, suture; sym, symplectic; vo, vomer; vpop, ventral part of preopercle; (?), uncertain; (le), left; (ri), right.

an updated and improved interpretation of the morphology of this genus. Perhaps most notably, the new specimens reveal the presence of an interopercle in *Besania*, which necessitates a revision of earlier ideas on the systematic affinities of the genus. In addition, the Prosanto Formation specimens are distinctly different from the Besano material, and are placed in a new species.

2. Material and Methods

The new material described here is from the top of Strel mountain, and from the Ducanfurrga, both localities of the Prosanto Formation in Canton Grisons, Switzerland. The Prosanto Formation forms a part of the marine Middle Triassic (Ladinian) of the Silvretta Nappe. It consists of up to 200 m of dark limestones and dolomites. The fossiliferous layers are thinly bedded and laminated. The depositional environment of the Prosanto Formation is interpreted as a regional basin with a stratified waterbody that resulted in oxygen-depleted bottom water. In the last ten years of the 20th century, a large number of new Prosanto Formation fossils have been recovered, including plants (calcareous algae), conifers, invertebrates (cephalopods, crustaceans), and vertebrates (fishes, reptiles). Further details of the geology, stratigraphy and paleoecology are described in Eichenberger (1986), Bürgin et al. (1991), Furrer (1995), and Furrer et al. (1992).

The material is stored in the Paleontological Institute and Museum, University of Zürich (PIMUZ). One specimen (PIMUZ A/I 3602) is from a private-collection (C. Obrist, Stein, Switzerland). Altogether, nine specimens were examined (PIMUZ A/I 2838, 2839, 2863, 3225, 3520, 3522, 3601, 3602 and 3746).

The specimens were photographed and the line-drawings were prepared with the aid of a Wild M8 stereomicroscope.

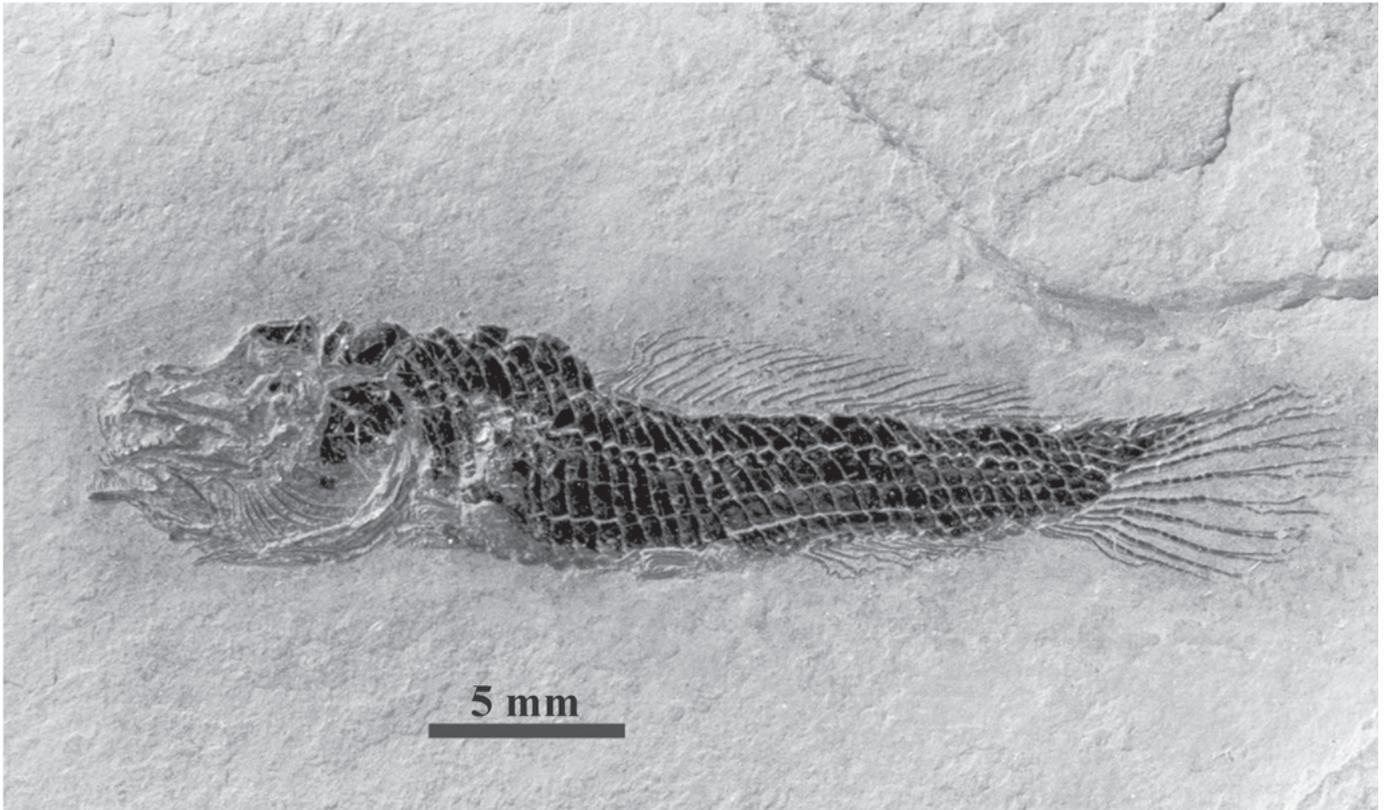


Fig. 3. A *Besania schaufelbergi* sp. nov. PIMUZ A/I 3602, juvenile specimen in lateral view.

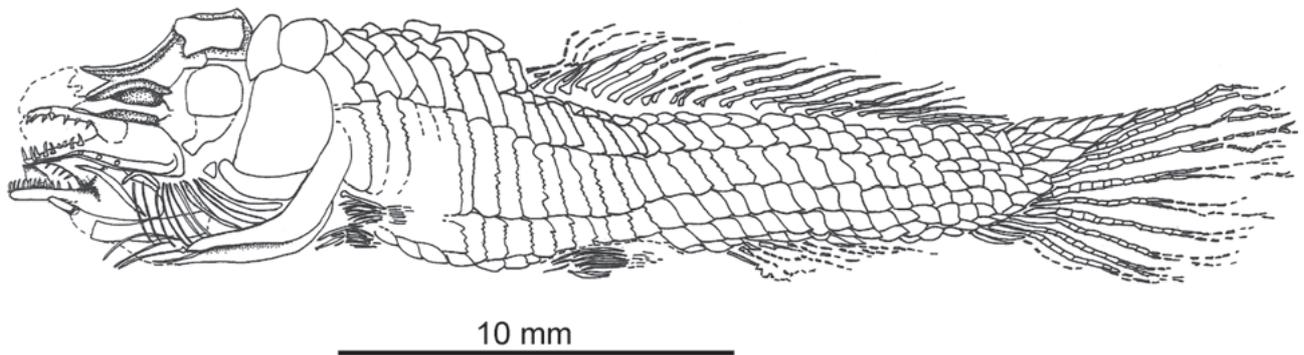


Fig. 3. B *Besania schaufelbergi* sp. nov. PIMUZ A/I 3602, camera lucida drawing of the juvenile specimen from Fig. 3A.

3. Systematic Paleontology

OSTEICHTHYES HUXLEY 1880
 ACTINOPTERYGII COPE 1887
 Division HALECOSTOMI *sensu* PATTERSON 1973
 Genus *BESANIA* BROUGH 1939

Type species. – *Besania micrognathus* BROUGH 1939, from Besano, Italy.

Emended Diagnosis. – An elongated fish with a row of deepened flank scales; three or more extrascapulars; long and narrow crescent shaped preopercle; interopercle present; more than 25 rays in the elongate dorsal fin; a convexly rounded caudal fin.

Besania schaufelbergi sp. nov.
 Figures 1–12

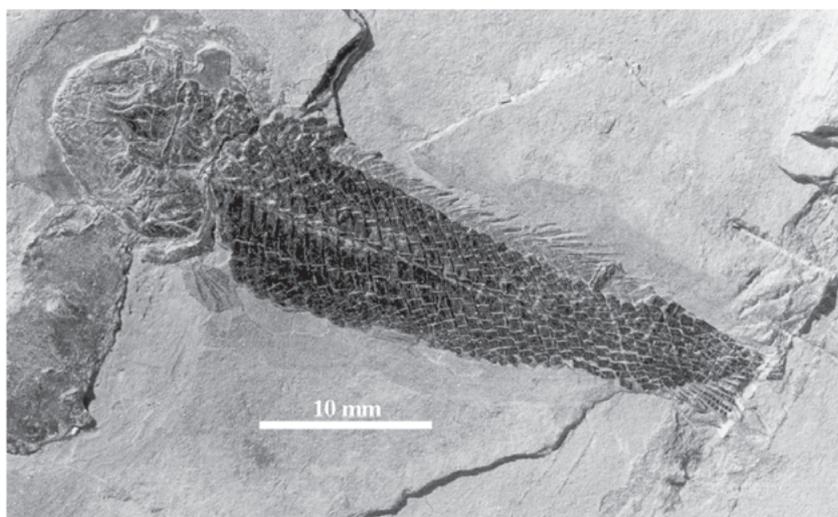


Fig. 4. *Besania schaufelbergi* sp. nov. PIMUZ A/I 2838, with body in lateral and skull in dorso-lateral view.

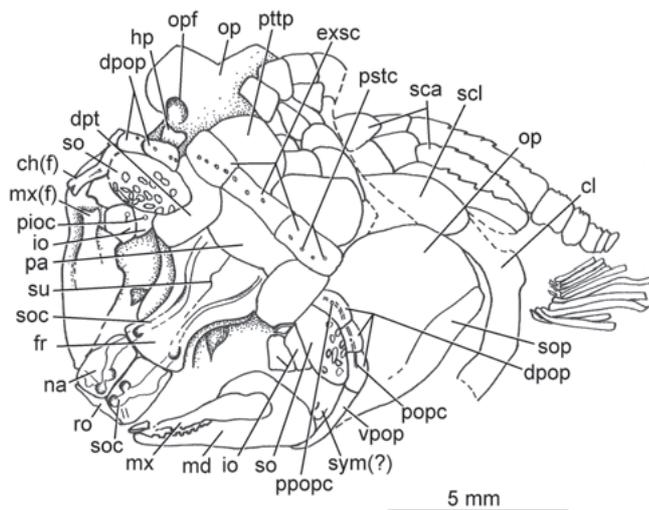


Fig. 5. *Besania schaufelbergi* sp. nov. PIMUZ A/I 2838, camera lucida drawing of the skull in Fig. 6. For abbreviations see Fig. 2.

Derivation of name. – The species is named after Elisabeth Schaufelberger (Zürich, Switzerland), in recognition of the large number of fossils she has collected from the Prosanto Formation.

Holotype. – PIMUZ A/I 3601 (Figs. 1 & 2).

Paratypes. – PIMUZ A/I 2838, 2839, 2863, 3225, 3522, 3602. The specimens vary in degree of completeness. PIMUZ A/I 2863, and 3602 appear to be juvenile specimens.

Locality and horizon. – Top of Strel mountain, Wiesen, Landwassertal, and Ducaufurrga near Davos, both in Canton Grisons, Switzerland; Prosanto Formation, Alpine Middle Triassic, Ladinian.

Diagnosis. – Typical *Besania*-like fish, with a maximum standard-length of 44 mm; 11 branchiostegal rays, 33 to 34 vertical scale rows, scales with serrated posterior margin, a small anal-fin with only eight fin rays.

Tab. 1. Measurement ratios for frontal and parietal of *Besania schaufelbergi* sp. nov.

	PIMUZ A/I 3602 juvenil	PIMUZ A/I 3601 subadult	PIMUZ A/I 2838 adult
frontal min. width (mm)	0,30	0,50	0,67
frontal max. width (mm)	1,00	1,67	2,07
frontal length (mm)	3,33	3,40	3,93
frontal ratio min./max. width	0,30	0,30	0,32
frontal ratio max. width/length	0,30	0,49	0,53
frontal ratio min. width/length	0,09	0,15	0,17
parietal max. width (mm)	0,8	1,4	1,42
parietal max. length (mm)	1,07	1,13	1,33
parietal ratio width/length	0,75	1,24	1,07
ratio length parietal/frontal	0,32	0,33	0,34

4. Description

Shape and size: A small fusiform fish. The standard-length of the shortest specimen PIMUZ A/I 3602 is 26 mm (Figs. 3, 4) and of the longest specimen PIMUZ A/I 2838 (Fig. 5) 44 mm. The ratio of skull- to standard-length is more or less 30 %. The caudal and anal fin are both relatively long, and the caudal fin is convexly rounded in outline (Figs. 3, 12).

Snout region: Two specimens of *Besania schaufelbergi* sp. nov. (PIMUZ A/I 3601, Figs. 1, 2, and PIMUZ A/I 2838, Figs. 6, 7) show the elements of the skull in dorsal view. The single rostral bone is relatively long and narrow. The nasals are paired and rectangular with prominent openings for the supra-orbital sensory canal, as is typical for *Besania*. The recess for the anterior external naris is apparently present on PIMUZ A/I 3601 (Fig. 2).

Skull-roof: The frontals are more-or-less fused. The anterior and median parts of the skull-roof are narrow whereas the pos-

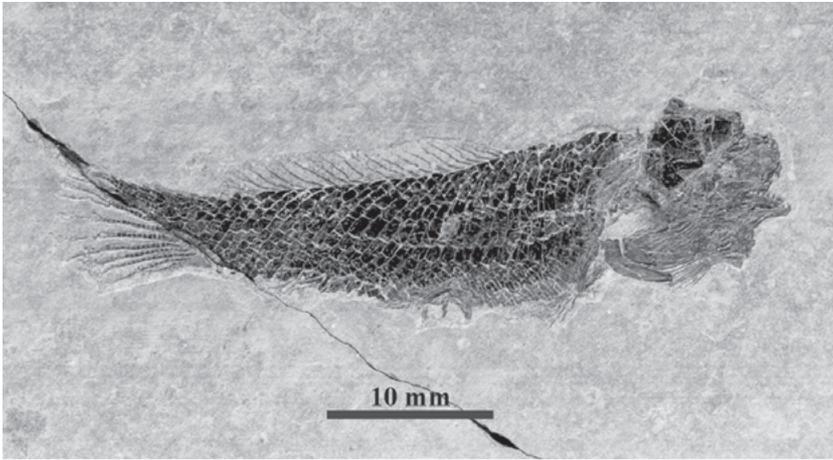


Fig. 6. *Besania schaufelbergi* sp. nov. PIMUZ A/I 3522, in lateral view.

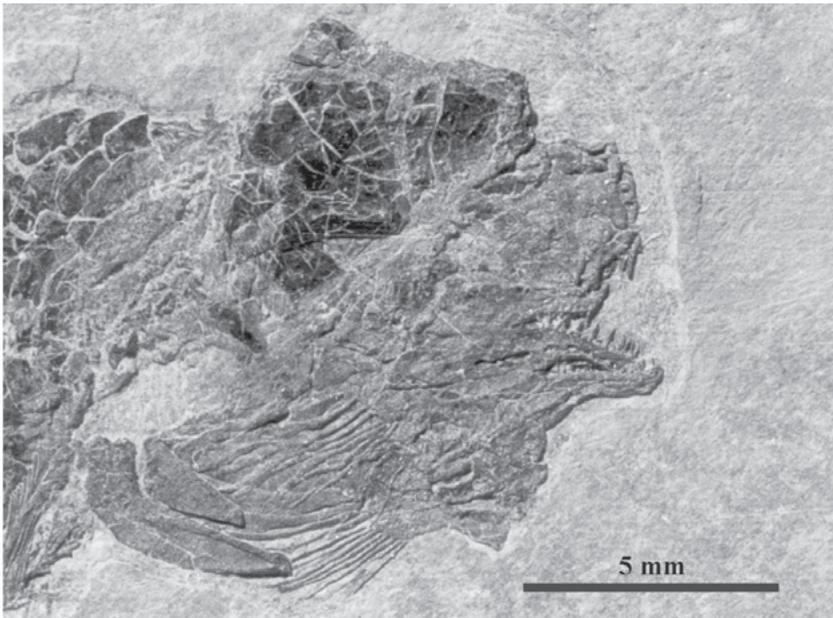


Fig. 7. A *Besania schaufelbergi* sp. nov. PIMUZ A/I 3522, skull in lateral view.

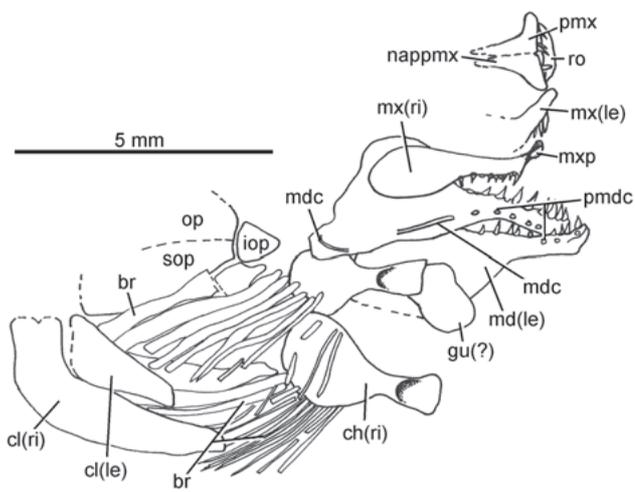


Fig. 7. B *Besania schaufelbergi* sp. nov. PIMUZ A/I 3522, camera lucida drawing of the skull of Fig. 7A. For abbreviations see Fig. 2.

terior bones are broader. The parietals are paired bones with an almost rectangular shape, but may be fused in some specimens (Fig. 5). The three or four rectangular extrascapulars are situated behind the posterior border of the parietal. Specimen PIMUZ A/I 2838 (Fig. 5) has a large rectangular median extrascapular, and somewhat smaller paired lateral extrascapulars, whereas PIMUZ A/I 3225 (Fig. 10) displays four rectangular extrascapulars, two on each side of the midline. There is no ornamentation on the skull roof.

Measurements of three specimens what we presume to be different developmental stages are shown in Table 1. The measurements show no significant differences between the ratio of the skull-bones of presumed juvenile and adult specimens.

Circumorbital series: The circumorbital series is represented by only one or two infraorbitals (Figs. 2, 5, 9), which are quadrangular in shape. In the holotype (PIMUZ A/I 3601), a small and slender bone with a sensory canal opening is located near

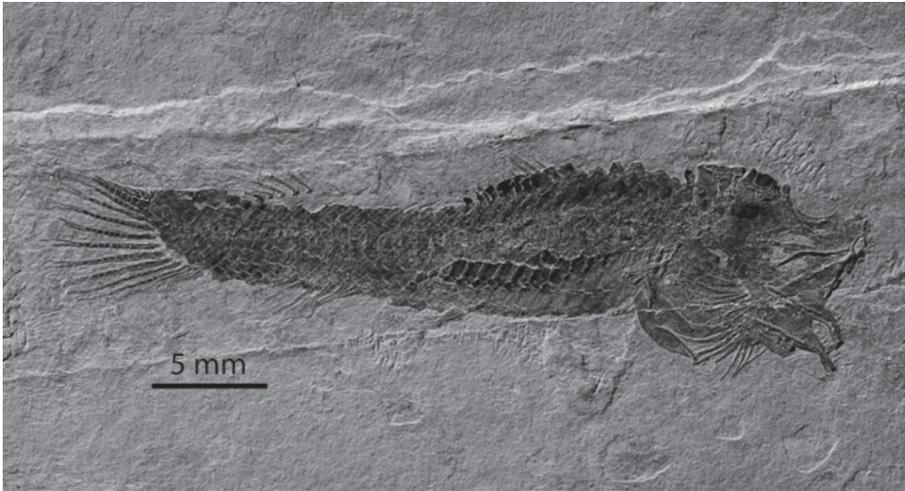


Fig. 8. *Besania schaufelbergi* sp. nov. PIMUZ A/I 3746, in lateral view with well exposed ceratohyal and branchiostegal rays.

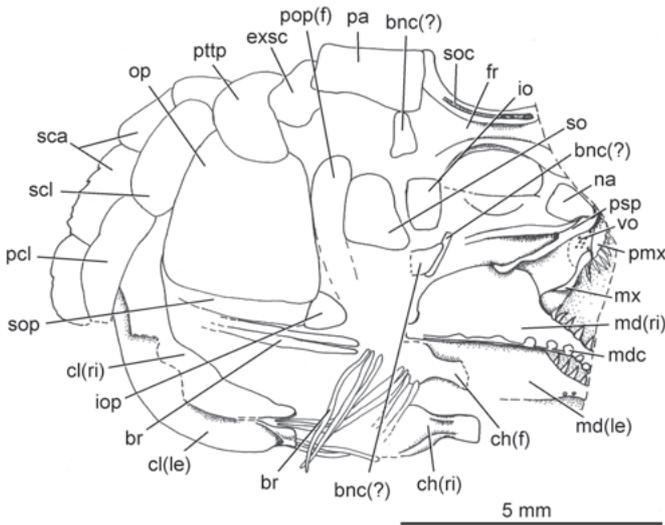


Fig. 9. *Besania schaufelbergi* sp. nov. PIMUZ A/I 2839, camera lucida drawing of the skull in lateral view. For abbreviations see Fig. 2.

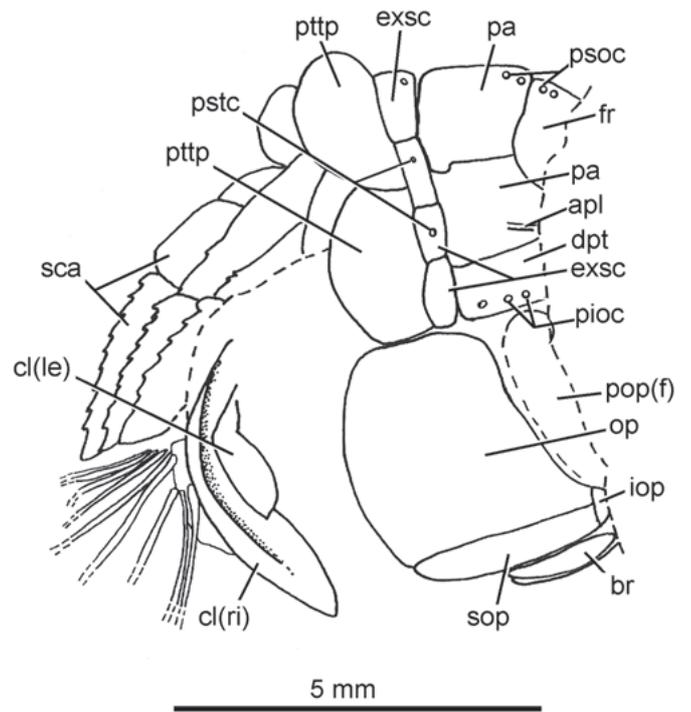


Fig. 10. *Besania schaufelbergi* sp. nov. PIMUZ A/I 3225, camera lucida drawing of the posterior skull region in lateral view. For abbreviations see Fig. 2.

the posterior border of the orbit. Its position suggests that it may be a dermosphenotic with a moderately curved anterior edge.

Cheek region: The cheek region is partly covered by suborbitals. Only one rectangular suborbital is preserved in the new material. In specimen PIMUZ A/I 2838 (Fig. 5), the suborbital and infraorbital bones are ornamented with oval and prolate tubercles. The preopercle is completely preserved in only one specimen (PIMUZ A/I 2838), and unlike Brough's (1939) description, it is long and narrow. The dorsal part of the preopercle is fragmented into three sub-rectangular elements on specimen PIMUZ A/I 2838. Because the preopercle of the other specimens is very incomplete, it is not possible to determine if this fragmentation is typical for *B. schaufelbergi* sp. nov.

Parasphenoid: The parasphenoid is visible but incompletely preserved in only one specimen (PIMUZ A/I 2839, Fig. 9). The bone is narrow anteriorly and broadens posteriorly. Grooves or foramina for nerves and muscles are not preserved. A portion of the vomer can be seen in the same specimen, situated anterior to the parasphenoid. The vomer bears many tiny teeth with rounded cusps.

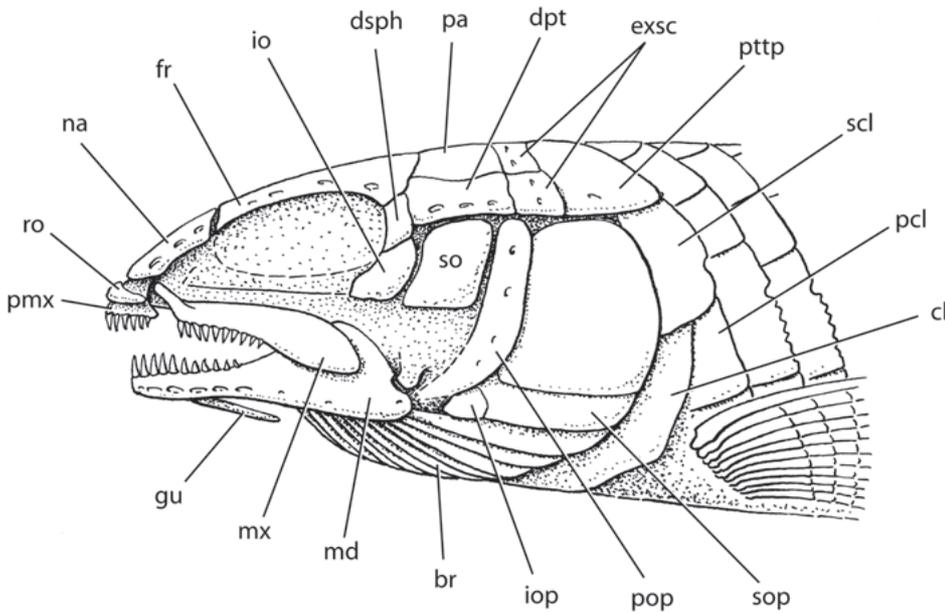


Fig. 11. *Besania schaufelbergi* sp. nov. Composite reconstruction of the skull in lateral and dorsal view based mainly on the holotype PIMUZ A/I 3601.

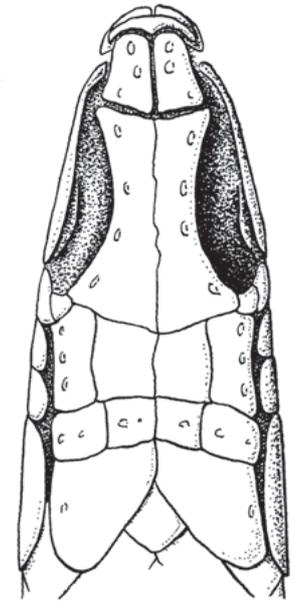
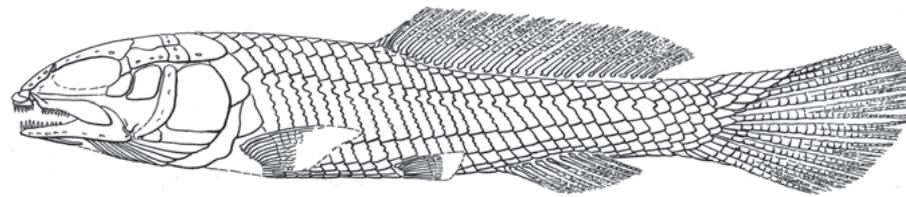


Fig. 12. *Besania schaufelbergi* sp. nov. Composite reconstruction based mainly on the holotype PIMUZ A/I 3601.



Upper jaw: The anterior portion of the upper jaw complex consists of a short, paired premaxillae. The premaxillary teeth are long and sharply pointed. In PIMUZ A/I 3522 (Figs. 6 & 7) the prominent nasal process is visible. The maxilla is relatively long and bears a prominent medial process at the anterior end, and a somewhat drop-shaped posterior portion. The tooth-row extends from the tip of the maxilla to its mid-portion. The teeth are much higher than broad and sharply pointed. There is no indication of a supramaxilla in any of the *Besania*-specimens from the Prosanto Formation or from Monte San Giorgio (Bürgin in prep.).

Lower jaw: The lower jaw is triangular in shape with a prominent coronoid process. Its teeth are sharply pointed and slightly recurved at their tips. The tooth row ends halfway along the length of the lower jaw. Individual elements of the lower jaw (angular, dentary and other bones) cannot be identified. A small indentation at the posterior end of the lower jaw presumably received the articular head of the quadrate, but the exact nature of the jaw articulation in *Besania* remains unsettled.

Hyoid-arch: PIMUZ A/I 2838 (Fig. 5) preserves the posterior

process of the hyomandibula. It is stout and triradiate with broad dorsal and ventral ends and a large articular process for the opercle. The rounded ventral tip of a narrow bone is located at the caudal edge of the lower jaw and might be part of the quadrate, or a symplectic, which would suggest a double jaw articulation. A splint-like symplectic is preserved in one of the Monte San Giorgio specimens.

Gill-cover: The gill-cover is formed mainly by the opercle. It is somewhat higher than broad and trapezoidal in shape with rounded dorsal and straight anterior edges. The subopercle is narrow with a dorsal edge that contacts the ventral border of the opercle. Anteriorly, the subopercle is bordered by the interopercle. Three specimens (PIMUZ A/I 2839, Fig. 9; PIMUZ A/I 3225, Fig. 10 and PIMUZ A/I 3522, Fig. 7) have a small, triangular interopercle, which is situated anterior to the subopercle. In *Besania schaufelbergi* sp. nov., the ceratohyal is large and deep and bears a row of ca. 11 long and thin branchiostegal rays along its ventral margin (Fig. 11). The uppermost two or three branchiostegal rays reach nearly as far up the side of the skull as the subopercle, and they are somewhat

broader than the more ventrally positioned rays. In specimen PIMUZ A/I 3522 (Fig. 7), an imperfectly preserved oval bone near the lower jaw and the ceratohyal may represent the a median gular.

Shoulder girdle: The large posttemporal contacts the extrascapulars anteriorly, and the adjacent posttemporal medially. More posteriorly the bone is convex in shape. The supra-cleithrum is subrectangular, with rounded corners. The largest shoulder girdle bone is the long, narrow and sickle-shaped cleithrum. The area of articulation for the scapulocoracoid is preserved on PIMUZ A/I 2839 (Fig. 9).

Sensory canal system: Openings for the supraorbital sensory canal are well-preserved on the nasals of specimen PIMUZ A/I 2838 (Fig. 5). The canal runs along the lateral edge of the frontal and ends inside the parietal (Fig. 10). Specimen PIMUZ A/I 3225 (Fig. 10) is the only one in which a sensory pit line is preserved on the skull-roof with the anterior one being visible near the rostral edge of the parietal. Only two separate openings are present on the infraorbitals, and dermosphenotics in the holotype PIMUZ A/I 3601 (Fig. 2), which mark the course of the infraorbital sensory canal. But it is not certain if the supraorbital and infraorbital sensory canals are fused in the dermosphenotic as in more derived fishes (e.g. *Amia*, Allis 1889, Grande & Bemis 1998). The mandibular sensory canal is located along the ventral edge of lower jaw, but the mandibular pit line is not preserved. Sensory openings are also preserved on the extrascapulars (Fig. 5) which belong to the supratemporal commissural canal. The preopercular sensory canal, which is marked by a groove, is located in the median portion of the preopercle of PIMUZ A/I 2838 (Fig. 5).

Fins: The paired fins are well-preserved. The fin rays are relatively short, but segmented and distally branched, with the leading fin ray of each fin unsegmented and being spinous. The number of rays in the pectoral fin is about 10 – 11, while the pelvic fin has no more than seven rays. The pelvic fins are located at scale row 10.

The well developed anal fin is located at scale rows 16 to 17. A complete anal fin with eight rays is preserved in specimen PIMUZ A/I 3602 (Fig. 3). The long dorsal fin consists of about 27 segmented and branched fin rays. The distal edge of the fin is truncated in outline. Two basal fulcra are present at the base of the dorsal fin, located at vertical scale row 10 or 11. The last fin ray occurs at scale row 30. In the supposed juvenile specimen PIMUZ A/I 3602 (Fig. 3) the rays are not branched.

In most specimens, the caudal fin is well preserved. It is convexly rounded in outline (Fig. 3). The dorsal edge bears eight to nine spine-like basal fulcra, followed by a row of fringing fulcra. In the holotype, the apices of the paired rows of basal fulcra row are visible. Only the caudal fin shows such paired basal fulcra. They are followed by about 13 segmented, and branched fin rays. The fin is bordered ventrally by two or three small and sinuous basal fulcra.

Squamation: All scales are covered by a thick but unornamented layer of ganoine. The scales are rectangular to rhom-

Tab. 2. Differences between the two species of the genus *Besania*.

	<i>B. micrognathus</i> BROUGH 1939	<i>B. schaufelbergi</i> sp. nov.
bones of the skull-roof are fused together or not	yes	no
number of fin-rays of the analis	about 12	8 (in only one specimen)
branchiostegal rays	8	11
number of vertical scale rows	36–37	33–34
posterior edge of scales	smooth	serrate

boidal in shape. Scales of the middle horizontal row are deeply rectangular (Fig. 3). Anteriorly, the width-to-length ratio of the deep flank scales is 4:1; posteriorly, the middle flank scales are longer than wide. The posterior margin of vertical scale rows one to 20 are distinctly serrated. More posteriorly, this margin is smooth. The scales that contain the lateral line sensory canal are characterised by an indentation at their caudal edge. Posteriorly, the squamation ends in a short upper caudal lobe with small rhomboidal scales, which are obliquely oriented and separated from them by a caudal hinge (Fig. 3). The number of vertical scale rows varies from 33 to 34.

5. Discussion

Recent excavations of the Palaeontological Institut University of Zürich in the Swiss part of the Alpine Middle Triassic at Monte San Giorgio in southern Switzerland (Canton Tessin) resulted in a large collection of actinopterygians, among them additional specimens of *Besania* (Bürgin in prep.). We found additional details, which further establish that *B. micrognathus* BROUGH 1939, the only hitherto known species of *Besania*, differs from *B. schaufelbergi* sp. nov. These differences include: number of fin-rays in the anal fin, number of branchiostegal rays; number of vertical scale rows; the bones of the skull-roof are not fused in *B. schaufelbergi*; and, as mentioned above, the nature of the posterior margin of the scales (Tab. 2). The two species are otherwise very similar in many other respects of their skull and body morphology.

With this new material, the phylogenetic position of *Besania* can be reassessed. Some characteristic features of the family Luganoiidae (deepened flank-scales, shape of skull-roof, rounded caudal fin) are found in the genus *Besania*, but, in many details, this genus is conspicuously different from *Luganoia*, the other genus placed in this family. The question is, whether these differences clearly discriminate the two genera? The two taxa share at least partly fused parietals, the presence of more than one paired extrascapular, and the convexly rounded shape of the caudal fin. They both have a row of deepened flank-scales, although in *Luganoia* the deepened flank scales end abruptly at the middle of the body and are followed by two scale-rows with the same width-to-length ratio as

the scales that are dorsal and ventral to these rows. In *Besania* the deep flank-scales run to the tail, and the width-to-length ratio is only gradually reduced. The most notable differences between the genera are in the shape of the preopercle, the presence/absence of an interopercle, and the shape of the maxilla.

In *Luganoia*, the preopercle is large, and suborbitals are absent (Brough 1939; Bürgin 1992). In contrast, *Besania* has a long and narrow, crescent-shaped preopercle and the suborbitals forming part of the cheek region, which are derived conditions in actinopterygians (Gardiner 1967).

The shape of the maxilla of *Luganoia*, is unusual (Brough 1939; Bürgin 1992: 107, fig. 124), and very unlike that in *Besania*. Also in *Luganoia*, a number of postmaxillars are present below the preopercle, and three anamestic postorbitals are present at the dorsal border of the preopercle (Bürgin 1992: 110). These elements are lacking in *Besania*. Perhaps most significantly, an interopercle is absent in *Luganoia* according to Brough (1939), McAllister (1968), and Patterson (1973), although the latter two authors believed that an interopercle could have been present. Bürgin (1992) described new specimens of *Luganoia lepidosteoides* BROUGH 1939, in which the lack of a distinct interopercle is confirmed. In contrast, the interopercle is clearly identifiable in *Besania*. Our conclusion is that the differences between the two genera are sufficient to remove *Besania* from the family Luganoiidae and the order Perleidiformes, because perleidiform fishes have no interopercle, usually the preopercle is wide and suborbitals are small or absent. In our interpretation, *Besania* is a typical halecostome fish (*sensu* Patterson 1973), with a mobile maxilla and an interopercle. Other basal halecostome fishes including *Prohalecites* (Tintori 1990), *Hulettia* (Schaeffer & Patterson 1984), *Acentrophorus* (Gill 1923), and *Aphanepygus* (Bartram 1977a) also lack a supramaxilla. The absence of a supramaxilla is plesiomorphic for the Halecostomi (Schaeffer & Patterson 1984).

Some morphological features of *Besania* are also found in other neopterygian fishes. A large number of extrascapulars are preserved in *Dapedium* (Wenz 1967; Thies 1988) and *Aphanepygus* (Bartram 1977b), whereas the number varies in *Prohalecites porroi* (Tintori 1990). A fragmented preopercle is known in different actinopterygians e.g. In *Aphanepygus*, the same condition is present in PIMUZ A/I 2838, the dorsal parts of the preopercle are called suprapreopercles (Bartram 1977a). In *Prohalecites* (Tintori 1990) and *Pholidoctenus* (Zambelli 1978), a small ventral split is seen in the preopercle. In *Lep-tolepis* (Nybelin 1974), the dorsalmost pointed portion of the preopercle is separate from the rest of the bone.

The shape of the ceratohyal is very similar to the one in *Macrosemius* (Bartram 1977b), and a row of thin branchiostegals is also observed in *Aphanepygus* (Bartram 1977a).

The prominent openings for the supraorbital sensory canal on the nasals are similar to the condition in *Prohalecites* (Tintori 1990), in which the openings of the canal are conspicuous. Also in *Besania*, most of the openings of the sensory canal-system are conspicuously large, and often the canal itself can be

observed similar to that described in macrosemiid fishes (Bartram 1977b).

A long dorsal fin is typical for the family Macrosemiidae. In *Macrosemius*, the tail is convexly rounded (Bartram 1977b). The condition of the dorsal fin is also similar in *Aphanepygus* (Bartram 1977a), and in amiids (Grande & Bemis 1998).

On the other hand, the dorsal part of the circumorbital series is formed by a large number of supraorbitals in *Aphanepygus* as in *Luganoia*. However, *Aphanepygus* lacks deepened flank scales. Furthermore, the construction of the opercular series is more like *Macrosemius*, but the Macrosemiidae do not have a gular (Bartram 1977b). Deepened flank scales are also known in the Pycnodontiformes, Perleidiformes, and other, more plesiomorphic families, and are not informative for phylogenetic studies. Due to the present preservation important details of the braincase and axial skeleton cannot be observed. Although our knowledge of the morphology of *Besania* is improving, its precise relationships remain enigmatic. A taxonomic placement in one of the halecostome subgroups is not possible at present, so we therefore propose to place *Besania* as *incertae sedis* within Halecostomi, as has also been suggested for *Aphanepygus* (Bartram 1977a), *Hulettia* (Schaeffer & Patterson 1984), and *Prohalecites* (Tintori 1990; Arratia & Tintori 1999).

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