Functional anatomy and mode of life of the latest Jurassic crinoid *Saccocoma*

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Loose elements of the roveacrinid *Saccocoma* from the Tithonian red Rogoża Coquina, Rogoźnik, Pieniny Klippen Belt, Poland, are used to test the contradictory opinions on the mode of life of *Saccocoma*. The investigated elements belong to three morphological groups, which represent at least two separate species: *S. tenella*, *S. vernioryi*, and a third form, whose brachials resemble those of *S. vernioryi* but are equipped with wings of different shape. The geometry of brachials' articular surfaces reveals that the arms of *Saccocoma* were relatively inflexible in their proximal part and left the cup at an angle of no more than 45°, then spread gradually to the sides. There is no evidence that the wings were permanently oriented in either horizontal or vertical position, as proposed by two different benthic life-style hypotheses. The first secundibrachial was probably more similar to the first primibrachial than to the third secundibrachial, in contrast to the traditional assumption. The winged parts of the arms were too close to the cup and presumably too stiff to propel the animal in the water efficiently. Swimming was probably achieved by movements of the distal, finely branched parts of the arms. The non-horizontal attitude of the winged parts of the arms is also not entirely consistent with the assumption that they functioned as a parachute. Moreover, the wings added some weight and thus increased the energy costs associated with swimming. The hydrodynamic benefits balancing these extra costs are not entirely clear, but it seems probable that the wings reduced the sinking rate of the animal not by increasing the pressure drag, as suggested by the parachute-analogy, but by increasing the surface drag (friction drag), which also harmonize with the presence of spines, reticulate sculpture and conspicuous vacuolar ornamentation in some species of *Saccocoma*.

Key words: Crinoidea, Roveacrinida, *Saccocoma*, brachial articulations, functional anatomy, Tithonian, Rogoża Coquina.

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Introduction

Saccocoma Agassiz, 1836 is a small roveacrinid (stemless microcrinoid) common in the Late Jurassic pelagic sediments of the Tethyan realm (Nicosia and Parisi 1979). Its most characteristic features are (1) the presence of lateral, rounded, wing-like expansions on proximal parts of the arms, (2) bowl-shaped, thin-walled cup with reticulate sculpture, and (3) the lack of a stem (Fig. 1). Complete, articulated specimens of the most common species, *Saccocoma tenella* (Goldfuss, 1831), from the famous Solnhofen lithographic limestone were described in detail by Jaekel (1892) in a classic work where he interpreted this animal as free living, pelagic and floating with the aid of the paddle-like lateral expansions called "Schwimmplatten". This interpretation has been generally accepted by subsequent researchers (e.g., Barthel et al. 1990; Hess 1999, 2002). Recently, however, some authors hypothesised a benthic lifestyle. They proposed that *Saccocoma* had been a mudsticker whose proximal arms either lay flat on the sediment surface (Milsom 1994) or were oriented vertically with the "Schwimmplatten" serving as a protection against the sedi-

ment (Manni et al. 1997). Still, Hess (1999, 2002) and Seilacher and Hauff (2004) rejected these views and supported the classic interpretation.

The aim of this study is to test the contradictory opinions on the mode of life of *Saccocoma* using loose saccocomid skeletal elements from the Tithonian of Rogoźnik (Pieniny Klippen Belt, Carpathians, southern Poland).

Material and methods

The investigated material was obtained by removing weathered crusts from blocks of red shelly limestone (Rogoża Coquina Member, Early to Middle Tithonian, Birkenmajer 1977) found at the base of the abandoned Rogoźnik quarry. Part of the material was originally collected and sorted by A. Pisera and J. Dzik in late 1970s, more was picked by the author in 2003 at the same locality. Ossicles were picked from the dried residue gained by scrubbing the weathered rock fragments with water and a brush. For scanning electron microscopy, specimens were fixed to the stubs with water-soluble glue so that they could be photographed from both sides.

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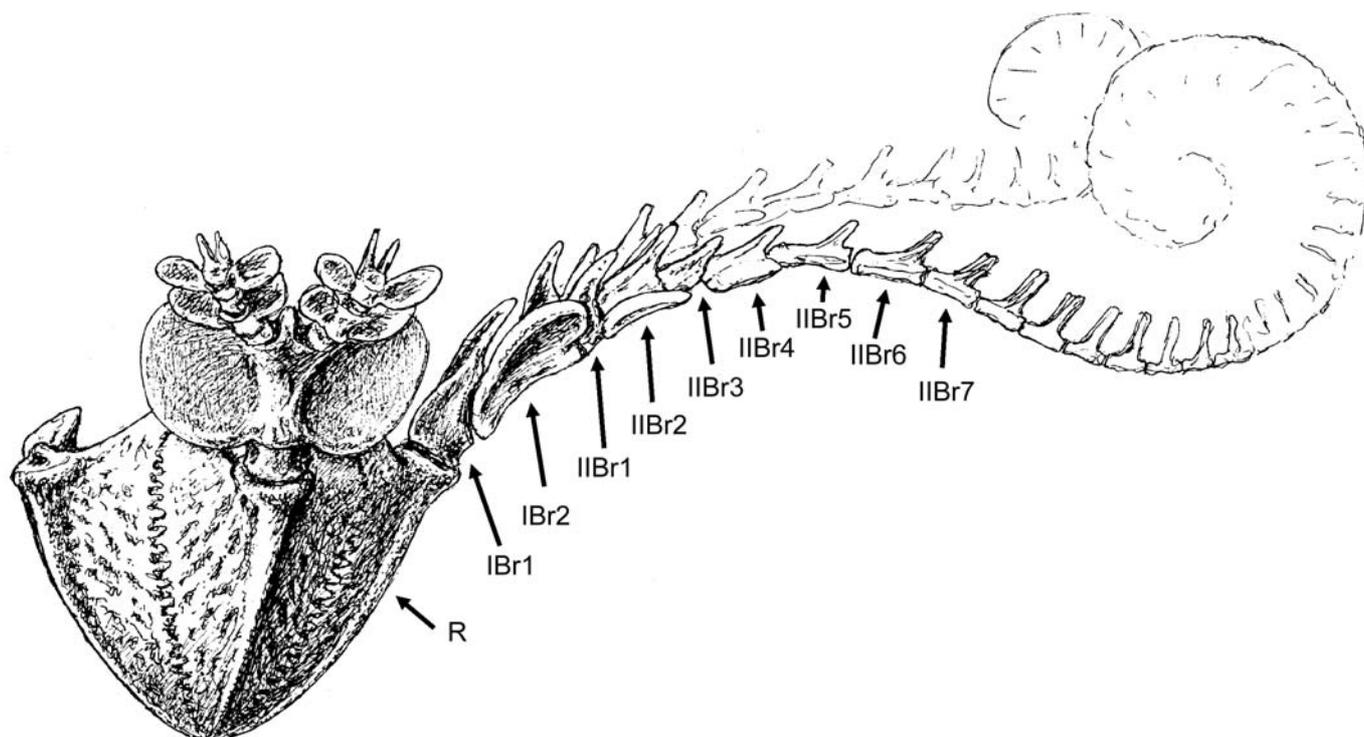
http://app.pan.pl/acta51/app51-261.pdf

Fig. 1. Restoration of *Saccocoma tenella* (Goldfuss, 1831). Some arms or their distal parts omitted for clarity (drawing by Jerzy Dzik based on a model constructed by the author).

To achieve the aims of the study, articulations of individual brachials have been analysed in detail. Identification and matching of the element types also required determining of species number and their intraspecific variability.

Institutional abbreviation.—ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Other abbreviations.—IBr1(2), first (second) primibrachial; IIBr1(2, 3, ...), first (second, third, etc.) secundibrachial; Ax, axillary; BrBr, brachials; R, radial.

Functional anatomy of *Saccocoma*

Brachial articulations and arrangement.—Articulations between brachials of saccocomids were discussed by Hess (1972, 1999, 2002). In his most recent work he illustrated articulations between radials and base of arms of *Crassicoma schattenbergi* (Hess, 2002). However, the arrangement and articulations of elements within the proximal part of the arm of *Saccocoma tenella*, presented here on Fig. 2, have never been explicitly illustrated before.

The articulation between the radial and the wingless first primibrachial serves as the point of attachment for the entire arm. The V-shaped muscle fields on the inner side of the radial correspond to two elongate, similarly V-shaped muscle fields on the oral surface of IBr1. The latter is connected with the winged second primibrachial by a fixed, non-muscular articulation (called "blocked" cryptosynarthry by Hess 2002), which is oblique in relation to the long axis of both ossicles (such "sloping" connections are distinctive for the Roveacrinida). As the ligamentary part of the radial's facet points upwards, the fixed IBr1/IBr2 complex must have been oriented at a rather small angle in the living animal. The second primibrachial is an axillary (the element where the arm branches) bearing two distal muscular facets, whose ligament pits point outwards at angle of about 45°. The following two elements, the wingless first and the winged second secundibrachials, are again stiffly joined by a sloping cryptosynarthry. Pisera and Dzik (1979) and Manni and Nicosia (1984) illustrated supposed IIBrBr1 of two species of *Saccocoma*, but the figured ossicles have rather non-sloping distal articulation surfaces and are in fact IIBrBr3. Since the second secundibrachial and the second primibrachial have identical proximal facets, the complementary element (IIBr1) must have had a sloping distal surface as in IBr1 and is probably hard to distinguish from it.

The second secundibrachial has a muscular distal articulation facet whose ligament pit again points outwards. The following wingless IIBr3 and winged IIBr4 are once more joined by cryptosynarthry or synostosis, but this time the articulation plane is nearly perpendicular to the arm's axis, rather than oblique. Consequently, these ossicles are easy to recognize. All following articulations are muscular, and
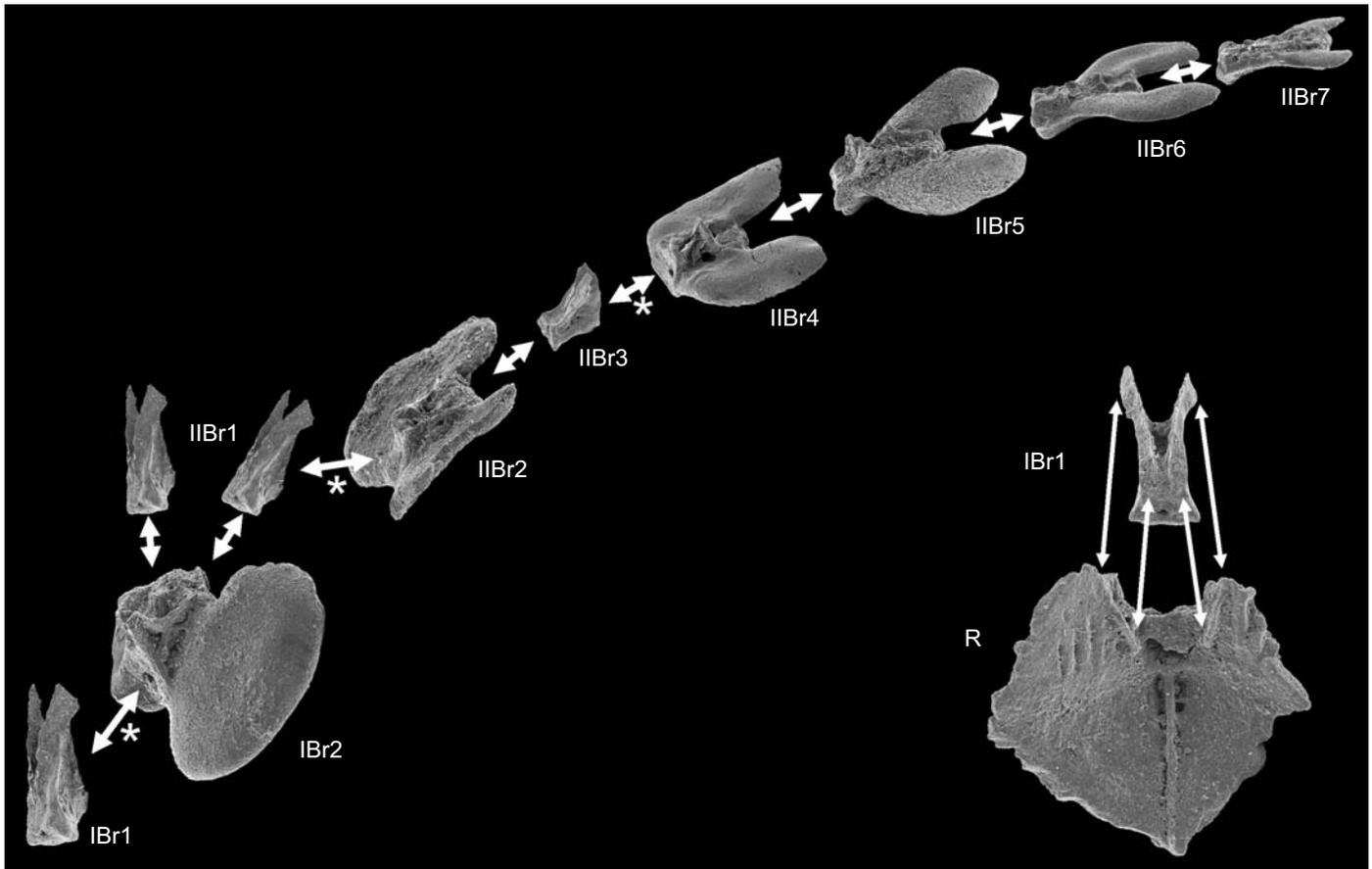
Fig. 2. Arrangement and articulation of proximal brachials in *Saccocoma tenella*. Asterisks denote non-muscular (cryptosynarthrial) articulations. Not to scale.

IIBr5–IIBr7 differ only in size and wing proportions. Hess (2002) assumed that in *Crassicoma* synostosis also occurs between IIBr5 and IIBr6. He also illustrated some supposedly distal secundibrachials of *Saccocoma quenstedti* with cryptosynarthrial facets at one end, and a bent muscular facet at the other end. Yet, no comparable ossicles have been found in the investigated material from Rogoźnik.

Arm position and mode of life.—Due to the upward-pointing radial articular facets and the fixed character of crypto-synarthrial connections in living *Saccocoma*, the most proximal part of the arms (IBr1–IBr2) must have been relatively stiff and left the cup at an angle of no more than 45°. The arms then spread gradually to the sides and were nearly horizontal at about IIBr4–IIBr5. The more distal parts (above IIBr7) had considerable flexibility. This can be observed in articulated specimens from Solnhofen, in which the proximal arms are relatively straight, but commonly curled distally.

Thus, Hess' (1999: fig. 220) reconstruction of *S. tenella* requires in my opinion some modification. In his drawing, IBr1 and IBr2 seem to be articulated by facets at a right angle to the arm axis, not by sloping cryptosynarthries that are nearly parallel to the axis. As shown in Fig. 2, such a connection is anatomically impossible; in fact, the arm would have to be broken to achieve such an orientation. The position of

the proximal arms in the reconstruction by Manni et al. (1997: fig. 3) is also not in accordance with the observed anatomical features. These authors do not take the angle at which the arms leave the cup and the slopes of the distal facet of IBr2 into consideration. In effect, the arms in their reconstruction are vertical instead of spreading gently to the sides. Manni et al. (1997) argue that *Saccocoma* was a benthic mud-sticker and that its vertically-oriented lateral wings served as a cover against the invasion of loose sediment. In my opinion, however, the actual position of the proximal arms does not support this view and is more in accordance with the classic pelagic model (Jaekel 1892, Hess 1999, 2002), in which this crinoid floated by the movement of broadly outstretched arms equipped with lateral wings (hence the name "Schwimmplatten"). However, this model is not without some problems. The winged parts of the arms were too close to the cup and presumably too stiff to efficiently propel the animal in the water. Still, this construction does not exclude a pelagic life style. Probably the distal, finely branched parts of the arms with their high oral processes were mobile enough to provide locomotion for this minute animal.

This assumption is at the base of Seilacher and Hauff's (2004) new hypothetical model: "snap-swimming". They interpret the coiling of the distal arms as seen in many articu-

lated Solnhofen specimens, not as a taphonomic artefact or a protective reflex against invasion of mud (Hess 2002), but as a part of the normal behaviour of this crinoid. According to their model, swimming proceeded by (1) an inward coiling of the arms through slow muscular action (recovery stroke), and (2) their rapid outstretching triggered by the spring-like action of aborally-placed ligament, which could instantly release the energy stored during coiling (active stroke). In this way, the crinoid could propel itself mouth-up in the water or at least actively prevent sinking.

This model explains the probable locomotory behaviour of *Saccocoma* and supports a pelagic mode of life, but is does not fully explain the function of the wings on the proximal part of the arms. The assumption (Jaekel 1892; Hess 1999, 2002; Seilacher and Hauff 2004) that they functioned as a parachute is not entirely consistent with their non-horizontal attitude. In fact, the second primibrachial, bearing the largest wings, is the most vertical. Moreover, the calcareous wings, although being very thin, added some weight, decreasing the buoyancy of the pelagic animal and thus inevitably increased the energy cost associated with it's constant struggle to keep afloat.

This cost can be estimated by measuring the participation of the wings' mass in relation to the mass of the entire skeleton. To achieve this, I constructed models of the cup and proximal parts of the arm of *Saccocoma* differing in proportions and measured their mass with and without the wings attached (the models were made from modelling mass; since I was seeking only relative values, the actual density of the original pieces was not important, assuming no substantial differences existed between the density of wings and other parts of the skeleton). The lateral expansions constituted roughly 25 to 15 % of the skeleton mass (cup and proximal brachials up to IIBr7). If one includes the numerous distal pieces, the proportion is smaller, probably about 5–10 % (however, these values are possibly too high, since the wings moulded from modelling mass may be not adequately thin). This does not seem an excessive overweight, but it could be noticeable for a pelagic animal. The hydrodynamic benefits balancing these extra costs are not entirely clear. One possible explanation is that the wings reduced the sinking rate of *Saccocoma* not exactly by increasing the pressure drag, as the parachute-analogy suggests, but mainly by increasing the animal's surface drag (viscous or friction drag). The latter results directly from viscous forces of water, which are significant for pelagic animals of small size (living at low Reynolds numbers). If so, the non-horizontal orientation of the largest wings would not hinder their traditionally assumed function. It would also harmonize with the presence of spines, reticulate sculpture, conspicuous vacuolar ornamentation and peculiar shape of wings in some species of *Saccocoma*, as all of these structures increase the surface drag. This assumption would be especially true for small, subadult individuals, as the relative significance of the surface drag decreases as the size of an aquatic animal increases.

Systematic palaeontology

Apart from articulated specimens in Solnhofen limestones, diverse loose elements of saccocomids are known from numerous localities (Sieverts-Doreck 1955, 1958; Verniory 1960, 1961, 1962a, 1962b; Hess 1972, 2002; Nicosia and Parisi 1979; Pisera and Dzik 1979; Holzer and Poltnig 1980; Manni and Nicosia 1984; Głuchowski 1987). Several species of *Saccocoma* have been described, some of which turned out to be preservational variants synonymous with *Saccocoma tenella* (Manni and Nicosia 1986; Manni et al. 1997; Hess 1999). Hertha Sieverts-Doreck also used some informal names in her unpublished notes (Hess 2002). These were used by Verniory (1961, 1962a) and Hess (1972) and subsequently referred to by Nicosia and Parisi (1979) and Pisera and Dzik (1979). Verniory (1962b) and Manni and Nicosia (1984) illustrated two more species. Finally, Hess (2002) revised the available material and drafts of Sieverts-Doreck. He distinguished two genera: the comparatively thick-walled Oxfordian to late Kimmeridgian *Crassicoma*, with several species that lack "Schwimmplatten" on the free brachials and were presumably necto-benthic, and the thin-walled early Kimmeridgian to Tithonian *Saccocoma*, bearing wing-like lateral expansions on proximal brachials. Four valid species—*S. tenella* (Goldfuss, 1831)*, S. quenstedti* Sieverts-Doreck and Hess, 2002, *S. longipinna* Hess, 2002, and *S. vernioryi* Manni and Nicosia, 1984—are currently recognised within the genus *Saccocoma*.

In the material from the red Rogoża Coquina at Rogoźnik, two known *Saccocoma* species and a third form of unclear status have been identified.

Class Crinoidea Miller, 1821
Subclass Articulata Zittel, 1879
Order Roveacrinida Sieverts-Doreck, 1952 in Moore 1952
Family Saccocomidae d'Orbigny, 1852
Genus *Saccocoma* Agassiz, 1836

Type species: *Comatula tenella* Goldfuss, 1831: by subsequent designation of Manni, Nicosia, and Tagliacozzo (1997), Lower Tithonian, Solnhofen, Germany.

Saccocoma tenella (Goldfuss, 1831)
Figs. 3A–E, 4A, B, 5A–D, H, I, 6A, B, E, F, H, I.

1831 *Comatula tenella* sp. nov.; Goldfuss 1831: 204, pl. 62: 1.
1831 *Comatula pectinata* sp. nov.; Goldfuss 1831: 205, pl. 62: 2.
1831 *Comatula filiformis* sp. nov.; Goldfuss 1831: 205, pl. 62: 3.
1892 *Saccocoma tenella* Goldfuss; Jaekel 1892: 659–694, pl. 29: 6, pl. 30.
1960 *Saccocoma tenella* Goldfuss; Verniory 1960: 250–257, figs. 1–9.
1979 *Saccocoma tenella* Goldfuss, 1862; Pisera and Dzik 1979: 810–811, fig. 3, pl. 1: 8, 9, pl. 2: 1–7, pl. 3: 1–3.
1980 *Saccocoma tenella* (Goldfuss, 1831); Holzer and Poltnig 1980: 207, fig. 2, pls. 1–3.
1987 *Saccocoma tenella* Goldfuss, 1862; Głuchowski 1987: 39–40, pl. 17: 1, 4–6, pl. 18: 1–5, pl. 19: 1–6, fig. 13: 7–10.
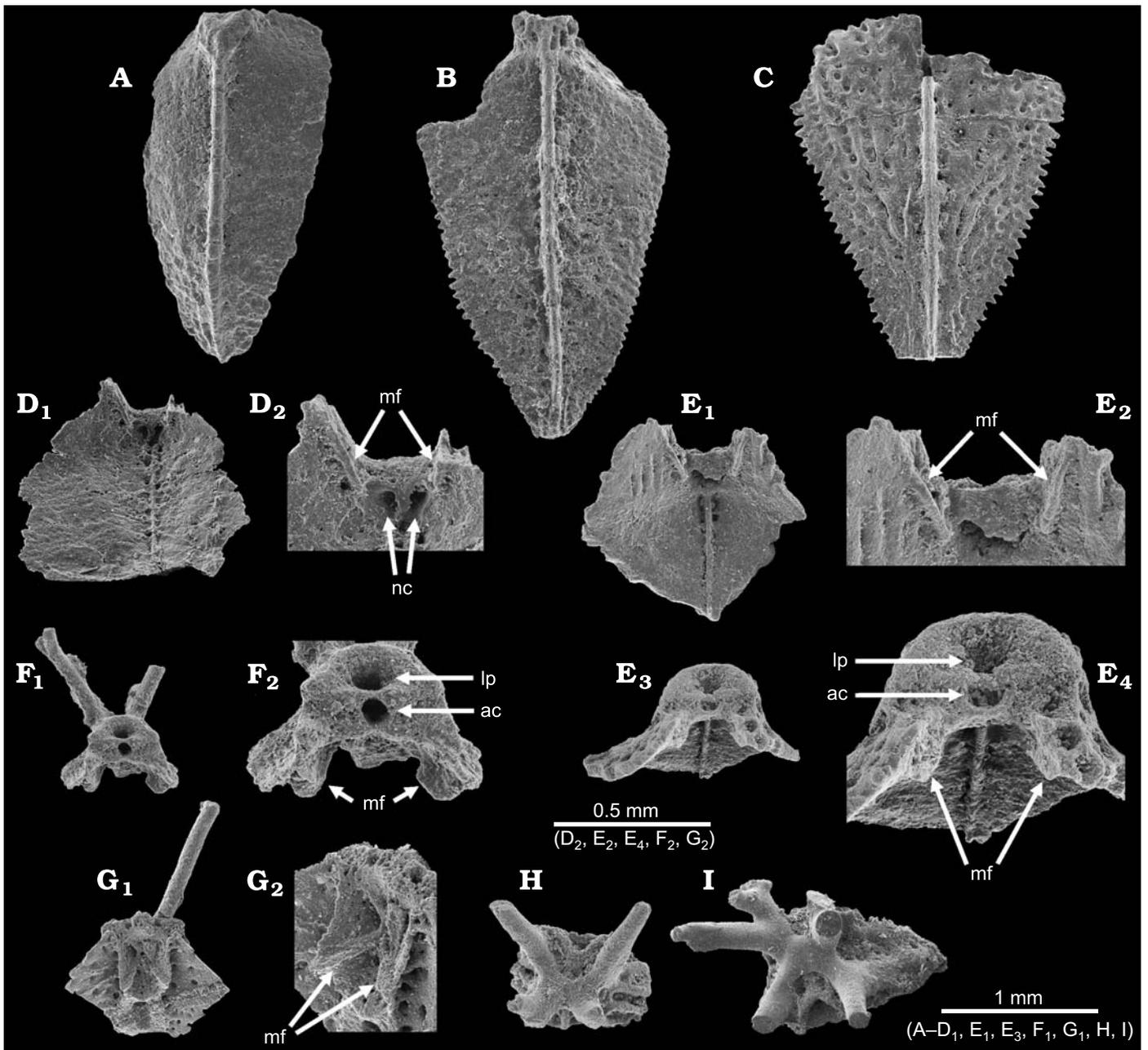2002 *Saccocoma tenella* (Goldfuss, 1831); Hess 2002: 19, figs. 12, 13.

Fig. 3. Radials of *Saccocoma* from Tithonian red Rogoża Coquina at Rogoźnik, Pieniny Klippen Belt, Poland. **A–E**. *Saccocoma tenella* (Goldfuss, 1831). **A**. ZPAL Ca.6/01, exterior view. **B**. ZPAL Ca.6/02, exterior view. **C**. ZPAL Ca.6/03, exterior view. **D**. ZPAL Ca.6/09, interior view (D_1) and details of the upper part (D_2, enlarged twice). **E**. ZPAL Ca.6/12, interior view (E_1) and details of the upper part (E_2, enlarged twice); oral view (E_3) and details of the articulation facet (E_4, enlarged twice). **F–I**. *Saccocoma vernioryi* Manni and Nicosia, 1984. **F**. ZPAL Ca.6/11, oral view (F_1) and details of the articulation facet (F_2, enlarged twice). **G**. ZPAL Ca.6/08, interior view (G_1) and muscle fields viewed from different angle (G_2, enlarged twice). **H**. ZPAL Ca.6/06, exterior view. **I**. ZPAL Ca.6/05, exterior view.

Material.—More than 100 radials, mostly broken, and more than 400 brachials.

Description.—Radial plates (Fig. 3A–E) resembling an arrow-head in outline, gently curved, thin. External (aboral) surface with pronounced median ridge and a more or less developed reticulate sculpture. Edges vary from straight to serrate. The bulbous articulation facet with well-developed ligament fossa bears no spines. Inner (oral) side rather smooth,

with a thin median ridge terminating at the base of the articulation facet, where openings of nerve canals may be seen. At the upper end, two ridges form a V-shaped surface for the attachment of muscles.

The first primibrachial (IBr1; Fig. 4A) is cylindrical, has distinct ligament fossae on the proximal end and two well-developed, low, distally elongate muscle fields on the oral side. The aboral side shows a large, sloping, non-muscular (cryptosynarthial or synostosial) distal articulation facet that
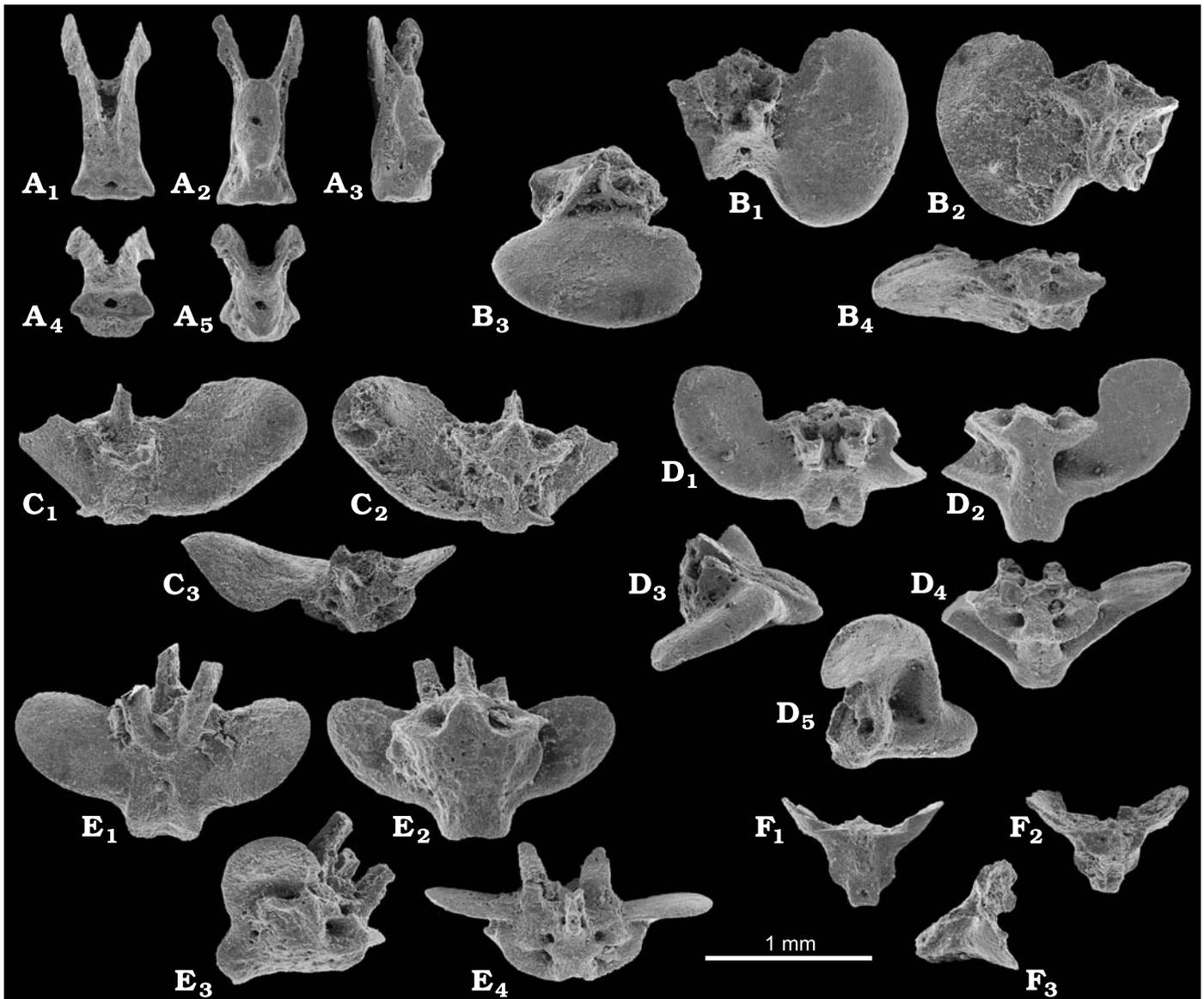
Fig. 4. First (**A**) and second (**B–F**) primibrachials of *Saccocoma* from Tithonian red Rogoża Coquina at Rogoźnik, Pieniny Klippen Belt, Poland. **A**, **B**. *Saccocoma tenella* (Goldfuss, 1831). **A**. ZPAL Ca.6/25, IBr1, oral (A_1), aboral (A_2), lateral (A_3), proximal (A_4), and distal (A_5) views. **B**. ZPAL Ca.6/16, IBr2 (IAx), oral (B_1), aboral (B_2), lateral/oral (B_3), and distal (B_4) views. **C**. *Saccocoma* sp., ZPAL Ca.6/19, IBr2 (IAx), oral (C_1), aboral (C_2), and distal (C_3) views. **D**, **E**.*Saccocoma* aff. *vernioryi* Manni and Nicosia, 1984. **D**. ZPAL Ca.6/18, IBr2 (IAx), oral (D_1), aboral (D_2), lateral (D_3), distal (D_4), and lateral/slightly aboral (D_5) views. **E**. ZPAL Ca.6/17, IBr2 (IAx), oral (E_1), aboral (E_2), lateral/slightly aboral (E_3), and distal (E_4) views. **F**. *S. vernioryi* Manni and Nicosia, 1984, ZPAL Ca.6/20, IBr2 (IAx), oral (F_1), aboral (F_2), and lateral (F_3) views.

in side view forms an angle of about 20° with the long axis of the ossicle.

The second primibrachial or primaxillary (IBr2 = IAx; Fig. 4B) bears two large, symmetrical, rounded, dish-like lateral expansions or wings ("Schwimmplatten"). Their proximal margins extend beyond the proximal articulation surface, which is non-muscular, sloping at an angle of about 20–30°, and well visible in oral view. The two distal muscular articulation facets are comparatively low in distal view, their ligament fossae can be seen aborally. On the oral side, there are two weak ridge-like oral processes and a median processus (usually broken).

The first secundibrachial (IIBr1) is probably more similar to the IBr1 than to the IIBr3 (see the chapter on functional anatomy). The second secundibrachial (IIBr2; Fig. 5B–D) generally resembles the IBr2 (IAx), except that it has only one muscular distal articulation facet, that it lacks the median processus, and that the proximal facet (sloping non-muscular) may be slightly bent to one side making the wing-like expansions more or less asymmetrical. The third secundibrachial (IIBr3; Fig. 5A) is again short, with the proximal articulation surface developed as in the IBr1, but with distinctly higher muscle fields. Its distal articulation surface is non-muscular and almost perpendicular (60–80°) to the ele-
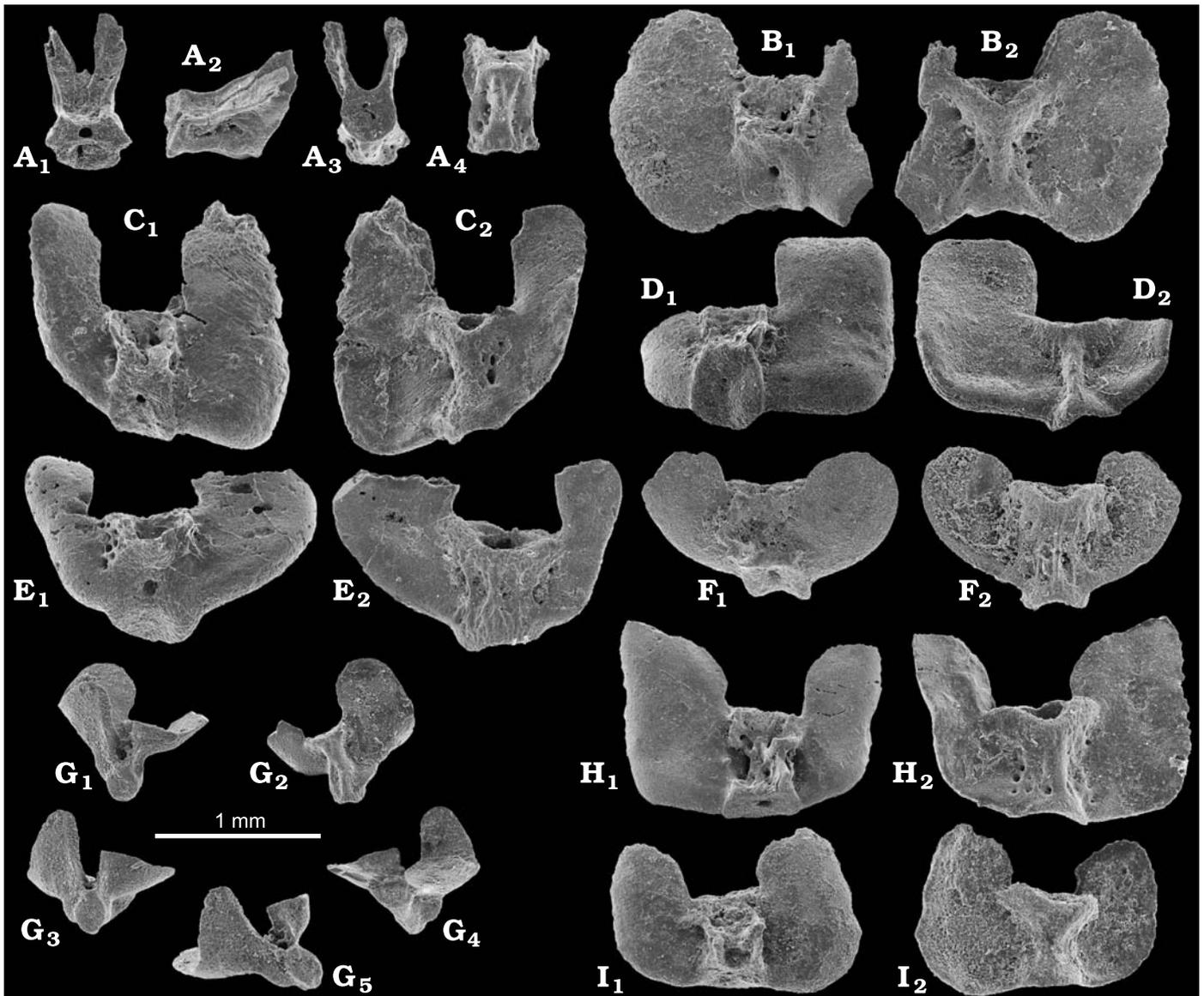
Fig. 5. First or third (**A**), second (**B–G**) and fourth (**H**, **I**) secundibrachials of *Saccocoma* from Tithonian red Rogoża Coquina at Rogoźnik, Pieniny Klippen Belt, Poland. **A**, **B**, **H**, **I**. *Saccocoma tenella* (Goldfuss, 1831). **A**. ZPAL Ca.6/21, IIBr1 or 3, proximal (A_1), lateral (A_2, proximal side to the left), distal (A_3), and aboral (A_4) views. **B**. ZPAL Ca.6/15, IIBr2, oral (B_1) and aboral (B_2) views. **H**. ZPAL Ca.6/27, IIBr4, oral (H_1) and aboral (H_2) views. **I**. ZPAL Ca.6/26, IIBr4, oral (I_1) and aboral (I_2) views. **C**, **D**. *Saccocoma tenella*? (Goldfuss, 1831). **C**. ZPAL Ca.6/14, IIBr2, oral (C_1) and aboral (C_2) views. **D**. ZPAL Ca.6/13, IIBr2, oral (D_1) and aboral (D_2) views. **E**, **F**. *Saccocoma* aff. *vernioryi* Manni and Nicosia, 1984. **E**. ZPAL Ca.6/23, IIBr2, oral (E_1) and aboral (E_2) views. **F**. ZPAL Ca.6/22, IIBr2, oral (F_1) and aboral (F_2) views. **G**. *Saccocoma vernioryi* Manni and Nicosia, 1984, ZPAL Ca.6/24, IIBr2, oral (G_1), aboral (G_2), proximal (G_3), distal (G_4), and lateral/proximal views.

ment's long axis. The fourth secundibrachial (IIBr4; Fig. 5H, I) has more or less asymmetric wing-like expansions, a non-muscular, non-sloping (almost perpendicular) proximal articulation surface, a muscular distal facet, and low, paired oral processes that are more pronounced than in the IBr2 or IIBr2. Secundibrachials of higher order (IIBr5–IIBr7; Fig. 6A, B, E, F) have progressively shorter wings, muscular articulation facets on both ends, and low but distinct oral processes. Even more distal secundibrachials (IIBr8 and higher; Fig. 6H, I) have high and flat (often more or less broken) oral processes and no or very short lateral wings.

Remarks.—Most of the investigated ossicles probably represent subadult individuals. The radial plates do not reach 7–8 mm, as reported in other studies (Głuchowski 1987; Holzer and Poltnig 1980), but only 2.5–3.5 mm at the most. The variability of their sculpture, first noted by Verniory (1960), reflects an ontogenetic change, as shown in detail by Holzer and Poltnig (1980): the smooth surfaces of small (below 2–2.5 mm) radials of young individuals became covered with a network of ridges and ribs as the animal grew.

The arrangement of the proximal brachials adopted here follows that of Jaekel (1892) who in his famous reconstruc-
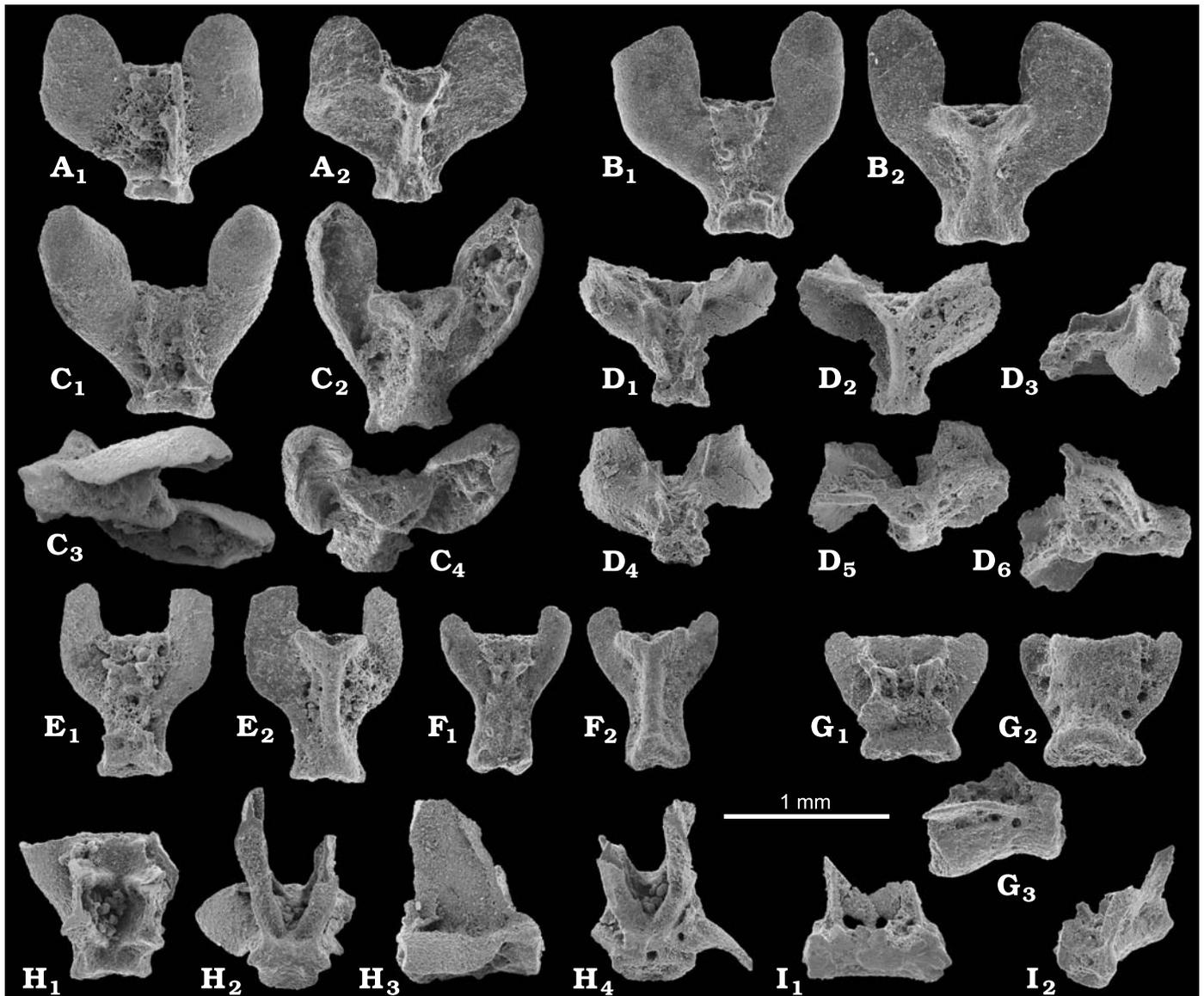
Fig. 6. Fifth (**A**), sixth (**B**, **C**), seventh (**F**, **G**) and more distal (**H**, **I**) secundibrachials of *Saccocoma* from Tithonian red Rogoża Coquina at Rogoźnik, Pieniny Klippen Belt, Poland. **A**, **B**, **E**, **F**, **H**, **I**. *Saccocoma tenella* (Goldfuss, 1831). **A**. ZPAL Ca.6/28, probably IIBr5, oral (A_1) and aboral (A_2) views. **B**. ZPAL Ca.6/29, probably IIBr6, oral (B_1) and aboral (B_2) views. **E**. ZPAL Ca.6/32, probably IIBr6 or 7, oral (E_1) and aboral (E_2) views. **F**. ZPAL Ca.6/30, probably IIBr7, oral (F_1) and aboral (F_2) view. **H**. ZPAL Ca.6/10, distal secundibrachial (IIBr8 and higher), oral (H_1), proximal (H_2), lateral (H_3, proximal side right), and distal (H_4) views. **I**. ZPAL Ca.6/31, distal brachial, lateral view (I_1) and articulation facet (I_2). **C**. *Saccocoma* sp., ZPAL Ca.6/34, probably IIBr6, oral (C_1), aboral (C_2), lateral/aboral (C_3), and distal/aboral (C_4) views. **D**. *Saccocoma vernioryi* Manni and Nicosia, 1984, ZPAL Ca.6/35, IIBr5, 6 or 7, oral (D_1), aboral (D_2), lateral (D_3, proximal side left), proximal (D_4), distal (D_5), and lateral (D_6, proximal side right) views. **G**. *Saccocoma* aff. *vernioryi* Manni and Nicosia, 1984, ZPAL Ca.6/33, probably IIBr7 or more distal secundibrachial, oral (G_1), aboral (G_2), and lateral (G_3, proximal side right) views.

tion illustrated the animal with five arms, each splitting at the second primibrachial (primaxillary) into two secondary arms, whose proximal parts consists of two wingless (IIBr1 and IIBr3) and five winged (IIBr2, IIBr4–IIBr7) secundibrachials. However, this is not necessarily the case, as Hess (1999: fig. 219) has shown in an articulated specimen with wings on third secundibrachials and, in one or two of the arms, with a second primibrachial that is not an axillary. This may be explained by pathological development or imperfect regeneration.

Saccocoma vernioryi Manni and Nicosia, 1984

Figs. 3F–I, 4F, 5G, 6D.

1972 *Saccocoma* sp. indet.; Hess 1972: 639, pl. 2: 24.
1972 Non-identifiable elements; Hess 1972: 639, pl. 2: 26.
1979 *Saccocoma* cf. *quenstedti* Verniory, 1961; Pisera and Dzik 1979: 811–813, fig. 4a, c–e.
1979 *Saccocoma* sp.; Pisera and Dzik 1979: 812, fig. 4b.
1984 *Saccocoma vernioryi* Manni and Nicosia, 1984: 91–97, figs. 1–16.
1987 *Saccocoma* cf. *quenstedti*; Głuchowski 1987: 40–41, pl. 17: 2, 3, fig. 13: 11.

Material.—More than 50 radials, about 15 brachials and many broken-off radial spines.

Description.—Radials (Fig. 3F–I) as in *Saccocoma tenella*, but equipped with two pairs of spines, one projecting upward and the other downward, at the base of the articulation facet. The spines may branch, but are usually broken in the studied material. The second primibrachial or primaxillary (IBr2 = IAx; Fig. 4F) is small (about 1 mm wide and long), triangular in outline, with a sloping non-muscular articulation facet on the proximal and two muscular facets on the distal side. The wings have a distinctive bell-shaped profile, different from dish-like wings of *S. tenella*. The second secundibrachial (IIBr2; Fig. 5G) generally resembles the IBr2, but it has only one distal articulation facet (muscular) and the wings are asymetrical. The only identified distal secundibrachial of higher order (IIBr5, IIBr6 or IIBr7) has muscular articulations at both ends and low, but distinct oral projections.

Remarks.—Although no articulated specimens of this species are known, the spiny radials can be unequivocally considered conspecific with the bell-shaped brachials, as Manni and Nicosia (1984) found such radials in strata where no other species of *Saccocoma* occurred. They described all types of ossicles, including the wingless IBr1, IIBr1, and IIBr3 which seem to correspond to their equivalents in *S. tenella* (except that, in my opinion, the first secundibrachial in both species must have been similar to the first primibrachial, not to the third secundibrachial, as I have explained earlier in this paper). The present material is not as rich; I identified only about a dozen very small and delicate IBr2 and IIBr2, evidently belonging to juvenile individuals (Figs. 4F, 5G), and a single poorly preserved secundibrachial of higher order (IIBr5, IIBr6 or IIBr7; Fig. 6D). Nevertheless, broken radials of this species are quite common; usually only the area around the articulation facet (with damaged spines attached) is preserved. There is also an abundance of broken-off spines.

A large second secundibrachial (IIBr2) and presumably two other brachials of this form have been illustrated by Pisera and Dzik (1979: 812, fig. 4c–e) under the name *Saccocoma* cf. *quenstedti*. These ossicles were attributed by Manni and Nicosia (1984) to *S. vernioryi*. They apparently represent adult individuals as opposed to the juvenile ones here described. However, in the present material there were no such elements.

Saccocoma aff. *vernioryi* Manni and Nicosia, 1984
Figs. 4D, E, 5E, F, 6G.

Material.—About 10 brachials.

Description.—This group of ossicles includes second primibrachials or primaxillaries (IBr2 = IAx; Fig. 4D, E) with relatively short wings which extend distally but not proximally. The large, sloping non-muscular proximal articulation facet projects beyond the proximal margin of the wings, as in *S. vernioryi*. However, the wings are not bell-shaped as in this species but flat or slightly concave, as in *S.tenella*. On the

aboral side, there is a more or less pronounced depression at the base of each wing (Fig. 4D$_2$), which may be overgrown by a broad lamella that extends from the central part of the ossicle to the sides (Fig. 4E$_2$) and leaves only narrow fissures visible in lateral views (Fig. 4E$_3$). This lamella has some small perforations and shows traces of reticulate sculpture. The oral side bears three large processes. The distal end of this ossicle is high, with two conspicuous muscular articulation facets (Fig. 4E$_4$). The corresponding ligament fossae are large and well-visible in the aboral view (Fig. 4E$_2$). With a developed aboral lamella, the ossicle has a compact and massive general appearance. The second secundibrachial (IIBr2; Fig. 5E, F) is similar to the IBr2, but has only one distal articulation facet and no median processus.

The only identified secundibrachial of higher order (IIBr5, IIBr 6, IIBr 7 or more; Fig. 6G) is short, broad, has small wings and well-developed proximal and distal muscular articulation facets with large ligament fossae. Its aboral side has a broad lamella and the oral surface shows roots of two presumably large processes.

Remarks.—The brachials described here resemble the brachials of adult *Saccocoma vernioryi* with regard to the protruding proximal articulation facet, high distal end and general outline. However, the wings are not bell-shaped, but flat or slightly concave. Additionally, on the aboral side there is a lamellar overgrowth that extends laterally and makes the elements look more robust and massive than those of *S. vernioryi*. A single broken radial with very massive spines (Pisera and Dzik 1979: 812, fig. 4b) may match these brachials. They either represent a species closely related to *S. vernioryi*, or simply belong to senior, highly calcified individuals. At the moment, there are not enough such elements to settle this issue.

Conclusions to the systematic part

In the investigated material, brachials show three morphologies, which seem to represent at least two separate species. The most abundant brachials are referred to *Saccocoma tenella*; they have rounded, dish-like wings, small oral processes and a low distal end. The much less common brachials with wings that have a peculiar bell-shaped outline are assigned to *S. vernioryi*. A few other brachials that lack the bell-like appearance but have nonetheless large proximal articulation facets projecting well beyond the proximal margin of the wings, as in *S. vernioryi*, are referred to *Saccocoma* aff. *vernioryi*. These brachials have also large oral processess, a high distal end and often exhibit a lamellar overgrowth extending from the central part to the sides on the aboral side. However, only two types of radials can be distinguished. One type carries spines at the base of the articulation facet and the other type lacks them. The spineless type belongs to *S. tenella*, the other to *S. vernioryi*, as described by Manni and Nicosia (1984). Most probably, *Saccocoma* aff. *vernioryi* had also spiny radials. If so, the two Tithonian species (*S. tenella* and *S.*

vernioryi) are closely related. They also seem to be related to the Kimmeridgian *S. quenstedti*, which bears one pair of spines and has a very distinctive pattern of coarsely reticulate sculpture on the radials as well as the brachials (see Verniory 1961; Hess 2002). Interestingly, some brachials of *Saccocoma* aff. *vernioryi* show traces of a rather coarse sculpture on the broad central part of the ossicle (Fig. $5E_2$, F_2) or even a perforated lamella extending to the sides (Figs. $4E_2$, E_3, $6G_2$, G_3). This contrasts with the usually smooth surface of the narrow central body of the brachials in *S. tenella* (Figs. $4B_2$, $5B_2$, D_2).

The investigated material also contains some brachials that seem to be intermediate between recognised species and thus hard to classify (Figs. 4C, 5C, D, 6C). This seems to be typical for saccocomids. Hess (2002) reported that, apart from easily distinguishable elements belonging to the main species of *Crassicoma*, he found many intermediate ossicles. Transitional forms may be an outcome of hybridisation between species, due to overlapping variability ranges of closely related species, or a reaction to changes in the environment.

Acknowledgements

References

Agassiz, L. 1836. Prodrome d'une Monographie des Radiaires ou Echinodermes. *Mémoires de la Société des Sciences Naturelles de Neuchâtel* 1 (for 1835): 168–199.

Barthel, K., Swinburne, N., and Conway Morris, S. 1990. *Solnhofen: a Study of Mesozoic Palaeontology*. 236 pp. Cambridge University Press, Cambridge.

Birkenmajer, K. 1977. Jurassic and Cretaceous stratigraphic units of the Pieniny Klippen Belt, Carpathians, Poland. *Studia Geologica Polonica* 45: 1–158.

Głuchowski, E. 1987. Jurassic and Early Cretaceous articulate crinoids from the Pieniny Klippen Belt and the Tatra Mts., Poland. *Studia Geologica Polonica* 94: 1–102.

Goldfuss, G. 1826–33. *Petrefacta Germaniae, Vol. 1*. 252 pp. Arnz, Düsseldorf.

Hess, H. 1972. Planktonic crinoids of Late Jurassic age from Leg 11, Deep Sea Drilling Project. *Initial Reports of the Deep Sea Drilling Project* 11: 631–643.

Hess, H. 1999. Upper Jurassic Solnhofen Plattenkalk of Bavaria, Germany. *In*: H. Hess, W.I. Ausich, C.E. Brett, and M.J. Simms (eds.), *Fossil Crinoids*, 216–224. Cambridge University Press, Cambridge.

Hess, H. 2002. Remains of saccocomids (Crinoidea: Echinodermata) from the Upper Jurassic of Southern Germany. *Stuttgarter Beiträge zur Naturkunde Serie B* 329: 1–57.

Holzer, H.-L. and Poltnig, W. 1980. Erster Nachweis einer Radialplatten-Fossillagerstätte der Schwebcrinoide *Saccocoma* im oberostalpinen Malm (Ostkarawanken, Kärnten). *Carinthia II* 170/90: 201–216.

Jaekel, O. 1892. Über Plicatocriniden, *Hyocrinus* und *Saccocoma*. *Zeitschrift der Deutschen Geologischen Gesellschaft* 44: 619–696.

Manni, R. and Nicosia, U. 1984. *Saccocoma vernioryi* n. sp., a new saccocomid from the Upper Jurassic of the central Italy. *Geologica Romana* 23: 91–97.

Manni, R. and Nicosia, U. 1986. *Saccocoma schwertschlageri* Walther, 1904 junior synonym of *Saccocoma tenellum* (Goldfuss), 1829. Evidence of autotomy in fossil crinoids. *Bollettino della Società Paleontologica Italiana* 24: 181–183.

Manni, R., Nicosia, U., and Tagliacozzo, L. 1997. *Saccocoma*, normal benthonic stemless crinoid: an opportunistic reply within mud dominated facies. *Palaeopelagos* 7: 21–132.

Miller, J.S. 1821. A Natural History of the Crinoidea or Lily-shaped Animals, with Observations on the Genera *Asteria*, *Euryale*, *Comatula* and *Marsupites*. 150 pp. Bryan and Co., Bristol.

Milsom, C.V. 1994. *Saccocoma*: A benthic crinoid from the Jurassic Solnhofen Limestone, Germany. *Palaeontology* 37: 121–129.

Moore, R.C. 1952. Crinoids. *In*: R.C. Moore, C.G. Lalicker, and A.G. Fisher (eds.), *Invertebrate Fossils*, 604–652. McGraw-Hill Book Co., New York.

Nicosia, U. and Parisi, G. 1979. *Saccocoma tenella* (Goldfuss)—Distribuzione stratigrafica e geografica. *Bollettino della Societá Paleontologica Italiana* 18: 320–326.

Orbigny, A. d'. 1852. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie startigraphique, Vol. 3*. 189 pp. Victor Masson, Paris.

Pisera, A. and Dzik, J. 1979. Tithonian crinoids from Rogoźnik (Pieniny Klippen Belt, Poland) and their evolutionary relationships. *Eclogae geologicae Helvetiae* 72: 805–849.

Seilacher, A. and Hauff, R.B. 2004. Constructional morphology of pelagic crinoids. *Palaios* 19: 3–16.

Sieverts-Doreck, H. 1955. Die Verbreitung die Crinoidengattung *Saccocoma* im Schwäbischen Jura. *Jahreshefte des Vereins für Vaterländische Naturkunde in Württemberg* 110: 118–120.

Sieverts-Doreck, H. 1958. Kleinreste von Echinodermen aus dem fränkischen Jura (Sammlung Schattenberg, Bamberg). Ein vorläufiger Bericht. *Bericht der naturforschende Gesellschaft Bamberg* 36: 15–21.

Verniory, R. 1960. Présence (et variétés) de *Saccocoma tenella* Goldfuss à Talloires (Haute-Savoie). *Archives des Sciences, Genève* 13: 250–257.

Verniory, R. 1961. Présence de *Saccocoma quenstedti* Doreck (in coll.) dans les gorges de la Méouge (Sisteron-Provence). *Archives des Sciences, Genève* 14: 315–320.

Verniory, R. 1962a. Quelques considérations sur les Saccocomidés (échantillonage, statistique, stratigraphie). *Archives des Sciences, Genève* 15: 388–390.

Verniory, R. 1962b. Une nouvelle forme de *Saccocoma* (Montbrand, Hautes-Alpes, France). *Archives des Sciences, Genève* 15: 391–397.

Zittel, K.A. von. 1879. *Handbuch der Paläontologie, Vol. 1*. 765 pp. R. Oldenbourg, München.