Remains of Saccocomids
(Crinoidea: Echinodermata)
from the Upper Jurassic of southern Germany

By Hans Hess, Basel

With contributions from manuscripts of Hertha Sieverts-Doreck †, Stuttgart

With 11 plates and 15 textfigures

Abstract

A rich fauna of mostly isolated saccocomid ossicles from Oxfordian to Upper Kimmeridgian strata of southern Germany, preserved in the Staatliches Museum für Naturkunde in Stuttgart, is described. The 6547 elements, cups, radials and brachials, collected since the 1930’s were studied by Sieverts-Doreck who proposed several new species and at least one new genus that were in part used in the literature, but were never formally established by designation of types. Sieverts-Doreck’s names are adopted here using the joint authorship Sieverts-Doreck & Hess for the following new taxa: the genus Crassicoma n. g. that includes the type species C. schattenbergi n. sp., C. feifeli n. sp., and C. mayr n. sp., all known from complete cups, as well as C. praeschattenbergi n. sp. and C. subornata n. sp., known from radials and brachials only. With the exception of the comparatively sturdy C. schattenbergi the brachials cannot always be assigned to a given species with certainty. The genus Saccocoma Agassiz is represented by S. quenstedti Sieverts-Doreck n. sp. and S. cf. tenella (Goldfuss).

The bulk of the material is from the Lower Kimmeridgian where the possibly partly benthic Crassicoma forms co-existed with the pelagic Saccocoma quenstedti. Remains of Saccocoma cf. tenella are from the Upper Kimmeridgian but this species was also reported from the Lower Tithonian. In addition to the German material Saccocoma longipinna Hess n. sp. from the Kimmeridgian-Tithonian boundary of the French Alps is presented. This form was described by Verniory in 1962 as Saccocoma n. sp. For Saccocoma tenella (Goldfuss) a lectotype is proposed.

Zusammenfassung

SIEVERTS-DORECK werden für die folgenden neuen Taxa mit der gemeinsamen Autorenschaft SIEVERTS-DORECK & Hess übernommen: Crassicoma n. g. mit der Typusart C. schattenbergi n. sp. und die ebenfalls durch Kelche belegten Arten C. prae schattenbergi n. sp. und C. feifeli n. sp., sowie die durch isolierte Radialia und Brachialia vertretenen Arten praeschattenbergi n. sp. und subornata n. sp. Mit Ausnahme der robusten C. schattenbergi bereitet die Zuordnung der Armglieder einige Mühe. Die Gattung Saccocoma Agassiz ist durch S. quenstedti SIEVERTS-DORECK & Hess n. sp. und S. cf. tenella (GOLDFUSS) vertreten.


1. Introduction

Saccocoms are mainly known for their most prominent representative, Saccocoma tenella, from the Upper Jurassic Plattenkalk of Bavaria (Hess 1999, 2000). Remains of saccocoms are, however, commonly found in Upper Jurassic sediments (SIEVERTS-DORECK 1955, 1958; VERNIORY 1961, 1962a, 1962b; Hess 1972, 2000; PISEREA & Dzik 1979; MANNI & NICOSIA 1984; KHUPP & MATYSZKIEWICZ 1997). The material described in this paper is preserved in the collections of the Staatliches Museum für Naturkunde in Stuttgart (collection numbers SMNS 64691–64847). It has been obtained from washings of marly sediments by K. SCHATTENBERG since the 1930’s (SIEVERTS-DORECK 1958) and later by K. FEIFEL and was studied by HERTHA SIEVERTS-DORECK since the 1950’s until her death in 1991. She has left numerous
notes and drafts but no manuscript ready for press. One of the reasons for this regrettable lack certainly is the large number of isolated and mostly very small ossicles and the complexity of the material (vividly described in SIEVERTS-DORECK’s notes; for example, not even the radials could be classified by her with certainty in many cases). Another reason may have been SIEVERTS-DORECK’s worry to publish an “unfinished” paper that might provoke critical reactions from others (see HAUDE 1992).

The present paper is in part based on the notes of SIEVERTS-DORECK to whom it is dedicated. In certain ways (lack of detailed stratigraphic record, no information on accompanying fauna, but also lack of important material mentioned by SIEVERTS-DORECK) this paper is of a preliminary nature, but I consider its publication worthwhile with the hope to stimulate future research on these fascinating crinoids.

Acknowledgments

The author extends special thanks to the responsible colleagues at the Stuttgart Museum: M. Urlichs for his help with the legacy of H. Sieverts-Doreck, G. Dietl for his support during my stay at the Museum, G. Schweigert for his valuable advice, constructive review of the manuscript and transformation of Quenstedt’s shorthand symbols into presently accepted stratigraphic units. The tricky nomenclatural questions were commented by G. Bloos and G. Schweigert whose help is gratefully acknowledged; the decisions presented in this paper are the author’s responsibility. M. Sander (University of Bonn) kindly made GOLDFUSS’ original of Comatula tenella available. D. Decrouet (Natural History Museum Geneva) helped with VERNORY’s original material. Thanks are also due to W. Riegraf (Münster) for information on the occurrence of saccocomid remains, to T. Baumiller (University of Michigan) for helpful suggestions, to W. Etter (Natural History Museum Basel) for his help with Fig.15 and to K. Foellmi (University of Neuchâtel) for access to the isotope analysis of some ossicles; these were performed by Z. Bender at the Institut für Petrographie und Geochemie of the University of Karlsruhe. The scanning electron micrographs were made by D. Mathys (Zentrum für Mikroskopie, University of Basel).

2. Occurrence

In the Upper Jurassic of southern Germany remains of saccocomids have been obtained mostly from marly sediments of Lower Kimmeridgian age. Some remains are from an Oxfordian locality in Upper Franconia; a number of ossicles were collected from Upper Kimmeridgian sediments at one locality in Swabia. One species (Saccocoma cf. tenella) was reported by SIEVERTS-DORECK from the Lower Tithonian of Swabia. Detailed stratigraphical and sedimentological information is unfortunately not available for the material described in the following.

According to W. RIEGRAF (pers. comm., 2000) saccocomid remains are absent (or very rare) from Oxfordian and Lower Tithonian sediments of the Swabian Alb. They also lack in the Zementmergel (Upper Kimmeridgian) of Allmendingen and Blaubeuren near Ulm; these marls were deposited under the influence of the Tethys and contain planktonic foraminifera and radiolarians and one would have expected them to contain also remains of saccocomids. Saccocomids (S. tenella) are common in the Nusplingen Lithographic Limestone of similar age. In RIEGRAF’s sampling remains of saccocomids are restricted to the middle part of the Lower Kimmeridgian (“Weisser Jura Gamma2”) and the middle part of the Middle Kimmeridgian (“Weisser Jura Delta2”), times of significant deposition of marls (sea level rise or transgression).

As pointed out by KEUPP & MATYSZKIEWICZ (1997) remains of saccocomids are characteristic of the so-called “Lombardia facies” which prograded on the epiconti-
nental platforms of the passive northern Tethyan shelf in southern Poland and the southern Franconian Alb during Late Oxfordian to Early Tithonian times. Remains of saccocomids are a significant part of Upper Jurassic pelagic limestones that also contain planctonic organisms such as radiolarians. The Lombardia facies marks the late transgressive systems tract as well as the presumed high stand deposits. The Saccocoma facies was thus deposited during phases of retrograding spongiolithic development. It appears that saccocomids from the sediments examined by Keupp and Matyszkiewicz all belong to the pelagic genus Saccocoma.

The saccocomids classified here in the genus Crassicoma are common in the Lower Kimmeridgian sponge facies of Swabia but such sediments also contain the pelagic Saccocoma quenstedti. It is obvious that additional field work is needed to elucidate the distribution of the Crassicoma and Saccocoma species and associated fauna in the different facies types.

3. Localities

The saccocomid material from Swabia (Schwaben), Upper Franconia (Oberfranken) and from the valley of the river Altmühl (Altmühltal) is contained in more than 200 cavity slides (Franke Zellen) numbered by the author in the Stuttgart collection. It consists mostly of disarticulated ossicles (radials and brachials), but a number of cups are also present; the ossicles from Swabia are generally better preserved than those from Franconia. According to informations (notes and draft manuscripts, sorted by the author and now preserved in the Stuttgart collection) of H. Sieverts-Doreck (see also Sieverts-Doreck 1955), the material was collected at the following localities (age names provided by G. Schweigert):

Swabia, Lacunosamergel Fm. (Lower Kimmeridgian)

<table>
<thead>
<tr>
<th>Locality (original collection)</th>
<th>Age</th>
<th>Sieverts-Doreck’s “species”</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tieringen, Kreis Balingen (Feifel)</td>
<td>Platynota Zone, sponge facies</td>
<td>Schattenbergi</td>
</tr>
<tr>
<td>Steige(*) Beuren–Erkenbrechtsweiler, Kreis Nürtingen</td>
<td>Divisum Zone</td>
<td>Quenstedti</td>
</tr>
<tr>
<td>Steige Neidlingen–Eckhof, Kreis Göppingen, about 100 m above the large bend on the upper slope (Feifel, Sieverts-Doreck)</td>
<td>Hypselocyclum Zone, mud facies</td>
<td>Schattenbergi, feifeli</td>
</tr>
<tr>
<td>Steige Neidlingen–Eckhof, large quarry</td>
<td>Platynota Zone, sponge facies</td>
<td>Quenstedti</td>
</tr>
<tr>
<td>Kornberg near Bad Boll, Kreis Göppingen (Feifel)</td>
<td>Hypselocyclum Zone, mud facies</td>
<td>Subornata, mayri, Schattenbergi, quenstedti</td>
</tr>
<tr>
<td>Hochalb near Auendorf, Kreis Göppingen</td>
<td>Platynota Zone, sponge facies</td>
<td>Subornata, mayri, feifeli, quenstedti</td>
</tr>
<tr>
<td>Hardtberg near Reichenbach im Täle, Kreis Göppingen, ascent to cross on the summit</td>
<td>Base of Platynota Zone</td>
<td>Subornata, mayri</td>
</tr>
<tr>
<td>Hardtberg near Reichenbach im Täle</td>
<td>Divisum Zone</td>
<td>Feifeli, quenstedti</td>
</tr>
</tbody>
</table>
**Steige** means a steep road

### Swabia, Untere Felsenkalke Fm. (Upper Kimmeridgian)

<table>
<thead>
<tr>
<th>Location</th>
<th>Formation, Zone, Facies</th>
<th>Fossil Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Steige Burladingen–Stetten</td>
<td>Platynota Zone, mud facies</td>
<td>quenstedti</td>
</tr>
<tr>
<td>Bossler near Gruibingen, Kreis Göppingen</td>
<td>Acanthicum Zone, sponge facies</td>
<td>quenstedti</td>
</tr>
<tr>
<td>Steige Beuren–Erkenbrechtsweiler, Kreis Nürtingen, small abandoned</td>
<td>Acanthicum Zone, sponge facies; reddish marly layer below a 1 m thick limestone bed</td>
<td>feifeli, quenstedti</td>
</tr>
<tr>
<td>quarry at the upper end of the Steige</td>
<td>with numerous platychonians</td>
<td></td>
</tr>
<tr>
<td>Steige Urach–Sirchingen, about 1 km before Sirchingen (FEIFEL)</td>
<td>Hybonotum Zone, sponge facies</td>
<td>n. sp., cf. tenella</td>
</tr>
</tbody>
</table>

*Note.* – SIEVERTS-DORECK (1955) assigned this locality (Nr. 12; Steige from Urach to Sirchingen) to the “Weijsjura Epsilon”, but this corresponds to the sponge facies of Hangende Bankkalke Fm. and is thus Lower Tithonian (G. SCHWEIGERT, pers. comm., 2002). In the “Weijsjura Zeta” (Lower Tithonian) she mentioned the localities 13 (Nusplingen), 14 (quarry at the upper end of the Steige from Taillingen to Neuweiler) und 15 (quarry of the cement factory Gerhausen near Blaubeuren, zoogenic facies of the Zementmergel). The material labelled *Saccocoma* n. sp., cf. *tenella*, is contained in slides 192–195 and was collected by FEIFEL; it is from locality 14, uppermost “Malm δ” (= Eu- doxus Zone, according to G. SCHWEIGERT), the quarry is now filled up.

### Swabia, Hangende Bankkalke Fm. (Lower Tithonian)

<table>
<thead>
<tr>
<th>Location</th>
<th>Formation, Zone, Facies</th>
<th>Fossil Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Würgau, quarry Höllein</td>
<td>Bimammatum Zone</td>
<td><em>schattenbergi, mayri</em></td>
</tr>
<tr>
<td>Würgau, quarry Höllein</td>
<td>Divisum Zone</td>
<td><em>schattenbergi</em></td>
</tr>
<tr>
<td>Stammberg near Peulendorf (type locality of</td>
<td>Planula Zone</td>
<td>*schattenbergi, mayri,</td>
</tr>
<tr>
<td><em>schattenbergi</em>)</td>
<td></td>
<td><em>crassipligma</em></td>
</tr>
<tr>
<td>Stammberg near Peulendorf (SIEVERTS-DORECK’s</td>
<td>Divisum Zone</td>
<td><em>schattenbergi, mayri</em></td>
</tr>
<tr>
<td>planned type locality for <em>mayri</em>)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Upper Franconia, Würgau reef complex, “Malm Alpha” (Oxfordian), “Beta” and “Gamma” (Lower Kimmeridgian)**

<table>
<thead>
<tr>
<th>Location</th>
<th>Formation, Zone</th>
<th>Fossil Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stammberg near Peulendorf (type locality of</td>
<td>Planula Zone</td>
<td>*schattenbergi, mayri,</td>
</tr>
<tr>
<td><em>schattenbergi</em>)</td>
<td></td>
<td><em>crassipligma</em></td>
</tr>
<tr>
<td>Stammberg near Peulendorf (SIEVERTS-DORECK’s</td>
<td>Divisum Zone</td>
<td><em>schattenbergi, mayri</em></td>
</tr>
<tr>
<td>planned type locality for <em>mayri</em>)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Note. – Not all the localities and “species” mentioned in Sieverts-Doreck’s notes or draft manuscripts are represented in the available slides. This is also true of material of C. schattenbergi from the Bimammatum Zone (expressed in Textfig. 14 with a question mark).

4. Morphotypes and generic classification

The saccocomids of the Upper Jurassic of southern Germany basically belong to three morphotypes (Sieverts-Doreck’s “Formgruppen”) that may be distinguished by cup morphology (including presence or absence of distinct basals), width of radial articular facets, ornamentation of cup and presence or absence of dish-like wings (Jaekel’s [1892] “Schwimmplatten”) on proximal brachials.

1. Cup more or less thick-walled, without lateral processes or spines, proximal brachials without lateral wings. This is Sieverts-Doreck’s “schattenbergi-Gruppe”, for which she reserved the new genus Crassicoma.

2. Cup thin-walled, with lateral processes or spines, proximal brachials without wings. This is Sieverts-Doreck’s “quenstedti-Gruppe”.

3. Cup thin-walled, without lateral processes or spines, proximal brachials with lateral wings. This is the group of Saccocoma tenella.

In her notes Sieverts-Doreck assigned to these morphotypes a number of “species”. For example, the group of schattenbergi contains schattenbergi, feifeli, subornata and mayri. The group of quenstedti consists mainly of this form, but Sieverts-Doreck’s notes hint at a certain overlapping of the quenstedti und tenella groups. The stratigraphically older forms that first appear in the Lower Kimmeridgian with the representative schattenbergi are quite different from the younger forms (quenstedti und tenella). I thus recognize in the present paper two genera, Crassicoma with 5 species, schattenbergi, prae schattenbergi, mayri, feifeli and subornata, and Saccocoma with 2 species, tenella and quenstedti. Other species mentioned by Sieverts-Doreck in her notes, such as crassipligma, pentangula in the schattenbergi group (= Crassicoma) and perplexa = spinosa in the quenstedti group (= Saccocoma), cannot at present be defined in a proper way. “Saccocoma mayri” is represented in Sieverts-Doreck’s documents by photographs of several characteristic cups from the Planula Zone (“Malm β”) and the Divisum Zone (“Malm γβ”) of Stammberg near Peulendorf, but these cups could unfortunately not be located in any of the slides. However, one incomplete but otherwise well-preserved cup is available in a slide from Würkgau to define the species. Sieverts-Doreck has also used other generic names in her notes, such as Eosaccocoma for schattenbergi, but I have retained those names that were already mentioned in the literature (Verniory 1961, 1962; Hess 1972, 2000; Manni & Nicosa 1984). Typical specimens of the four main representatives of Crassicoma, namely schattenbergi, prae schattenbergi, feifeli and subornata are easily recognized, but there are many ossicles (radials and primibrachials) that are intermediate between one or the other of these species. They are described and figured in relation to the most similar species. The radials of two of the species recognized here, subornata and prae schattenbergi, are of similar size and have a similar surface structure. They may be distinguished by their inner side and by their thickness (the prae schattenbergi radials are very compact and show open nerve canals on the inner side). The open nerve canals of the prae schattenbergi radials suggest that they may represent the juvenile stage of a larger species with now
overgrown canals, such as *schattenbergi* occurring in the same strata. The material is, however, not large enough to demonstrate corresponding growth stages and I therefore propose to consider *praeschattenbergi* as a separate species for the time being. With some exceptions secundibrachials are more difficult to classify and a number of assignments are provisional. A glossary of frequently used terms is given in Pl. 1 where radials and brachials from different species of the genus *Crassicoma* are figured.

5. Brachial articulations

Brachial articulations are best seen on the comparatively sturdy and therefore well-preserved brachials of *Crassicoma schattenbergi*. They may be summarised as follows: R-IBr1 = muscular (with an angle of about 60° between ligamentary and...
muscular parts (Textfigs. 1a, 7); IBr1 – IBr2 (IAx) = “blocked”, sloping cryptosynarthrial (Textfigs. 1b, 7); IAx – IIBr1 = muscular (with an angle of about 45° between ligamentary and muscular parts) (Textfig. 8); IIBr1 – IIBr2 = “blocked”, sloping cryptosynarthrial (Textfigs. 4–6); IIBr2 – IIBr3 = muscular (commonly with scalloped muscle areas) (Pl. 2); IIBr3 – IIBr4 = cryptosynarthry or synostosis (non-sloping = perpendicular to arm axis) (Pl. 2); IIBr4 – IBr5 = muscular (ligamentary part elevated, muscle fields scalloped and lower) (Pl. 2); IIBr5 – IIBr6 = synostosis (according to SIEVERTS-DORECK in her notes). Higher brachials of \textit{C. schattenbergi} appear to have only muscular articulations, but SIEVERTS-DORECK mentioned in her notes also the occurrence of synostoses. This could not be ascertained with the available material. The distribution of articulation types of \textit{C. schattenbergi} thus corresponds to that of \textit{Saccocoma tenella} which is known from complete specimens. It may be assumed that it also corresponds to the other \textit{Crassicoma} species described in the present paper. For the “blocked” cryptosynarthries between the primibrachials and the first two secundibrachials SIEVERTS-DORECK planned to use the term “fulcro-synarthry”. It is characterized by a weak fulcral ridge on the distal face of the proximal brachial and a corresponding weak median furrow on the proximal face of the distal brachial; the shallow ligament fossae are along the edge of the ossicle. I prefer to use the name “blocked” cryptosynarthry because typical synarthries have fulcral ridges on opposite facets.

Pinnule sockets only occur in distal brachials, not in proximal brachials up to IIBr4 or 5 so that there is a proximal pinnule gap. The number of pinnule-bearing brachials is quite small. It may be assumed that pinnules or ramules occurred in a way comparable to \textit{Saccocoma tenella}.

I have followed in most cases SIEVERTS-DORECK’s arrangement of the proximal brachials on the hypothetical arms. In her notes or draft manuscripts no reconstruction of the proximal or indeed of any arm region could be found. I have therefore tried to arrange the different brachials on the base of their articular facets. The match between radial and the two primibrachials of \textit{C. schattenbergi} is good (Textfig. 7). The combination of the axillary IBr2 with the first secundibrachial (IIBr1) and of the IIBr1 with the second secundibrachial (IIBr2) is hampered by the fact that either the first two secundibrachials cannot readily be distinguished or that there are hardly any IIBr1 ossicles in the material. One possible combination (Pl. 2; Textfigs. 9, 10) shows a primaxillary with the first two secundibrachials. As expected (and known from \textit{Saccocoma tenella}) IBr2 and IIBr1 form an angle of about 45° so that the arm bends away from a vertical position at this point (see also Textfig. 8). However, the IBr2 and IIBr1 do not match well because there is a certain gap between the muscle fields (Textfig. 8; Pl. 2), by contrast the aboral ligament fossae match (Textfig. 9). In addition, the scalloped muscle fields of IIBr1 interfere to some extent with the median interradial prolongation of the axillary IBr2 (Textfig. 8). For this reconstruction first secundibrachials that are almost triangular in side view were chosen; the muscular and cryptosynarthrial facets form an angle of 60°–70° (Pl. 2). Pl. 2 also shows a second secundibrachial (IIBr2) with a good match between its presumed proximal cryptosynarthrial facet and the corresponding distal facet of the IIBr1. This secundibrachial has a presumed distal muscular facet which is bent but otherwise almost parallel to the cryptosynarthrial facet. This is unfortunately the only such brachial in the material. SIEVERTS-DORECK did not refer to the articulation between IBr2 and IIBr1. She thought that the brachials with a triangular outline were second
Figs. 7–10. *Crassicoma schattenbergi*. Sieverts-Doreck & Hess n. g. n. sp, Lower Kimmeridgian. (7) Exterior (a) and lateral view (b) of radial (R) and primibrachials (IBr), see also Pl. 2, Stammberg (R, slide 14, SMNS 64697; IBr1, slide 17, SMNS 64698; IBr2, slide 21, SMNS 64699, with partly intact muscle field on the right side, left muscles field broken off); (8) exterior/distal view IBr2 (slide 75, Michelsberg, SMNS 64700) and IIBr1 (slide 34, Stammberg, SMNS 64701) see also Pl. 2; (9) exterior view of IBr2 (slide 67, Kornberg, SMNS 64702) and first secundibrachial (IIBr1) with proximal facet (slide 66, Kornberg, SMNS 64703, see also Pl. 5, fig. 14) with well-matching aboral part of the muscular facets (* aboral ligament fossae*); (10) lateral view of IIBr1 (slide 49, Neidlingen-Eckhof, SMNS 64694, see also Textfig. 4) and IIBr2 (slide 34b, Stammberg, SMNS 64705, see also Pl. 2) (Photographs Hess). – Scale bars = 1 mm.
secundibrachials (see Pl. 3, Figs. 6–7) and combined them with third se-
cundibrachials (IIBr3) that have a bent, scalloped proximal muscular facet (Pl. 3, Fig.
5) and a distal synostosial facet (Pl. 3, Figs. 8–9). This combination is shown in Pl. 5,
Figs. 1–4. The match is quite good but we are left with the problem of the missing
first secundibrachial. The scalloped muscle fields of these facets indicate strong mus-
cular activity of the animals during life. The distal facet of the IIBr3, a very flat cryp-
tosynarthry or, better, a synostosis (Pl. 3, Figs. 8–9) connects to the IIBr4; in view of
the overall similarity of IIBr3 and IIBr4 it is not always possible to know in which
position they originally were. Problems also exist in the more distal brachials of
Saccoma quenstedti. In slide 188, for example, all brachials have a bent muscular facet
at one end and a sloped cryptosynarthrial facet at the other. As shown by Text-
fig. 11 these facets do not match and it is something of an enigma how the brachials
connected.

6. Methods

The slides with the material as assembled and sorted by SIEVERTS-DORECK have
been numbered by the author so that ossicles removed from the slides can be traced
back to the original slides.

In a first step the different forms or species have been differentiated on the basis
of cups and/or isolated radials. In a second step the primibrachials have been as-
signed to the “cup species”, followed, in a third step, by the proximal se-
cundibrachials and further brachials, wherever possible.

A few SEM pictures were taken by W. E. REIF around 1980 for SIEVERTS-DORECK
(see Pl. 3). Most of the scanning electron micrographs are from gold coated (20 nm)
samples photographed by DANIEL MATHYS at the Zentrum für Mikroskopie of the
University of Basel using a Philips XL30 ESEM. A large number of microscopic pictures were taken by the author with a Nikon Coolpix mounted on a Leica stereomicroscope (enlargements up to x48, partly using camera zoom). In view of their generally reduced depth of field only a limited number of these photographs have been used for the present paper; the whole collection is contained on a CD-ROM (372 pictures) deposited with the material in the Stuttgart Museum. These pictures with attached text can be examined with FotoStation. They are also contained in a Word for Windows document (“SaccocomaPictures”). The microphotographs have been numbered from the bottom up on the plates, starting from the cup or the radials (proximal or aboral position), followed by the proximal and the distal brachials (distal or oral position upward), thus representing their position during life. In line with current usage the terms “oral” and “aboral” are preferred to “ventral” and “dorsal”; however, for the views of individual ossicles I have preferred the easier terms “exterior”, “interior” and “lateral”. In a number of ossicles with sloping facets (e.g. the first primibrachials, IBrl) the interior view also shows the proximal facet and the exterior view the distal facet, this is expressed as “interior/proximal” or “exterior/distal” view.

7. Systematics

The following species names were proposed by SIEVERTS-DORECK in her notes and draft manuscripts and were consequently used by several authors (VERNIORY 1961, 1962a, 1962b; TURNER 1965; HESS 1972). However, no type specimens were designated and no type locality and horizon were published. In addition, published descriptions are very brief and do not include a discussion of variability and relationships. The same is true for the proposed genera which were used by SIEVERTS-DORECK somewhat inconsistently. TURNER (1965) suggested that the names Saccocoma schattenbergi and S. feifeli (and also S. quenstedti) are available according to ICZN Art. 13. I have adopted SIEVERTS-DORECK’s names using the joint authorship SIEVERTS-DORECK & HESS. The different taxa are formalized by designation of types and characterized according to present usage. A preliminary report on this material has been published by the author (HESS 2000).

Order Roveacrinida SIEVERTS-DORECK in MOORE et al., 1952
Family Saccocomidae D’ORBIGNY, 1852

Diagnosis. – Cup bowl-shaped, composed of radials that may be thick-walled in early forms, basals small or vestigial; minute central piece may be present, but mostly fused with basals; radials and brachials in advanced forms with lightened skeleton as well as wings, some forms with spines on the cup; one form without arms but oral cover plates.

Genus Crassicoma SIEVERTS-DORECK & HESS n. g.

Type species: Crassicoma schattenbergi n. sp.
Derivation of name: After the relatively thick-walled cup of the type species (in comparison with Saccocoma tenella).
Diagnosis. – Cup low, composed of thick-walled to thinner radials with interradial processes and basals that may be fused with a central piece, radial cavity shallow; aboral pole sunk or with protruding knob; radials articulated to each other by flat synostoses; outer surface of radials coarsely reticulate or pitted to finely rugose, without median ribs; lower edge truncated; muscle fields of radials strongly developed, attached to the dagger-like interradial processes, in some forms encroaching from the base of the processes on the inner wall of the radial; first primibrachials high and flat with narrow profile, with wing-like lateral processes apparently forming a protective wall around the oral side of the cup, proximal facet with ligamentary part forming an angle of 60° to 80° with the commonly scalloped muscle fields situated on the inner side, distal facet a flat cryptosynarthry visible on about half the outer surface and nearly parallel (angle about 20°) to the inner side.

Crassicoma schattenbergi Sieverts-Doreck & Hess n. sp.  
[Saccocoma schattenbergi Sieverts-Doreck, manuscript name]  

Holotype: Cup with basals, Pl. 4, Fig. 1 (slide 1, SMNS 64734, designated by Sieverts-Doreck); diameter: 4 mm, height 2.1 mm.  
Paratypes: Cup, Pl. 4, Fig. 2 (slide 2, SMNS 64735); radial, Textfig. 7 (slide 14, SMNS 64697); IBr1, Textfig. 7 (slide 17, SMNS 64698); IBr2, Textfig. 7 (slide 21, SMNS 64699), all Lower Kimmeridgian, Stammberg; radial, Pl. 4, Fig. 6 (slide 46, SMNS 64739), Lower Kimmeridgian, Neidlingen-Eckhof.  

Derivation of name: Dedicated to K. Schattenberg who collected most of the Franconian material described in this paper.  

Type locality and horizon: Stammberg, Lower Kimmeridgian (“Malm β” = Planula Zone), holotype; Lower Kimmeridgian (“Malm γ3”, Divisum Zone), paratypes.  

Stratigraphic and geographic distribution: Kimmeridgian (Planula Zone to Divisum Zone), Swabia (Steige Neidlingen-Eckhof, Kornberg); Kimmeridgian (Planula Zone to Divisum Zone), Franconia (Stammberg).  

Material: see Appendix. The list given in the Appendix includes the typical thick-walled schattenbergi radials and all brachials that can be assigned to the type species or to comparable species (Crassicoma cf. schattenbergi). The best material (radials and brachials) are from a locality at the Steige Neidlingen-Eckhof, about 100 m above the large curve (Hypselocyclum Zone). However, Stammberg in Franconia has been selected as the type locality because of the presence of complete cups in the Lower Kimmeridgian (Planula Zone and Divisum Zone).  

Diagnosis. – Cup rather large, composed of thick-walled radials with finely rugose to pitted outer surface and truncated lower edge, interradial processes of radials with triangular cross-section, muscle fields attached to process facing the axial canal, ligamentary part of articulation facet sunk between the processes, openings for nerve canals not exposed on inner side of radials; aboral pole sunk, with five small basals and central piece; first primibrachials flat, with scalloped wing-like processes; second primibrachial (primaxillary) with interradial spine, ligamentary part and muscle fields at an angle of more than 90°, muscular areas supported orally by pillars; distal facet of first secundibrachial with cryptosynarthry; distal facet of
second secundibrachial with sunken muscle fields; synostosial articulation between third and fourth secundibrachials; further brachials mostly dumb-bell shaped, pin-nules present, but few.

Description. – Cup/radials: *Crassicoma schattenbergi* is a large saccocomid. The cups are low and composed of thick-walled radials with pronounced dagger-like interradial processes that are triangular in cross-section; the outer surface of the radials is finely rugose or pitted and the lower edge truncated. The radials are broadly joined by a flat synostosis. The ossicles consist of essentially two layers (Pl. 3, Fig. 2, at the bottom): an outer layer with loose stereom and an inner layer with denser stereom that contains the nerve canals. The articular facet consists of two parts (Pl. 4, Fig. 6a). The horizontal space at the base of the processes has a broad aboral ligamentary pit and a ridge with a large axial canal and adjoining interarticular ligament fossae (Pl. 4, Fig. 6a; Pl. 5, Fig. 8). The scalloped muscle fields are on the radially directed flank of the processes and form an angle of more than 90° with the ligamentary part of the facet. The aboral pole is sunk, with 5 small but distinct basals and a centrale (Pl. 4, Fig. 4).

The IBr1 are leaf-like, with a thicker proximal part whose articular facet has a horizontal ligamentary part that corresponds to the radial; the inner side has a V-shaped central part with a broad, flat furrow, flanked by two triangular exterior wings that carry the scalloped muscle fields with 4 lobes (Pl. 1, Fig. 6). The muscle area thus forms an angle with the ligamentary area similar to that of the corresponding area on the radial. The outer (aboral) side has a short elevated proximal part with a reticulate surface that prolongs onto the side wings and a long, broadly triangular “blocked” cryptosynarthry with a large, almost rectangular, central canal (Pl. 3, Fig. 3). The side wings may have been in contact in the living animal, forming a protective wall around the body cavity. Smaller ossicles are thicker, with the narrow synarthrial facet somewhat protruding (Pl. 4, Fig. 12); the ambulacral furrow on the inner side (between the muscle fields) is deeper than in the larger ossicles.

The second primibrachials (IBr2) or first axillaries (IAx) are wedge-shaped or flat-triangular in side view (Textfig. 7b; Pl. 2); the proximal facet is a cryptosynarthry corresponding to the distal facet of the IBr1; some well-preserved ossicles have a long interradial spine separating the two distal muscular facets (Textfig. 2; Pl. 4, Fig. 15; Pl. 5, Fig. 12); these facets have a ligamentary part with aboral ligament pit, ridge and inconspicuous interarticular ligament pits that is at a right angle to the long axis (Pl. 5, Fig. 11); in side view the muscle fields are more or less in prolongation of the proximal cryptosynarthry, thus forming an angle of about 135° with the ligamentary part (Textfig. 7b; Pl. 2). Some of the smaller ossicles have a proximal facet with the cryptosynarthry (about 2/3 of the facet) followed distally by two wings flanking a rather deep furrow (Textfig. 3).

As discussed in Section 5 a distinction between first and second secundibrachials is difficult in the available material. In any case, IIBr1 or IIBr2 are nearly triangular or wedge-shaped, with one muscular and one cryptosynarthrial facet (Textfigs. 4–6, 10; Pl. 2; Pl. 5, Figs. 3, 13). As a rule these facets form an angle of about 45° with the arm axis. The muscular facets of these brachials are scalloped and bent (Pl. 3, Figs. 6, 7; Pl. 5, Figs. 16–17).

The third secundibrachial (IIBr3) is characterized by a proximal muscular facet and a very flat distal cryptosynarthry or, better, a synostosis. The ossicles are comparatively short and the two facets subparallel (Pl. 5, Figs. 2, 4). The scalloped mus-
cle fields of the proximal facet are deepened (Pl. 2; Pl. 3, Fig. 5; Pl. 5, Fig. 18); the distal facet is a horseshoe-shaped synostosis (Pl. 3, Figs. 8, 9; Pl. 5, Fig. 19).

The proximal facet of the fourth secundibrachial (IIBr4) is the mirror image of the distal facet of third secundibrachial (Pl. 2), the muscle fields of the distal facet are sunk.

Fifth secundibrachials (IIBr5) have not been defined with certainty, but the brachials following IIBr4 become progressively more elongate (Pl. 5, Fig. 22) and dumb-bell shaped in exterior or interior view (Pl. 5, Figs. 20, 23, 25). Articulations are muscular (Pl. 5, Figs. 20–23, 25), with a deep aboral ligament pit visible from the outside (Pl. 3, Fig. 10); on some better preserved ossicles are wings for the attachment of the muscles (broken off in most brachials) (Pl. 5, Fig. 25). Some secundibrachials of unknown position have a (proximal?) muscular and a (distal?) synostosial facet (Pl. 5, Fig. 24). Only a small percentage of the brachials (10 % or less) have pinnule sockets (Pl. 5, Figs. 26, 27).

Relationships. – *Crassicoma schattenbergi* has a compact cup, quite different from the strongly developed reticulate structure of *Saccocoma quenstedti* and *S. tenella* where the skeleton is reduced to the supporting elements: it also lacks wings or processes on the brachials (Schwimmplatten).

The cup of *schattenbergi* superficially resembles the equally sturdy *Pseudosaccocoma*, a species where the cup is covered by a compact layer of calcite and whose arms are unknown. According to KÄSTLE (1982) *Pseudosaccocoma* has a dicyclic cup that is completely overgrown by the first columnal (called “Hüllkörper” by BACH-MAYER 1958) and is therefore not related to the Saccocomidae but rather to the Isocrinidae.

Articulation types observed here correspond to those of pelagic Saccocomidae (*Saccocoma tenella*, see Hess 1999) and to representatives of other Roveacrinida (SIEVERTS 1933; PECK 1943, 1948; DESTOMBES 1984). All these Roveacrinida have strongly imbricating proximal brachials (IBr1 – IBr2 and IIBr1 – IIBr2) united by cryptosynarthries; there is also a pronounced pinnule gap on the proximal arms. Differences in cup shape, presence of centrale (fused infrabasals?) and basals, development of processes for the attachment of muscles, presence of spines and wings as floating aids appear to be adaptations to different lifestyles of these crinoids and are thus an expression of morphological plasticity.

**Crassicoma cf. schattenbergi**

A large number of radials are similar in outline to the typical thick-walled *schattenbergi* radials, but they are thinner, with an outer surface that is more strongly pitted or reticulate (Pl. 4, Figs. 7–10; Pl. 5, Figs. 5–9). Because the radials are thinner their nerve canals to the basals are more visible on the inner side (Pl. 4, Figs. 7, 8b; Pl. 5, Fig. 9). The majority of the radials occur together with the more typical *schattenbergi* radials; an ecophenotypic variation therefore seems unlikely. In accordance with SIEVERTS-DÖRECK in her notes they are here considered as a variety, but they may also belong to a separate species. Typical radials of *C. subornata* have a more finely sculptured surface. The first primibrachial with weakly sculptured surface (Pl. 4, Fig. 11) is provisionally assigned to *schattenbergi*, it may belong to another species.
Crassicoma praeschattenbergi Sieverts-Doreck & Hess n. sp.
[Saccocoma praeschattenbergi Sieverts-Doreck, manuscript name]

**Holotype**: Radial, Pl. 6, Fig. 4 (slide 146, SMNS 64777, designated by Hess); width 0.8 mm, height 0.9 mm.

**Paratypes**: Radial, Pl. 6, Fig. 1 (slide 130, SMNS 64775), height and width 0.8 mm; radial Pl. 1, Fig. 2 and Pl. 6, Fig. 2 (slide 130, SMNS 64711), Himmelreich near Bargau.

**Derivation of name**: Considered to be closely related to *schattenbergi*.

**Type locality and horizon**: Himmelreich near Bargau, Lacunosamergel Fm., Lower Kimmeridgian.

**Stratigraphic and geographic distribution**: Kimmeridgian (Platynota Zone), Swabia (Himmelreich near Bargau, slopes of Michelsberg)

**Material**: see Appendix.

**Diagnosis.** – Radials small, low, rather thick-walled, with broad interradial processes, surface finely rugose, muscle fields strongly encroaching on inner side, openings for commissure and canals to basals exposed on inner surface; basals well developed.

**Description.** – This is a small species known mainly from radials (at least it has not been possible to assign brachials with certainty). The radials are low, rather thick-walled, with broad interradial processes and a finely sculpured, convex surface. The lower edge is notched, indicating the presence of distinct basals (Pl. 6, Fig. 4). The aboral ligament pit of the articular facet is large and visible on the outer surface (Pl. 6, Fig. 1), the nerve canal is rounded rectangular and the adjoining shallow interarticular fossae are of similar size (Pl. 6, Figs. 1–3). The inner surface shows not only the lateral openings for the ring commissure but also the opening of the nerve canals to the basals (Pl. 1, Fig. 2). The muscle fields strongly encroach on the inner side of the radials (Pl. 1, Fig. 2; Pl. 6, Fig. 3). A number of brachials may belong to this species, assignments are based on the finely sculptured surface, size, morphology of articular facets and occurrence. They include broad (Pl. 6, Fig. 7) or narrower (Pl. 6, Fig. 8) first primibrachials with cryptosynarthrial facets of different length. The matching pair of slender, first and second primibrachials (Pl. 6, Figs. 9–10) may also belong to this species. The same is true for a IIBr2 with a proximal cryptosynarthrial facet (Pl. 6, Fig. 11) and a IIBr3 whose distal facet is a very narrow synostosis (Pl. 6, Fig. 12). Assignment of the brachial in Pl. 6, Fig. 13, perhaps the proximal facet of a IBr1, is more doubtful. Distal secundibrachials with muscular facets are figured in Pl. 6, Figs. 14–15.

**Relationships.** – The radials of *praeschattenbergi* have a surface structure that is similar to that of *C. subornata*. They may be distinguished by their inner side and by their thickness (the *praeschattenbergi* radials are very compact and show open nerve canals on the inner side). It cannot be ruled out that *praeschattenbergi* radials may represent the juvenile stage of *schattenbergi* occurring in the same strata, but they could also be the result of paedomorphosis and thus belong to a distinct species.

Crassicoma subornata Sieverts-Doreck & Hess n. sp.
[Saccocoma subornata Sieverts-Doreck, manuscript name]

Holotype: Radial, Pl. 7, Fig. 2 (slide 137, SMNS 64789, designated by Hess); width 0.8 mm, height 0.9 mm.
Paratypes: Radial, Pl. 1, Fig. 3 and Pl. 7, Fig. 6 (slide 114, Michelsberg, SMNS 64712); IB1, Pl. 7, Fig. 9 (slide 132, Himmelreich, SMNS 64795); IB2, Pl. 7, Fig. 13 (slide 133, Himmelreich, SMNS 64799); all Lacunosamergel Fm., Lower Kimmeridgian.

derivation of name: After the weakly sculptured radials.

type locality and horizon: Michelsberg, Lower Kimmeridgian (Lacunosamergel Fm., Zone of Sutneria platynota).

Stratigraphic and geographic distribution: Kimmeridgian (Platynota Zone – Hypselocyclum Zone, mostly mud facies) in the Swabian Alb between Erkenbrechtsweiler (southwestern part) and Heubach (Bargau, northeastern part of the area).

Material: see Appendix; it contains numerous cups and radials, one isolated basal cone and isolated primibrachials (IB1 and IA).

Diagnosis. – Radials thin, aborally straight, not curved, surface only weakly rugose, articular facet with large muscle fields that encroach from the side wall of the interradial processes on the inner wall to form distinct notches; lower edge of radials broad, indicating presence of rather large basals; primibrachials rather long and slender; more distal brachials dumb-bell shaped with weakly rugose surface.

Description. – The radials are thin and rather high, aborally straight, not curved; the articular facet has large muscle fields that encroach from the side wall of the interradial processes on the inner wall (Pl. 7, Figs. 4 and 6). The lower edge of the radials is rather broad, indicating a relatively large basal circle, in some radials the edge is notched (Pl. 7, Fig. 6) for the articulation with distinct basals. The surface of the radials is only weakly sculptured in most radials (Pl. 7, Figs. 2–3, 5). On the inner side the nerve canals of the ring commissure are partly exposed (Pl. 7, Figs. 4, 6), but the paired nerve canals to the basals are mostly enclosed within the radials with just the openings visible (Pl. 1, Fig. 4; Pl. 7, Fig. 4). Brachials assigned to this species have a surface structure similar to that of the radials (Pl. 7, Figs. 9, 13, 23, except Fig. 21 whose surface structure resembles C. schattenbergi). The first primibrachials are comparatively slender, with a roughly rectangular cryptosynarthrial distal facet and a more or less circular axial canal (Pl. 7, Fig. 9); the second primibrachials are also mostly slender (Pl. 7, Fig. 12). The secundibrachials include cryptosynarthrial (Pl. 7, Figs. 14–15, 17), synostial (Pl. 7, Figs. 19–20) and muscular facets (Pl. 7, Figs. 16, 18, 22, 23). The more distal brachials are constricted around the middle part and are thus strongly dumb-bell shaped (Pl. 7, Figs. 22–23).

Relationships. – C. subornata differs from C. schattenbergi by its thinner, aborally straight radials; the interradial processes are also thinner and the muscle fields encroach more strongly on the inner side. On their surface C. subornata radials and brachials are more finely sculptured. The first primibrachials of C. subornata have less developed exterior wings and their cryptosynarthrial facet is roughly rectangular with a circular axial canal, not triangular with a more rectangular axial canal. C. praeschattenbergi has much sturdier, lower radials with partly exposed nerve canals.

Note. – A number of radials assigned to C. subornata are rather narrow (Pl. 7, Fig. 7) indicating a comparatively higher cup; they may be juvenile.

Crassicoma feifeli Sieverts-Doreck & Hess n. sp.
[Saccocoma feifeli Sieverts-Doreck, manuscript name]

Holotype: Cup, Pl. 1, Fig. 1 and Pl. 8, Fig. 2 (slide 83, SMNS 64710, designated by Hess); diameter 1.1 mm, height 0.3 mm.

Paratypes: Cup, Pl. 8, Fig. 3 (slide 101, Hardtberg, SMNS 64811); partial cup, Pl. 8, Fig. 4 (slide 91, Beuren-Erkenbrechtsweiler, SMNS 64812); radial with attached basals, Pl. 8, Fig. 6 (slide 105, Hardtberg, SMNS 64814); radial, Pl. 8, Fig. 7 (slide 99, Hardtberg, SMNS 64815); all Lacunosamergel Fm., Lower Kimmeridgian.

Derivation of name: In honour of K. FeiFEL (1873–1959) who was the first to isolate saccocomids from washed material from the Swabian Upper Jurassic.

Type locality and horizon: Steige Beuren-Erkenbrechtsweiler, Lacunosamergel Fm., Lower Kimmeridgian.

Stratigraphic and geographic distribution: Platynota Zone (Lower Kimmeridgian) to Acanthicum Zone (Upper Kimmeridgian) of the middle Schwabenalb.

Material: see Appendix. It contains numerous cups and radials, one isolated basal circlet and a few isolated primibrachials (IBr1 and IBr2) whose assignment is provisional.

Diagnosis. – Cup very small, low, aboral pole with small basals and centrale mostly fused into cone or knob protruding from the aboral surface, interradial processes rounded, lappet-like; radials with truncated lobes bearing the articular facets, outer surface reticulate to pustulate, less so near interradial sutures; thickness of radials quite variable; articular facets comparatively small, aboral ligament pit of radial facets large, almost vertical and visible in side view of the cup, area of axial canal and very small interarticular ligament pits forming part of the upper edge of the cup, the somewhat larger muscle fossae almost horizontal and visible only in oral view, thus forming an angle with the aboral ligament fossa; primibrachials provisionally assigned to this species very narrow and long, reticulate, articular facets small, ambulacral furrow conspicuous.

Description. – The cup is very small and low, at the aboral pole are small basals that are mostly fused with the centrale into a knob protruding from the aboral surface (Pl. 8, Figs. 1, 3). A partly broken cup shows that the knob is a fusion product of the five basals with the centrale (Pl. 8, Fig. 4). Such a “basal cone” has also been found isolated (Pl. 8, Fig. 9). A few radials have their basals still attached (Pl. 8, Fig. 6). The interradial processes of the radials are rounded, lappet-like (Pl. 8, Fig. 3). Seen from below (aborally, Pl. 8, Fig. 1) or above (orally, Pl. 8, Fig. 2) the cup shows the characteristic truncated lobes of the radials with their articular facets. These are comparatively small, the aboral ligament fossa is large, almost vertical and exposed when the cup is viewed from the side (Pl. 8, Fig. 3). The area of the axial canal with shallow, small interarticular ligament fossae is part of the upper rim of the cup (Pl. 8, Fig. 5), the somewhat larger muscle fields are almost horizontal and visible only from above (Pl. 1, Fig. 1); they thus form an angle with the aboral ligament fossa. The outer surface of the cup is reticulate to pustulate, less so near interradial sutures (Pl. 8, Fig. 1). Isolated radials are nearly triangular in exterior view, with the aboral ligament fossa and its pit showing up (Pl. 8, Fig. 7). This pit is separated by a thin ridge from the somewhat larger axial canal (Pl. 8, Fig. 8); the separating ridge may be broken so that pit and axial canal form one opening (Pl. 8, Fig. 5). Primibrachials provisionally assigned to this species are very narrow and long, their surface is reticulate. The articular facets are small and the ambulacral furrow is conspicuous (Pl. 8, Figs. 10–11). Similarly elongate primibrachials have been described for other roveacrinids. They include first primibrachials of Saccocoma sp. and S. cf. subornata, respectively, from Upper Jurassic sediments drilled off the coast of Florida (Hess 1972, figs. 9 and 21), but also first and second primibrachials of the Triassic Osteocrinus (Kristan-Tollmann 1970, figs. 5, 11; 1977, figs. 7–8) and brachials of...
Cretaceous roveacrinids (Peck 1943, pl. 76, figs. 30–36). The Triassic forms also have cups prolonged aborally into a spine; the reason for the occurrence of such elongate primibrachials in saccocomids is unclear.

Note. – Thickness of the radials and their ornamentation are quite variable.

Relationships. – C. feifeli differs from the other species of Crassicoma by the small size and the very characteristic shape of the cup, with an aboral knob of fused basals and centrale protruding from the flat base. The interradial processes are not dagger-like as in C. schattenbergi and C. subornata, the aboral ligament fossa of the radial articular facet is directed outward at nearly a right angle to the muscle fields on the rim of the cup.

Crassicoma mayri Sieverts-Doreck & Hess n. sp.
[Saccocoma mayri Sieverts-Doreck, manuscript name]

Holotype: Cup, Pl. 9, Fig. 1 (slide 213, SMNS 64819, designated by Hess); diameter 2.4 mm, height 0.9 mm.

Derivation of name: Dedicated to F. X. Mayr (deceased 1974), former Professor at the University of Eichstätt.

Type locality and horizon: Würgau, Oxfordian (“Malm α2”, Bimammatum Zone).

Stratigraphic and geographic distribution: “Malm α2” (Bimammatum Zone), Würgau. According to Sieverts-Doreck’s notes it also occurs in “Malm β” (Planula Zone) of Stammberg near Peulendorf (mainly isolated radials), and “Malm γ3” (Divisum Zone) of the same location.

Material: Only the single cup (slide 213) from Würgau has been found in the material preserved at the Stuttgart Museum. It has been labelled by Sieverts-Doreck as “cf. mayri”, but there is no doubt that it belongs to the same species as the cups available as photographs only and assigned by Sieverts-Doreck to mayri. Sieverts-Doreck considered Stammberg as the type locality (the holotype from the Divisum Zone). A number of relatively narrow radials from Neidlingen-Eckhof (slide 148) with a reticulate to pitted surface may provisionally be assigned to this species (Pl. 9, Fig. 2).

Diagnosis. – Cup low, bowl-shaped, five-lobed in outline, aborally tapered, interradially depressed; aboral pole with a small knob of fused basals and centrale.

Description. – The holotype (Pl. 9, Fig. 1) is a bowl-shaped cup, it is five-lobed in outline and aborally tapered. The radials are convex, the interradial areas therefore depressed. The aboral pole is sunk, with a small knob of probably fused basals and centrale rising from the center. The cup is very low in side view, with the articular facets at the upper edge of the radials; the aboral knob is not visible in side view. The cup may originally have been provided with interradial processes, but these are not preserved on the holotype. The outer surface is finely pitted to rugose. The radial figured on Pl. 9, Fig. 2 possibly belongs to this species. It is convex and has a reticulate surface; the aboral ligament is hardly visible from the outside. There are rather small interradial processes.

Relationships. – According to Sieverts-Doreck C. mayri occurs mostly together with C. schattenbergi, both species appear to be closely related and belong to the same morphotype. C. mayri differs from C. schattenbergi in the convex aboral pole, thinner radials and a more strongly pentalobate outline of the cup which is also lower. C. feifeli is similarly low bowl-shaped in side view, but it has a knob protruding from the aboral surface; the radials have truncated lobes that bear articular facets directed outward and thus visible from the side. The surface of the C. feifeli radials is more strongly sculptured than that of C. mayri.
Genus *Saccocoma* Agassiz, 1836

[[Saccocoma Agassiz, 1836, p. 193]

**Type species:** *Comatula tenella* Goldfuss, 1831, p. 204, pl. 62, fig. 1; subsequent designation by Manni, Nicosia & Tagliacozzo, 1997, p. 130; Hess, 1999, p. 218 (= *Comatula pectinata* Goldfuss, 1831, p. 205; *Comatula filiformis* Goldfuss, 1831, p. 205; Lombardia Brönnimann, 1955, p. 43).

**Diagnosis.** – Cup a hemisphere or open bowl with deep radial cavity, very thin-walled, surface covered by network of anastomosing ribs that reinforce area beneath the articular facets where antler-like processes may be present; basal knob of fused basals and centrale mostly indistinct; articular facet to the first primibrachial small; first primibrachials short, without wing-like processes; second primibrachial (first axillary) and some of the secundibrachials with dish-like lateral wings, the more distal brachials may have paired vertical oral processes.

**Remarks.** – According to Rasmussen (1978, p. T924) *Comatula pectinata filiformis* Goldfuss 1831 is the type species of *Saccocoma*, as designated by Jaekel (1918, p. 92) who thought that this form was devoid of Schwimmplatten (dish-like lateral wings on the proximal brachials). Jaekel (ibid.) proposed the name *Saccoma* for *Saccocoma tenella* (with Schwimmplatten). Because the Solnhofen saccocomids clearly belong to a single species with Schwimmplatten on the proximal brachials and paired vertical oral processes on the more distal brachials (Textfigs. 12, 13) tenella and pectinata are conspecific and *Saccoma* is a junior synonym of the valid genus *Saccocoma*. Interestingly, Jaekel’s famous reconstruction of *Saccocoma tenella* (1892, pl. 30) has both the Schwimmplatten and the oral processes like those shown in his pl. 29 of “*Saccocoma pectinata*”.

*Comatula tenella* (Goldfuss, 1831)

Textfigs. 12, 13

**Lectotype:** Textfig 13, an individual on the original slab of Goldfuss (1831, p. 204, Pl. 62, fig. 1), No. 423, Institut für Paläontologie, University of Bonn. Designated herein.

**Type locality and horizon:** Solnhofen, Lower Tithonian.

**Remarks.** – I have chosen to designate a lectotype for this important species, using a specimen of *Comatula tenella* (Goldfuss 1831, pl. 62, fig. 1) now preserved in the collections of Bonn University. The original 15 x 15 cm and 4 mm thick slab contains 5 reasonably well-preserved subadult specimens (cup diameter about 3 mm) and two coprolites composed of saccocomid remains; all individuals are similar with regard to cup and brachials. I have not been able to assign with certainty one of the individuals to Goldfuss’ fig. 1A or 1D; his reconstructions of a whole animal in natural size (fig. 1B) and a part enlarged (fig. 1C) are incorrect, with the enlarged picture showing two arms with dish-like brachials throughout. I have therefore chosen the best preserved individual on the original slab for designation as the lectotype (Textfig. 13). This individual shows the essential parts, cup, proximal brachials with Schwimmplatten and more distal brachials with paired oral processes. The specimens figured by Goldfuss in pl. 62, fig. 2 (referred to *C. pectinata* and found near Eichstätt) have been lost (M. Sander, pers. comm. 2002). An adult specimen from the Eichstätt area is shown in Textfig. 12. It has all the characteristics of the lectotype and of the fine specimen figured by Hess (1999, fig. 219), now preserved in the Basel Natural History Museum (collection number M 9999); this specimen was found in the Upper Solnhofen Formation of the Langenaltheim Haardt quarry (see Meyer & Schmidt-Kahler 1994, fig. 59, p. 76), a quarry in the area of the lectotype.

*Comatula cf. tenella* (Goldfuss, 1831)

[= *Saccocoma* n. sp., cf. *tenella* – Sieverts-Doreck (manuscript)]

**Stratigraphic and geographic distribution:** Ossicles of this species were collected by Feifel in a quarry at the upper end of the Steige from Taüllingen (Kreis Balingen) to
Neuweiler, an outcrop of Untere Felsenkalke; the locality is thus of Upper Kimmeridgian age ("Malm δ", Eudoxus Zone). As mentioned in Section 3 this species has also been reported from the Lower Tithonian of Sirchingen.

Material: see Appendix. The material mostly consists of radials and brachials with lateral processes or wings (Schwimmplatten). The radials are all more or less broken, in only one instance is the radial articular facet preserved.

Description. – The radials are very thin and therefore more or less broken. They are rather flat, indicating a conical and rather high cup (1 to 2 mm), with a more

Fig. 12. *Saccocoma tenella* (GOLDFUSS) on the lower side of a slab from the Upper Solnhofen Formation (Lower Tithonian), Wintershof near Eichstätt. (a) Aboral view of completely crushed cup with well-preserved structure and small centrale, note IBr2 with lateral wings (Schwimmplatten); (b) aboral (exterior/distal) view of axillary IBr2 of another individual with intact, porcelain-like lateral wings and visible aboral ligament fossae (aol); (c) proximal view (articular facet) of secundibrachial (individual a) with paired oral processes (arrows); all specimens on this slab have secundibrachials with paired vertical processes and Schwimmplatten. Natural History Museum Basel M 10000 (a and c), M 10001 (b) (Photographs Hess). – Scale bars = 1 mm.
or less sculptured surface. A number of plates show a central rib (Pl. 9, Fig. 11) or a pair of ribs (Pl. 9, Fig. 10), but these may lack in others (Pl. 9, Fig. 8). The outer surface is distinctly sculptured in a somewhat variable pattern (Pl. 9, Figs. 8, 10a, 11a). The inner surface is quite smooth, with two parallel ribs in a number of ossicles (Pl. 9, Figs. 10b, 11b); the ribs may hide the nerve canals leading to the basal piece. The lateral edges of the radials are distinctly serrate. The articular facet is comparatively small, with the aboral ligament pit visible from the surface (Pl. 9, Fig. 9). The axillary brachials (presumably second primibrachials, IBr2) have a strongly sloping cryptosynarthrial facet that is visible from the inside (orally) (Pl. 9, Fig. 12b) and two

Fig. 13.  *Saccocoma tenella* (GOLDFUSS), lectotype chosen from one of the individuals on the original slab of GOLDFUSS (1831: 204, pl. 62, fig. 1); aboral view with cup and proximal arms; IAx = second primibrachial (primaxillary); black arrows indicate lateral wings (Schwimmplatten), white arrows indicate oral processes (*GOLDFUSS*’ *Co-matula pectinata*). Solnhofen, Lower Tithonian; Institut für Paläontologie der Universität Bonn, no. 423 (Photograph Hess). – Scale bar = 1 mm.
muscular distal facets whose aboral ligament pit is visible from the outside (aboral-ly) (Pl. 9, Fig. 12a). The outer surface of the IBr2 is reticulate and the sides are drawn out into rounded wings (Schwimmplatten) that are mostly broken. Non-axillary brachials either have a cryptosynarthrial or a synostosial facet at one end and a muscular facet at the other end, or they bear two muscular facets; a number have lateral wings with a dense inner and a transparent outer part (Pl. 9, Fig. 13). Other brachials are elongate, stick-like; in some the proximal parts of broken-off oral processes (similar to those of S. tenella) are still visible.

Relationships. – The Swabian form is closely related to Saccocoma tenella of the Plattenkalk facies of Bavaria. The main difference is in the less well developed central rib on most of the radials from Swabia. A form similar to the present one has been reported by Verniory (1960) from the Kimmeridgian of Haute-Savoie (France). (It should be noted that in Verniory’s terminology the Solnhofen limestone is also of Kimmeridgian age, see Verniory 1962a: 390.) The radials found at the French location have a surface varying from almost smooth to coarsely reticulate. This variability also occurs in the Swabian material. The brachials are quite comparable to those described by Verniory and to those of S. tenella from Bavaria. Verniory was not sure whether the French material represents more than one species, but he also mentioned that the main morphotypes were connected by intermediates. Both Verniory’s material and the present one may represent a species different from tenella but I refrain from establishing a species solely on the basis of somewhat differently sculptured radials.

Saccocoma quenstedti Sieverts-Doreck & Hess n. sp.
[manuscript name]

Saccocoma quenstedti Doreck (in coll.). – Verniory, p. 315, figs. 1–11.

Holotype: Cup, Pl. 10, Fig. 1 (slide 151, SMNS 64832, designated by Hess); diameter 2.5 mm, height 1.8 mm.
Paratypes: Radials Pl. 10, Fig. 2 (slide 153, SMNS 64833), Pl. 10, Fig. 3 (slide 154, SMNS 64834).

Derivation of name: Dedicated to F. A. Quenstedt, the famous German palaeontologist.

Type locality and horizon: Upper Kimmeridgian (Acanthicum Zone), Bossler near Gruibingen.

Stratigraphic and geographic distribution: Lower Kimmeridgian (Platynota Zone) to Upper Kimmeridgian (Acanthicum Zone), Swabia (several localities), Lower Kimmeridgian, Franconia (Stammberg).

Material: See Appendix. It consists of a few complete cups (whose antler-like processes are broken off), some complete radials and a large number of broken radials, mostly the reinforced part around the articular facet with the processes emanating from there. A large number of brachials is also available.

Diagnosis. – Cup pentagonal in outline, aborally convex with small basal knob; radials with paired antler-like lateral processes of variable shape that extend outward from the aboral part of the articular facet; radials strongly sculptured around the thickened base of the lateral process beneath the radial facet, but finely reticulate to
smooth in the interradial areas, no median rib; muscle fields on inner edge of radials; wings of brachials commonly perforated.

**Description.** – The hemispheric cup is pentagonal in outline, with the radial parts around the facets forming the angles (Pl. 10, Fig. 7); it is aborally convex with a small, non-protruding basal knob (Pl. 10, Fig. 1). Starting from the thickened base beneath the small radial facet with its lateral processes the surface of the radial is strongly sculptured with anastomosing ribs (Pl. 10, Fig. 2) that disappear near the interradial sutures, leaving 5 bands of smooth area around the sutures (Pl. 10, Fig. 1). There is no pronounced median ridge. Paired antler-like lateral processes of variable shape extend outward from the aboral part of the radial articular facet. These processes are very irregular (Pl. 10, Figs. 2–6); some have rounded tips, others are pointed or even bifurcate. The material contains a large number of broken radials such as those figured, with only the area around the facet preserved (Pl. 9, Fig. 7). The muscle fields are at the inner edge of the radials (Pl. 9, Fig. 7b). First primibrachials have not been identified with certainty. Axillary second primibrachials (IBr2, IAx) are easily recognized, however (Pl. 9, Figs. 4, 5). The proximal facet of these ossicles is a sloping cryptosynarthry (Pl. 9, Fig. 5). The distal facet is muscular, with the aboral ligament fossae visible from the outside (Pl. 9, Fig. 4). The surface of the ossicles is coarsely reticulate, with the lateral wings commonly perforated (Pl. 9, Figs. 4, 5). The perforations may, however, be artifacts due to preservation, as indicated by brachials with well-preserved, dense lateral wings (Schwimmplatten, see Pl. 9, Fig. 6). Proximal and distal secundibrachials and distal brachials occur in wide variety of shapes (Pl. 10, Figs. 9–16). Some of the, presumably proximal, brachials have one synostosial facet (Pl. 10, Fig. 8), others of similar width have muscular facets at both ends (Pl. 10, Fig. 9). Especially puzzling are distal brachials with a bent muscular facet at one end and a sloped cryptosynarthrial one at the other; as discussed above (Textfig. 11, p. 10) and also shown in Pl. 10, Figs. 10–16 the facets of these ossicles do not match if one assumes that the mostly perforated skeletal processes occur on only one side of the ossicles (the side opposite the ambulacral furrow). All these brachials share a light, reticulate skeleton.

**Relationships.** – *S. quenstedti* is closely related to *S. vernioryi* Manni & Nicosia (1984) with which it shares branched antler-like spines on the radials. This Tithonian species from central Italy has two pairs of spines, one directed upward, the other downward. The proximal secundibrachials of *S. vernioryi* have lateral wings with a different shape and no distal secundibrachial comparable to those figured in Pl. 10, Figs. 10–16 were described by the authors.

*Saccocoma longipinna* Hess n. sp.

[= *Saccocoma* n. sp., Verniory 1962b, p. 391]

1962b *Saccocoma* n. sp. – Verniory, p. 391, figs. 1–8
1979 *Saccocoma* sp. – Nicosia & Parisi, p. 323, fig. 2

**Holotype:** The secundibrachial, Pl. 11, Fig. 6 (Verniory 1962b, fig. 6); length 2.2 mm. Muséum d’Histoire Naturelle de Genève (repository number in Decrouez & Proz, in preparation).

**Paratypes:** Radials, Pl. 11, Figs. 1–2 (Verniory 1962b, figs. 1–2); secundibrachial, Pl. 11, Fig. 4 (Verniory 1962b, fig. 4). Muséum d’Histoire Naturelle de Genève (repository numbers in Decrouez & Proz, in preparation).

**Derivation of name:** Referring to the elongate wings on the proximal brachials.
Type locality and horizon: Montbrand (Pays du Buëch, Hautes-Alpes, France), marls at the Kimmeridgian-Tithonian boundary (F. ATROPS, pers. comm., 2002). According to the notes left by VERNIORY the material is from part J 6 of the profile (LEFLAIVE, 1955–56) along the road from La Faurie to Montbrand, about 1800 m from Montbrand. This part of the section, labelled “Kimmeridgien”, is a 15 m thick succession of vertical limestone beds with chert nodules, followed by 1.5 m of vertical marls that contained the saccocomids.

Material: VERNIORY (1962b) figured 4 incomplete radials (three of them with articular facet) and 5 brachials; in the text he mentioned 17 well-preserved brachials. An inventory will be published shortly (DECROUET & PROZ, in preparation).

Diagnosis. – Radials thin, lateral edges only weakly serrate or straight, inner surface smooth; outer surface smooth near the interradial edges but with spongiform or reticulate sculpture at the thickened base of the articular facet; secundibrachials with a prolonged lateral wing on one side, reaching a length of more than 5 times the length of the body, and a much shorter wing with the outline of a half circle on the other side.

Remarks. – When this paper went into print the specimens described by VERNIORY (1962b) and belonging to his private collection were thought to have been lost after his unexpected death in 1962. Fortunately, the material was found just in time for the final proof. VERNIORY’s plate is here reproduced (Pl. 11) as a tribute to his skills in observation and drawing.

Description (translated in part from VERNIORY’s paper). – The (mostly broken) radials are about 2.6 mm high and about 2 mm wide and roughly triangular with a pronounced, thickened and sculptured central part forming the base of the articular facet; the width of the facet is about a third of that of the ossicle. The articular facet shows a distinct aboral ligament pit and two shallow, somewhat smaller interarticular ligament fossae (Pl. 11, Fig. 2). The muscle fields are situated on the inner side and form an open V with an angle of 80 to 110° (Pl. 11, Fig. 3). Proximal winged secundibrachials have a short body with a very elongate wing on one side and a much shorter wing on the other side. Their exact position is unknown, but part of them may be second secundibrachials (IIBr2) because such brachials have sloping proximal cryptosynarthries and distal muscular facets. According to Verniory the winged secundibrachials all appear to have a proximal cryptosynarthrial facet and a distal muscular facet so that (unwinged) intermediate ossicles with proximal muscular facets and distal cryptosynarthries must have been interposed between the winged ossicles (as in S. tenella, cf. Pl. 11, Fig. 9), but such brachials were not found. The slightly asymmetric body has a spongiform outer surface; the inner side shows a strongly sloping cryptosynarthry proximally and muscle fields extending from the corresponding distal facet toward the upper edge of the cryptosynarthrial facet (Pl. 11, Fig. 6). The wings (“expansions natatoires”) are very asymmetric; one has an enormous length, reaching 6.35 times the length of the body; the other is a semicircle emanating from the body. The two wings are not on the same plane but form an angle of 170°-150°. VERNIORY found nearly the same number of ossicles with the large wing to the “right” and to the “left” (“left”: 8 ossicles, “right”: 9 ossicles). It appears probable that the “right” and “left” brachials alternated on the arm, preventing cumbersome imbrication during movement of the arm (Pl. 11, Fig.11).

Relationships (in part translated from VERNIORY’s paper). – The radials lack the pronounced median rib of S. tenella and the spines emanating from the base of the articular facets of S. quenstedti and S. vernioryi. Winged brachials in S. tenella and S. vernioryi are more or less symmetric and not strongly asymmetric as in Sac-
Brachials of *S. quenstedti* have a certain asymmetry (see Verniory 1961, fig. 8–10) but the larger wing is not elongate.

8. Similar saccocomids from other localities

*Saccocoma quenstedti* was described by Verniory (1961) from the Kimmeridgian of Provence (southern France). The broken radials and the axillary IBr2 are very similar to the corresponding ossicles from the present material and also no IBr1 have been found. However, some secundibrachials in the French material have different lateral wings of quite different size. *Saccocoma vernioryi*, a form similar to *quenstedti*, was described by Manni & Nicosia (1984) from the Upper Jurassic (Lower to Middle Tithonian) of central Italy. These authors attributed the broken radials, described by Pisera & Dzik (1979) from the Tithonian of Rogoznik (Poland) under the name of *Saccocoma cf. quenstedti* to the same species. Gluchowski (1987) described radials and brachials of *Saccocoma tenella* from the Dursztyn Limestone Formation (Lower-Middle Tithonian to Lower Berriasian) of the Pieniny Klippen Belt (Poland); interestingly, he also described, from the same strata, radials with branched spines at the base of the arm facets assigned to *Saccocoma cf. quenstedti*. According to Manni & Nicosia (1984) the Tithonian *S. vernioryi* differs from the essentially Kimmeridgian *S. quenstedti* by two pairs of spines on the radial below the articular facet.

On the ocean floor east of the Florida coast the “Glomar Challenger” drilled in 1970 in a depth of 5300 m and a sediment depth of 260 m Upper Jurassic sediments. These contained elements of saccocomids very similar to those described in the present paper (Hess 1972). The following species were recognized by the author after contacting H. Sievert-Doreck: *quenstedti*, *schattenbergi* and *subornata*. Ossicles of *S. tenella* were not found.

9. Taphonomy and mode of life

Saccocomids occur in southern Germany from the Oxfordian to the Tithonian (Textfig. 14). The latest species, *Saccocoma tenella*, is also the best known and should therefore serve as the starting point for the following discussion. Functional morphology and taphonomy indicate that it was a pelagic form, feeding while actively moving through the water column (Hess 1999). Life on the bottom as advocated by Milsom (1994) and Manni et al. (1997) is not supported by the facts (Keupp & Matyszkiewicz 1997; Hess 2000). The Early Tithonian Plattenkalk facies is characterized by extremely fine-grained, even-layered lime mudstones. The very fine sediment, probably brought in by periodic storms, could have blocked the food grooves, impairing the crinoids’ feeding abilities and preventing further movement. In this scenario, the immobilized animals sank to the bottom in a cloud of settling sediment; by virtue of their higher density and their center of gravity near the cup the crinoids would have reached the bottom in life position before the bulk of the sediment. The very common curled-up specimens with their orally enrolled arms must have resulted from muscular contractions of the brachials, presumably to protect the food grooves against invasion of mud. Occasionally, the animals may have been further traumatized after reaching the bottom, thereby casting off their arms; this preserva-
Fig. 14. Stratigraphic range of saccocomids in southern Germany (photographs from other figures, reduced to same scale). Cup of *Crassicoma schattenbergi*, SMNS 64734 (holotype), Stammberg; cup of *C. mayri*, SMNS 64819 (holotype), Würgau; cup of *C. feifeli*, SMNS 64811 (paratype), Hardtberg; radial of *C. praeschattenbergi*, SMNS 64775 (paratype), Himmelreich; radial of *C. subornata*, SMNS 64789 (holotype), Michelsberg; cup of *Saccocoma quenstedti*, SMNS 64832 (holotype), Bossler; radial of *S. cf. tenella*, SMNS 64826, Tailfingen-Neuweiler (the occurrence in the Lower Tithonian is SIEVERTS-DORECK’s [1955] locality Nr. 12, at the road from Urach to Sirchingen, see Section 3); crushed cup of *S. tenella* (for comparison), Wintershof near Eichstätt, Natural History Museum Basel M 10000. The figure indicates the occurrence of ossicles that were contained in the slides examined by the author; some species may have had a broader range (see Appendix).
tional state is known as “Saccocoma schwertschlageri” (Manni & Nicosia 1986). The uncommon specimens with outstretched arms (Hess 1999, fig. 219) may have perished from natural causes. The pelagic lifestyle of Saccocoma tenella and their position in the food chain is also proven by the common occurrence of coprolites that are composed of crinoidal remains (Müller 1969); Saccocoma appears to have been preyed upon by teuthoid cephalopods (Janicke 1970), and by ammonites (Schweigert & Dietl 1999; Dietl & Schweigert 2001). The coiled nature of coprolite Lumbricaria intestinum Münster leaves little doubt that these coprolites descended directly to the sea floor from an animal living and feeding in the water above (Hess 2000). The coprolites were contemporaneous with the crinoids, because both are preserved on beds interpreted to be lithified early by a bacterial film. A pelagic lifestyle may also be assumed for the other Saccocoma species (S. quenstedti, S. vernioryi and S. longipinna) with their essentially similar morphology of light skeleton and floating aids.

The compact nature with low, thick-walled cups and broad arms as well as the absence of any floating aids suggest that the Crassicoma forms, especially the early C. schattenbergi and C. mayri, were essentially benthic. However, the presence of articulations with strongly developed muscle fields as well as loss of the stem indicates that these forms may at times have been active swimmers, thus increasing the crinoids’ feeding capacity. Isolated ossicles of saccocomids are of course allochthonous so that different lifestyles may have been possible at the same time. Similar to Saccocoma tenella the arms of Crassicoma schattenbergi and related species formed an angle of approximately 45° at the axillary second primibrachial (Textfig. 8). It appears that, in contrast to S. tenella (Hess 1999, fig. 220), the secundibrachials were again in a more vertical position during life (Pl. 2). This suggests that the Crassicoma species were neither fully pelagic nor fully benthic. Instead, perhaps, they could rise from the bottom to catch food or to move to other places, such movements being supported by the well-developed muscles. The absence of the floating aids that occur in Saccocoma, such as processes on the radials, wings on the proximal brachials and vertical processes or baffles on the more distal brachials also indicates a life that was not permanently spent floating. It has been proposed by Milsom (1998) that during feeding roveacrinids sank passively. This may be true for Crassicoma rather than for the purely pelagic Saccocoma. Saccocomids share with the other members of the order Roveacrinida the sloping cryptosynarthries between the two primibrachials and the first and second secundibrachials. Such sloping cryptosynarthries appear to be characteristic of small or very lightly built, partly or fully pelagic crinoids and must have served a function for such a mode of life. Non-sloping synostoses only occur between more distal secundibrachials (the first at IIBr3-IIBr4) where the arms of roveacrinids could break due to stress. The comparatively large surface of the sloping “blocked” cryptosynarthries may have stabilized the lowermost part of the arms of these small or fragile animals, thus protecting the area of the cup with its exposed soft parts. As described above the side wings on the first primibrachials of Crassico-

ma schattenbergi may have formed a protective wall around the body cavity. Such protection would have been more important for a partly benthic form with a low, shallow cup than for a truly pelagic form like S. tenella with a rather high cup and short, rod-like first primibrachials.
T. BAUMILLER (pers. comm., 2002) suggested to use isotopic signatures in a number of ossicles of presumed benthic and pelagic species. The δ^{18}O of skeletal calcite is commonly correlated with temperatures and salinity of the water in which the organism grows. The equilibrium δ^{18}O of calcite that crystallizes in water of a particular isotopic composition varies inversely with temperature according to a known equation (ETTER 1994). Assuming that the subtropical ocean at Lower Kimmeridgian times was well stratified the 18O/16O ratio is an indication of water depth (Textfig. 15). To obtain meaningful values the conditions under which the elements were formed should exclude significant seasonal fluctuations in temperature; conversely, the organisms in question should have had a short life span. Under such reasonable assumptions one can distinguish the relatively deep-dwelling species, which will have formed their skeleton in colder water (and thus have a more positive δ^{18}O), from the shallower forms in the same sediment sample.

The isotope values of ossicles of three species from the Lower Kimmeridgian (Platynota Zone) of Michelsberg were determined by Z. B. ENDER at the Institut für Petrochemie und Geochemie, University of Karlsruhe (Results from the second run may be more reliable because of a somewhat larger sample size, K. FOELLMI, pers. comm. 2002), see also Textfig. 15.

![Graph showing the ratio of δ^{18}O in biogenic calcite as a function of temperature during formation (from ETTER 1994, Fig. 4.23; paleotemperatures according to DODD & STANTON 1990), with values of saccoomid ossicles from the Lower Kimmeridgian of Michelsberg.](image-url)
With the exception of the second run of slide 112 the $\delta^{13}C$ values of the three samples vary little and agree well with those of Jurassic pelagic limestones. The range of the $\delta^{18}O$ values indicate pelagic rather than benthic forms (K. Foellmi, pers. comm. 2002); the differences may suggest that the animals spent most of their lives at somewhat different depths. Not unexpectedly, the pelagic $S. quenstedti$ has the most negative value, corresponding to a (surface) temperature of more than 30°C. $Crassicoma$ cf. $schattenbergi$, with the most positive value corresponding to a temperature of 27°C, may have spent most of its life closer to the bottom. In contrast, $C. feifeli$ would have lived near the surface. This makes sense if the slender brachials of Pl. 8, Figs. 10 and 11 really belonged to this minute saccocomid. The degree of diagenetic overprinting by the transformation of the porous skeleton into solid calcite is difficult to assess at this time. It is evident that more data are needed, including information on lithology and facies, to bolster the results from this very limited sample.

Milsom (1998) suggested that roveacrinids exploited two different lifestyles; (1) benthic with the ability to swim, and (2) nektonic. She assumed that the forms with wings and spines on the cup and proximal brachials (i.e. $Saccocoma quenstedti$) had limited arm mobility and were benthic. In contrast, nektonic forms have an enlarged dorsal (radial) cavity and extreme arm mobility but are virtually devoid of ornamentation and show evidence for skeletal lightening. Such a differentiation is not apparent in the present material. Forms of the genus $Crassicoma$ with a sunk aboral pole ($schattenbergi$, mayri and probably $praeschattenbergi$) have a rather sturdy skeleton, $feifeli$ with a comparable skeleton has a protruding aboral pole in form of a knob. All these forms have a shallow radial cavity. Representatives of the genus $Saccocoma$ have a deep radial cavity and light skeleton combined with spines on the cup and/or wings on the brachials, characters that don’t make sense in a benthic lifestyle. Due to their special arrangement the lateral wings on the proximal part of the arms do not seem to have hindered their mobility (Hess 1999, 2000; see also Pl. 11, Fig. 9). Type of arm articulations are overall comparable between the two genera. Well-developed, scalloped muscle fields on the proximal brachials and broad muscle fields on the sturdy, dumb-bell shaped distal brachials of $Crassicoma schattenbergi$ as described in this paper are a prerequisite for forms that were at times active swimmers.

### 10. Phylogeny

Apart from the mass occurrences of $Saccomoma tenella$ in the Early Tithonian Plattenkalk facies saccocomids appear to be most common in the Lower Kimmeridgian (Platynota to Divisum Zones, see Textfig.14). In these strata all 5 recognized species of $Crassicoma$ ($schattenbergi$, $praeschattenbergi$, $subornata$, mayri, $feifeli$) occur, but also $Saccocoma quenstedti$. $Crassicoma mayri$ is the first to appear, with an occurrence in the Oxfordian (the occurrence of $Crassicoma schattenbergi$ in strata of this age was reported by Sieverts-Doreck but is not substantiated by the available

<table>
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<th>$\delta^{13}C$</th>
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<td>2.25/2.58</td>
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<td>-2.34/-3.05</td>
<td>2.09/1.20</td>
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<td>$Saccocoma quenstedti$, 10 brachials</td>
<td>188</td>
<td>-2.82/-3.05</td>
<td>2.20/2.06</td>
</tr>
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</table>
material). Saccocoma cf. tenella was found in the Upper Kimmeridgian (but may also have occurred in the Lower Tithonian); S. vernioryi is restricted to the Tithonian. Saccocoma longipinna is known from the Kimmeridgian-Tithonian boundary. Saccocomids thus started to radiate in the early Late Jurassic with compact forms lacking floating aids such as winged brachials (Crassicoma mayri and C. schattenbergi). C. schattenbergi, one of the two early forms, has a cup with primitive characteristics (distinct basals and a centrale) and such an arrangement can also be inferred for C. prae schattenbergi from the profile of the radials. With the exception of C. schattenbergi the Crassicoma forms are very small, especially in comparison with Saccocoma tenella, but also with other Saccocoma species (Textfig. 14). Other forms from the Lower Kimmeridgian, such as C. subornata and a number of radials of uncertain status (C. cf. schattenbergi) are comparatively slender so that there is no clear-cut succession from thick-walled to thin-walled forms. The presence of the pelagic S. quenstedti in the same Lower Kimmeridgian sediments that also furnished the thick-walled and presumed benthic C. schattenbergi adds to confuse the picture. Sieverts-Doreck thought that C. subornata was an early, primitive form but was not sure about its position within Crassicoma. It may be assumed that the ancestor of the primitive, thick-walled Crassicoma species had a stem (if only at the larval stage), but how this was lost and how the peculiar sloping cryptosynarthries of the proximal brachials developed is open. Axicrinus alexandri Kristan-Tollmann (1977), a primitive roveacrinid with well-developed basals from the Upper Triassic of the southern Alps, has characteristics that resemble those of Crassicoma schattenbergi and may thus be ancestral to this Upper Jurassic species, but no intermediate forms are known that could bridge the gap. The phylogeny of the different Upper Jurassic saccocomids, including their origin, is thus unsolved; a problem they share with the other roveacrinids.

11. References


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Plate 1

Glossary of terms.
(1) Oral view of cup of Crassicoma feifeli SIEVERTS-DORECK & HESS n. g. n. sp., holotype, Lower Kimmeridgian, Beuren-Erkenbrechtsweiler (slide 83, SMNS 64710);
(2) interior view of radial of Crassicoma praeschantzenbergi SIEVERTS-DORECK & HESS n. g. n. sp., Lower Kimmeridgian, Himmelreich near Bargau (slide 130, SMNS 64711);
(3) interior view of radial of Crassicoma subornata SIEVERTS-DORECK & HESS n. g. n. sp., Lower Kimmeridgian, Michelsberg (slide 114, SMNS 64712);
(4) exterior view of radial of Crassicoma cf. schattenbergi, Lower Kimmeridgian, Michelsberg (slide 60, SMNS 64713);
(5) radial facet of Crassicoma feifeli, Lower Kimmeridgian, Hardtberg near Reichenbach (slide 99, SMNS 64714);
(6) interior/proximal view of IBr1 of Crassicoma schattenbergi SIEVERTS-DORECK & HESS n. g. n. sp. with scalloped muscle fields, Lower Kimmeridgian, Steige Neidlingen–Eckhof (slide 48, SMNS 64715) (Photographs MATHYS). – Scale bars = 1 mm.
Plate 2

Articulations (connections indicated by arrows) between radial and base of arms of *Crassicoma schattenbergi* Sieverts-Doreck & Hess n. g. n. sp., Lower Kimmeridgian.

Left side, lateral view of radial (R, slide 14, Stammberg, SMNS 64697), first primibrachial (IBr1, slide 17, Stammberg SMNS 64698) and second (axillary) primibrachial (IBr2 = 1Ax, slide 21, Stammberg, SMNS 64699).

Right side, IBr2 (slide 75, Michelsberg, SMNS 64719), two first secundibrachials (IIBr1, Stammberg; left, slide 37, SMNS 64696; right slide 34, SMNS 64701), second secundibrachial (IIBr2, slide 34, Stammberg, SMNS 64705), oblique lateral view of third secundibrachial (IIBr3, slide 34, Stammberg, SMNS 64722) and fourth secundibrachial (IIBr4, slide 36, Stammberg, SMNS 64723), proximal (slide 36, Stammberg, SMNS 64724) and distal view of IIBr4 (slide 36, Stammberg, SMNS 64725) (Photographs Mathys). For a discussion on the position of IIBr1 and IIBr2 see text.

pr = proximal, di = distal. – Scale bars = 1 mm.
Plate 3

Crassicoma schattenbergi Sieverts-Doreck & Hess n. g. n. sp., Lower Kimmeridgian, Steige Neidlingen-Eckhof.

(1) Exterior view of radial (slide 46, SMNS 64726);
(2) interior view of radial with openings for ring commissure, the interradial processes are broken off, note dense inner and spongiform outer layer (slide 46, SMNS 64727);
(3) exterior/distal view of IBr1 (slide 48, SMNS 64728);
(4) interior/proximal view of IBr1 (slide 48, SMNS 64715);
(5) oblique proximal view of IIBr3 with bent muscular facet (other side is a synostosis) (slide 50, SMNS 64729);
(6, 7) lateral view (6) of IIBr1 or IIBr2 (according to Sieverts-Doreck, see text) with muscular facet at left and crypto-synarthrial proximal facet downward and exterior/distal view (7) with muscular facet (slide 49, SMNS 64730);
(8) distal facet of IIBr3 (synostosis) (slide 49, SMNS 64731);
(9) distal facet of another IIBr3 with synostosis (inverted position) (slide 49, SMNS 64732);
(10) exterior view of distal brachial with two muscular facets (slide 58, SMNS 64733).

(Photographs W. E. Reif, except Fig. 10 = Mathys). – Scale bars = 1 mm.
Plate 4

*Crassicoma schattenbergi* Sieverts-Doreck & Hess n. g. n. sp. (1–6, 12–16) and *Crassicoma cf. schattenbergi* (7–11).

1. Cup, holotype (slide 1, Lower Kimmeridgian, Stammberg, SMNS 64734) (a) aboral view, (b) aboral/lateral view;
2. cup, paratype (slide 2, Lower Kimmeridgian, Stammberg, SMNS 64735);
3. thick-walled radial, paratype (slide 7, Lower Kimmeridgian, Stammberg, SMNS 64736) (a) exterior view, (b) interior view, (c) lateral view;
4. basal circlet with centrale (that is missing in the holotype, fig. 1) (slide 74, Lower Kimmeridgian, Michelsberg, SMNS 64737) (a) aboral, (b) oral;
5. exterior view of relatively narrow radial (slide 14, Lower Kimmeridgian, Stammberg, SMNS 64697), see also Fig. 7 and Pl. 2;
6. thick-walled radial, paratype (slide 46, Lower Kimmeridgian, Neidlingen-Eckhof, SMNS 64726) (a) exterior/distal view with interradial processes and their scalloped muscle fields, (b) lateral view.

7. *Crassicoma cf. schattenbergi*, interior view of broken radial with nerve canals to basals (slide 69, Lower Kimmeridgian, Kornberg, SMNS 64740);
8. thin radial (slide 60, Lower Kimmeridgian, Michelsberg, SMNS 64741), exterior view (a), interior view (b);
9. relatively flat radial with one intact interradial process (slide 52, Lower Kimmeridgian, Neidlingen-Eckhof, SMNS 64742) (a) exterior view, (b) interior view;
10. lateral view of rather thin radial (slide 12, Lower Kimmeridgian, Stammberg, SMNS 64743);
11. weakly sculptured first primibrachial (IBr1) of *Crassicoma cf. schattenbergi* (slide 17, Lower Kimmeridgian, Stammberg, SMNS 64698) (a) lateral view, (b) exterior/distal view, see also Textfig. 7 and Pl. 2.
12. *Crassicoma schattenbergi*, (a) exterior/distal view, (b) interior/proximal view of IBr1 (slide 71, Lower Kimmeridgian, Neidlingen-Eckhof, SMNS 64745);
13. exterior/distal view of very broad IBr1 (slide 71, Neidlingen-Eckhof, SMNS 64746);
14. exterior/distal view of narrow (juvenile?) IBr1 (slide 71, Neidlingen-Eckhof, SMNS 64747);
15. second primibrachial (IBr2) (slide 21, Stammberg, SMNS 64692) (a) exterior/distal view, (b) interior/proximal view;
16. third secundibrachial (IIBr3) (slide 50, Neidlingen-Eckhof, SMNS 64748) (a) distal view, (b) proximal view.

(Photographs Hess). – Scale bars = 1 mm.
HESS, SACCOCOMIDS FROM THE UPPER JURASSIC OF SOUTHERN GERMANY
Plate 5

Crassicoma schattenbergi n. g. n. sp. Sieverts-Doreck & Hess (Figs. 1–4, 10–27) and radials of *Crassicoma cf. schattenbergi* (Figs. 5–9), Lower Kimmeridgian:

(1, 2) Exterior view of IIBr2 (slide 49, Neidlingen-Eckhof, SMNS 64749) and IIBr3 (slide 50, Neidlingen-Eckhof, SMNS 64750);

(3, 4) lateral/interior view of IIBr2 (slide 49, Neidlingen-Eckhof, SMNS 64751) and IIBr3 (slide 50, Neidlingen-Eckhof, SMNS 64752);

(5) lateral/exterior view of radial (slide 69, Kornberg, SMNS 64753);

(6) exterior view of radial (slide 12, Lower Kimmeridgian, Stammberg, SMNS 64754);

(7) exterior view of radial (slide 60, Michelsberg, SMNS 64713);

(8) radial articular facet (slide 60, Michelsberg, SMNS 64755);

(9) interior view of radial (slide 12, Lower Kimmeridgian, Stammberg, SMNS 64756);

(10) exterior/distal view of IBr1 (slide 61, Kornberg, SMNS 64757);

(11) exterior/distal view of IBr2 (slide 62, Kornberg, SMNS 64758);

(12) oblique lateral view of IBr2 with preserved interradial process (slide 120, Michelsberg, SMNS 64759);

(13) proximal/lateral view of IIBr1 (slide 66, Kornberg, SMNS 64760);

(14) exterior/lateral view of strongly sculptured IIBr1(?) (slide 66, Kornberg, SMNS 64703, see also Textfig. 9);

(15) exterior/proximal view of IIBr1 (slide 66, Kornberg, SMNS 64762);

(16) distal view of IBr2, right muscle field broken away (other side is a cryptosynarthry) (slide 49, Neidlingen-Eckhof, SMNS 64763);

(17) proximal view of IIBr3, one scalloped muscle field broken away (other side is a synostosis) (slide 50, Neidlingen-Eckhof, SMNS 64764);

(18) proximal view of IIBr3 (slide 65, Kornberg, SMNS 64765);

(19) distal view of IIBr3, synostosis (slide 65, Kornberg, SMNS 64766);

(20) interior view of distal brachial, ambulacral furrow and two muscular facets (slide 65, Kornberg, SMNS 64767);

(21) exterior/proximal or distal view of distal brachial (slide 65, Kornberg, SMNS 64768);

(22) oblique exterior/proximal view of distal brachial (slide 58, Neidlingen-Eckhof, SMNS 64769);

(23) interior view of short distal brachial, with two muscular facets (slide 58, Neidlingen-Eckhof, SMNS 64770);

(24) interior/distal view of IIBr3 with synostosis (slide 58, Neidlingen-Eckhof, SMNS 64771);

(25) interior view of short distal brachial with muscular facets (slide 58, Neidlingen-Eckhof, SMNS 64772);

(26) exterior view of distal brachial with pinnule facet (slide 55, Neidlingen-Eckhof, SMNS 64773);

(27) oblique exterior view of distal brachial with pinnule facet, ambulacral furrow to the right (slide 43, Stammberg, SMNS 64774).

(Photographs Mathys). – Scale bars = 1 mm.
Plate 6

Crassicoma praeschattenbergi Sieverts-Doreck & Hess n. g. n. sp., Lower Kimmeridgian.

(1) Exterior view of radial, paratype (slide 130, Himmelreich, SMNS 64775);
(2) Interior view of radial, paratype (see also Pl. 1, fig. 2) (slide 130, Himmelreich, SMNS 64711);
(3) Interior/distal view of radial to show the deep muscle fields (slide 131, Himmelreich, SMNS 64776);
(4) Radial, holotype (slide 146, Himmelreich, SMNS 64777) (a) exterior/distal view, (b) exterior view, (c) interior view, note notches for basals;
(5) Radial (slide 138, Michelsberg, SMNS 64778) (a) exterior view, (b) interior view;
(6) Radial with broad interradial process (slide 130, Himmelreich, SMNS 64779) (a) exterior view, (b) interior view;
(7) IBr1 (slide 147, Himmelreich, SMNS 64780) (a) interior view, (b) exterior view;
(8) IBr1 (slide 132, Himmelreich, SMNS 64781) (a) interior view, (b) exterior view;
(9) Oblique interior/proximal view of IBr1 (slide 131, Himmelreich, SMNS 64782) and
(10) Matching oblique interior/proximal view of IBr2 (slide 131, Himmelreich, SMNS 64783);
(11) Proximal/interior view of IIBr2 with cryptosynarthry (slide 131, Himmelreich SMNS 64784);
(12) Distal view of IIBr3 with narrow synostosis (slide 131, Himmelreich, SMNS 64785);
(13) Proximal view of IIBr1 (?) of Crassicoma praeschattenbergi or Crassicoma subornata (slide 131, Himmelreich, SMNS 64786);
(14, 15) Distal brachials with muscular facets (slide 131, Himmelreich, SMNS 64787–64788) (14) exterior, (15) interior view.

(Photographs Mathys, except Figs. 4–8 = Hess). See text for assignment of brachials. – Scale bars = 1 mm.
Plate 7

*Crassicoma subornata* SIEVERTS-DORECK & Hess n. g. n. sp., Lower Kimmeridgian.

(1–8) Radials.

(1) Exterior view (slide 137, Michelsberg, SMNS 64788);
(2) holotype, exterior view (slide 137, Michelsberg, SMNS 64789);
(3) exterior view of paratype with intact interradial processes (slide 128, Hochalb, SMNS 64790);
(4) interior view (slide 137, Michelsberg, SMNS 64791);
(5) exterior view (slide 114, Michelsberg, SMNS 64792);
(6) interior view of paratype with lower margin notched for basals (slide 114, Michelsberg, SMNS 64712);
(7) interior view of small, narrow radial (slide 139, Hardtberg, SMNS 64793);
(8) radial articular facet (slide 143, Hochalb, SMNS 64794).

(9–23) Brachials.

(9) Exterior/distal view of IBr1, paratype (slide 132, Himmelreich, SMNS 64795);
(10) interior/proximal view of IBr2 (slide 127, Hochalb, SMNS 64796);
(11) interior/proximal view of IBr1 with muscle fields partly broken away (slide 126, Hochalb, SMNS 64797);
(12) interior/proximal view of narrow IBr2 (slide 133, Himmelreich, SMNS 64798);
(13) exterior/distal view of IBr2, paratype (slide 133, Himmelreich, SMNS 64799);
(14) proximal view of IIBr2 (slide 134, Himmelreich, SMNS 64800);
(15) proximal view of II Br2 with one muscle field broken away (slide 117, Michelsberg, SMNS 64801);
(16) proximal view of IIBr3 (other side is a synostosis) (slide 117, Michelsberg, SMNS 64802);
(17) oblique distal view of II Br1 (slide 117, Michelsberg, SMNS 64803);
(18) proximal view of IIBr3 (other side is a synostosis) (slide 126, Hochalb, SMNS 64804);
(19) distal view of IIBr3 with synostosis (slide 126, Hochalb, SMNS 64805);
(20) interior/distal view of IIBr3 with synostosis (slide 117, Michelsberg, SMNS 64806);
(21) exterior view of distal brachial, possibly another species of *Crassicoma* because of the more sculptured surface (slide 117, Michelsberg, SMNS 64807);
(22) interior view of brachial (slide 117, Michelsberg, SMNS 64808);
(23) exterior view of brachial (slide 117, Michelsberg, SMNS 64809).

(Photographs Mathys). – Scale bars = 1 mm (unless indicated otherwise).
Plate 8

Crassicoma feifeli SIEVERTS-DORECK & HESS n. g. n. sp., Lower Kimmeridgian.
(1) Cup, aboral view (slide 83, Beuren-Erkenbrechtsweiler, SMNS 64810);
(2) oral view of cup (see also Plate 1, Fig. 1), holotype (slide 83, Beuren-Erkenbrechtsweiler, SMNS 64710);
(3) lateral view of cup with interradial processes, paratype (slide 101, Hardtberg, SMNS 64811);
(4) oblique aboral view of cup with two radials missing, paratype, note basals partly fused with centrale (slide 91, Beuren-Erkenbrechtsweiler, SMNS 64812);
(5) oblique oral view of cup (slide 82, Beuren-Erkenbrechtsweiler, SMNS 64813);
(6) interior view of radial with two basals, note encroaching muscle fields (slide 105, Hardtberg, SMNS 64814);
(7) exterior view of radial, paratype (slide 99, Hardtberg, SMNS 64815);
(8) radial articular facet (slide 99, Hardtberg, SMNS 64714);
(9) oblique oral view of basal circlet (basal cone), the centrale is just visible at the bottom (slide 98, Beuren-Erkenbrechtsweiler, SMNS 64816);
(10) oblique interior view of IBr1 provisionally assigned to C. feifeli, note deep ambulacral furrow (slide 105, Hardtberg, SMNS 64817);
(11) exterior view of IBr2 provisionally assigned to C. feifeli (slide 111, Hardtberg, SMNS 64818).

(Photographs Mathys). – Scale bars = 1 mm (unless indicated otherwise).
Plate 9

(1) **Crassicoma mayri** Sieverts-Doreck & Hess n. g. n. sp.; cup, holotype, Oxfordian, Würgau (slide 213, SMNS 64819) (a) aboral view, (b) lateral view (c) lateral/oral view, m = muscle field, aol = aboral ligament;

(2) **Crassicoma cf. mayri**, Lower Kimmeridgian, exterior view of radial (slide 148 Neidlingen-Eckhof, SMNS 64820);

(3) **Crassicoma feifeli** Sieverts-Doreck & Hess n. g. n. sp., Lower Kimmeridgian, aboral view of cup with ring of fused basals, centrale missing (slide 83, Beuren-Erkenbrechtsweiler, SMNS 64821).

*Saccocoma quenstedti* Sieverts-Doreck & Hess n. sp., Lower Kimmeridgian (4–7).

(4) Exterior view of IBr2 (slide 171, Neidlingen-Eckhof, SMNS 64822);

(5) proximal/interior view of IBr2 (slide 177, Hardtberg, SMNS 64823);

(6) proximal/exterior view of axillary brachial (IBr2?) with Schwimmplatte (broken away on left side (slide 165, Bossler, SMNS 64824);

(7) part of a radial with lateral processes (m = muscular facet), (slide 157, Bossler, SMNS 64825) (a) aboral view, (b) distal (oral) view.

*Saccocoma cf. tenella* (Goldfuss), Upper Kimmeridgian, Tailfingen-Neuweiler (8–13).

(8) Exterior view of radial (articular facet broken off) (slide 194, SMNS 64826);

(9) exterior view of upper part of radial with articular facet (slide 194, SMNS 64827);

(10) small radial (slide 192, SMNS 64828) (a) exterior view, (b) interior view;

(11) radial (slide 194, SMNS 64829) (a) exterior view, (b) interior view;

(12) IBr2 (slide 193, SMNS 64830) (a) exterior view, (b) interior/proximal view;

(13) exterior (a) and interior (b) view of brachial with one preserved Schwimmplatte, note dense stereom extending from the body and transparent stereom at the margin, the lower (proximal) facet (13b) is a cryptosynarthry (slide 195, SMNS 64831.)

(Photographs Hess = 1, 7, 10–13, Mathys = 2–6, 8, 9). – Scale bars = 1 mm.
Plate 10

*Saccocoma quenstedti* **SIEVERTS-DORECK & Hess** n. sp., Lower Kimmeridgian.

1. Oblique aboral view of cup, *holotype* (slide 151, Bossler, SMNS 64832);
2. *exterior view of radial, paratype* (slide 153, Bossler, SMNS 64833);
3. *interior view of radial, paratype* (slide 154, Bossler, SMNS 64834);
4. Distal view of broken radial with intact processes (slide 157, Bossler, SMNS 64835);
5. Distal view of broken radial with intact processes (slide 157, Bossler, SMNS 64836);
6. Distal/lateral view of broken radial with intact processes (slide 155, Bossler, SMNS 64837);
7. Oral view of cup with partly preserved lateral processes (slide 150, Bossler, SMNS 64838);
8. *exterior/distal view of secundibrachial with partly preserved lateral wings* (slide 178, Hardtberg, SMNS 64839);
9. *exterior view of secundibrachial with muscular facets at both ends and partly preserved lateral flange on one side* (slide 178, Hardtberg, SMNS 64840);
10–16, SMNS 64841–64847 *secundibrachials in lateral* (10–12, 14–16) and *proximal/interior view* (13) with bent muscular facet and ambulacral furrow, *brachials have a bent muscular facet at the lower* (proximal?) *end and a sloped cryptosynarthrial or synostial facet at the upper* (distal) *end,* (10, 11, 16: slide 188, Michelsberg; 12, 15: slide 177, Hardtberg; 13: slide 179, Hardtberg; 14: slide 182, Hardtberg).

(Photographs **MATHYS**). – Scale bars = 1 mm (unless indicated otherwise).
Plate 11


1. Part of radial with articular socket, (1a) outer surface of broken radial, (1b) schematic cross-section through cup;
2. Articular facet of radial;
3. Inner side of upper part of broken radial with V-shaped muscle fields;
4. Outer side of proximal brachial (IIBr1 or 2 or 3);
5. Outer side of proximal brachial (IIBr1 or 2 or 3);
6. Inner side of proximal brachial (IIBr1 or 2 or 3) with strongly sloping cryptosynarthry, holotype;
7. Oral view of muscular brachial articular facet;
8. Outer side of proximal brachial (IIBr2 or IIBr3);
9. Arrangement of proximal secundibrachsials of *Saccocoma tenella* starting from IAx, winged brachials are interleaved with wingless brachials;
10. Hypothetical arrangement of ossicles of *S. longipinna* on two neighbouring arms;
11. Hypothetical arrangement of “right” and “left” winged brachials of *S. longipinna* alternating on one arm. Proximal end of ossicles is directed downward, distal end is directed upward.

Upper (vertical) scale bar (1 mm) for Figs. 4–8; lower (horizontal) scale bar (1 mm) for Figs. 1–3. – Copied from VERNIORY (1962b).
Appendix: List of material

Note. – As explained in Section 5 the assignment of first and second secundibrachials is problematic. Slides may include ossicles of other species, as indicated.

**Crassicoma schattenbergi**

Planula Zone, Stammberg

Slide 1: one cup (holotype).

Slides 3, 6, 7, 13: radials (3: 2; 6: 2; 7: 3, 13: 4).

Divisum Zone, Stammberg.

Slide 2: one cup.

Slides 4, 5, 11, 14: radials (4: 1 radial + 1 brachial; 5: 2; 9: 3; 11: 50; 14: 6).


Slides 30-33: IBr1 – juvenile (broad ossicles) or small (long) ossicles from other species (30: 4; 31: 33; 32: 37; 33: 23).

Slides 42-45: mostly dumb-bell shaped distal brachials with muscular/muscular articulations (42: 8; 43: 9; 44: 74; 45: 6).

Hypselocyclum Zone, Steige Neidlingen–Eckhof

Slides 46, 47: radials and various brachials (includes “SEM originals”, photographed by REIF) (46: 5 + 1 cf. schattenbergi; 47: 1 + 6 cf. schattenbergi); 48: 1 radial, 2 IBr1, 49: 21 IBr2; 50: 34 IBr3 with synostosis/muscular articulations; 51: 4 IBr4 with synostosis/muscular articulations).


Slide 57: 5 IBr1 + 3 IBr2; 71: 24 IBr1.

Slides 56, 58: unsorted material (58: mainly schattenbergi).

Hypselocyclum Zone, Kornberg near Boll

Slide 59: 5 radials; 61: 63 IBr1; 62: 7 IBr2; 63: 20 brachials, unsorted; 64: about 150 mostly dumb-bell shaped unsorted brachials, belonging to schattenbergi; 65: 32 brachials, including IBr1, IBr3 or IBr4 with synostosis/muscular articulations; 66: 36 unsorted brachials (IBr1, IBr3, IBr2, variety of schattenbergi and others); 67: 27 IBr2.

Platynota Zone, Michelsberg

Slide 60: 1 radial + 22 radials of cf. schattenbergi; 74: 1 basal circlet with centrale; 75: 16 IBr1 + 6 IBr2; 76: 4 IBr1 + 2 IBr1 or IBr2 + 2 distal brachials + 1 radial of feifeli.

**Crassicoma cf. schattenbergi** (radials only)

Planula Zone, Stammberg


Divisum Zone, Stammberg

Slide 10: 1.

Hypselocyclum Zone, Steige Neidlingen–Eckhof


Platynota Zone, Michelsberg

Slide 60: 22 (partly also cf. subornata).

Hypselocyclum Zone, Kornberg

Slide 59: 11; 69: 34 (could also be subornata).
Divisum Zone, Hardtberg
Slide 70: 18 (possibly subornata).

Divisum Zone, Würgau
Slide 9: 3.

Platynota Zone, Roggenmühle
Slide 73: 3.

Crassicoma praeschattenbergi
Platynota Zone, Himmelreich near Bargau
Slide 130: 29 radials; 131: 83 radials + 5 IB1r + one IB2r + 3 distal brachials + 22 thinner radials (cf. subornata) 132: 65 IB1r; 146: 4 radials, 147: one IB1r.

Platynota Zone, slopes of Michelsberg
Slide 138: 4 radials, 147: one IB1r.

Platynota Zone (clay facies), slopes of Michelsberg
Slides 112–115: radials (thin-walled); 112: 112 radials feifeli + one schattenbergi + 28 subornata; 113: 6 radials; 114: 4 radials; 115: 16 radials; 116: 7 IB1r; 117: 50 brachials with synostosis/muscular and muscular/muscular articulation, muscular/muscular = dumb-bell shaped. Slides 118–123 (“sp. sp.” according to SIEVERTS-DORECK); 118: 33 IB1r (some may belong to schattenbergi); 119: 48 IB2r; 120: 55 IB2r; 121: 54 proximal secundibrachials (mostly strongly sculptured = schattenbergi?, but some finely sculptured = subornata); 122: one brachial (strongly sculptured, assignment doubtful); 123: 50 unsorted brachials (mostly subornata).

Crassicoma subornata
Platynota Zone, Steige Beuren–Erkenbrechtsweiler
Slide 124: 2 axillaries and 7 other brachials.

Platynota Zone (Clay facies), Hochalb near Auendorf
Slide 125: 10 slender IB1r with grooved outer surface; 126: 13 IB1r and brachials with synostosis/muscular articulation, outer surface reticulate (possibly schattenbergi); 127: 24 IB2r. Slides 128, 129: (“sp. sp.” according to SIEVERTS-DORECK). 128: 33 radials (9 = subornata, 11 = feifeli, 13 = cf. schattenbergi); 129: about 50 unsorted brachials (some subornata but mostly reticulate, some with pinnule sockets = cf. schattenbergi). Slide 143: 34 radials (one = praeschattenbergi).

Platynota Zone, Himmelreich near Bargau
Slide 132: 66 slender IB1r (may be partly praeschattenbergi); 133: 68 IB2r; 134: 28 IB1r(1 or 2); 135: 128 finely sculptured brachials, mostly dumb-bell shaped, some with pinnule sockets; 136: about 600 brachials, unsorted with regard to position on arm (similar to 135).

Divisum Zone, Hardtberg
Slide 139: 70 radials + 2 IB2r + 4 secundibrachials; 140: + one radial + 23 IB1r + 24 IB2r + 19 distal brachials; 141: 27 radials (mostly broken) + 15 IB1r + 28 IB2r + 89 distal brachials (18 with pinnule socket); 142: one IB1r.

Hypselocyclum Zone, Kornberg near Boll
Slide 144: one radial (robust, finely sculptured) + one secundibrachial; 145: one brachial (strongly dumb-bell shaped, “Saccocoma sp.”).

Crassicoma feifeli
Acanthicum Zone, Steige Beuren–Erkenbrechtsweiler
Slides 82–97: cups (82: 10; 83: 19; 84: 6; 85: 28; 86: 15; 87: 1; 88: 2; 89: 1; 90: 1; 91: 5; 92: 11; 93: 12; 94: 3; 95: 3; 96: 53; 97: 43). Slide 98: 5 radials + isolated basal cone.
Divisum Zone, Hardtberg near Reichenbach
Slides 99–106, 110: cups and radials, some brachials of doubtful assignment (99: 8 cups + 37 radials; 100: 5 cups + 9 partial cups + 3 radials; 101: one cup + one IBr1; 102: 2 cups + 57 radials; 103: 65 radials; 104: unsorted radials + IBr1 + distal brachials of *feifeli* and *schattenbergi*; 105: one cup + 6 IBr1 + one IBr2, part of the brachials may belong to *quenstedti*; 106: 4 cups; 110: one cup).

Hypselocyclum Zone, Steige Neidlingen–Eckhof
Slide 107: 89 radials; 108: 25 radials (thinner than normal, variety?); 111: one IBr2, probably belonging to *feifeli*.

Divisum Zone, Stammberg near Peulendorf
Slide 109: 2 cups.

Platynota Zone (Clay facies), slopes of Michelsberg
Slide 112: 112 radials *feifeli* + one *schattenbergi* + 28 *subornata*.

Crassicoma *mayri*
Slide 213: one cup from Würgau (Bimammatum Zone).

Crassicoma *cf. mayri*

Lacunosamergel Formation, Steige Neidlingen–Eckhof
Slide 148: 18 radials (relatively narrow, outer surface reticulate-pitted, interradial process).

Saccocoma *quenstedti*

Acanthicum Zone (spongiolithic facies), Bossler
Slide 149: one cup; 150: one partial cup; 151: 5 cups; 152: 4 cups; 153: 57 broken radials; 154: 3 broken radials; 155: 98 broken radials; 156: 17 broken radials; 157: 16 broken radials + 7 brachials; 158: 2 radials; 159: 4 broken radials; 160: 11 mostly broken radials; 161: 72 mostly broken radials; 162: 88 mostly broken radials; 163: about 700 broken radials; 164: 11 brachials (Schwimmpfaffen); 165: 2 brachials (Schwimmpfaffen).

Divisum Zone, large quarry, Steige Neidlingen–Eckhof

Divisum Zone (spongiolithic facies), Hardtberg
Slide 175: 2 broken radials + 29 mostly proximal brachials; 176: 7 broken radials + 30 mostly proximal brachials; 177: 3 broken radials + 42 proximal and distal brachials; 178: 75 mostly distal brachials; 179: 102 mostly distal brachials; 180: 14 brachials, (one axillary), perhaps belonging to *Crassicoma feifeli*; 181: one brachial, possibly *C. feifeli*; 182: 6 brachials with aboral process.

“Malm γ3” (Divisum Zone), Stammberg near Peulendorf
Slide 183: one probably juvenile cup without distinct processes; 184: 2 cups.

Acanthicum Zone, Steige Burladingen–Stetten (“tief”)
Slide 185: 18 broken radials + one brachial.

Acanthicum Zone, Steige Beuren–Erkenbrechtsweiler
Slide 186: 3 radials.

Hypselocyclum Zone (Clay facies), Kornberg near Boll
Slide 187: 8 broken radials + 8 brachials (Schwimmpfaffen).

Platynota Zone (Clay facies), slopes of Michelsberg
Slide 188: 79 mostly long brachials + 2 long axillaries.
Platynota Zone, Hochalb near Auendorf

Slide 189: one broken radial + one brachial (Schwimmplatten) + one long distal brachial; 190: 5 broken radials + 23 brachials (Schwimmplatten).

Platynota Zone, Steige untere Roggenmühle near Geislingen

Slide 191: (Coll. J. Schmidt 1946): 8 broken radials, 20 brachials (mostly with Schwimmplatten).

*Saccocoma* cf. *tenella*

Untere Felsenkalke Formation (Eudoxus Zone) quarry at the upper end of the Steige from Tailfingen (Kreis Balingen) to Neuweiler

Slide 192: 40 broken radials + one IBr2 + one brachial; 193: 30 brachials with Schwimmplatten (8 axillaries); 194: 22 mostly broken radials + 7 brachials; 195: about 17 broken radials + 115 brachials (with Schwimmplatten) + about 92 distal, elongate brachials + one centrale.

Unclassified ossicles

The following material has been sorted by Sieverts-Doreck only to a very limited degree.

Slide 196: Divisum Zone, Steige Beuren-Erkenbrechtsweiler; numerous radials and brachials of several species.

Slide 197: Platynota Zone, untere Roggenmühle near Geislingen; numerous brachials (IBr1, IAx, IIBr)

Slide 198: Platynota Zone (Clay facies), Himmelreich near Bargau; one broken radial of *S. quenstedti*, other crinoid ossicles, ophiuroids.

Slide 199: Hybonotum Zone, Steige Urach–Sirchingen; part of a cup, possibly belonging to *C. feifeli*


Slides 204, 205: Platynota Zone (Clay facies), slopes of Michelsberg; 204: numerous secundibrachials (dumb-bell shaped), some ophiuroids; 205: some elongate brachials, one axillary.

Slide 206: Hypselocyclum Zone, Steige Neidlingen–Eckhof; various echinoderms (ophiuroids, numerous saccocomid brachials), foraminifera.

Slides 207–209: Hypselocyclum Zone (Clay facies), Kornberg near Boll; 207: one elongate IBr1; 208: one elongate IBr1; 209: one elongate IAx.


Slides 212, 213: “Malm α2” Bimammatum Zone, Würgau; 212: 8 elongate brachials (“sp. D”).