



The Cretaceous crab *Rathbunopon*: revision, a new species and new localities

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With 6 figures and 1 table

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Abstract: The crab genus *Rathbunopon* is exclusively known from Cretaceous rocks, mainly from Europe. Here two new European localities are presented: one in the Albian/Cenomanian of northern Spain yielding well-preserved specimens of *Rathbunopon obesum*, and one from the lower Aptian at the German-Austrian border yielding *Rathbunopon schrattenkalkensis* n. sp. Both are found in association with coral reefs. Based upon a revision of the genus, we place *Rathbunopon* within the Prosopidae. Furthermore, *Homolopsis tuberculata* is transferred to *Rathbunopon*. Placement of '*Rathbunopon*' *atherfieldensis* in *Rathbunopon* is not tenable; we place it here within the Homoloidae in open nomenclature. With the addition of *R. tuberculatum*, *Rathbunopon* is interpreted to have evolved in the Hauterivian and diversified in the Albian/Cenomanian. Whereas *R. obesum* resided mainly in reefal settings, *Rathbunopon* species lived in a variety of environments and are suggested to be generalists.

Key words: Cretaceous, decapod, Spain, Austria, Germany, Aptian, Albian, Cenomanian, brachyura, *Rathbunopon*.

1. Introduction

Species of the Cretaceous decapod crustacean *Rathbunopon* STENZEL, 1945 have been reported mainly from Europe with only one occurrence in North America. The type species, *Rathbunopon polyakron* STENZEL, 1945, was described from Texas, USA. Most species are known from Great Britain. Here, we report on two localities, one in Spain and one at the German-Austrian border, yielding *Rathbunopon obesum* (VAN STRAELEN, 1944) and *Rathbunopon schrattenkalkensis* n. sp., respectively. The latter discovery represents the first decapod known to us from this locality and Formation. Furthermore, the genus *Rathbunopon* is revised, and its paleoenvironment and evolution are discussed.

2. Locality and stratigraphy

The abandoned Koskobilo quarry in northern Spain is located about 50 km SSW from the city of San Sebastian (Fig. 1a). Here, Albian/Cenomanian reefal limestones crop out at the edge of the Aldoirar patch reef and are part of the Albinez Unit within the Eguino Formation (LÓPEZ-HORGUE et al. 1996). The age assignment is based on ammonites from both under- and overlying strata, which are dated as late Albian and middle Cenomanian, respectively (LÓPEZ-HORGUE et al. 1996). In addition, orbitolinid foraminifera, typical of Early to mid-Cretaceous strata in southern Europe, have been recorded from this decapod-bearing unit. Crabs in the Koskobilo quarry have been found mainly at the south-

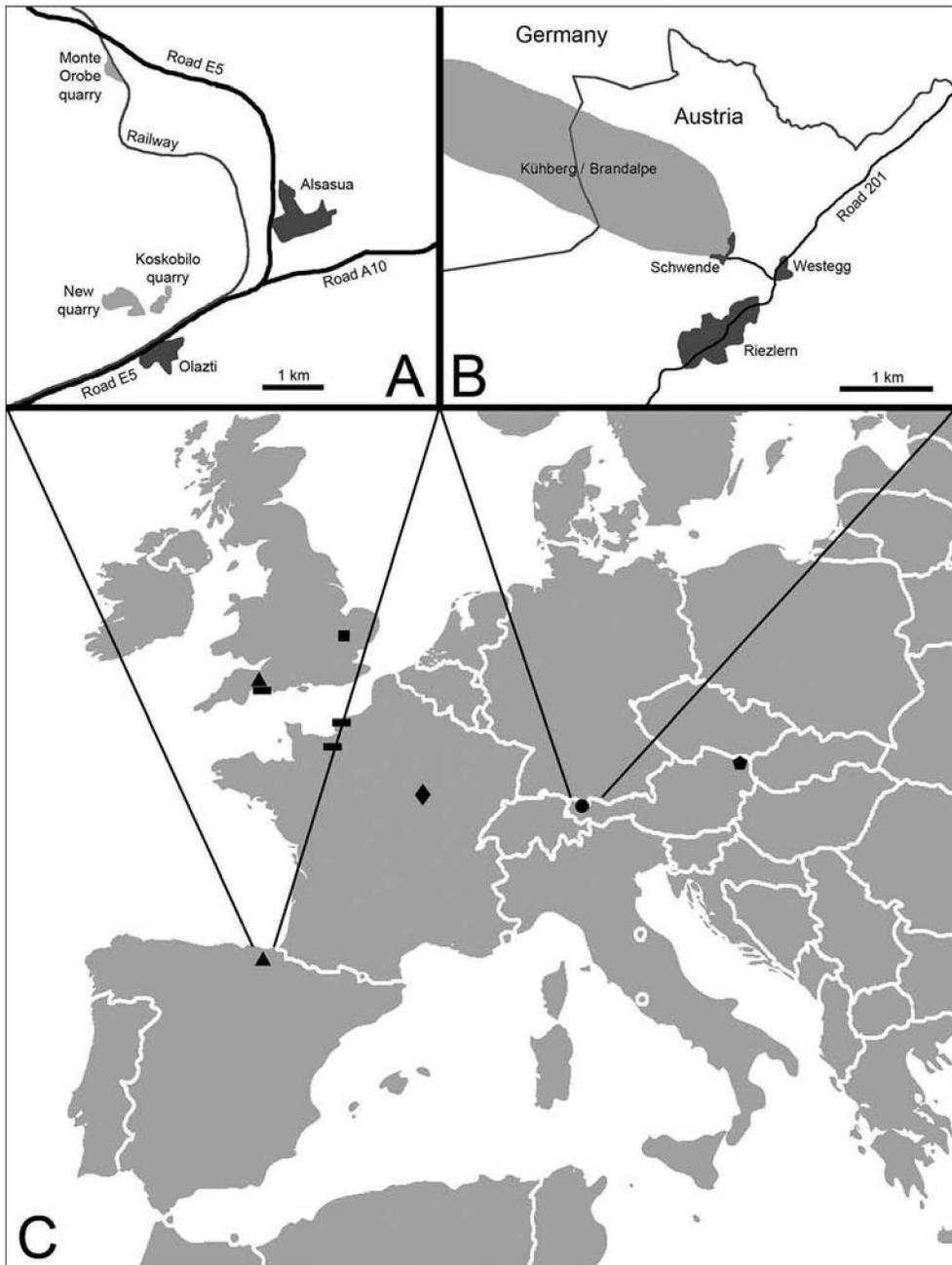


Fig. 1. Map showing localities from where *Rathbunopon* spp. was reported in this study and in literature. **A** – Alsasua, northern Spain, and surroundings showing the Koskobilo and Monte Orobe quarries. **B** – Location of the Kühberg/Brandalpe at the German-Austrian border. **C** – *Rathbunopon* spp. in Europe. Circle = *R. schrattenkalkensis*; triangle = *R. obesum*; square = *R. oblitum*; diamond = *R. tuberculatum*; rectangle = *R. woodsii*; pentagon = *Rathbunopon* sp.; *Rathbunopon polyakron* from Texas (USA) is not displayed here.

ern wall during collecting since 2008. Earlier reports on decapods from this quarry can be found in FRAAIJE et al. (2009) and KLOMPMAKER et al. (2011). Decapods from this quarry are from a similar lithology and age as the decapods from the nearby Monte Orobe quar-

ry (VAN STRAELEN 1940, 1944; RUIZ DE GAONA 1943; BATALLER 1950; VIA BOADA 1981, 1982; GÓMEZ-ALBA 1989; LÓPEZ-HORGUE et al. 1996; FRAAIJE et al. 2008).

The second locality is the Kühberg/Brandalpe, on the German-Austrian border, about two km NW of

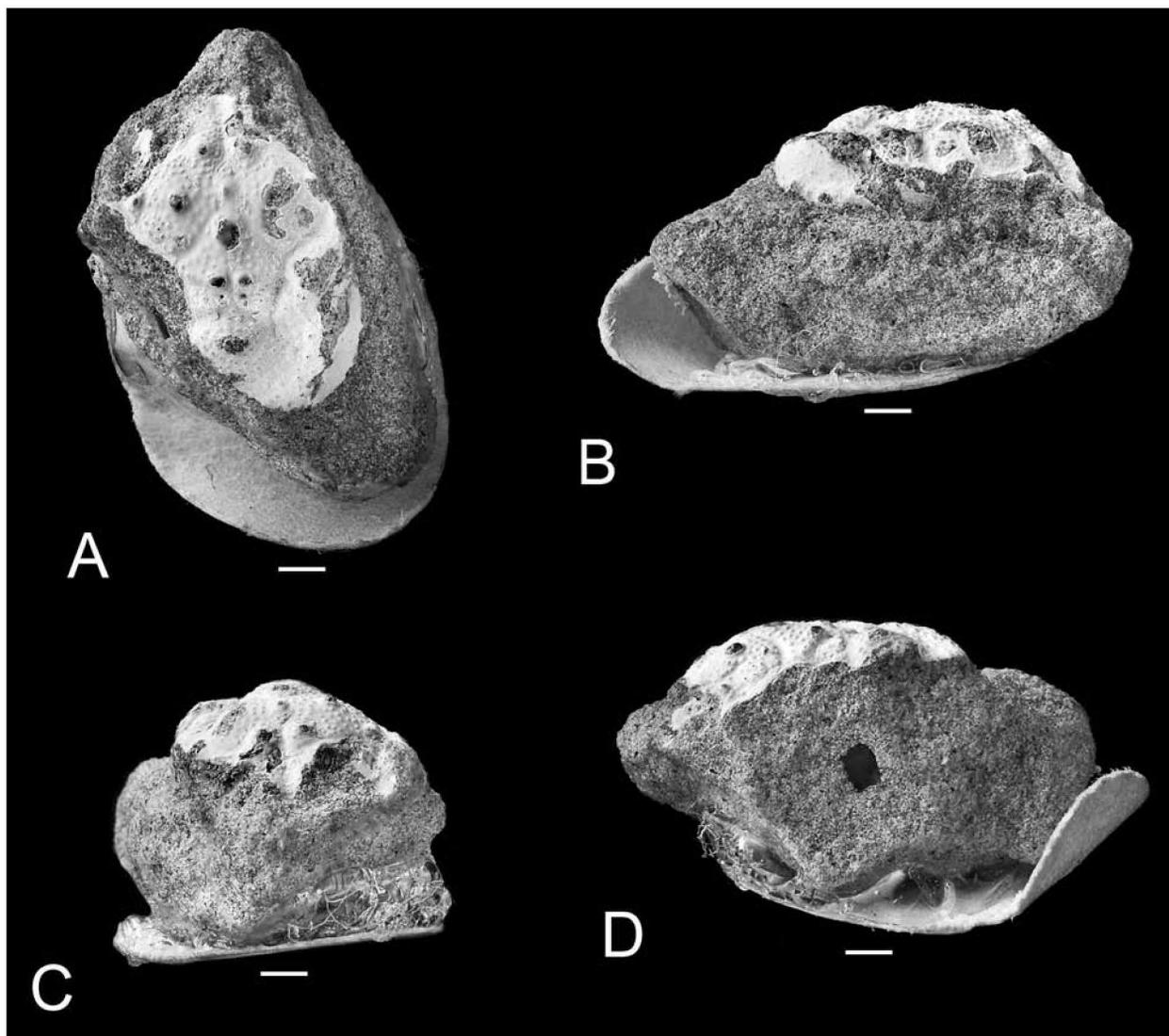


Fig. 2. The type specimen of '*Rathbunopon*' *atherfieldensis* WRIGHT, 1997. **A** – Dorsal view; **B** – right lateral view; **C** – frontal view; **D** – left lateral view. Scale bars equal 1 mm. Copyright: The Natural History Museum, London; Photos by PHIL CRABB.

Riezlern, western Austria (Fig. 1b). The outcrops on this mountain consist of a dark-grey reefal limestone in which corals are abundant. These strata belong to the Schratenkalk Member of the Schratenkalk Formation, which is interpreted to be early Aptian in age (BOLLIGER 1988; CsÁSZÁR et al. 1994).

3. Systematic paleontology

Infraorder Brachyura LINNAEUS, 1758

Section Dromiacea DE HAAN, 1833

Superfamily Homolodromioidea ALCOCK, 1900

Family Prosopidae v. MEYER, 1860

Discussion: Historically, *Rathbunopon* has been placed within the Prosopidae (STENZEL 1945; WITHERS 1951; WRIGHT & COLLINS 1972). SCHWEITZER et al. (2010), however, decided to put it into the Glaessneropsidae in their list of all known fossil decapods. We put it back into the prosopids based on the following criteria: a) *Rathbunopon* resembles other prosopids, especially *Prosopon* v. MEYER, 1835, much more than other glaessneropsids in terms of the location of the regions (see SCHWEITZER & FELDMANN 2009: fig. 2, WEHNER 1988: pl. 1), b) *Rathbunopon* fits the generic diagnosis of the Prosopidae in SCHWEITZER & FELDMANN (2009) and c) it exhibits an augenrest (separated from the actual orbit by a small ridge, sensu SCHWEITZER & FELDMANN 2009), which is unknown in the Glaessneropsidae but present in the Prosopidae (see SCHWEITZER & FELDMANN 2009).

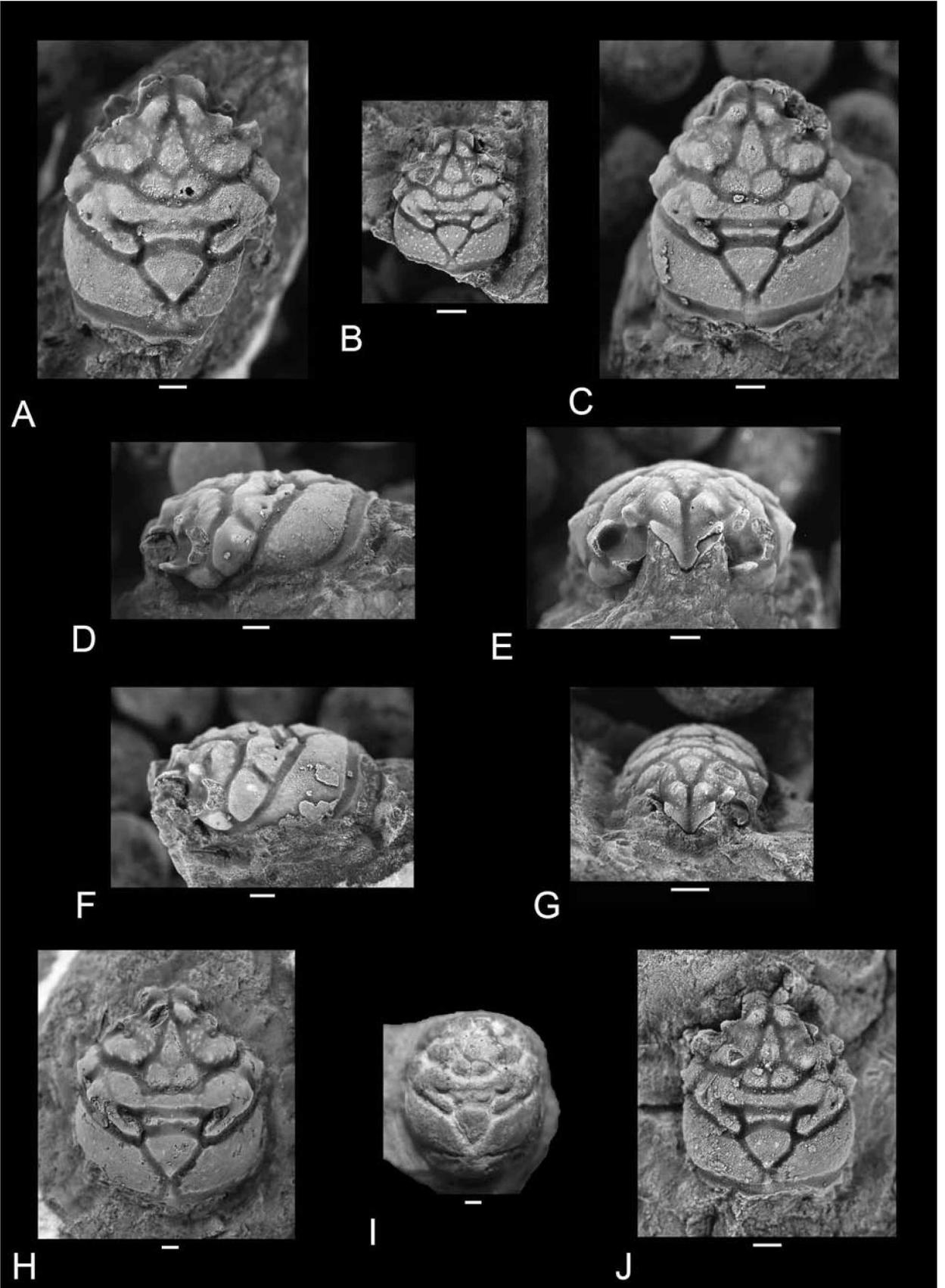


Fig. 3.

Genus *Rathbunopon* STENZEL, 1945

Type species: *Rathbunopon polyakron* STENZEL, 1945.

Other species included: *Rathbunopon obesum* (VAN STRAELEN, 1944); *R. oblitum* (CARTER, 1898); *R. schratenkalkensis* new species; *R. tuberculatum* (VAN STRAELEN, 1936); *R. woodsi* WITHERS, 1951.

Emended diagnosis: Carapace subovoid, slightly longer than wide, strongly convex transversely. Triangular rostrum strongly downturned, with median groove. Well-developed augenrest surrounded by several projections. No rim defining lateral margin. Convex posterior margin with strong groove in front of it. About equally strong, pronounced cervical and branchiocardiac grooves. Subtriangular mesogastric region, usually with three tubercles/raised areas. Epigastric region defined by a tubercle. Cardiac region usually subtriangular. Mesobranchial region bilobed (modified after WRIGHT & COLLINS 1972).

Discussion: Placement of *Rathbunopon atherfieldensis* WRIGHT, 1997 (see SCHWEITZER et al. 2010) in this genus is erroneous. The urogastric region of *R. atherfieldensis* does not fit with the description in the diagnosis of the genus in WRIGHT & COLLINS (1972: 21, “double bar-like urogastric lobe”). Furthermore, the metagastric region is absent in *R. atherfieldensis*, whereas it is mentioned in the generic description of STENZEL (1945). It is also absent in homolids. Moreover, the mesogastric region has a distinctly longer anterior extension than other species of *Rathbunopon*. In addition, it is more subpentagonal, especially posteriorly, and it exhibits four tubercles/raised areas instead of three as in all other species of *Rathbunopon*. The posteriormost two tubercles are placed more toward the longitudinal axis/middle of the mesogastric region compared to other species of *Rathbunopon* in which they often mark the outer side of the mesogastric region. Overall, the latter region is very reminiscent of that in homolids (e.g., *Homolopsis edwardsii* BELL, 1863, *Latheticocarcinus atlanticus* (ROBERTS, 1962), *L. declinatus* (COLLINS, FRAAYE & JAGT, 1995), *L. pikeae* (BISHOP & BRANNEN, 1992) and *L. punctata* (RATHBUN, 1917)). Additionally, the crescent-shaped urogastric lobes of *R. atherfieldensis* (as indicated in WRIGHT 1997: fig. 14) cannot be found in any *Rathbunopon*, but are present in homolids such as *H. edwardsii*, *L. atlantica*, and *L. punctata*. Furthermore, the cardiac region in *R. atherfieldensis* exhibits strong tubercles, not seen in other species of *Rathbunopon*, but present in homolids. The tubercle arrangement of one larger, anterior tubercle and one smaller posterior one on the cardiac region is similar to that region in *H. edwardsii*. The shape of the mesobranchial region is more reminiscent

of homolids than of *Rathbunopon*. In the latter there is a groove incising the inner part in dorsal view. A *linea homolica* was, however, not mentioned by WRIGHT (1997: 137), even though the specimen was “strongly arched in transverse section.” The presence of a *linea homolica* could neither be confirmed nor refuted based on illustrations (Fig. 2). Unfortunately, no details on the orbits/augenrests are given in the description of *R. atherfieldensis*, as this might be the sole, other discrimination between homolids, which do not have true orbits (sensu WRIGHT & COLLINS 1972: 42), and species of *Rathbunopon* which exhibit well-developed orbits. A picture (Fig. 2C) of the frontal part of the specimen, however, shows no clear evidence of pronounced orbits/augenrests. In conclusion, *R. atherfieldensis* does not fit with *Rathbunopon* based on the characters discussed and the fact that there is only one partly preserved specimen available. Although definite placement within a genus within the Homolidae is tempting, we refrain from doing so because of the relatively poor preservation of the specimen compared to other specimens presented here. Instead, we place *R. atherfieldensis* in open nomenclature within the Homolidae.

WRIGHT (1997: 135) mentioned that *Homolopsis tuberculata* VAN STRAELEN, 1936 might be a *Rathbunopon*, which seems justified judging from the illustrations and description of the species. The epigastric, protogastric and mesogastric regions occur on the same location as in *R. obesum*, *R. polyakron* and *R. woodsi* judging from VAN STRAELEN (1936: pl. 4, fig. 4) and photographs provided by the Muséum d’Histoire naturelle in Auxerre, where the type specimen is housed. Moreover, the mesogastric region is subdivided into three parts and it is subtriangular, which is also seen in *R. obesum*, *R. oblitum*, *R. polyakron* and *R. woodsi*. Consistent with *Rathbunopon* spp., the frontal/rostral region is strongly downturned and also exhibits a median groove, the former which is not the case in homolids. In addition, the epibranchial region seems to exhibit a tubercle, as in *R. obesum*, *R. polyakron* and *R. woodsi*. The mesobranchial protuberances in the type specimen of *H. tuberculata* also occur in species of *Rathbunopon*, notably in *R. woodsi* and *R. polyakron*. VAN STRAELEN (1936) did not mention the presence of a *linea homolica* in *H. tuberculata*, a key character of homolids and known at least since CARTER (1898) described this fracturing of the carapace near the lateral margin. Furthermore, the three protuberances paralleling the rim of the augenrest would suggest the augenrests are at least somewhat defined, whereas homolids have poorly defined orbits (SCHWEITZER 2001) and no augenrests. In conclusion, it seems reasonable to transfer tentatively *H. tuberculata* to *Rathbunopon* until new material is available, as the assignment of *R. tuberculatum* is based on a single, incomplete specimen.

Fig. 3. Specimens of *Rathbunopon obesum* (VAN STRAELEN, 1944) from Koskobilo except for I. **A-C** – Dorsal views of the carapace (MAB k3068, MAB k3142 and MAB k3141). **D, F** – Left lateral views (MAB k3068 and MAB k3141). **E, G** – Frontal views (MAB k3068 and MAB k3142). **H, J** – Dorsal views of the carapace (MAB k2611 and MAB k3140). **I** – Dorsal view of a topotype from Monte Orobe (MSGB9577). Scale bars equal 1 mm.

Rathbunopon obesum (VAN STRAELEN, 1944)

Figs. 3-4, 5c

*1944 *Homolopsis obesa* VAN STRAELEN, p. 6-10, pl. 1, fig. 3, 3^a.1950 *Homolopsis obesa*. – BATALLER, p. 150.1972 *Rathbunopon obesum*. – WRIGHT & COLLINS, p. 23-24, pl. 1, fig. 8.1981 *Rathbunopon obesum*. – VIA BOADA, p. 250.1996 *Rathbunopon obesum*. – LÓPEZ-HORGUE et al., p. 93.

Diagnosis: Carapace longer than wide, subovoid, with well-delineated regions, strongly convex transversely. Widest part near mid-length. Grooves fairly deep, branchiocardiac groove as strong as cervical groove. Triangular rostrum with median groove, strongly downturned. Protogastric and epibranchial regions with one tubercle. Mesogastric region with two raised areas posteriorly, and one anteriorly instead of distinct tubercles. Distinctive, subcircular augenrests. Metagastric and mesobranchial regions well-connected. Subtriangular cardiac region.

Description: For the description, the terminology of Fig. 4 is used, which differs from that of STENZEL (1945: fig. 16) for the hepatic and epibranchial regions. Measurements of the specimens are provided in Table 1. Carapace subovoid, slightly longer than wide, widest part near mid-length, strongly convex transversely and moderately convex longitudinally. Frontal/rostral margin convex, with small axial notch in dorsal view; in frontal view strongly downturned at about right angles with longitudinal axis, triangular with rounded tip and median groove. Augenrests subcircular, about forwardly directed; upper margin bearing relatively salient projection. Outer-augenrest projection lanceolate, with a broad base. Infra-augenrest margin defined as a large and salient projection, much more advanced than the supra-augenrest. Curved anterolateral margin highly irregular due to grooves and bulbous regions. First portion of posterolateral margin notched by branchiocardiac groove, broadly arched posteriorly. Posterior margin slightly sinuous with

faint axial concavity. Grooves U-shaped in cross section, smooth and pronounced. Cervical groove sinuous, straight posterior to mesogastric region, pronounced in lateral view. Branchiocardiac groove anterolaterally oriented, as pronounced as cervical groove, but less sinuous, curving anteriorly below subhepatic region and extending along flanks of cardiac region as straight elements. Groove between metabranchial region and posterior rim strongest, follows posterior margin and fades out laterally.

Regions strongly delineated generally, many tubercles/raised regions on anterior carapace. Prominent, subcircular epigastric region somewhat inclined, with strong tubercle flanking the anterior end of mesogastric region. Ellipsoidal protogastric region with tubercle on innermost part, well-delineated posteriorly, more weakly delineated anteriorly, positioned lateral to mid-part of mesogastric region. Subtriangular mesogastric region longer than wide, with slightly concave lateral margins, weakly subdivided into an elongated, frontal part narrowing anteriorly, and two subcircular/elliptical raised regions posteriorly. Small hepatic region obscured by the swollen protogastric lobe. Swollen subtriangular subhepatic region only visible in lateral view, with longest axis directed anteriorly, bounded by anteriorly curving branchiocardiac groove on the lower side, and two grooves on the upper side. Epibranchial region subquadrate to subtriangular, oriented laterally, with an outwardly oriented tubercle situated near the innermost part. Mesobranchial region bilobed with small depression near the outermost part; well-connected with transverse metagastric region. Urogastric region 5-7 times wider than long, narrowest in center, defined by transverse grooves. Triangular cardiac region large, as long as wide, usually with three small granules forming a posteriorly directed triangle; upper margin as wide as urogastric and often slightly convex. Subtriangular/subrectangular metabranchial region largest region on the dorsal carapace. Tiny triangular intestinal region posterior to cardiac region with one edge oriented anteriorly, splits metabranchial regions.

The specimens from Koskobillo do not exhibit complete cuticles and show few scattered pustules on the internal

Table 1. *Rathbunopon* spp.; measurements (in mm) of five specimens of *R. obesum* from Koskobillo (Spain), one (*R. obesum*) from Monte Orobe (Spain) and one (*R. schrattenkalkensis*) from the Kühberg/Brandalpe (German-Austrian border). L1 = Maximum length along longitudinal axis, inclusive of rostrum; W1 = maximum width; L2 = mesogastric length, grooves not included; W2 = mesogastric width, grooves not included; W3 = frontal/rostral width; W4 = orbital width (dorsal view).

	L1	W1	L1/W1	L2	W2	L2/W2	W3	W4
MAB k2611, Koskobillo	13.5	11.4	1.18	4.3	3.2	1.34	3.7	2.2
MAB k3140, Koskobillo	7.5	6.1	1.23	2.3	2.0	1.15	2.3	1.4
MAB k3068, Koskobillo	10.4	7.8	1.33	2.7	2.2	1.23	2.7	1.9
MAB k3141, Koskobillo	10.1	7.0	1.44	2.5	2.0	1.25	2.3	-
MAB k3142, Koskobillo	5.2	4.0	1.30	1.6	1.2	1.33	1.4	-
MSGB9577, Monte Orobe	8.1	7.4	1.09	2.1	2.0	1.05	-	-
MAB k3139, Kühberg/Brandalpe	8.3	8.0	1.04	2.3	1.9	1.21	-	-

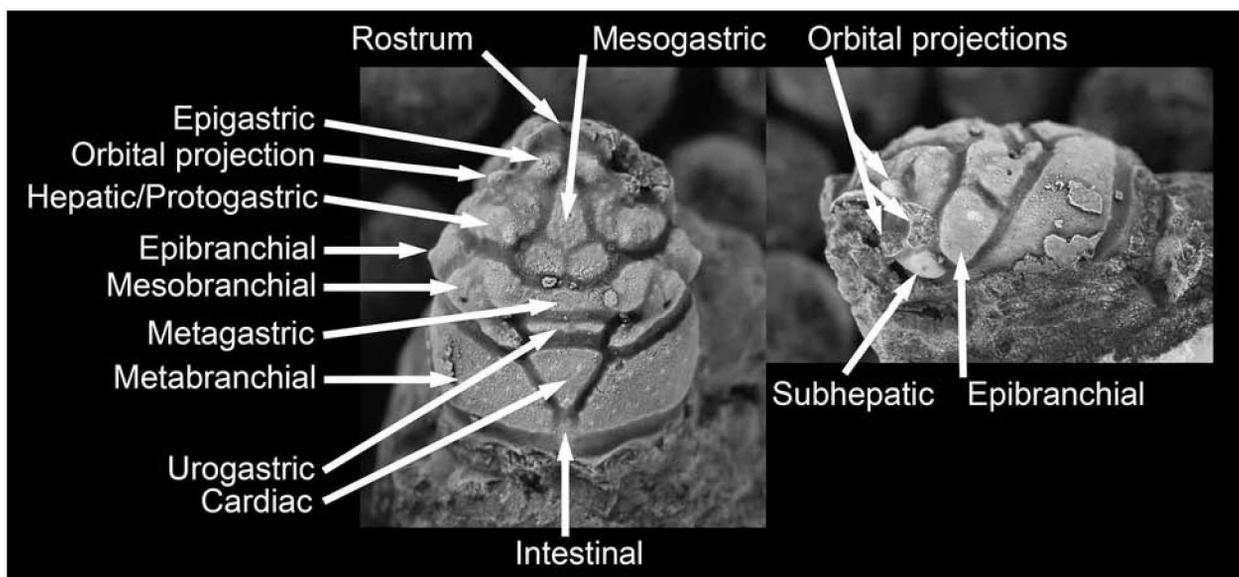


Fig. 4. A specimen (MAB k3141) of *Rathbunopon obesum* (VAN STRAELEN, 1944) with the terminology of the regions used in this study indicated in dorsal and lateral view.

mould of the carapace, which are especially abundant on the mesogastric regions and in the depression between the epigastric and protogastric regions. Abdomina, venters and appendages are not preserved.

Material examined: Specimens MAB k3140-3142, 3068, 2611 from Spain, Koskobilo quarry. These specimens are deposited in the Oertijdmuseum De Groene Poort, Boxtel, The Netherlands. In addition, a topotype from Monte Orobe quarry, MGSB9959, was studied. This specimen is housed in the Museo Geológico del Seminario de Barcelona, Spain. VAN STRAELEN (1944) did not mention where the original type specimen from Monte Orobe was housed, nor did he provide inventory numbers. The type specimen was not encountered in the collections of Museo Geológico del Seminario de Barcelona nor in the collection of the Institut Royal des Sciences naturelles de Belgique in Brussels. Hence, a neotype should be designated in the future.

Occurrence: Specimens from Koskobilo and Monte Orobe, northern Spain, were discovered in the Albian/Cenomanian reefal limestones of the Albinez Unit within the Eguino Formation (LÓPEZ-HORGUE et al. 1996).

Discussion: Neither obvious ontogenetic changes were observed in the studied specimens, nor any variation unrelated to ontogeny. The single specimen of *Rathbunopon oblitum* was not traced according to WRIGHT & COLLINS (1972). Hence, the comparison must be based on the description by CARTER (1898) and the line drawing of the specimen. The cervical groove is positioned more anteriorly in *R. oblitum* than in *R. obesum*. *Rathbunopon oblitum* appears to exhibit three tubercles on the mesogastric region, whereas *R. obesum* has three raised parts. The urogastric region in *R.*

oblitum is significantly larger than in *R. obesum*. The cardiac region is different as well: subpentagonal in *R. oblitum*, but triangular in *R. obesum*. The metabranchial regions are connected posteriorly in *R. oblitum*, whereas a small intestinal region was found for *R. obesum* subdividing the two metabranchial regions. However, this difference might also be due to the probable weathering of the specimen (WRIGHT & COLLINS 1972). The augenrests of *R. oblitum* are small and “four diameters apart” (WRIGHT & COLLINS 1972: 22). In *R. obesum* the augenrests are fairly large and more closely spaced. The concave posterior margin displayed in CARTER (1898: pl. 2, fig. 4) could be a mistake by the artist according to WRIGHT & COLLINS (1972). Lastly, the length-width ratio is larger in *R. obesum* than in *R. oblitum*.

Rathbunopon obesum resembles the type species, *R. polyakron* (Fig. 5A), but, overall, *R. polyakron* has a more tubercular character. The mesogastric region of *R. polyakron* exhibits three distinct subcircular tubercles, whereas this is not the case in specimens of *R. obesum*, which has three raised parts. Moreover, the mesogastric region is significantly longer in *R. obesum* because of a longer anterior process. The tubercles on the mesobranchial and the protogastric regions of *R. polyakron* are more pronounced than in *R. obesum*. The cardiac region in *R. polyakron* is more bulbous and rounder compared to the relatively flat and distinctly triangular cardiac region in *R. obesum*. Furthermore, the augenrest is oval in *R. polyakron*, whereas it is subcircular in *R. obesum*. The widely spaced pits in front of the urogastric region, as seen in the holotype of *R. polyakron*, are absent in *R. obesum*. WRIGHT & COLLINS (1972) mentioned that the tuberculation in *R. polyakron* would have been more extreme than in *R. obesum*, based on the specimen from Great Britain. No evidence for this could be found. Lastly, the metagastric region is well-connected

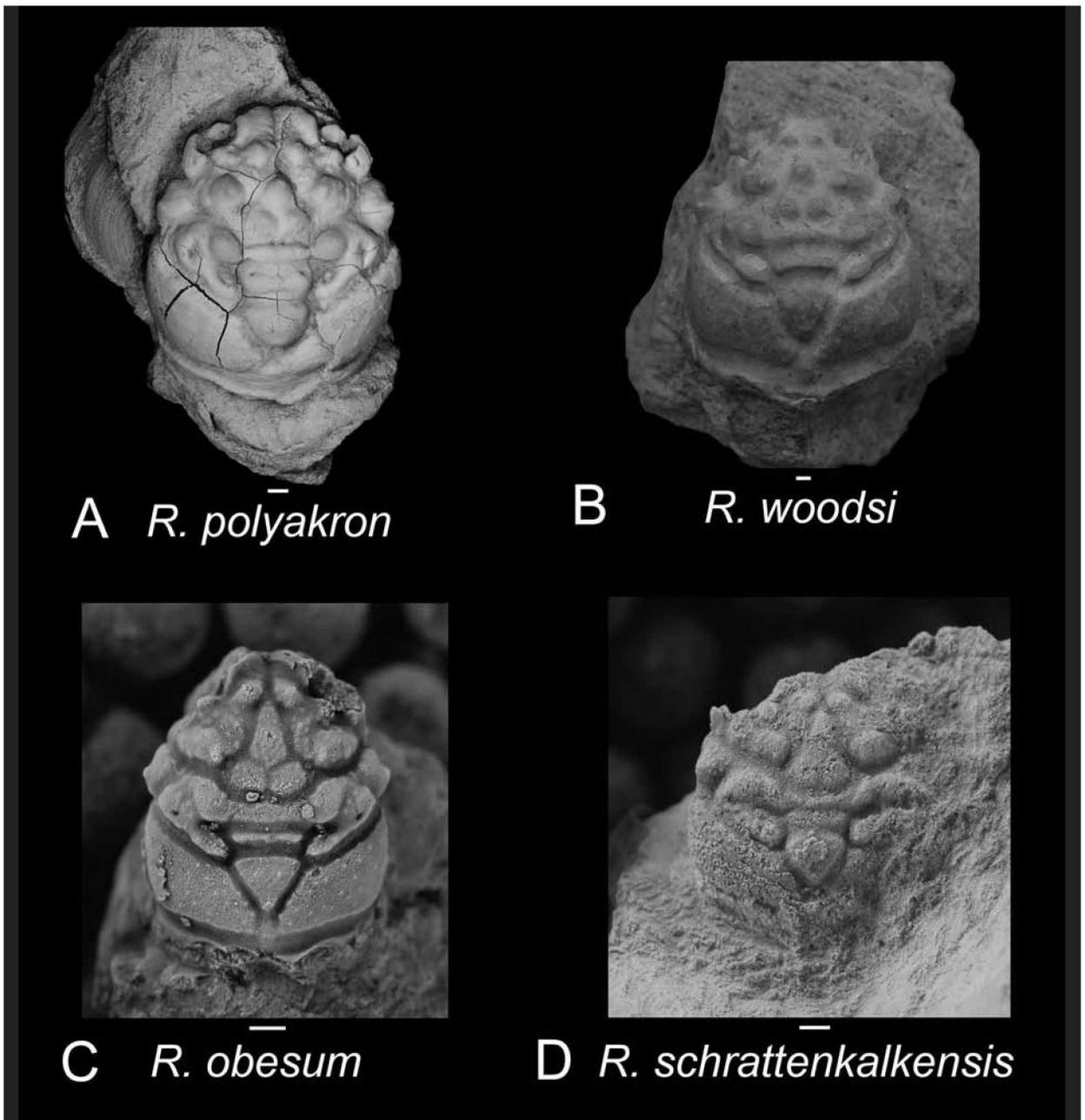


Fig. 5. Several species of *Rathbunopon* in dorsal view for comparison. **A** – Holotype of *Rathbunopon polyakron* STENZEL, 1945 (Bureau of Economic Geology, The University of Texas, BEG 21097). **B** – Holotype of *Rathbunopon woodsi* WITHERS, 1951 (Sedgwick Museum, Cambridge, SM B50779). **C** – Specimen of *Rathbunopon obesum* (VAN STRAELLEN, 1944) (MAB k3141) from Koskobilo, Spain. **D** – Holotype of *Rathbunopon schrattenkalkensis* n. sp. (MAB k3139). Scale bars equal 1 mm.

with the mesobranchial region in *R. obesum*, but weakly connected in *R. polyakron*.

For differences with *R. schrattenkalkensis* n. sp. (Fig. 5D) see below. *Rathbunopon obesum* differs from *R. tuberculatum* in its epibranchial region bearing one instead of two tubercles and in its rim of the augenrest exhibiting only

one tubercle instead of three subparallel protuberances. Additionally, the mesobranchial protuberances in *R. tuberculatum* are less pronounced in *R. obesum*. *Rathbunopon obesum* differs from *R. woodsi* (Fig. 5B) in that the latter has its maximum width posterior to the mid-length, whereas *R. obesum* has its widest part near the mid-length. WITH-

ERS (1951) mentioned the anterior process of the mesogastric region to exhibit a tubercle in *R. woodsi*, which is a raised triangle in *R. obesum*. Similarly, the posteriormost parts of *R. woodsi* consist of tubercles, whereas they are raised areas in *R. obesum*. Moreover, the mesogastric region is significantly longer in *R. obesum* because of a longer anterior process. The most obvious difference is that in *R. woodsi* the metabranchial regions take up significantly more space on the carapace.

WRIGHT (1997) reported two specimens of *R. obesum* from the Cenomanian of Klement, northeastern Austria. Detailed analysis of high-quality pictures of the best preserved specimen (BMNH IC 14), however, seems to show a somewhat rounder cardiac region and a rounder posterior margin of the mesogastric region in comparison with the specimens from Spain, which might be a preservation artifact. The poor preservation of the two specimens does not allow an unambiguous assignment to *R. obesum*. Hence, we refer the specimens to *Rathbunopon* sp.

Rathbunopon schrattenkalkensis n. sp.

Fig. 5D, 6

Holotype: MAB k3139, housed in the Oertijdmuseum De Groene Poort, Boxtel, The Netherlands. For measurements see Table 1.

Etymology: After the lower Aptian Schrattenkalk Member of the Schrattenkalk Formation in which the specimen was discovered.

Diagnosis: Carapace subovoid, about as long as wide, widest part in metabranchial region, slightly convex transversely and longitudinally. Grooves fairly deep, branchiocardiac groove as strong as cervical groove. Hepatic region present as separate tubercle. Protogastric and epibranchial regions consisting of one tubercle. Mesogastric region with two raised areas posteriorly, and one anteriorly instead of distinct tubercles. Metagastric and mesobranchial regions interconnected. Metagastric and urogastric regions equally long. Subtriangular, slightly swollen cardiac region. Cuticle with indented pustules.

Description: Carapace subovoid, about as long as wide, widest part in metabranchial region, slightly convex transversely and longitudinally. Frontal/rostral margin with axial notch in dorsal view; in frontal view downturned. Augenrests and orbits not preserved. Upper margin of the augenrest bears one orbital tubercle; outer projection lanceolate. Curved anterolateral margin highly irregular due to grooves and bulbous regions. First portion of posterolateral margin notched by branchiocardiac groove, arched posteriorly. Posterior part lateral margin strongly arched in lateral view. Posterior margin not preserved. Grooves U-shaped in cross section, smooth and pronounced. Cervical groove slightly sinuous. Branchiocardiac groove anterolaterally oriented, equally pronounced as cervical groove.

Regions strongly delineated generally, many tubercles/raised regions on anterior carapace. Epigastric region with tubercle flanking anterior end of mesogastric region. Pro-

togastric region ellipsoidal and tubercular. Subtriangular mesogastric region longer than wide, with slightly concave lateral margins, weakly subdivided anteriorly into an elongated, frontal part narrowing, and posteriorly into two subcircular/elliptical raised regions. Small hepatic region consists of a tubercle, situated in between tubercle on upper part of augenrest and outer projection. Epibranchial region subquadrate, oriented laterally, with a tubercle situated near innermost part pointing upward. Mesobranchial regions bilobed, connected with transversely oriented metagastric region. Urogastric region wider than long. Swollen, triangular cardiac region as long as wide; upper margin as wide as urogastric region. Subtriangular/subrectangular metabranchial region is largest region on the dorsal carapace.

Cuticle preserved on left metabranchial region exhibits a pustulate character; pustules indented in the center and on the epibranchial region, where the pustules are smaller. Abdomen, venter and appendages are not preserved.

Occurrence: The specimen from the Kühberg/Brandalpe on the German-Austrian border was found in reefal limestones of the lower Aptian Schrattenkalk Member of the Schrattenkalk Formation.

Discussion: The specimen closely resembles *Rathbunopon obesum*, although some key differences exist. The widest part is in the metabranchial region in *Rathbunopon schrattenkalkensis* n. sp., not close to mid-length as in *R. obesum*. Overall, *R. schrattenkalkensis* is significantly less convex, both longitudinally and transversely. This could be due to the compression of the carapace, which would explain the fact that its length-width ratio is lower than in *R. obesum*. But, no breakage of the carapace was observed in lateral view, which suggests this was not caused by diagenesis (Fig. 6). The hepatic region is not fused with the protogastric region as in *R. obesum*, but there is a tubercle developed anterolaterally to the protogastric region in *R. schrattenkalkensis*. The tubercle on the epibranchial region is more upwardly directed than in *R. obesum* in which it is laterally oriented. Furthermore, in *R. obesum* the antero-axial part of the mesobranchial region is more pronounced resulting in a more sinuous cervical groove. The metagastric and urogastric regions are equally long in *R. schrattenkalkensis*, whereas the metagastric region is about twice as long compared to the urogastric region in *R. obesum*. The metagastric region in *R. schrattenkalkensis* is lower compared to the mesobranchial region, but about equally high in *R. obesum*. The urogastric region is less defined by the grooves compared to *R. obesum*. The cardiac region in *R. schrattenkalkensis* seems to have slightly rounder edges and is more swollen. The posterior part of the lateral margin is stronger arched in *R. schrattenkalkensis* than in *R. obesum* in lateral view. The number of differences and the fact that specimens of *R. obesum* do not show any variation warrant the description of this specimen as a new species.

The single specimen of *R. oblitum* exhibits a cervical groove that is more anteriorly positioned in *R. oblitum* than in *R. schrattenkalkensis*. *Rathbunopon oblitum* appears to exhibit three tubercles on the mesogastric region, whereas *R. schrattenkalkensis* has three raised parts instead. The urogastric region in *R. oblitum* is significantly larger than in

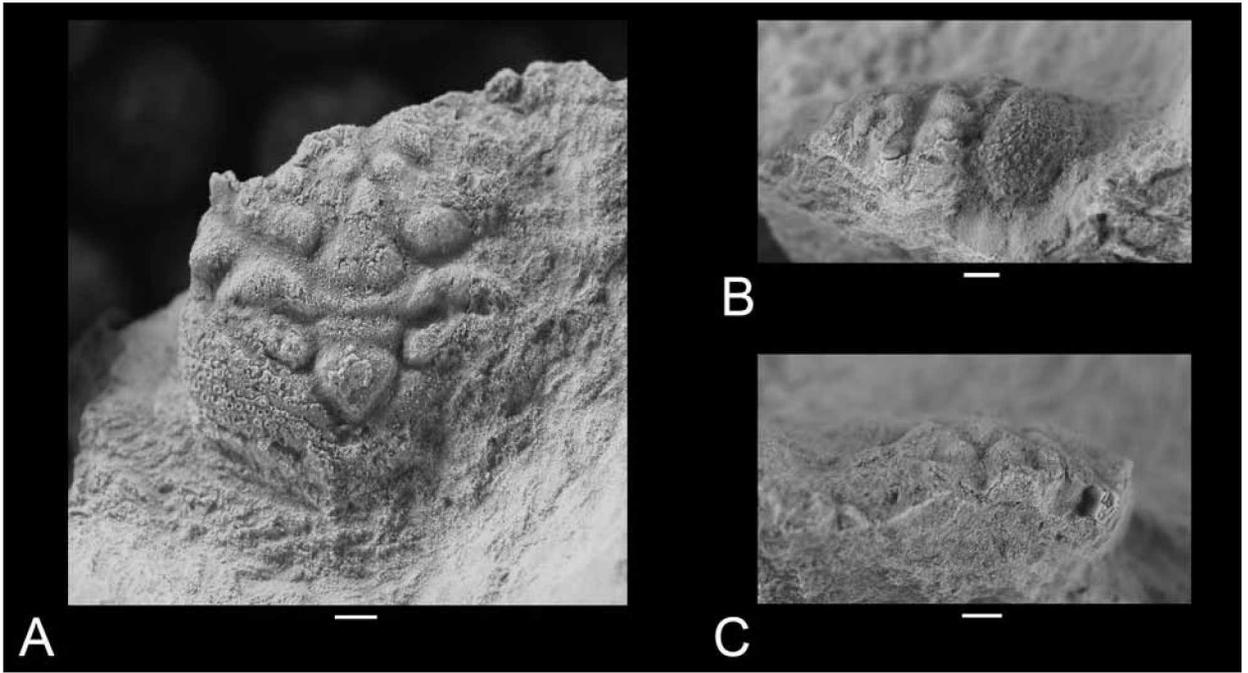


Fig. 6. The monotypic holotype of *Rathbunopon schrattenkalkensis* n. sp. (MAB k3139). **A** – Dorsal view; **B** – lateral view; **C** – frontal view. Scale bars equal 1 mm.

R. schrattenkalkensis. The cardiac region is subpentagonal in *R. oblitum*, but triangular in *R. schrattenkalkensis*.

Rathbunopon polyakron (Fig. 5A) has a more tubercular character than *R. schrattenkalkensis*. The mesogastric region of *R. polyakron* exhibits three distinct subcircular tubercles, whereas this is not the case in *R. schrattenkalkensis*, which exhibits three raised parts. Moreover, the mesogastric region is significantly longer in *R. schrattenkalkensis* because of a longer anterior process. The proto-gastric tubercle on *R. polyakron* is more pronounced than in *R. schrattenkalkensis* as well as the tubercles on the meso-branchial regions lateral to the metagastric region. The cardiac region of *R. polyakron* is more bulbous and exhibits a rounder posterior edge than in *R. schrattenkalkensis*. The widely spaced pits in front of the urogastric region, as seen in the holotype of *R. polyakron*, are absent in *R. schrattenkalkensis*.

Rathbunopon schrattenkalkensis differs from *R. tuberculatum* by its epibranchial region bearing one instead of two tubercles and by its margin of the augenrest showing two tubercles (inclusive of hepatic region) instead of three parallel tubercles.

Rathbunopon schrattenkalkensis differs from *R. woodsi* (Fig. 5B) in its ornamentation. WITHERS (1951: 180) mentioned that *R. woodsi* “must either have been smooth or very finely granulated” based on the surface of the cuticle being preserved in some places. Based on the cuticle preserved on the left metabranchial region *R. schrattenkalkensis* appears to have exhibited distinct pustules at least on some parts of the carapace. Furthermore, WITHERS (1951) men-

tioned the anterior process of the mesogastric region to exhibit a tubercle in *R. woodsi*, which is a raised triangle in *R. schrattenkalkensis*. Similarly, the posteriormost parts of *R. woodsi* consist of tubercles, whereas these are raised areas in *R. schrattenkalkensis*. Moreover, the mesogastric region is significantly longer in *R. schrattenkalkensis*. The most obvious difference is that the metabranchial regions are relatively larger in *R. woodsi*.

4. Evolution and paleoenvironment

Based upon the finds thus far known, *Rathbunopon* evolved in the Early Cretaceous (Hauterivian) and then diversified in the Albian and Cenomanian. *Rathbunopon obesum*, *R. polyakron*, *R. schrattenkalkensis*, *R. tuberculatum* and *R. woodsi* resemble each other closely, whereas *R. oblitum* seems more distantly related. Given the Hauterivian age of the *R. tuberculatum*, this species might have given rise to the younger *R. obesum*, *R. polyakron*, *R. schrattenkalkensis*, and *R. woodsi*. WRIGHT & COLLINS (1972) suggested that *Rathbunopon* might have derived from *Prosopon* v. MEYER, 1835 after BEURLIN (1928), who recognized that *Prosopon tuberosum* v. MEYER, 1840 and *R. oblitum* show similarities. Indeed, *Rathbunopon* and some prosopids (e.g., *Prosopon abbrevatum* SCHWEITZER &

FELDMANN, 2009, *P. aculeatum* v. MEYER, 1857, and *P. verrucosum* REUSS, 1858) show a high degree of similarity, especially in the regions posterior to the cervical groove (see SCHWEITZER & FELDMANN 2009: fig. 2). We, thus, propose that *Proposon* might have been a predecessor of *Rathbunopon*.

Hitherto, *Rathbunopon obesum* was known from the Cenomanian sands in Wilmington, Devon, southwestern Great Britain (WRIGHT & COLLINS 1972), and from the Albian/Cenomanian reefal limestones of Monte Orobe, northern Spain (VAN STRAELEN 1944) (Fig. 1C). The new finds from Koskobilo, from the same strata as Monte Orobe (4 km N of Koskobilo), add a third locality where *R. obesum* has been found. *Rathbunopon obesum*, thus, resided mostly in reefal environments.

The holotype of *R. polyakron* was discovered in the Cenomanian of Texas, USA (Grayson marl, Wasita Group, Comanche Series) (STENZEL 1945). The upper Albian specimen of *R. oblitum* was found in the Cambridge Greensand, Cambridge, southeastern England (CARTER 1898; WRIGHT & COLLINS 1972). *Rathbunopon woodsii* was found in a Cenomanian limestone at Beer Head, Devon, southwestern England (WITHERS 1951; WRIGHT & COLLINS 1972). Additionally, this species was also encountered in the Cenomanian of Pétreval (BRETON & COLLINS, this volume) and Le Billot (BRETON 2009), northwestern France. In the former case the rock was a calcareous, glauconitic sandstone with some chalk; in the latter a sandy glauconite/calcareous sandstone (BRETON 2009). The Hauterivian *R. tuberculatum* was found in a grey limestone in the vicinity of Auxerre, France (VAN STRAELEN 1936). The sole specimen of *R. schrattenkalkensis* was found in an Aptian coral reef environment near the German-Austrian border. Species of *Rathbunopon* were thus able to cope with a variety of environments and are considered to be generalists.

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