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***Gabaleryon*, a new genus of widespread early Toarcian polychelidan**

lobsters

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Polychelidan lobsters are decapod crustaceans with a unique anatomy: a dorsoventrally flattened carapace, four to five pairs of chelate appendages and a completely reduced rostrum. These crustaceans, like most other malacostracans are mostly preserved in outcrops in which exceptional preservation occurs, the Fossil-Konservat-Lagerstätten. Unfortunately, Lagerstätten are rare, and therefore disjointed both geographically and stratigraphically. This study focuses on a new genus of polychelidan lobster, *Gabaleryon*, with the description of two new species, *Gabaleryon coquelae* (Toarcian, France), and *G. garassinoi* (Toarcian, Italy). The long-standing question of the generic assignment of *Eryon moorei* (Toarcian, United-Kingdom) is herein solved and the species is ascribed to *Gabaleryon*. The occurrences of these three species and a fourth, *Gabaleryon* sp. 1 (Toarcian, Germany), provide a first palaeobiogeographic indication that the Fossil-Lagerstätten in which they occur were linked during Toarcian times. Besides, the occurrence of a possible fifth species of *Gabaleryon* in the late Bajocian – early Bathonian of France would extend the stratigraphic distribution of the new genus. Finally these new species increase our knowledge of the fossil polychelidans and place the Toarcian as their second peak of palaeobiodiversity, after that at the Kimmeridgian-Tithonian boundary.

Key words : Fossil-Lagerstätte, palaeobiogeography, Early Jurassic, Crustacea, Polychelida, Toarcian Oceanic Anoxic Event.

Introduction

Polychelidan lobsters (Polychelida) are fascinating decapod crustaceans characterized by an unusual morphology: a dorsoventrally flattened body, a complete reduction of rostrum and four to five chelae (up to three in other decapod crustaceans). Fossil polychelidan lobsters are almost exclusively known from Fossil-Lagerstätten – outcrops in which exceptional preservation occurs. For this reason, distribution of polychelidans is geographically and stratigraphically discontinuous. Though polychelidans occur abundantly from the Middle Triassic to Late Jurassic, they become extremely rare during the Cretaceous and then disappear from the fossil record. Yet, they are represented in modern environments by only one family, the Polychelidae Wood-Mason, 1874 (Fig. 1). Another discontinuity can be seen in their geographical distribution. While extant species are distributed worldwide (Galil 2000), fossil polychelidans seem mostly confined to Europe (e.g., Glaessner 1969; Garassino & Schweigert 2006; Feldmann *et al.* 2013; Audo 2014; Audo *et al.* 2014a, 2014b, 2014c; Bravi *et al.* 2014); with very few occurrences outside Europe: Canada (1 specimen: Feldmann *et al.* 2013); India (1 specimen: Feistmantel 1877); Lebanon (2 larval specimens: Haug *et al.* 2015); Japan (5 specimens: Karasawa *et al.* 2003); and Siberia (5 specimens: Chernyshev 1930).

As with other crustaceans and arthropods (Wills 2001), these discontinuities are probably due to their low preservation potential. Indeed, the fossil diversity of polychelidans is almost entirely documented from their occurrences in Fossil-Lagerstätten (Fig. 1). The apparent fossil diversity of polychelidans clearly reaches a peak at the Kimmeridgian-Tithonian boundary. This period coincides with the extensive deposition of plattenkalks, such as the celebrated Solnhofen-type outcrops, which have yielded many species of polychelidans (Oppel 1862; Garassino & Schweigert 2006; Audo *et al.* 2014a, 2014b). The second peak in diversity occurs during the Sinemurian, with the deposits at Osteno (Italy: Pinna 1968, 1969; Teruzzi 1990) and Lyme-Regis (United Kingdom: Woods 1925), which also yielded many species of polychelidans. The third peak of polychelidans diversity occurs in the early Toarcian. Most early Toarcian polychelidan species are documented from the celebrated Holzmaden area and a few other German outcrops (Beurlen 1928, 1930, 1944; Kuhn 1952; Hauff & Hauff 1981). Among these Toarcian species, many are assigned to the genus *Proeryon* Beurlen, 1928, which has a geographically wide range, since it occurs in Germany, France and Siberia (Audo 2014).

In this study, we describe recently discovered specimens of Polychelida from the Toarcian of Brenoux (France) and reinvestigate closely allied species from rarely studied outcrops in France, England, Italy and Germany, all Toarcian in age. In addition, we studied one younger specimen from the late Bajocian – early Bathonian of Sennecey-le-Grand (France). Our new observations allow the description of one new genus and two new species. This taxonomic work improves our knowledge of polychelidan fossil diversity and allows us to study their palaeobiogeographic significance.

Institutional abbreviations. **BRLSI**, Bath Royal Literary and Scientific Institution, Bath, United Kingdom; **MNHN.F**, Collection de Paléontologie, Muséum national d’Histoire naturelle, Paris, France; **MSNM**, Museo civico di Storia naturale di Milano.

Geological settings and stratigraphy

All studied specimens were collected in five outcrops (Fig. 2) located in France (Brenoux), England (Strawberry Bank), Italy (two outcrops of Sogno Formation) and Germany (Engetal valley), which are all dated into the early Toarcian. An additional specimen from Sennecey-le-Grand (late Bajocian – early Bathonian, France) will also be considered.

Brenoux

Brenoux’s outcrop lies at the north-eastern flank of the Balduc inlier, near the village of Brenoux (Lozère department, France, about 5 km of Mende). Rocks cropping out in Balduc are dated from the late Pliensbachian to the Aalenian (Coquel-Poussy 2013). Among these, the Toarcian sequence is mostly represented by the so-called *schistes-carton*: bituminous, thinly bedded calcareous marls. At the base of these marls, a greyish limestone bed occurs. A second limestone bed is intercalated within the marls, about one meter above the first one. The lower limestone bed (basal Toarcian) has yielded a beautifully preserved fauna including many fishes attributed to *Leptolepis* cf. *coryphaenoides* (Bronn, 1830), two polychelidans and a fragment of a cephalopod with its ink sac.

Strawberry Bank

The Strawberry Bank Lagerstätte yielded a diverse fossil fauna consisting of marine nektonic animals such as fish, crocodiles (Pierce & Benton 2006), ichthyosaurs (Caine & Benton 2011; Marek *et al.* 2015), cephalopods and crustaceans together with abundant insects from a nearby land mass (Williams *et al.* in press). The fossils are preserved in buff-coloured calcareous nodules composed of poorly sorted biomicritic mudstone. The fossils are generally

articulated and preservation is very fine; the vertebrates are typically three-dimensional (showing little or no compaction) and numerous delicate and soft tissue structures are preserved (Williams *et al.* 2015). However, this Lagerstätte is known from just one collection made in the 1840s by Charles Moore from a quarry on the edge of the town of Ilminster, Somerset, England (Copp *et al.* 1999). Unfortunately the quarry was infilled in the late 1850s and its exact location is currently unknown. There is little or no local exposure, but fortunately Moore (1866) recorded the section, which alongside his collection held by BRLSI, enables precise lithostratigraphic correlation. Moore's extensive Strawberry Bank collection was largely ignored until the last decade (Williams *et al.* 2015), though at the time of writing the fossils were the subject of intense scientific scrutiny. Other comparable sites which preserve coeval faunas include Whitby in Northern England, Holzmaden in Southern Germany, and several sites in France (e.g. Charnay in South-East France) (Williams *et al.* 2015).

Outcrops of Sogno Formation

The Sogno ("the dream") Formation crops out on the southern flank of the mount Brughetto, *ca* 10 km southeast of Lecco, Province of Lecco, Lombardy, Italy, and on the southern flank of the mount Cornizzolo (*ca* 8 km southwest of Lecco). During Toarcian, the Sogno Formation was deposited on the edge of the Trento Plateau. Three lithologies are recognized in this formation; the basal one is dated into the early Toarcian (Tenuicostatum ammonite biozone) and yields a varied fauna including exceptionally preserved fossils (Tintori 1977; Gaetani & Poliani 1978; Garassino & Teruzzi 2001; Schweigert *et al.* 2003; Garassino & Gironi 2005; Delfino & Dal Sasso 2006). This fauna comprises actinopterygian fishes (*Leptolepis coryphaenoides*, *Pachycormus* sp., *Pholidophorus* sp.), a marine reptile (possibly *Pelagosaurus* Bronn, 1842), crustaceans (?*Antrimpos* Münster, 1839, *Gabaleryon garassinoi* nov. gen., nov. sp., *Uncina alpina* Schweigert *et al.*, 2003, ?*Etallonia* Oppel, 1861), bivalves (*Bositra* sp.), cephalopods (see Tintori 1977) and fragments of terrestrial plants (see Tintori 1977).

Engetal valley

The studied specimen from the Northern Calcareous Alps comes from the middle part of the Allgäu Formation (today part of the Austroalpine Allgäu Nappe), which includes dark, bituminous, sometimes manganiferous shales (so-called *Manganschiefer*). These bituminous shales can be dated with the help of some ammonites listed by Jacobshagen (1965) as early Toarcian in age. The exact locality is situated in the Engetal valley, southwest of the town of

Pfronten, in the southernmost part of Germany, *ca* 2 kilometres north of the Austrian border. Besides the new specimen of polychelidan lobster, a single chela of *Uncina alpina* Schweigert, Garassino, Hall, Hauff & Karasawa, 2003 was found at this locality. Although these finds point to some potential for exceptional preservation, the locality was never systematically sampled.

Sennecey-Le-Grand

The outcrop lies about 2 km south of the town of Sennecey-le-Grand (Saône-et-Loire department, France). This outcrop is mostly known for yielding beautifully preserved echinoderms (Meyer 1990), including articulated asteroids, ophiuroids and crinoids (Lang 2012); but is still poorly documented in scientific literature. The outcrop belongs to the *Marnes à Acuminata* Formation which is dated into the late Bajocian – early Bathonian (Pellenard *et al.* 1998).

Material and methods

Examined material

In total, 23 specimens were used in this study:

- 2 specimens collected from the base of Toarcian at Brenoux (Lozère Department, France) by Nathalie Coquel-Poussy (specimen MNHN.F.A51506 and one housed in Nathalie Coquel-Poussy's private collection).
- 1 specimen of *Eryon moorei* Woodward, 1866 (holotype: BRLSI M1247) from Ilminster (Somerset, United Kingdom), historically collected by Charles Moore.
- 19 specimens ascribed to *Proeryon hartmanni* (Meyer, 1836) (Garassino & Gironi 2005), from the Sogno formation at mount Cornizzolo (MSNM i26211-i26216, i26218, i26220, i26221, i26223-i26225, i26227, i26233-i26237, i26284).
- 1 specimen ascribed to *Coleia* cf. *banzensis* Kuhn, 1952 (Garassino & Teruzzi 2001), from the Sogno formation at mount Brughetto (MSNM i10850).

Imagery

The study of the holotype of *Eryon moorei* and the specimen of *Coleia* cf. *banzensis* are based on high-resolution pictures. Specimens from Brenoux and mount Cornizzolo were imaged using cross-polarized lights and/or UV fluorescence photography. These techniques help achieving a greater contrast between the fossil and matrix either by removing most

surface reflection (cross-polarization) or by fluorescence of mineral occurring in the fossil (yellow fluorescence under UV light).

Systematic palaeontology

Class **Malacostraca** Latreille, 1802

Order **Decapoda** Latreille, 1802

Suborder **Pleocyemata** Burkenroad, 1963

Polychelida Scholtz & Richter, 1995

Superfamily **Eryonoidea** Haan, 1841

Family **Coleiidae** Van Straelen, 1925

Genus *Gabaleryon* nov. gen.

Included species. *Gabaleryon coquelae* nov. sp., *Gabaleryon garassinoi* nov. sp., *Gabaleryon moorei* (Woodward, 1866) nov. comb.

Type species. *Gabaleryon coquelae* nov. sp.

Occurrence. Toarcian (France, England, Italy, Germany) – late Bajocian – early Bathonian (France) (?).

Etymology. A combination of the Gabali, Gallic tribe that inhabited the region, where the type species occurs and *Eryon* Desmarest, 1817, generic name for the first described species of Polychelida Scholtz & Richter, 1995.

Diagnosis. Dorsoventrally flattened carapace, with an ovoid outline in dorsal view; ocular incision widely open laterally; cervical and postcervical incisions forming minute indentations of lateral margin; axial carina on pleonites 2 to 5 cut by the deep posterior transverse groove; very rounded scaphocerite.

Comments. *Gabaleryon* nov. gen. is ascribed to Polychelida by its four pairs of chelate pereopods, its dorsoventrally flattened carapace and the absence of rostrum, which is replaced by a concave frontal margin (Fig. 3F). It is distinguished from all other polychelidan genera by its unique combination of characters. It differs from all genera of polychelidan lobsters, with the exception of *Proeryon* Beurlen, 1928 (Coleiidae), *Willemoesiocaris* Van Straelen, 1925 (Coleiidae), *Palaeopolycheles* Knebel, 1907 (Coleiidae), and *Tethyseryon* Bravi *et al.*, 2014 (Coleiidae), by an axial carina on pleonal terga cut by posterior transverse groove (Fig. 3). It differs from all these genera by very shallow cervical and postcervical incisions (Fig. 3). Furthermore, it differs from *Willemoesiocaris* and *Palaeopolycheles* by its short anterolateral angle (Fig. 3). *Gabaleryon* nov. gen. seems phylogenetically related to

Proeryon. Indeed, it possesses characteristics also known in *Proeryon*: a short anterolateral angle, a wide and rounded scaphocerite and pleonal terga with an axial carina cut by posterior transverse groove. *Proeryon* is currently ascribed to Coleiidae. For this reason, it seems reasonable to place *Gabaleryon* within the same family. However, we point out that the diverse Coleiidae are considered as possibly paraphyletic (Audo *et al.* 2014c) and the familial assignment of *Gabaleryon* may change.

Gabaleryon coquelae nov. sp.

Figs 3F, 4

2013 *Eryon* sp.; Coquel-Poussy: 10-13, figs 10-11.

Etymology. The specific epithet honours Nathalie Coquel-Poussy, who discovered the type material and introduced it to the scientific community.

Type material. Holotype with part and counterpart of a flattened, subcomplete specimen in dorsal view (MNHN.F.A51506); Paratype with part and counterpart of a flattened, subcomplete specimen in ventral view (N. Coquel-Poussy's private collection).

Type locality. Brenoux (Lozère department, France).

Type age. Early (basal) Toarcian (Coquel-Poussy 2013).

Occurrence. Hitherto only known from the type locality.

Diagnosis. Dorsoventrally flattened carapace, with an ovoid to subrectangular outline in dorsal view; ocular incision widely open laterally; shallow cephalothoracic grooves; postcervical groove effaced or absent between branchial carina and median line; cervical and postcervical incisions forming minute indentations of lateral margin; axial carina on pleonites 2 to 5 cut by deep posterior transverse groove; very rounded scaphocerite; first pereopod with long palm; long uropod.

Description.

Shape of carapace. — Dorsoventrally flattened carapace, with ovoid outline in dorsal view; concave frontal margin; short anterolateral angle; lateral margin cut by ocular, cervical and postcervical incisions; large ocular incision widely open laterally and closed ventrally; anterolateral margin slightly convex, subparallel to longitudinal axis; cervical and postcervical incisions opening in the first half of the lateral margin; very small cervical incision; straight mediolateral margin slightly shorter than anterolateral margin; very small postcervical incision; posterolateral margin slightly convex; rounded posterolateral angle, contiguous with pleon, extending shortly along first pleonite; concave posterior margin, wider than frontal margin.

Carinae and grooves of carapace. — Postrostral and postcervical carinae separated by cervical groove; slightly raised postrostral and postcervical carinae, poorly preserved; postorbital carina not visible; branchial carina extending anteriorly from posterolateral angle toward ocular incision cut by postcervical and cervical grooves, not reaching ocular incision; shallow and curved cervical groove cutting deeply median line in the middle of carapace length; shallow and transverse postcervical groove, not preserved between branchial carina and median line.

Pleon and telson. — Pleon and telson slightly longer than carapace; pleon slightly narrower than carapace; pleonite 1 poorly preserved; pleonites 2-6 of decreasing width; tergum of pleonites 2 to 6 crossed by a pair of transversal grooves converging medially and cutting axial carina, anterior one being slightly deeper than the other and separated from pleonite anterior margin by a slightly cambered zone; pleonites 2-5 tergopleura not preserved; subtriangular telson strengthened by two longitudinal carinae.

Eye and cephalic appendages. — Large eye slightly projected from ocular incision; antennula not preserved; antenna with short basipodite carrying (1) very rounded scaphocerite strengthened by median carina and (2) endopod forming a long flagellum measuring about one third of carapace length; other cephalic appendages not preserved.

Thoracic appendages. — Third maxilliped with reniform ischium, and stout merus-dactylus; first pereopod distinctly larger than others, with dactylus and pollex strongly curved distally, palm as long as dactylus and subtriangular carpus; chelate pereopods 2-4 decreasing in size distally, with dactylus and pollex slightly shorter than palm and slightly curved distally; pereopod 5 not preserved.

Pleonal appendages. — Pleopods 1-5 not preserved; uropods with short basipodite carrying (1) elongate uropodal exopod, almost as long as telson, strengthened by longitudinal carina and distally cut by diaeresis and (2) rounded uropodal endopod, almost as long as telson, strengthened by longitudinal carina.

Ornamentation. — Pleonal tergum covered by numerous tubercles between anterior and posterior transverse grooves, not preserved elsewhere.

Gabaleryon moorei (Woodward, 1866) nov. comb.

Fig. 5

1866 *Eryon moorei* Woodward: 499-500, pl. 25 fig. 3.

1877 *Eryon moorei* Woodward; Woodward: 11.

1881 *Eryon moorei* Woodward; Woodward: 530.

1888 *Eryon moorei* Woodward; Spence Bate: 116.

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1891 *Eryon moorei* Woodward; Krause: 176.

1911 *Eryon moorei* Woodward; Woodward: 307.

1924 *Eryon moorei* Woodward; Balss: 175.

1925 *Eryon moorei* Woodward; Van Straelen: 119.

1925 *Coleia moorei* (Woodward); Woods: 21, pl. 5 fig. 5.

1929 *Proeryon moorei* (Woodward); Glaessner: 340.

1952 *Proeryon moorei* (Woodward); Kuhn: 159.

2005 *Proeryon moorei* (Woodward); Garassino & Gironi: 59.

2006 *Coleia moorei* (Woodward); Garassino & Gironi: 95.

2007 *Coleia moorei* (Woodward); Teruzzi & Garassino: 95.

2010 *Coleia moorei* (Woodward); Schweitzer *et al.*: 44.

Type material. Holotype by monotypy (BRLSI M1247), part of flattened, subcomplete specimen in dorsal view.

Type locality. Strawberry Bank (Ilminster, Somerset, United Kingdom).

Type age. Early Toarcian (Serpentinum ammonite biozone; Woods 1925).

Occurrence. Hitherto only known from the type locality.

Emended diagnosis. Dorsoventrally flattened carapace, with ovoid outline in dorsal view; ocular incision widely open laterally; deep cephalothoracic grooves; postcervical groove marked between branchial carina and median line; cervical and postcervical incisions forming minute indentations of lateral margin; axial carina on pleonites 2 to 5 probably cut by deep posterior transverse groove; first pereopod with stocky palm; uropods as long as telson, with uropodal exopod cut by very rounded diaeresis.

Description.

Shape of carapace. — Dorsoventrally flattened carapace, with ovoid outline in dorsal view; concave frontal margin; short anterolateral angle; lateral margin cut by ocular, cervical and postcervical incisions; large ocular incision widely open laterally; anterolateral margin slightly convex, subparallel to longitudinal axis; cervical and postcervical incisions opening in first half of lateral margin; very small cervical incision; straight mediolateral margin slightly shorter than anterolateral margin; very small postcervical incision; posterolateral margin slightly convex; rounded posterolateral angle, contiguous with pleon, extending shortly along first pleonite; concave posterior margin, wider than frontal margin.

Carinae and grooves of carapace. — Postrostral carina not preserved; postcervical carinae strongly raised posteriorly; postorbital carina not visible; branchial carina extending anteriorly from posterolateral angle toward ocular incision cut by postcervical and cervical

grooves, not reaching ocular incision; deep and curved cervical groove cutting deeply median line in middle of carapace length; deep postcervical groove, extending transversally from postcervical incision toward branchial carina, shallower from branchial carina to median line, curving slightly forward near median line, not cutting median line.

Pleon and telson. — Pleon and telson slightly longer than carapace; pleon slightly narrower than carapace; pleonite 1 shorter than others; pleonites 1-5 with subrectangular terga; pleonite 6 with subtrapezoidal tergum; tergum of pleonites 2 to 6 crossed by pair of transversal grooves converging medially; pleonites 2-5 with lanceolate tergopleura, poorly preserved; pleonite 6 with narrow tergopleura; subtriangular telson strengthened by two longitudinal carinae.

Eye and cephalic appendages. — Not preserved

Thoracic appendages. — Large pereopod 1; pereopod 1 palm stout, slightly longer than dactylus, with curved outer margin; other pereopods not preserved.

Pleonal appendages. — Pleopods 1-5 not preserved; uropods with short basipodite carrying (1) elongate uropodal exopod, strengthened by longitudinal carina and distally cut by strongly curved diaeresis and (2) rounded uropodal endopod, almost as long as telson, strengthened by longitudinal carina.

Ornamentation. — Pleonal tergum covered by fine tubercles between anterior and posterior transverse grooves, not preserved elsewhere.

Comments. *Eryon moorei* possesses an ovoid carapace in outline in dorsal view, an ocular incision widely open laterally, very small cervical and postcervical incisions and posterior transverse groove on pleonites cutting median line. All these characters are diagnostic of *Gabaleryon* nov. gen. and justify the assignment of *Eryon moorei* to this genus. *Gabaleryon moorei* nov. comb. differs from *G. coquelae* nov. gen., nov. sp. by its slightly deeper cephalothoracic grooves (shallower in *G. coquelae*), a postcervical groove between marked branchial carina and median line (effaced or absent in *G. coquelae*), a first pereopod with palm slightly stockier and with more curved margins (more slender and with straight margins in *G. coquelae*) and shorter uropodal endopod and exopod (longer in *G. coquelae*). It also differs from *Gabaleryon garassinoi* nov. gen., nov. sp. by a more ovate carapace (subrectangular in *G. garassinoi*) a slightly shorter carapace (slightly shorter than pleon and telson; carapace as long as pleon and telson in *G. garassinoi*) and uropodal endopod and exopod shorter than the telson (longer than the telson in *G. garassinoi*).

Gabaleryon garassinoi nov. sp.

Figs 6-7

2001 *Coleia* cfr. *banzensis* Kuhn; Garassino & Teruzzi: 190-191, fig. 3.

2005 *Proeryon hartmanni* (Meyer); Garassino & Gironi: 56-63, figs 4-9.

Etymology. The specific epithet honours Alessandro Garassino, who was the first palaeontologist to study the fossil crustaceans from the Sogno Formation, Lombardy, Italy.

Type material. Holotype from mount Cornizzolo with part of a flattened, subcomplete specimen in dorsal view (MSNM i26215). – 18 paratypes from mount Cornizzolo: MSNM i26211-i26214, i26216, i26218, i26220, i26221, i26223-i26225, i26227, i26233-i26237, i26284. – 1 paratype from mount Brughetto: MSNM i10850.

Type locality. Sogno Formation of mount Cornizzolo (Province of Lecco, Lombardy, Italy).

Type age. Early Toarcian (Tenuicostatum ammonite biozone after Tintori 1977).

Occurrence. Early Toarcian of Sogno Formation (mounts Cornizzolo and Brughetto; Province of Lecco, Lombardy, Italy)

Diagnosis. Dorsoventrally flattened carapace, with subquadrate outline in dorsal view; ocular incision widely open laterally; deep cervical groove; postcervical groove faint between branchial carina and median line; cervical and postcervical incisions forming minute indentations of lateral margin; axial carina on pleonites 2 to 5 cut by posterior transverse groove; short telson, very rounded scaphocerite; first pereopod with stocky palm, elongate uropods with exopod cut by very curved diaeresis.

Description.

Shape of carapace. — Dorsoventrally flattened carapace, with subrectangular outline in dorsal view; concave frontal margin; short anterolateral angle; lateral margin cut by ocular, cervical and postcervical incisions; large ocular incision widely open laterally; anterolateral margin slightly convex, subparallel to longitudinal axis; cervical and postcervical incisions opening in first half of lateral margin; very small cervical incision; straight mediolateral margin slightly shorter than anterolateral margin; very small postcervical incision; posterolateral margin slightly almost straight; subquadrate posterolateral angle, contiguous with pleon, extending shortly along first pleonite; concave posterior margin, wider than frontal margin.

Carinae and grooves of carapace. — Well-marked postrostral carina not reaching anterior margin; well-marked postcervical carina extending from cervical groove to posterior margin; postorbital carina poorly preserved; well-marked branchial carina extending anteriorly from posterolateral angle toward cervical grooves; deep and curved cervical groove

cutting deeply median line in middle of carapace length; deep postcervical groove, extending transversally from postcervical incision toward branchial carina, very shallow (and poorly preserved) from branchial carina to median line; shallow branchiocardiac groove, extending along branchial carina and curving posteriorly toward median line.

Pleon and telson. — Pleon and telson as long as carapace; pleon slightly narrower than carapace; pleonite 1 slightly shorter than others; pleonites 1-5 with subrectangular terga; pleonite 6 with subtrapezoidal tergum; tergum of pleonites 2 to 6 crossed by pair of transversal grooves converging medially; pleonites 2-5 with lanceolate tergopleura, poorly preserved; pleonite 6 with tergopleura narrow; subtriangular telson strengthened by two longitudinal carinae.

Eye and cephalic appendages. — Large eye slightly projected from ocular incision; antennula not preserved; antenna with short basipodite carrying (1) very rounded scaphocerite strengthened by median carina and (2) endopod with a poorly preserved flagellum.

Thoracic appendages. — Large pereopod 1; pereopod 1 palm stout, slightly shorter than dactylus, with curved outer margin; chelate P2-P4, smaller than P1, poorly preserved.

Pleonal appendages. — Pleopods 1-5 not preserved; uropods with short basipodite carrying (1) elongate uropodal exopod, longer than telson, strengthened by longitudinal carina and distally cut by strongly curved diaeresis and (2) rounded uropodal endopod, longer than telson, strengthened by longitudinal carina.

Ornamentation. — Carapace covered with fine tubercles; pleon covered by slightly coarser tubercles.

Comments. Polychelidans from Sogno Formation were initially interpreted as *Coleia* cf. *banzensis* by Garassino & Teruzzi (2001) based upon the shape of specimens from mount Brughetto. Later, Garassino & Gironi (2005) provided new material from another outcrop of the same formation in mount Cornizzolo and assigned all specimens to *Proeryon hartmanni* (Meyer, 1836) based upon the shape of carapace, serration of lateral margin, presence of a diaeresis and carapace grooves (note that the branchiocardiac groove identified by Garassino & Gironi (2005) is herein considered as postcervical groove). Our reinvestigation of the well-preserved specimens from mount Cornizzolo and one from mount Brughetto leads us to a different conclusion. The new species differs clearly from species of *Proeryon* by its subrectangular carapace (more or less pyriform in *Proeryon* species), its shallow cervical and postcervical incisions (deeper in *Proeryon* species). The new species possess an ovoid, almost subquadrate carapace in outline in dorsal view, an ocular incision widely open laterally, very small cervical and postcervical incisions, posterior transverse groove on pleonites cutting

Gabaleryon new genus of widespread polychelidan lobster

median line and a very rounded scaphocerite. All these characters are diagnostic of *Gabaleryon* nov. gen. and justify the assignment to this genus. *Gabaleryon garassinoi* nov. sp. differs from *G. coquelae* and *G. moorei* by its subquadrate carapace (more ovate in *G. coquelae* and *G. moorei*), its postcervical groove shallow between both branchial carinae (well-marked in *G. moorei*, effaced or absent in *G. coquelae*), its P1 palm stockier and with slightly more curved margin (slightly more elongated and with straight margins in *G. coquelae*), its short telson (more elongated in *G. coquelae*) and longer uropodal endopod and exopod (shorter in *G. moorei*).

Gabaleryon sp. 1

Fig. 8A

Examined material. One specimen, part and counterpart (Tobias Klöck's and Giuseppe Gulisano's private collections).

Occurrence. Early Toarcian of Engetal valley (Allgäu Formation) near Pfronten, southernmost Germany.

Description. Dorsoventrally flattened carapace with concave frontal margin, and lateral margin cut by large ocular incision. Pleon and telson about as long as carapace; pleonite 1 slightly shorter than others; pleonites 4 to 6 crossed by an axial carina and a pair of transverse grooves, the posterior one cutting axial carina. Telson subtriangular, strengthened by pair of longitudinal carinae. First pereopod large, with palm with straight margins, dactylus and pollex as long as palm. Uropod poorly preserved, about as long as telson; uropodal exopod with curved diaeresis.

Comments. This specimen is assigned to *Gabaleryon* nov. gen. on the basis of its ovoid carapace, its posterior transverse groove cutting the axial carina on pleonal terga and its uropodal exopod with curved diaeresis. The straight P1 palm is similar to that of *Gabaleryon coquelae*, and differs from those of *G. garassinoi* nov. sp. and *G. moorei* nov. comb., which are more curved. This specimen preserves a spiny crest along P1 carpus. Such a crest is lacking or not preserved in *G. coquelae* – due to a poor preservation of carpus – and lacking in *G. garassinoi* and *G. moorei*. In addition, the generally poor preservation of the lateral margins of the carapace due to its superposition with first pereopods does not allow, in our opinion, to compare further this specimen with other species of *Gabaleryon* or to describe it as new species. The occurrence of this specimen in southernmost Germany is important as it extends the known palaeogeographic range of *Gabaleryon*.

?*Gabaleryon* sp. 2

Fig. 8B

Examined material. One specimen (David Gluck's private collection).

Occurrence. Late Bajocian – early Bathonian of Sennecey-le-Grand, Eastern France.

Description. Dorsoventrally flattened carapace, ovoid in outline in dorsal view, poorly preserved. Pleon about as long as carapace; s1 slightly shorter than others; s2-s6 crossed by a pair of transverse grooves cutting median line. First pereopod large, with stout palm with curved lateral margins; P1 dactylus and pollex incompletely preserved.

Comments. This specimen displays an ovoid carapace and axial carina on pleonites 2 to 5 cut by the deep posterior transverse groove. These characteristics are typical of *Gabaleryon*. However, it is not possible to assess the presence of a diaeresis nor the shape of the frontal margin. For these reasons, we cannot assign with confidence this specimen to *Gabaleryon*. It shall also be noted that the chela of first pereopod seems by far stouter than that of other species.

The occurrence in the late Bajocian – early Bathonian of a specimen with a morphology rather similar to that of Toarcian species of *Gabaleryon* suggests that this morphotype may have survived for 15 Ma.

Discussion

The Toarcian in Europe

During the Toarcian, most of Western Europe, including all the localities cited herein, was covered by a relatively shallow epicontinental sea at the then North-Western margin of the Tethys Ocean (Golonka 2007). The early Toarcian was marked by a global anoxic event (T-OAE) indicated by a carbon isotope excursion lasting between 0.3 and 0.6 Ma (Boulila *et al.* 2014; Huang & Hesselbo 2014) reaching its peak in the Falciferum subzone (183 Ma), after the deposition of the Sogno Formation and Brenoux outcrops, and approximatively when the Strawberry Bank Lagerstätte was deposited (Williams *et al.*, in press). The Engetal valley outcrop was deposited around the time when T-OAE occurred, in the early Toarcian. However, its relation with the T-OAE is not precisely known, since this outcrop is not currently dated precisely enough. Resulting from the volcanic activity of the Karoo-Ferrar igneous province and/or destabilization of gas hydrates (Emmanuel *et al.* 2006), the T-OAE was associated with up to 4 Ma of oceanic temperature fluctuation and other climatic perturbations resulting in substantially elevated marine global extinction rates (Little *et al.* 1995; Wignall *et al.* 2005; Suan *et al.* 2010): approximately 5% of families and 26% of genera (Danise *et al.* 2015) most notably amongst the ammonites (Macchioni & Cecca 2002),

the brachiopods (Vörös 2002; García Joral *et al.* 2011), and the foraminifera (Caruthers *et al.* 2013).

Distribution of Toarcian polychelidans

With the addition of the species described herein, the Toarcian is now recognized as the second peak of fossil diversity of polychelidan lobsters, with 5 genera and 10 species (8 genera and 15 species for Kimmeridgian-Tithonian; 4 genera and 9 species for Sinemurian) (Fig. 1).

Toarcian polychelidans can be divided into five main taxa:

1. *Gabaleryon* with the four herein described taxa, from France, United Kingdom, Italy and Germany;
2. *Proeryon*, with *Proeryon hartmanni* (Meyer, 1836), *P. hauffi* Beurlen, 1944, *P. laticaudatus* Beurlen, 1928, and *P. zehentbaueri* Audo, Schweigert, Saint Martin & Charbonnier, 2014 from Germany (see species listed in Audo *et al.* 2014c), *E. calvadosii* Morière, 1883 (probably a *Proeryon*, judging from the shape of carapace) from France and *Proeryon viluensis* Chernyshev, 1930 from Siberia – these last two species are considered to be junior synonyms of *P. hartmanni* by Audo (2014).
3. “*Coleia*” *sinuata* Beurlen, 1928;
4. “*Palaeopolycheles*” *crymensis* Levitski, 1974;
5. *Eryon sibiricus* (Chernyshev, 1930) (see Audo 2014 for generic assignment).

All of these species, except “*Palaeopolycheles*” *crymensis* (from the Toarcian-Aalenian boundary), date from the early Toarcian. This suggests that the early Toarcian, despite its biological crisis, was rather favourable to the preservation of polychelidans or/and to their diversification. In fact, *Gabaleryon coquelae* nov. gen., nov. sp. and *G. garassinoi* nov. sp. occur just before or at the beginning of the T-OAE anoxic event; *G. moorei* occurs during T-OAE.

Several reasons may explain the abundance of polychelidan lobsters in early Toarcian: it is possible that the preservation of crustacean carcasses was favoured by a low oxygenation of the seawater. A diversification of polychelidan lobsters is also possible, perhaps linked with the extinction of competitors and/or predators. If true, it would imply a trend opposed to that of other animal taxa which suffered from the extinctions during the T-OAE event. Unfortunately, it is currently impossible to test these hypotheses due to the lack of quantitative information on polychelidans in the fossil record.

Palaeoecology

Most studied specimens are complete and in anatomical connection, including the articulation between cephalothorax and pleon, which is one of the first to break (Allison 1986; 1988; Plotnick 1986). This preservation suggests little to no post-mortem transport, which implies that polychelidans were probably autochthonous or parautochthonous to their burial environments. It is quite possible that some or all of these Toarcian polychelidan lobsters were tolerant to hypoxic or even anoxic conditions, with factors such as food availability being more significant factors in their distribution. It has been demonstrated that this can be the case with modern decapod crustacean communities (Hendrickx 2001) and at Strawberry Bank, which was an anoxic depositional environment, there is at least one example of a fish (BRLSIM1389), which shows indications of scavenging that could only be attributed to a decapod crustacean. Many extant polychelidans are opportunistic scavengers (Firth & Pequegnat 1971; Lagardère 1973; Gore 1984; Cartes & Abelló 1992) and hence it seems likely that they may have contributed to the scavenging of fish remains in Strawberry Bank.

Palaeobiogeography

The localities where *Gabaleryon* occurs are scattered across Western Europe and were deposited in slightly different contexts (Fig. 2):

- Brenoux was deposited under the shallow Toarcian epicontinental sea, near several small islands; no terrestrial fauna has been documented there yet. This locality dates from the early Toarcian, but its precise ammonite biozone is unknown.
- Strawberry Bank was deposited in a similar context, except it was closer to the large landmass of the London-Brabant Massif and preserves an abundant terrestrial fauna. This locality is perhaps the youngest (Serpentinum biozone, Falciferum subzone).
- The Sogno Formation outcrops were deposited on the edge of the Trento Plateau separated from the others by the land mass of Corsica-Sardinia and a narrow deep basin. This locality is slightly older than Strawberry Bank.
- The siliciclastic claystones of the Engetal valley (Allgäu Formation) accumulated in moderately deep basins, which developed after the drowning of the previously developed carbonate platforms of the Northern Calcareous Alps. In the early Toarcian, the widespread Anoxic Event effected these deposits and led to temporary oxygen depletion at the sea floor.

Despite these differences, the Sogno Formation and Strawberry Bank are associated by their vertebrate faunas, with the occurrences in both outcrops of the fishes *Pachycormus*

Agassiz, 1833, *Leptolepis* Agassiz 1833 and *Pelagosaurus* Bronn, 1842. *Leptolepis* also occurs in Brenoux, however, this genus needs to be reviewed (Coquel-Poussy 2013) and therefore is currently not a good palaeobiogeographical proxy.

The description of *Gabaleryon* nov. gen. from Brenoux, Strawberry Bank and Sogno Formation provides additional palaeobiogeographical evidence linking France, United Kingdom and Italy. The occurrence of one species of *Gabaleryon* in each of these localities possibly indicates limited provincialism. Indeed, *G. coquelae* nov. sp., *G. moorei* nov. comb. and *G. garassinoi* nov. sp. are closely allied species.

Gabaleryon is therefore a relatively widespread genus of polychelidan, occurring from United Kingdom to Germany. Indeed, by comparison, most other polychelidan lobster genera are either documented from a single outcrop or geographically close outcrops. Only two other genera have a greater palaeogeographic distribution: *Coleia* Broderip, 1835, which still first occur in the Carnian of Japan (Karasawa *et al.* 2003) and occurs later in Europe (Glaessner 1969), but require to be reinvestigated; and *Proeryon* Beurlen, 1928, which occurs from France to Siberia during Toarcian.

Conclusions

The description of a new genus and two new species improves our knowledge of the fossil diversity of polychelidan lobsters. The assignment of *Eryon moorei* Woodward, 1866 to a new genus, also shows that the diversity of polychelidans has for a long time been underestimated. Above all, the precise taxonomic identification of these fossils allows us to link four widely separated outcrops.

At the time of writing, a single phylogeny (Ahyong 2009) has been proposed to assess relationships between polychelidans. This phylogeny was an important step toward a better comprehension of polychelidan diversity. However, the description of new morphotypes of polychelidans implies that we now require a more complete phylogeny with more focus on fossil species. A preliminary phylogeny focused on fossil polychelidans was recently proposed by Audo (2014), however, more work is required to assess the reliability of these early results. Yet, following these initial results, *Gabaleryon* seems to be closely related to *Proeryon* and *Tethyseryon* (Audo 2014). It is therefore an important step to understand phylogenetic relationships among polychelidans.

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Gabaleryon new genus of widespread polychelidan lobster

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Figures

Figure 1. Generic and specific diversity of polychelidans across time with indication of major Fossil-Lagerstätten in which they occur. References: basis for record, Audo (2014); 1, Ahyong (2009), Chan (2010) and WoRMS (2015); 2, Galil (2000).

Figure 2. Palaeogeographical map of Western Europe during the mid-Toarcian (simplified after Bassoulet *et al.* 1993) and location of Brenoux (1), Strawberry Bank (2), Outcrops from Sogno Formation (3), Engetal valley (4). Abbreviations: **A**, Apulia; **ACP**, Apennine carbonate platform; **Al**, Alborán; **AM**, Armorican Massif; **Dm**, Dalmatia; **IM**, Iberian Meseta; **K**, Kabylia; **LBM**, London-Brabant Massif; **MC**, Massif Central; **TP**, Tisza Plate; **Trp**, Trento Plateau; **TuB**, Tuscany Basin.

Figure 3. Comparison of the general outline of carapaces and third pleonite (right sides omitted) of the type species of each genus of fossil Polychelida: **A**, *Adamanteryon fourneti* Audo, Schweigert, Saint Martin & Charbonnier, 2014; **B**, *Antarcticheles antarcticus* Aguirre-Urreta, Chernoglasov & Medina 1990; **C**, *Coleia antiqua* Broderip, 1835; **D**, *Cycleryon propinquus* (Schlothheim, 1822); **E**, *Eryon cuvieri* Desmarest, 1817; **F**, *Gabaleryon coquelae* nov. gen., nov. sp.; **G**, *Hellerocaris falloti* (Van Straelen, 1923); **H**, *Knebelia bilobata* (Münster, 1839); **I**, *Palaeopentacheles roettenbacheri* (Münster, 1839); **J**, *Palaeopolycheles longipes* (Fraas, 1855); **K**, *Proeryon hartmanni* (Meyer, 1836); **L**, *Pseudocoleia mazzolenii* Garassino & Teruzzi, 1993; **M**, *Rosenfeldia triasica* Garassino, Teruzzi & Dalla Vecchia, 1996; **N**, *Soleryon amicalis* Audo, Charbonnier, Schweigert & Saint Martin, 2014; **O**, *Tethyseryon campanicus* Bravi, Garassino, Bartiromo, Audo, Charbonnier, Schweigert, Thévenard & Longobardi, 2014; **P**, *Tetrachela raiblana* (Bronn, 1858); **Q**, *Tropifer laevis* Gould, 1857; **R**, *Voulteryon parvulus* Audo, Schweigert, Saint Martin & Charbonnier, 2014; **S**, *Willemoesiocaris ovalis* (Van Straelen, 1923); **T**, *Wrangelleryon perates* Feldmann, Schweitzer & Haggart, 2013. Illustrations not to scale.

Figure 4. *Gabaleryon coquelae* nov. gen., nov. sp. from the early Toarcian of Brenoux, France. **A-B**, holotype MNHN.F. A51506, part, dorsal view in cross-polarized light (A) and interpretative line-drawing (B). **C-D**, paratype (N. Coquel-Poussy pers. coll.) part, ventral view in UV-light (C) and interpretative line-drawing (D). Abbreviations: **a1**, antennula; **a2**, antenna; **ba**, uropodal basipodite; **bc**, branchial carina; **c**, postcervical groove; **ca**, carpus; **ci**, postcervical incision; **da**, dactylus; **di**, diaeresis; **e1e**, cervical groove; **en**, uropodal endopod; **ex**, uropodal exopod; **me**, merus; **mXP3**, third maxilliped; **o**, eye; **P1-P5**, pereopods 1 to 5;

P?, indeterminate pereopod; **pc**, postcervical carina; **po**, postorbital carina; **pr**, postrostral carina; **pro**, propodus; **px**, pollex; **s1-s6**, pleonites 1 to 6; **sc**, scaphocerite; **t**, telson Scale bars, 1 cm. Photographs, D. Audo (A) and P. Loubry (C).

Figure 5. *Gabaleryon moorei* (Woodward, 1866) nov. comb. from the early Toarcian of Strawberry Bank, United Kingdom. **A**, holotype BRLSI M1247, dorsal view. **B**, interpretative line-drawing. Abbreviations: **a1**, antennula; **a2**, antenna; **ba**, uropodal basipodite; **bc**, branchial carina; **c**, postcervical groove; **da**, dactylus; **di**, diaeresis; **en**, uropodal endopod; **ex**, uropodal exopod; **P1**, pereopod 1; **po**, postorbital carina; **s1-s6**, pleonites to 6; **sc**, scaphocerite; **t**, telson. Scale bars, 1 cm. Photograph, M. Williams.

Figure 6. *Gabaleryon garassinoi* nov. gen., nov. sp. from mount Cornizzolo, Italy. **A-B**, holotype MSNM i26215, part, dorsal view in cross-polarized light (A) and interpretative line-drawing (B). **C-D**, paratype MSNM i26211 interpretative line-drawing (C) and part, dorsal view, cross-polarized light (D). **E**, paratype (MSNM i26284), ventral view, cross-polarized light. Abbreviations: **a2**, antenna; **ba**, uropodal basipodite; **c**, postcervical groove; **ca**, carpus; **da**, dactylus; **di**, diaeresis; **e1e**, cervical groove; **en**, uropodal endopod; **ex**, uropodal exopod; **md**, mandible; **me**, merus; **o**, eye; **P1**, pereopod 1; **pro**, propodus; **px**, pollex; **s1-s6**, pleonites 1 to 6; **sc**, scaphocerite; **t**, telson. Scale bars, 1 cm. Photographs, D. Audo, copyright MSNM.

Figure 7. *Gabaleryon garassinoi* nov. gen., nov. sp. from mounts Cornizzolo and Brughetto, Italy. **A-B**, paratype MSNM i26214 from mount Cornizzolo, dorsal view, cross-polarized light (A) and interpretative line-drawing (B). **C-D**, paratype MSNM i10850 from mount Brughetto, dorsal view (C) and interpretative line-drawing (D). Abbreviations: **a**, branchiocardiac groove; **a1**, antennule; **a2**, antenna; **ba**, uropodal basipodite; **bc**, branchial carina; **c**, postcervical groove; **da**, dactylus; **di**, diaeresis; **en**, uropodal endopod; **e1e**, cervical groove; **ex**, uropodal exopod; **o**, eye; **P1-P5**, pereopod 1 to 5; **P?**, indeterminate pereopod; **pc**, postcervical carina; **pr**, postrostral carina; **px**, pollex; **s1-s6**, pleonite 1 to 6; **t**, telson. Scale bars, 1 cm. Photographs, D. Audo (A) and A. Garassino (MSNM) (B), both copyright MSNM.

Figure 8. Other probable occurrences of *Gabaleryon* nov. gen. **A**, *Gabaleryon* sp. 1 from the Toarcian of Pfronten, Germany, natural light, with superimposed interpretative line-drawing. **B**, ?*Gabaleryon* sp. 2 from the late Bajocian – early Bathonian of Sennecey-le-Grand, France, dorsal-view in cross-polarized light. Scale bars, 1 cm. Photographs, Tobias Klöck (A) and D. Audo (B).

Figure 1

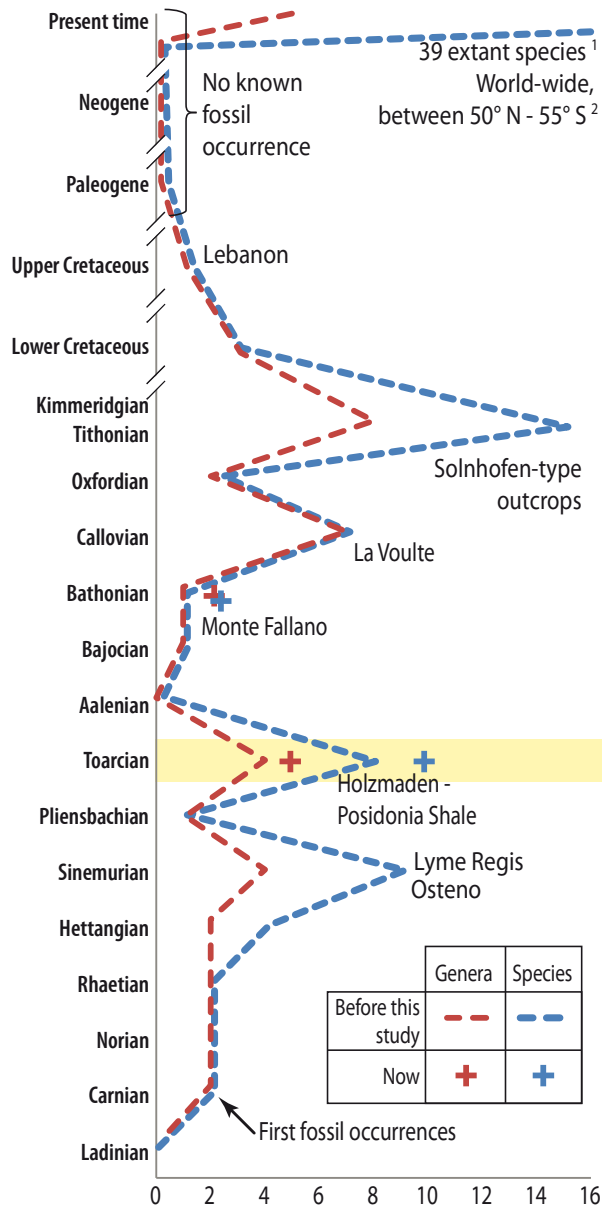


Figure 2

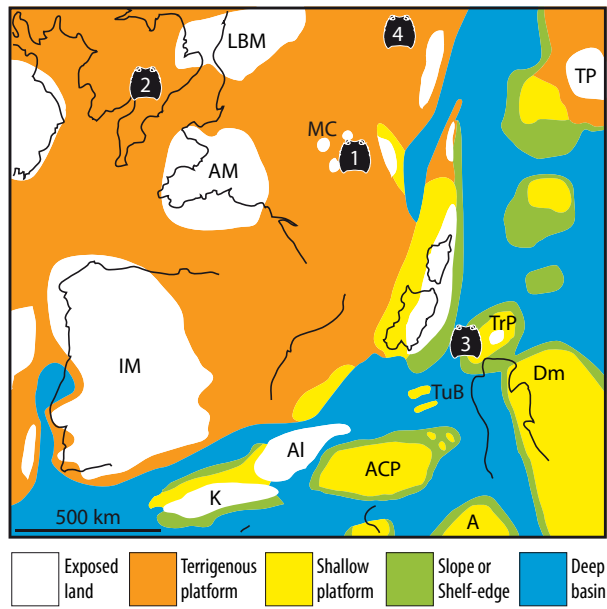
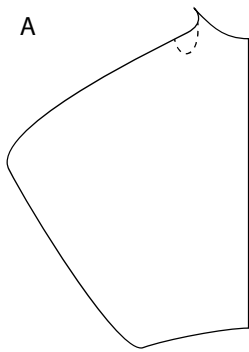
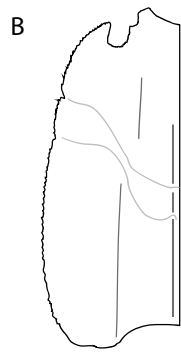


Figure 3



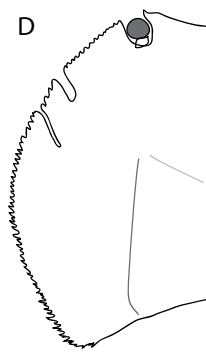
Adamanteryon



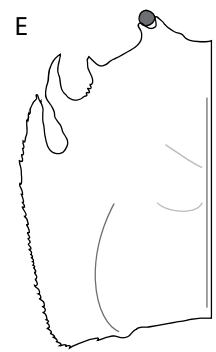
Antarcticheles



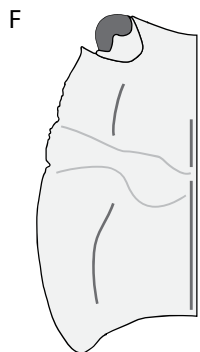
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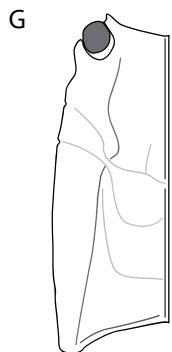
Cycleryon



Eryon



Gabaleryon



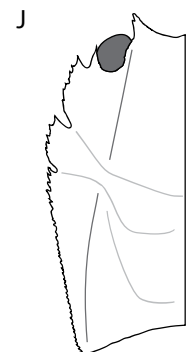
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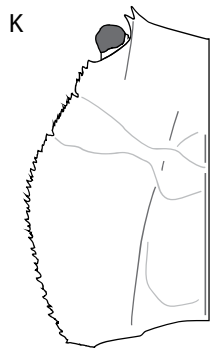
Knebelia



Palaeopentacheles



Palaeopolycheles



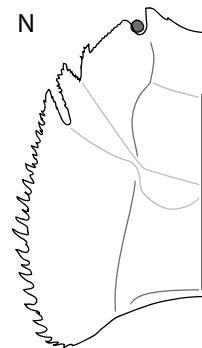
Proeryon



Pseudocoleia



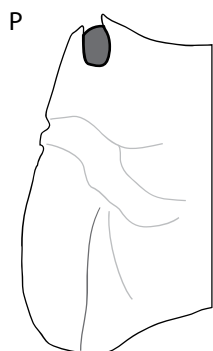
Rosenfeldia



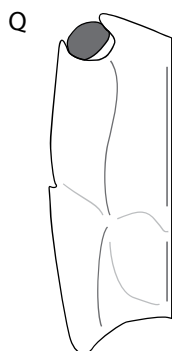
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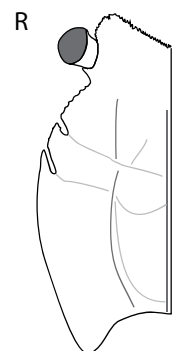
Tethyseryon



Tetrachela



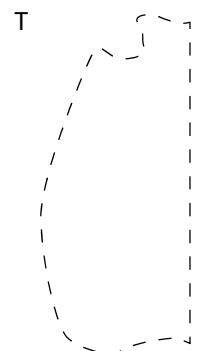
Tropifer



Voulteryon



Willemoesiocaris



Wrangelleryon

Figure 4

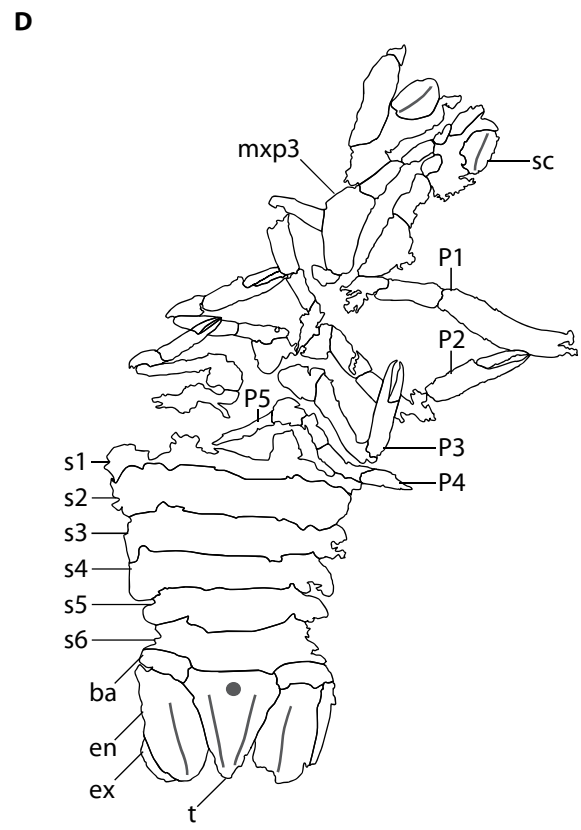
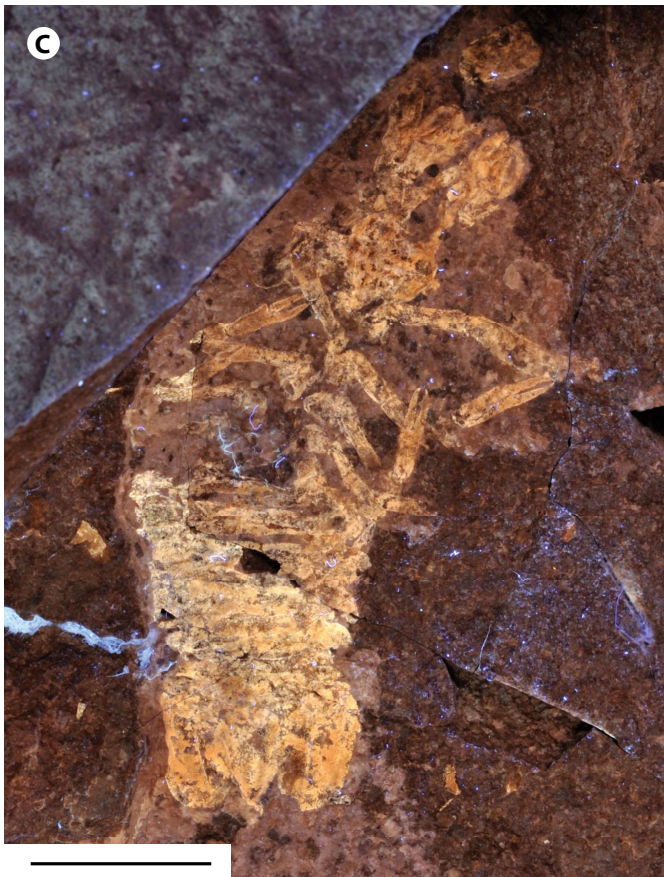
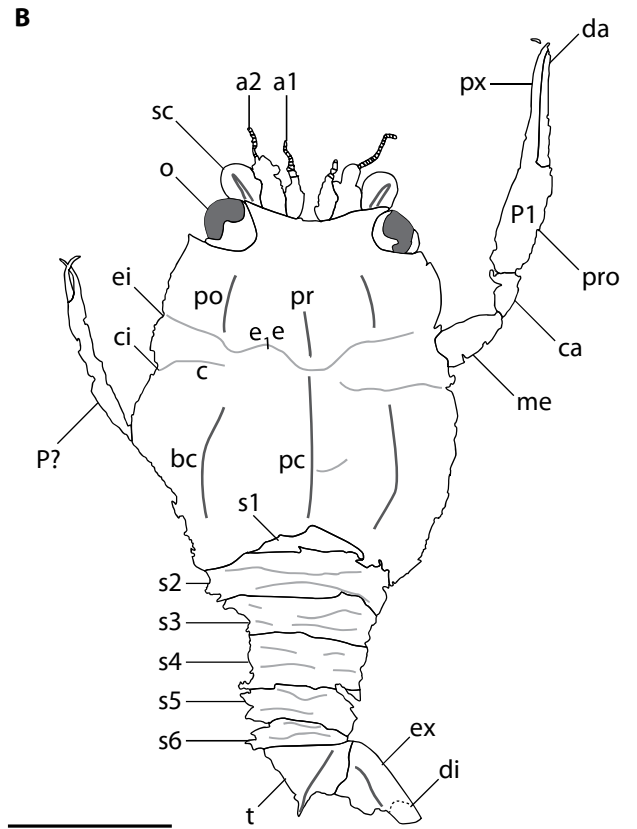


Figure 5

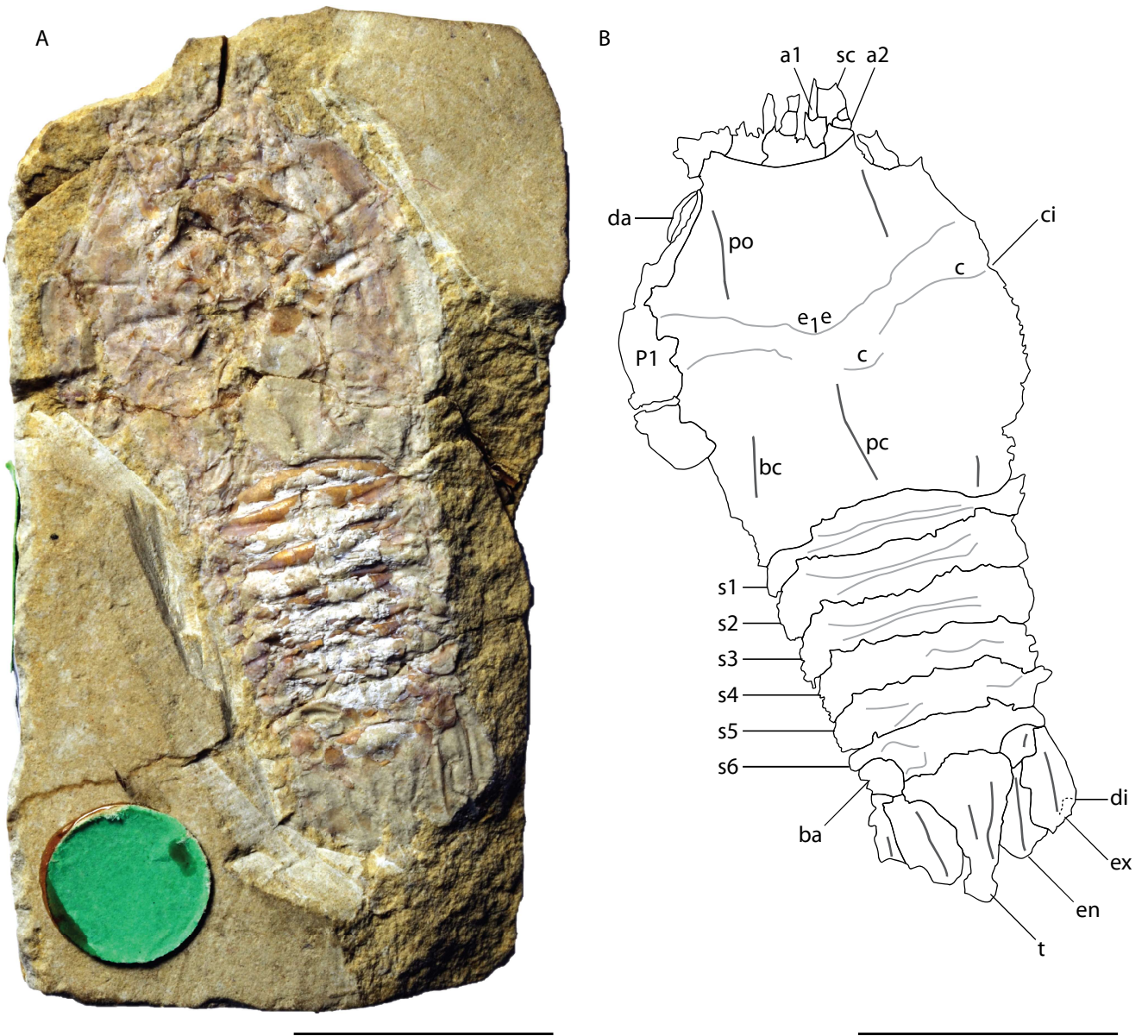


Figure 6

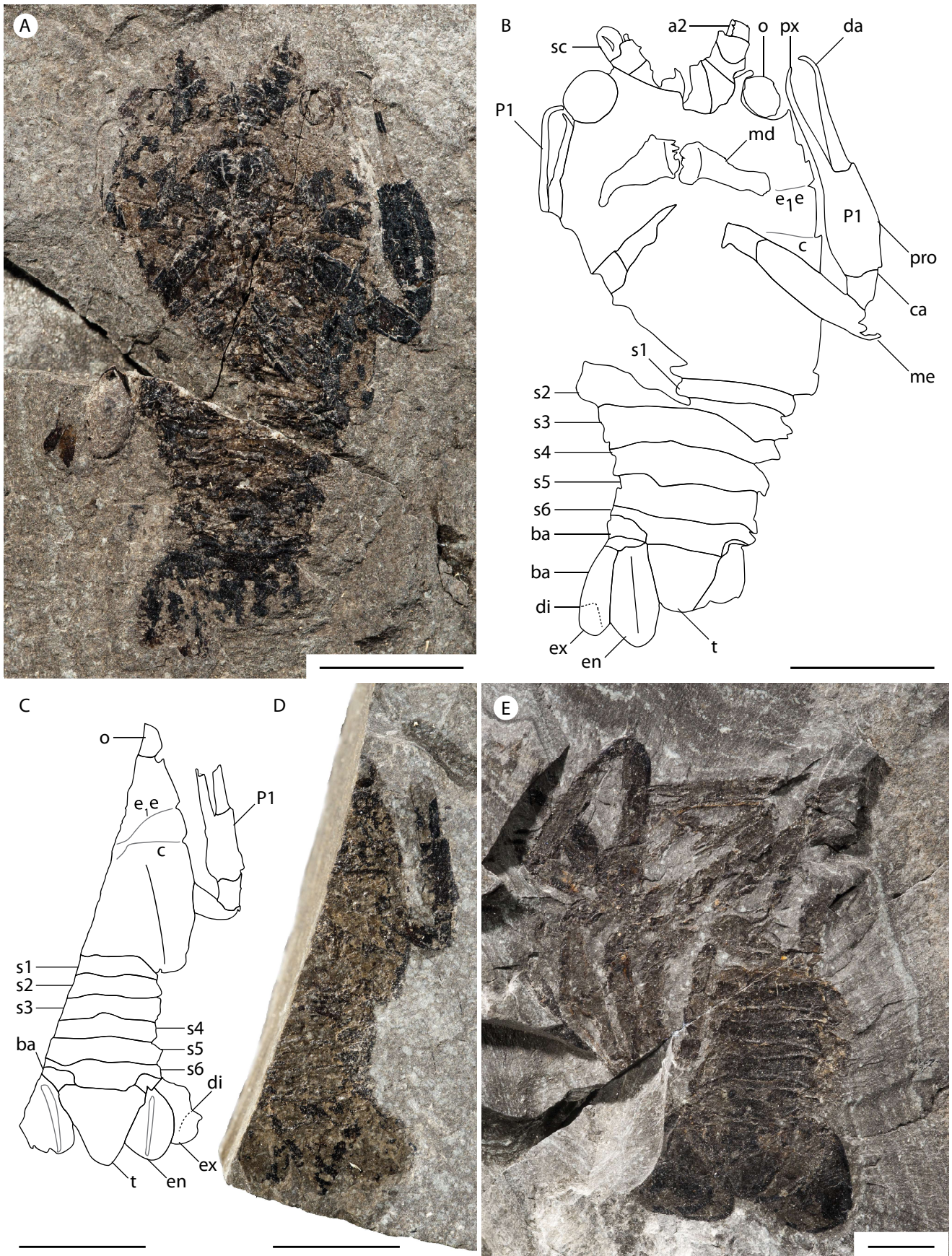


Figure 7

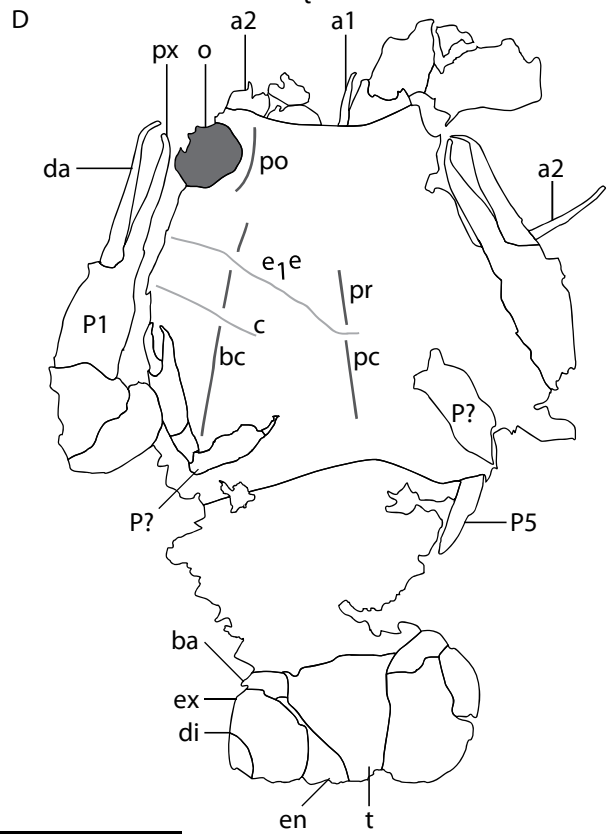
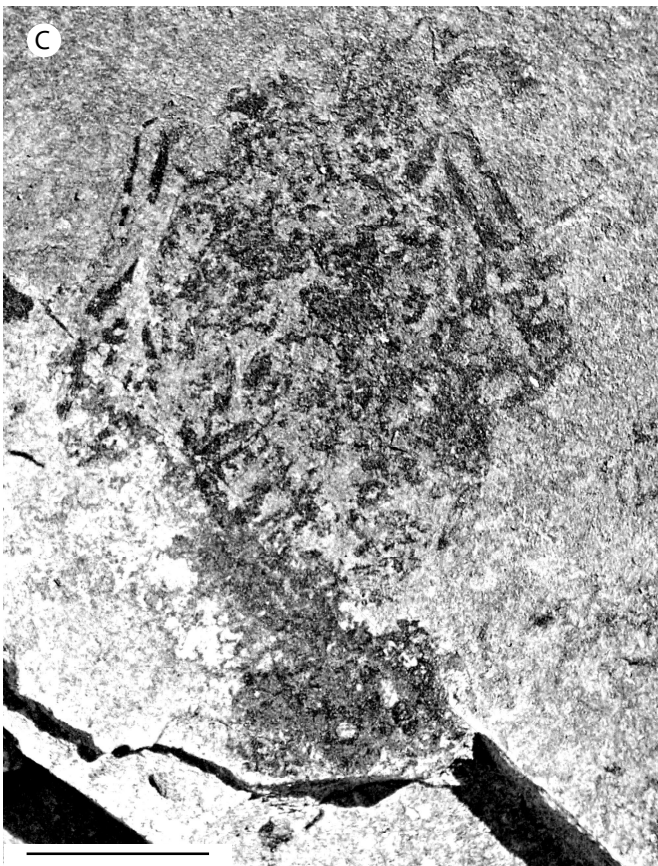
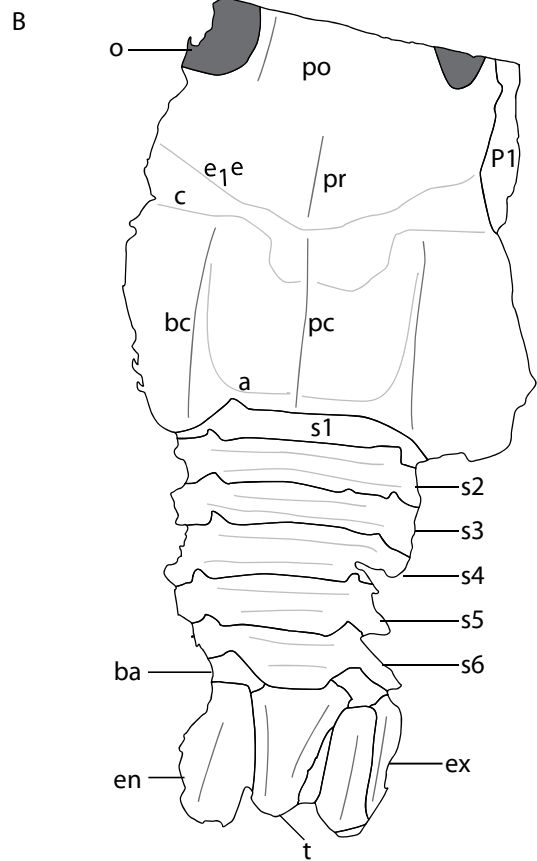


Figure 8

