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On unreported historical specimens of marine arthropods from the Solnhofen and Nusplingen Lithographic Limestones (Late Jurassic, Germany) housed at the Muséum national d'Histoire naturelle, Paris

Sur des spécimens historiques inédits d'arthropodes marins des Calcaires Lithographiques de Solnhofen et Nusplingen (Jurassique supérieur, Allemagne) conservés au Muséum national d'Histoire naturelle, Paris

Unreported specimens of marine arthropods from Solnhofen

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ABSTRACT

We report and illustrate several unpublished fossil specimens of marine arthropods, housed at the Muséum national d'Histoire naturelle in Paris (France) and coming from the Solnhofen and Nusplingen Lithographic Limestones (Late Jurassic, Germany). Notably, we describe specimens of *Antrimpos undenarius* Schweigert, 2001, *Eryma modestiforme* (Schlotheim, 1822) and *Mecochirus longimanatus* (Schlotheim, 1820). *Mecochirus foresti* Secrétan, 1968 is considered as a junior synonym of *Mecochirus longimanatus*. A revision of the specimens previously described is also realized. This contribution thus provides new information on the *Antrimpos* species from the Solnhofen Plattenkalks and gives a complete overview of the fossil marine arthropods coming from these Plattenkalks which are available at the MNHN.

KEY WORDS

Crustacea, Decapoda, Jurassic, Plattenkalk, Solnhofen, Nusplingen, Germany, collections, conservation.

RÉSUMÉ

Plusieurs spécimens fossiles d'arthropodes marins inédits, conservés au Muséum national d'Histoire naturelle à Paris (France) et provenant des Calcaires lithographiques de Solnhofen et de Nusplingen (Jurassique supérieur, Allemagne), sont décrits et illustrés. Nous décrivons notamment des spécimens d'*Antrimpos undenarius* Schweigert, 2001, d'*Eryma modestiforme* (Schlotheim, 1822) et de *Mecochirus longimanatus* (Schlotheim, 1820). *Mecochirus foresti* Secrétan, 1968 est considéré comme un synonyme plus récent de *Mecochirus longimanatus*. Une révision des spécimens décrits précédemment est également réalisée. Cet article fournit ainsi de nouvelles informations sur les espèces d'*Antrimpos* présentes dans les Plattenkalks de Solnhofen et donne un aperçu complet des arthropodes marins fossiles provenant de ces localités et disponibles au MNHN.

MOTS CLÉS

Crustacea, Decapoda, Jurassique, Plattenkalk, Solnhofen, Nusplingen, Allemagne, collections, conservation.

INTRODUCTION

The fossil record of marine arthropods delivered by Plattenkalks is particularly diverse and spans several continents (Africa, South America, North America, Europe) and geological era (Cretaceous, Jurassic, Carboniferous). Among these Plattenkalks, the Solnhofen Lithographic Limestones (Bavaria, Germany) are particularly remarkable and deliver beautifully preserved specimens of decapod crustaceans, stomatopods, mysidaceans, and xiphosurans (about 130 taxa; Arratia *et al.* 2015).

The collection of marine arthropods coming from Solnhofen at the Muséum National d'Histoire Naturelle (MNHN, Paris, France) is the result of 250 years of accumulation,

ensuing from exchanges with German institutions, wars pillage, purchases and donations (Charbonnier & Garassino 2012). Most of the specimens have been described in a previous paper (Charbonnier & Garassino 2012) but here, we report other specimens discovered in the MNHN collections, notably several specimens of the penaeid shrimp *Antrimpos undenarius* Schweigert, 2011 from the d'Orbigny collection.

This collection, assembled by the French naturalist Alcide d'Orbigny (1802-1857), was purchased by the MNHN and specimens were inventoried in a catalogue composed of 27 fascicles (Lauriat-Rage 2002). In 1898, a dedicated room (called after his name) was allocated in the newly built Gallery of Palaeontology: “la salle d'Orbigny”. However, the moving of the invertebrate collections, including arthropods, to another building in 2019-2020 required to map beforehand these collections and has led to the discovery of historical specimens that have not been published before.

MATERIAL AND METHODS

COLLECTION ARRANGEMENT. — As introduced by Charbonnier & Garassino (2012), the fossils housed in the National Museum of Natural History (MNHN; Paris, France) are dispersed between several collections and buildings, explaining why new specimens are regularly discovered. Because all the paleontological specimens housed at the MNHN will soon move in a single building, a mapping of the invertebrate collections has been realized. As a result, unreported historical specimens of marine arthropods from the Solnhofen Lithographic Limestones were discovered in the drawers of the institution and are the subject of this paper. The specimens already described by Charbonnier & Garassino (2012) will not be mentioned, unless the fossils are re-attributed to new taxa.

FOSSIL LOCALITIES. — Our localities encompass Late Jurassic marine Plattenkalks (i.e. very finely grained limestone precipitated under quiet conditions) of southern Germany (see Audo *et al.* 2014a: fig 1. for localization) where soft-bodied fossils, including arthropods, were preserved in lagoonal calcareous muds. The diversity of organisms is exceptionally important and the quality of the record is remarkable. Among marine arthropods, taxa such as penaeoidean and caridean shrimps, polychelidan, erymid and glypheid lobsters have notably been recorded (for general reviews see Garassino & Schweigert 2006, Schweigert 2011; Charbonnier & Garassino 2012; Winkler 2012; Schweigert *et al.* 2016).

The Solnhofen Lithographic Limestones, ranging from the late Kimmeridgian to the early Tithonian (Schweigert 2007), are located in the southern Franconian Alb (SW Germany). They include a large set of localities yielding Plattenkalks, such as Eichstätt, Painten, Solnhofen, globally referred to as “Solnhofen” in many old collections (Garassino & Schweigert 2006). Used since the late Stone Age as construction stones, fossils were traded by the quarrymen from the 18th century (Barthel *et al.* 1990: 4-10). These Plattenkalks deliver marine and terrestrial remains, among which jellyfish and feathered dinosaurs (the famous *Archaeopteryx*) are probably the most remarkable ones. Polychelidan, erymid and glypheoidean lobsters as well as caridean and penaeoidean shrimps account for the majority of Solnhofen crustaceans, the latter being the most abundant (Barthel *et al.* 1990: 129). Among xiphosurans, we can cite the *Mesolimulus* species, which is one of the best-known marine arthropods encountered in Solnhofen (Barthel *et al.* 1990: 138).

The Nusplingen Lithographic Limestone is a small fossil Lagerstätte, from the late Kimmeridgian, located in the western part of the Swabian Alb (SW Germany). The site includes two close quarries and delivers over 400 taxa of microfossils, land plants, invertebrates, vertebrates and ichnofossils remains (Dietl & Schweigert 2004, 2011). The first fossils from the Nusplingen Lithographic Limestone were reported in the middle of the 19th

century (Fraas 1855), and after a commercial use of the limestones, it is now a Protected Excavation Area dedicated to scientific excavation (Dietl & Schweigert 2004). Well-preserved caridean and penaeoidean shrimps and polychelidan lobsters, are typical of the Nusplingen Plattenkalk.

SYSTEMATICS. — The following list of Decapoda and Mysidacea crustaceans and limulids (Xiphosurida) housed in the MNHN is arranged taxonomically. It includes 117 specimens which are all presented Table 1.

Table 1. List of the 117 specimens of marine arthropods coming from the Southern Germany Lithographic Limestones and housed in the MNHN, Paris. Caption: bold: specimens newly described (this work); italic: specimens re-attributed (this work); n: number of specimens; - : not observed.

Taxa	Charbonnier & Garassino (2012)	This work	Total
DECAPODA	Collection numbers	Collection numbers	n
Aegeridae			
<i>Aeger spinipes</i> (Desmarest, 1817)	MNHN.F.B13441	<i>MNHN.F.B13440</i> , B13441, <i>B13442</i>	3
<i>Aeger tipularius</i> (Schlotheim, 1822)	MNHN.F.A33509, B13440, B13442, B13443, R03389, MNHN.GG.2004/57291, 2004/8072	MNHN.F.A33509, B13443, MNHN.GG.2004/8072	3
<i>Aeger insignis</i> Oppel, 1862		<i>MNHN.GG.2004/57291</i>	1
<i>Acanthochirana longipes</i> (Oppel, 1862)	MNHN.F.A42003		0
<i>Acanthochirana cordata</i> (Münster, 1839)		<i>MNHN.A33503</i> , <i>A42003</i> , <i>R03389</i>	3
Penaeidae			
<i>Antrimpos speciosus</i> Münster, 1839	MNHN.F.A33504, A33519, A33548, B13465, R03502, MNHN.GG.2004/8086	MNHN.F.A33504, A33519, A33548, B13465, R03502, MNHN.GG.2004/8086	6
<i>Antrimpos undenarius</i> Schweigert, 2011		MNHN.F.A06834, A49608, A49609, A49610, A49615, A49616, A49622, A49623, A49624	9
<i>Rauna angusta</i> Münster, 1839	MNHN.F.A42004	-	-
<i>Bylgia hexadon</i> Münster, 1839	MNHN.F.A33503		0
<i>Albertoppelia kuempeli</i> Schweigert & Garassino, 2004	MNHN.F.A33521	-	-
<i>Drobna deformis</i> Münster, 1839	MNHN.F.A33531	-	-
Caridea			
<i>Hefriga serrata</i> Münster, 1839	MNHN.F.B13464, MNHN.GG.2004/8237	-	-
Erymidae			
<i>Eryma modestiforme</i> (Schlotheim, 1822)	MNHN.F.A33507, B13446, B13448, B13450, B13452, B13463, MNHN.GG.2004/7462, 2004/8078-7471	MNHN.F.A32408 , A33507, A70905 , A70906 , B13446, B13448, B13450, B13452, B13463, MNHN.GG.2004/7462, 2004/8078-7471	11
<i>Palaeastacus fuciformis</i> (Schlotheim, 1822)	MNHN.F.B13449, MNHN.GG.2004/8245, 2004/7998-8106	MNHN.F.B13449, MNHN.GG.2004/8245, 2004/7998-8106	3
<i>Pustulina minuta</i> (Schlotheim, 1822)	MNHN.F.B13444, B13445, MNHN.GG.2004/8101	MNHN.F.B13444, B13445, MNHN.GG.2004/8101	3
Glypheidae			
<i>Glyphe pseudoscyllarus</i> (Schlotheim,	MNHN.F.A33506, B13447, B13462,	-	-

1822)	MNHN.GG.2004/7463					
Mecochiridae						
<i>Mecochirus longimanatus</i> (Schlotheim, 1820)	MNHN.F.A33508, A33533, A33534, A33535, A33536, A33537, A33538, A33539, A33540, A33541, A33542, A33546, A42005, A42007, B13453, B13454, B13456, B13457, R03397; MNHN.GG.2004/7461, 2004/8073, 2004/8075, 2004/8080, 2004/8081, 2004/8102, 2004/8232, 2004/8231	27	MNHN.F.A33508, A33533, A33534, A33535, A33536, A33537, A33538, A33539, A33540, A33541, A33542, A33546, A42005, A42007, A70929 , B13453, B13454, B13456, B13457, R03397; MNHN.GG.2004/7461, 2004/8073, 2004/8075, 2004/8080, 2004/8081, 2004/8102, 2004/8232, 2004/8231	28		28
Palinuridae						
<i>Palinurina longipes</i> (Münster, 1839)	MNHN.F.A30691, A30773, A33510, A33511, A33512, B13455, B13458, B13460	8	-	-		8
Eryonidae						
<i>Cycleryon propinquus</i> (Schlotheim, 1822)	MNHN.F.A33518, A33543, A42006, B13436, MNHN.GG.2004/8071	5	MNHN.F.A33518, A33543, A42006, B13436, MNHN.GG.2004/8071	5		5
<i>Cycleryon orbiculatus</i> (Münster, 1839)	MNHN.F.B13434	1	MNHN.F.B13434	1		1
<i>Eryon cuvieri</i> (Desmarest, 1817)	MNHN.F.A32407, A33501, A33520, A33544, A33545, B13437, B13438, B13439, B13451, R03402, R65101, MNHN.GG.2004/7997, 2004/8109, 2004/8004, 2004/8218, 2004/8220	16	MNHN.F.A32407, A33501, A33520, A33544, A33545, B13437, B13438, B13439, B13451, R03402, R65101, MNHN.GG.2004/7997, 2004/8109, 2004/8004, 2004/8218, 2004/8220	16		16
STOMATOPODA						
Sculdidae						
<i>Sculda pennata</i> Münster, 1840	MNHN.F.B13466	1	-	-		1
MYSIDACEA						
Mysidacea						
<i>Elder ungulatus</i> (Münster, 1839)	MNHN.F.A33549, B13467, MNHN.GG.2004/8217	3	MNHN.F.A33549, B13467, MNHN.GG.2004/8217	3		3
XIPHOSURA						
Lumulidae						
<i>Mesolimulus walchii</i> (Desmarest, 1817)	MNHN.F.A33516, B13432, B13433, MNHN.GG.2004/747	4	MNHN.F.A33516, B13432, B13433, MNHN.GG.2004/747	4		4
TOTAL		104		99		117

ABBREVIATIONS

Institutions

MNHN.F: Muséum national d'Histoire naturelle, Paris (France), Paleontological collection.

MNHN.GG: Muséum national d'Histoire naturelle, Paris (France), Geology collection.

CM: Carnegie Museum of Natural History, Pittsburgh (USA).

SMNS: Staatliches Museum für Naturkunde, Stuttgart (Germany).

Anatomy

a = branchiocardiac groove

ac = antennal carina

as = antennal spine

a1 = antennula

a2 = antenna

b = antennal groove

b₁ = hepatic groove

c = postcervical groove

d = gastro-orbital groove

di = diaeresis

e = eye

e₁e = cervical groove

egs = epigastric spine

gc = gastro-orbital carina

hs = hepatic spine

ip = intercalated plate

Mxp3 = third maxilliped

oc = orbital carina

P1–P5 = pereopods 1–5

r = rostrum

rs = rostral spines

sc = scaphocerite

ss = supraorbital spine

s1–s5 = pleonal somites 1–5

COMMENTED SYSTEMATIC LIST

Class MALACOSTRACA Latreille, 1802

Superorder EUCARIDA Calman, 1904

Order DECAPODA Latreille, 1802

Suborder DENDROBRANCHIATA Bate, 1888

Superfamily Penaeoidea Rafinesque, 1815

Family Aegeridae Burkenroad, 1963

Genus *Aeger* Münster, 1839

TYPE SPECIES. — *Macrourites tipularius* Schlotheim, 1822, by subsequent designation of Woods (1925).

Three species are known from the Solnhofen Lithographic Limestones (Schweigert *et al.* 2016). All are present in the palaeontological collections of the MNHN (Fig. 1).

***Aeger tipularius* (Schlotheim, 1822)**

(Fig.1A-C)

DIAGNOSIS FROM SCHWEIGERT ET AL. (2016). — Very short smooth rostrum; Mxp3 extremely long, with movable spines; chelate P1-P3; P1-P2 bearing long movable spines; P3 with spiny chelae; achelate P4-P5 and spineless; P3 slightly larger than P1-P2; well-developed pleopods; uropodal exopod with rounded diaresis.

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed seven specimens. Careful examination leads us to re-identify some of them. Three specimens, MNHN.F.A33509 (Solnhofen), B13443 (Eichstätt), MNHN.GG.2004/8072 (unknown locality), are maintained as *A. tipularius*, while four others are attributed to *Aeger spinipes* (Desmarest, 1817), *A. insignis* (Oppel, 1862), and *Acanthochirana cordata* (Münster, 1839).

COMMENTS. — Our assignation is based on the very short and smooth rostrum. The carapace groove pattern typical of *Aeger* — with a cervical groove steeply inclined, not joined to the dorsal margin but joined to the antennal groove; an oblique and sinuous branchiocardiac groove crossing all the carapace from the posterior margin to the hepatic region; and a hepatic groove joined anteriorly to the cervical groove and posteriorly to the branchiocardiac groove (see diagnosis in Charbonnier *et al.* 2017: 36) — is particularly visible on specimen A33509 (Fig. 1A-B).

***Aeger spinipes* (Desmarest, 1817)**

(Fig.1D)

DIAGNOSIS FROM SCHWEIGERT ET AL. (2016). — Extremely elongate rostrum, with one medium ventral tooth; Mxp3 extremely long, with movable spines; chelate P1-P3; P1-P2 bearing long movable spines; P3 with smooth chelae; achelate P4-P5 and spineless; P3 slightly larger than P1-P2; well-developed pleopods; uropodal exopod with rounded diaresis.

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed and figured only one specimen (MNHN.F.B13441, Eichstätt). We add two specimens from Solnhofen, MNHN.F. B13440, B13442 (Fig. 1D), formerly identified as *A. tipularius*.

COMMENT. — Our assignation is based on the extremely elongate rostrum.

***Aeger insignis* Opperl, 1862**

(Fig. 1E-F)

DIAGNOSIS FROM SCHWEIGERT ET AL. (2016). — Short rostrum, with one ventral tooth distally; Mxp3 extremely long, with movable spines; chelate P1-P3; P2 with spiny chelae; P3 with spiny elements and chelae; achelate P4-P5; uropodal exopod with rounded diaresis.

STUDIED MATERIAL. — Charbonnier & Garassino (2012) did not mention this species. We add one specimen from Solnhofen, MNHN.GG.2004/57291 (formerly identified as *A. tipularius*).

COMMENT. — Our assignation is based on the elongate rostrum bearing one median ventral tooth, particularly visible in UV light (Fig. 1F).

Genus *Acanthochirana* Strand, 1928

TYPE SPECIES. — *Udora cordata* Münster, 1839 (partim), by subsequent designation of Glaessner(1929).

DIAGNOSIS FROM CHARBONNIER ET AL. (2017). — Rostral carina with spines pointing forward; smooth rostrum, spineless; one epigastric spine in the third anterior of dorsal margin; weak cervical groove, not joined to dorsal margin; oblique branchiocardiac groove joined to hepatic groove at level of strong hepatic spine; short hepatic groove backward directed; cephalic region with postorbital spine; hypertrophied Mxp3 with rows of movable spines; branch-like Mxp3 dactylus; chelate P1-P3; achelate P4-P5; uropodal exopod without diaeresis.

***Acanthochirana cordata* (Münster, 1839)**

(Fig. 2)

STUDIED MATERIAL. — We studied three specimens, MNHN.A33503, R03389 (Solnhofen) and A42003 (Eichstätt), respectively attributed by Charbonnier & Garassino (2012) to *Bylgia hexadon* Münster, 1839, *Aeger tipularius*, and *Acanthochirana longipes* (Oppel, 1862).

COMMENTS. — Charbonnier & Garassino (2012) identified the specimen MNHN.F.A42003 as *A. longipes*. Careful examination of this specimen leads us to a different identification. Among the criteria listed in the diagnosis by Schweigert *et al.* (2016), the number of dorsal rostral teeth and the elongation of Mxp3 are the most important to distinguish *A. cordata* from *A. longipes*. Since it was impossible to count the teeth on our specimens, we use the ratio Mxp3 length / cephalothorax length. Based on drawings from Oppel (1862), the ratio is ≤ 1 for

A. cordata while $\gg 1$ for *A. longipes*. The ratio measured on this specimen is of 0.9, implying an assignation to *A. cordata*.

Specimen A33503 (Fig. 2A-B), previously attributed to *Bylgia hexadon*, was misidentified: it clearly shows elongate Mxp3 with moveable spines characteristic of aegerid shrimps. More precisely, the length of Mxp3 fits well with those observed in *Acanthochirana*. Additionally, this specimen shows a spiny rostral carina prolonged by a smooth rostrum and an epigastric spine, which allow us to ascribe the specimen to *Acanthochirana cordata*.

Specimen R03389 (Fig. 2C-D), previously attributed to *Aeger tipularius*, was also misidentified: it clearly shows elongate Mxp3 with moveable spines characteristic of aegerid shrimps but the length of Mxp3 fits well with those observed in *Acanthochirana*. Also, the carapace groove pattern is typical of *Acanthochirana*, showing a weak cervical groove not joined to the cervical margin, an oblique branchiocardiac groove joined to the hepatic groove near the strong hepatic spine and a short hepatic groove backward directed (see diagnosis in Charbonnier *et al.* 2017: 32).

Family Penaeidae Rafinesque, 1815

Genus *Antrimpos* Münster, 1839

TYPE SPECIES. — *Antrimpos speciosus* Münster, 1839, by subsequent designation of Glaessner(1929).

TRANSLATION OF THE ORIGINAL DIAGNOSIS FROM MÜNSTER (1839). — Antennules short; antennae very long, with a very long scaphocerite; chelate P1-P3, increasing in length,

with movable dactyli; cylindric flattened cephalothorax; rostrum dentate; pointed telson and subrounded uropodal exopod.

TRANSLATION OF THE EMENDED DIAGNOSIS FROM OPPEL (1862). — Antennules very short, of different length, antennae of twice the length of the body, rostrum dentate, spiny Mxp3; chelate P1-P3, increasing in length, and achelate P4-P5; S5 longest; cuticle smooth except on the dorsal area of the carapace, which is covered with small pits.

TRANSLATION OF THE EMENDED DIAGNOSIS FROM VAN STRAELEN (1925). — Rostrum dentate – often on both sides; antennules of different length; antennae to twice length of body; chelate P1-P3 and achelate P4-P5.

EMENDED DIAGNOSIS FROM GLAESSNER (1969). — Antennules very short, antennae to twice length of body, rostrum dentate, carapace smooth, thin; length of pereopods increasing from 1 to 3; 6th abdominal somite longest.

EMENDED DIAGNOSIS FROM SCHWEIGERT ET AL. (2016). — Carapace subrectangular, laterally flattened; rostrum elongate slightly turned upward distally, with nine dorsal teeth and one ventral tooth distally; epigastric tooth; Mxp3 short and smooth; uropodal exopod with a subrounded diarsis.

EMENDED DIAGNOSIS (PRESENT WORK). — Carapace subrectangular, laterally flattened; elongate rostrum slightly turned upward distally, with several dorsal teeth and one ventral tooth; longitudinal rostral carina; epigastric tooth; postorbital spine; very strong and asymmetrical hepatic spine, with elongate dorsal segment and short ventral one; concave

cervical groove rimming the upper segment of hepatic spine; subhorizontal hepatic ridge below hepatic spine; s1-s3 with rounded median lateral processes (subtle in s3); Mxp3 short and smooth; chelate P1-P3, increasing in length, achelate P4-P5; uropodal exopod with a subrounded diarsis.

***Antrimpos speciosus* Münster, 1839**

(Fig. 3)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) mentioned 6 specimens: 3 specimens from Solnhofen (MNHN.F.A33519, A33548, R03502); 2 specimens from Eichstätt (MNHN.F. A33504, B13465) and 1 specimen from an unknown locality (MNHN.GG.2004/8086). Collections Boué, de Roissy, Hoffstetter, Manchester Museum, d'Orbigny.

COMMENTS. — Specimen MNHN.F.A33504 (Fig. 3A-C) shows a well-preserved rostrum and a well-marked hepatic spine, while specimen A33519 (Fig. 3G-H) shows evidence of preserved muscle fibres near somites 1 and 2 (see also Briggs *et al.* 2005). For comparison, specimens from the Carnegie Museum of Natural History (CM-33420; from Robalino *et al.* 2016; Fig. 3D-E) and from the private collection of Roger Frattigiani (Laichingen, Germany; figured in Schweigert 2015: fig. 568 and Fig. 3F) are also illustrated.

***Antrimpos undenarius* Schweigert, 2001**

(Figs 4-5)

TRANSLATION OF THE DIAGNOSIS FROM SCHWEIGERT (2001). — Large-sized species of the genus *Antrimpos*, rostrum with 11 dorsal spines, the posterior one [= hepatic spine] being separated from the others, and one ventral spine located just before the foremost dorsal spine. Long propodite on P3.

STUDIED MATERIAL. — Charbonnier & Garassino (2012) did not mention this species. Nine specimens MNHN.F.A06834, A49608, A49609, A49610, A49615, A49616, A49622, A49623 and A49624 from Nusplingen were re-discovered in the Collection d'Orbigny. All these specimens are labelled “Nusplingen, Mr Bérolzingen, 13^e” (Fig. 4A). The family von Beroldingen is an old family of nobles originating from Switzerland; Baron Franz Coelestin von Beroldingen (1740-1798) was known as a mineral and fossil collector and after his death, his nephew, Count Joseph Ignace von Beroldingen (1780-?), sold his mineral collection to the London museum (British Museum of Natural History 1904). In our case, “Mr Bérolzingen” refers to Paul Ignaz Josef Graf von Beroldingen (1804-1875), another nephew of Baron von Beroldingen, who offered the *Antrimpos* specimens from Nusplingen to Alcide d'Orbigny. von Beroldingen probably got them by exchanging fossils with Oscar Fraas (1824-1897) as the two of them knew each other. Indeed, in a letter from 1863, “Mr Bérolzingen” mentioned several fossils from the Tertiary of Swabia, including the Jurassic taxon *Squatina acanthoderma* from Nusplingen, which was described by Oscar Fraas in 1855 (Mayer 1976). Number “13^e” refers to the thirteenth geological stage of d'Orbigny, which is the Oxfordian. Additional specimens of *A. undenarius* coming from the SMNS collection are presented in Fig. 5 for comparison.

COMMENTS. — According to Schweigert (2017), *Antrimpos undenarius* is the most abundant prawn of the Nusplingen Plattenkalk. The d'Orbigny specimens are characteristically

preserved by a coating made of iron oxides (Figs 4B, D, E, H, 5A-E) and embedded in relatively coarse lithographic limestones. The orientation of the corpses (pleon in lateral view and carapace in dorso-ventral view, as in Figs 4H, 5A-C, E) is also characteristic of the fossil prawns from Nusplingen. Thus, the preservation in complete dorsal view, as for A49610 (Fig. 4D) and SMNS 66122 (Fig. 5F) is rather rare. Furthermore, the preservation in 3D of the rostrum is particularly remarkable on specimens SMNS 80482 and SMNS 66122 (Fig. 5C, F). On specimens housed at the MNHN, the diagnostic anatomical characters of the species are poorly preserved and observed alternatively in several specimens (Fig. 4C, E, G). For instance, the rostrum with numerous dorsal teeth (Fig. 4G), the strong hepatic spine, the hepatic ridge, the median lateral processes on s1-s3 are typical of *Antrimpos*. The large size of the specimens is compatible with *A. undenarius*.

Infraorder ASTACIDEA Latreille, 1802

Superfamily Erymoidea Van Straelen, 1925

Family Erymidae Van Straelen, 1925

PRELIMINARY REMARKS. — *Eryma modestiforme* (Schlotheim, 1822) (Fig. 6), *Palaeastacus fuciformis* (Schlotheim, 1822) (Fig. 7) and *Pustulina minuta* (Schlotheim, 1822) (Fig. 7) are the three most common erymids found in the Solnhofen Lithographic Limestones. Numerous specimens are almost complete, but the compression often impedes the identification of the carapace grooves, which are important for the systematic of the Erymidae. Instead, we use the general ornamentation and the features of the P1 chelae (shape and ornamentation) to distinguish the erymid lobsters. Indeed, *P. fuciformis* and *P. minuta* have P1 chelae with a subrectangular propodus bearing short and wide fingers, while the fingers of *E. modestiforme* are longer than the propodus and are progressively narrowing to their distal extremity.

Moreover, *E. modestiforme* is ornamented by small tubercles and depressions, while *P. minuta* is covered by coarse rounded tubercles and *P. fuciformis* bears strong spines on its carapace and its P1 propodus.

Genus *Eryma* Meyer, 1840

TYPE SPECIES. — *Macrourites modestiformis* Schlotheim, 1822, by subsequent designation of Glaessner(1929).

Eryma modestiforme (Schlotheim, 1822)

(Fig. 6)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed 8 specimens: 6 specimens coming from Solnhofen (MNHN.F.A33507, B13448, B13450, B13452, B13463, MNHN.GG.2004/7462), 1 specimen from Eichstätt (B13446) and 1 specimen from an unknown locality (MNHN.GG.2004/8078-7471). Only two of them were figured (MNHN.F.B13450 and B13446); we thus figure three other specimens (MNHN.F.A33507 – Fig. 6B, B13452 – Fig. 6E and B13463 – Fig. 6A) and add three new specimens, 1 specimen from Eichstätt (MNHN.F.A32408 – Fig. 6H); 1 specimen from Painten (MNHN.F.A70906 – Fig. 6G) and 1 specimen from an unknown locality (MNHN.F.A70905 – Fig. 6C). Collections Boué, Schwarzschild, A. Milne-Edwards, Hoffstetter, Manchester Museum, Férussac, Sauzières.

COMMENTS. — *Eryma modestiforme* and *E. veltheimii* (Münster, 1839) are the two species encountered in the Solnhofen Lithographic Limestones, the former being the most common.

E. modestiforme is known by numerous specimens, almost complete, stored notably in European palaeontological collections (e.g. Paris, Berlin, London, Brussels, Basel). Among the MNHN collection, four specimens clearly show the intercalated plate characteristic of the erymid lobsters: MNHN.F.A32408, A33507, A70905, B13463, B13450 (Fig. 6A-D, H; see also Charbonnier & Garassino 2012: fig. 3b). All the specimens exhibit a short P1 propodus with a dense ornamentation, allowing us to ascribe the fossils to the species *E. modestiforme* (the propodus is more elongate and smooth in *E. veltheimii*). Moreover, three specimens show additional characters, diagnostic of *E. modestiforme*: (1) on the specimens MNHN.F.A70905 (Fig. 6C-D) and B13452 (Fig. 6E-F), the carapace groove pattern, in particular the junction between the postcervical and the branchiocardiac grooves (Devillez *et al.* 2016; Devillez & Charbonnier 2017), is easily identifiable; and (2) the morphology of the P1 chelae of the specimen MNHN.F.A32408 (Fig. 6H), shows a subrectangular propodus, thin fingers progressively narrowing to their distal extremity and without teeth on their occlusal margins.

The historical specimen MNHN.F.A32408, figured by Desmarest (1822: pl. 11, fig. 5), shows the typical mode of preservation and lithology of the Bavarian Lithographic Limestones (Fig. 6H) but the locality of this specimen may be misleading. Desmarest (1822: p. 136) refers to “Aichstedt”, which is also the locality indicated on the original label, while the locality “Aichtät” is specified on the specimen. In a letter about the Franconian geology to A. Brongniart, L. de Buch (1823) evokes the lithographic limestones exploited at “Eichstedt” and “Solenhofen”, in the Altmühl valley. However, there is no locality spelled “Eichstedt” next to the Altmühl River (instead, Eichstedt (Altmark) is a city located approx. 80 km west to Berlin) but “Eichstätt”. Thus, the designations “Aichtät”, “Aichstedt” and “Eichstedt” in the mentioned publications are likely orthographic variations referring to the same locality, nowadays spelled Eichstätt.

Genus *Palaeastacus* Bell, 1850

TYPE SPECIES. — *Astacus sussexiensis* Mantell, 1824, by subsequent designation of Glaessner(1929).

***Palaeastacus fuciformis* (Schlotheim, 1822)**

(Fig. 7A-C)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) mentioned three specimens: two from Solnhofen (MNHN.F.B13449; MNHN.GG.2004/8245) and one from an unknown locality (MNHN.GG.2004/7998-8106). We do not change their attribution.

COMMENTS. — Since only one specimen (MNHN.F.B13449) was figured by Charbonnier & Garassinno (2012), we additionally figure the specimen MNHN.GG.2004/8245 (Fig. 7A-C), which is particularly well-preserved; notably, the ornamentation is nearly complete.

Genus *Pustulina* Quenstedt, 1857

TYPE SPECIES. — *Pustulina suevica* Quenstedt, 1857, by subsequent designation of Glaessner(1929).

***Pustulina minuta* (Schlotheim, 1822)**

(Fig. 7D)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) mentioned three specimens: two from Eichstätt (MNHN.F.B13444, B13445) and one specimen from an unknown locality (MNHN.GG.2004/8101). We do not change their attribution.

Family Mecochiridae Van Straelen, 1925

Genus *Mecochirus* Germar, 1827

TYPE SPECIES. — *Macrourites longimanatus* Schlotheim, 1820, by subsequent designation of Woods (1927).

***Mecochirus longimanatus* (Schlotheim, 1820)**

(Fig. 8)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed 27 specimens including two specimens described as *Mecochiria foresti* by Secrétan (1968). We add a new specimen from Solnhofen (MNHN.F.A70929).

COMMENTS. — We localized the type material of *Mecochiria foresti* Secrétan, 1968. She listed five syntypes but figured only two (MNHN.F.A33537 – Fig. 8A-B, A33539 – Fig. 8F-G), which are dorsoventrally flattened. According to Förster (1971), these specimens show diagnostic characters of *Mecochirus longimanatus*, and *Mecochiria* is a junior synonym of *Mecochirus*. This view was followed by Schweitzer *et al.* (2010: 20), who, however, maintained *Mecochirus foresti* as a separate species. Our examination of the two syntypes did not evidence any significant morphological differences to distinguish two species. Hence, we consider *M. foresti* as a junior synonym of *M. longimanatus*.

Specimen MNHN.F.A70929 (Fig. 8C-E) arrived in the MNHN collections in December 1930, through Mr Gravigny, Charles Brongniart's son-in-law. The carapace exhibits the typical

cervical groove and the orbital and gastro-orbital carinae. P1 is very elongate and P2 shows a strong and stout propodus as described by Garassino & Schweigert (2006).

Infraorder POLYCHELIDA Scholtz & Richter, 1995

Family Eryonidae De Haan, 1841

PRELIMINARY REMARKS. — To date, the following eryonid species have been reported from the Solnhofen Lithographic Limestones: *Cycleryon propinquus* (Schlotheim, 1822), *Cycleryon orbiculatus* (Münster, 1839), *Cycleryon elongatus* (Münster, 1839), *Cycleryon wulfi* Garassino & Schweigert, 2004, *Eryon cuvieri* Desmarest, 1817, *Knebelia bilobata* (Münster, 1839), *Knebelia schuberti* (Meyer, 1836), and *Knebelia totoroï* Audo, Schweigert, Haug, Haug, Saint Martin & Charbonnier, 2014 (Audo *et al.* 2014b). Audo *et al.* (2014a) mentioned additional species including *Soleryon schorri* from Wattendorf and *Soleryon* sp. from Zandt.

Genus *Cycleryon* Glaessner, 1965

TYPE SPECIES. — *Macrourites propinquus* Schlotheim, 1822, by original designation.

***Cycleryon propinquus* (Schlotheim, 1822)**

(Fig. 9)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed five specimens (Table 1). We do not change their contribution.

COMMENTS. — The specimen MNHN.F.B13436 (Fig. 9A) is preserved in ventral view and exhibits asymmetrical first pereopods: the right P1 presents the usual aspect whereas the left one is much more reduced. According to Van Straelen (1925) and Audo (2014), this physiology is not native but rather due to a regenerative heterochely. The crista dentata (serrated inner margin of the third maxilliped ischium) is visible.

Genus *Eryon* Desmarest, 1817

TYPE SPECIES. — *Eryon cuvieri* Desmarest, 1817, by monotypy.

***Eryon cuvieri* Desmarest, 1817**

(Fig. 9)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed 16 specimens including the lectotype (Table 1).

COMMENTS. — Three of the specimens figured are in ventral view (Fig. 9 C-G), allowing the observation of nicely preserved details such as the mandibles exhibiting sharp triangular teeth of uneven size (specimen MNHN.F.GG2004/8220; Fig. 9D-E). Indeed, the preservation is usually excellent: the antennae, antennules and eyestalks of the specimens MNHN.F.A33545 and GG2004/8218 are clearly visible and they exhibit between eight and ten pereopods. The dorsally preserved specimen MNHN.F.B13439 (Fig. 9H) is also well-preserved and evidences delicate details on the carapace (branchiocardiac, postcervical and cervical grooves), telson (punctuations and carinae). The other specimen (A33501; Fig. 9B) present some calcite bundles on the left chela.

Superorder PERACARIDA Calman, 1904

Order MYSIDACEA Boas, 1883

Suborder and Family uncertain

Genus *Elder* Münster, 1839

TYPE SPECIES. — *Elder ungulatus* Münster, 1839, by subsequent designation of Opper (1862).

***Elder ungulatus* Münster, 1839**

(Fig. 10)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed three specimens from Solnhofen (MNHN.F.A33549, B13467; MNHN.GG.2004/8217) but figured none. We do not change their contribution.

COMMENTS. — Specimen MNHN.F.A33549 (Fig. 10) presents some pereopods with terminal dactylus, some pleopods, the tail fan, and the hooked rostrum, which is isolated from the body. The carapace (cephalothoracic shield) is not preserved, neither the pleon. This configuration evokes an exuvia or a predated specimen. Intriguingly, some pereopods exhibit apodemes as if the muscles were stripped off.

Class MEROSTOMATA Dana, 1852

Order XIPHOSURIDA Latreille, 1802

Family Limulidae Riek & Gill, 1971

Genus *Mesolimulus* Størmer, 1952

TYPE SPECIES. — *Limulus walchii* Desmarest, 1817, by monotypy.

Mesolimulus walchii (Desmarest, 1817)

(Fig. 11)

STUDIED MATERIAL. — Charbonnier & Garassino (2012) listed four specimens from Solnhofen (MNHN.F.A33516, B13432, B13433; MNHN.GG.2004/7473) but figured only one specimen (MNHN.F.A33516). We do not change their contribution.

COMMENTS. — Specimen MNHN.F.B13432 (Fig. 11A) is poorly preserved and exhibit many calcite bundles (as dumbbells and spheres), mostly at the rear of the prosoma. According to Briggs & Wilby (1996), among the arthropods of Solnhofen, *Mesolimulus* is the taxon the most commonly subject to calcite crystals bundles development (we illustrate a specimen of *Eryon cuvieri* with calcite bundles on Fig. 9B). Such crystals are believed to be formed during the early stage of diagenesis, due to microbial activity. Specimen MNHN.F.B13433 (Fig. 11B) is a dorsal view of a slightly deformed specimen; the prosoma, carapace and telson are beautifully preserved.

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Figures

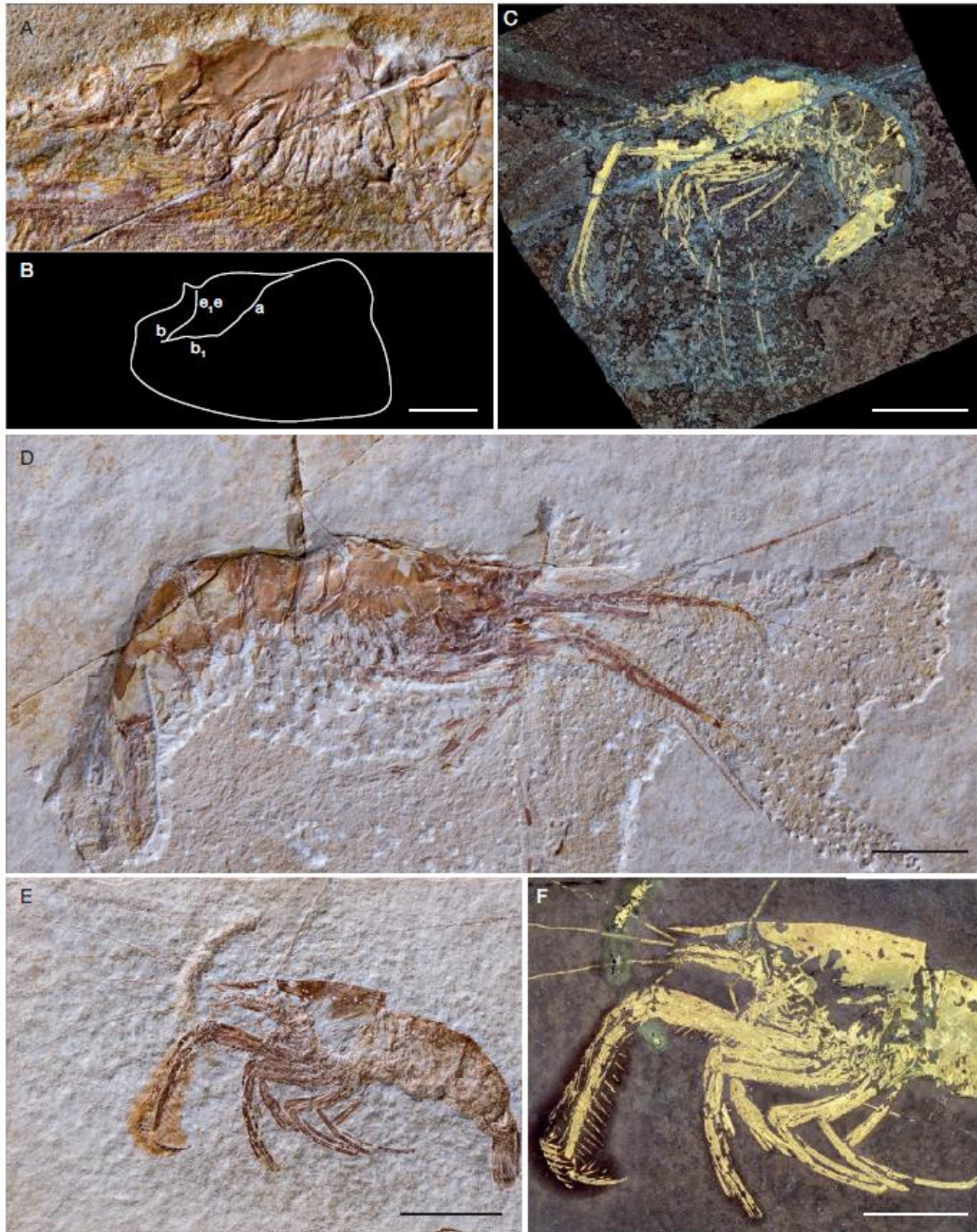


Fig. 1. — **A-C**, *Aeger tipularius* (Schlotheim, 1822), specimen MNHN.F.A33509 from Solnhofen; **A**, natural light; **B**, interpretation of the carapace grooves; **C**, UV light; **D**, *Aeger spinipes* (Desmarest, 1817), specimen MNHN.F.B13442 from Solnhofen; **E**, **F**, *Aeger insignis* Oppel, 1862, specimen MNHN.GG.2004/57291 from Solnhofen; **E**, natural light; **F**, UV light. Scale bars: A, C, 1 cm; B, D, 2 cm; E, 3 cm. Abbreviations: a, branchiocardiac groove; b, antennal groove; b1, hepatic groove; e, e, cervical groove. Photographs: L. Cazes. Line drawing: G.P. Odin.

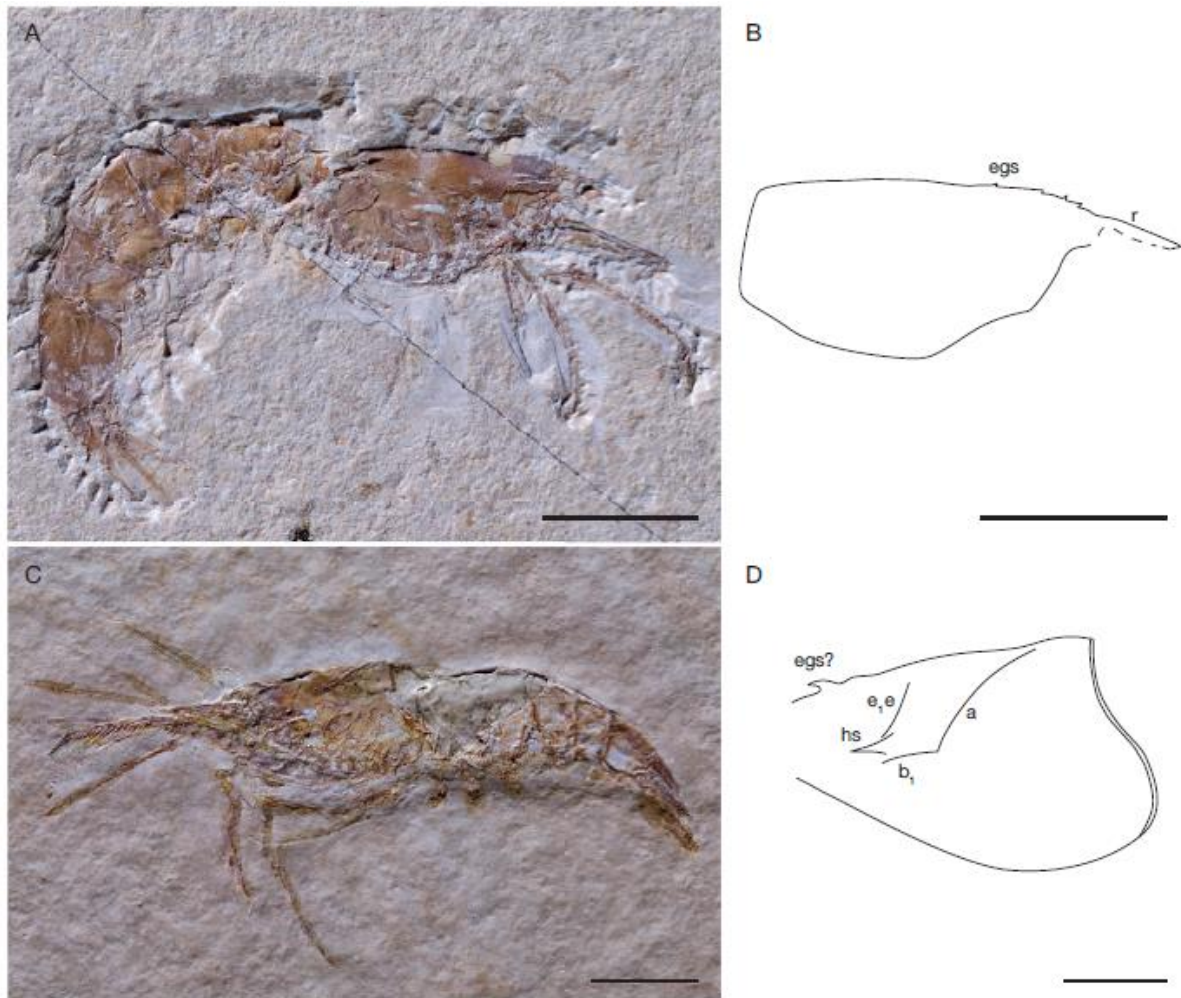


Fig. 2. — *Acanthochirana cordata* (Münster, 1839): **A, B**, specimen MNHN.F.A33503 from Solnhofen; **A**, natural light; **B**, interpretation of the carapace; **C, D**, specimen MNHN.F.R03389 from Solnhofen; **C**, visible light; **D**, interpretation of the carapace. Scale bars: A, B, D, 1 cm; C, 2 cm. Abbreviations: a, branchiocardiac groove; b1, hepatic groove; e1e, cervical groove; egs, epigastric spine; hs, hepatic spine; r, rostrum. Photographs: L. Cazes. Line drawing: G.P. Odin

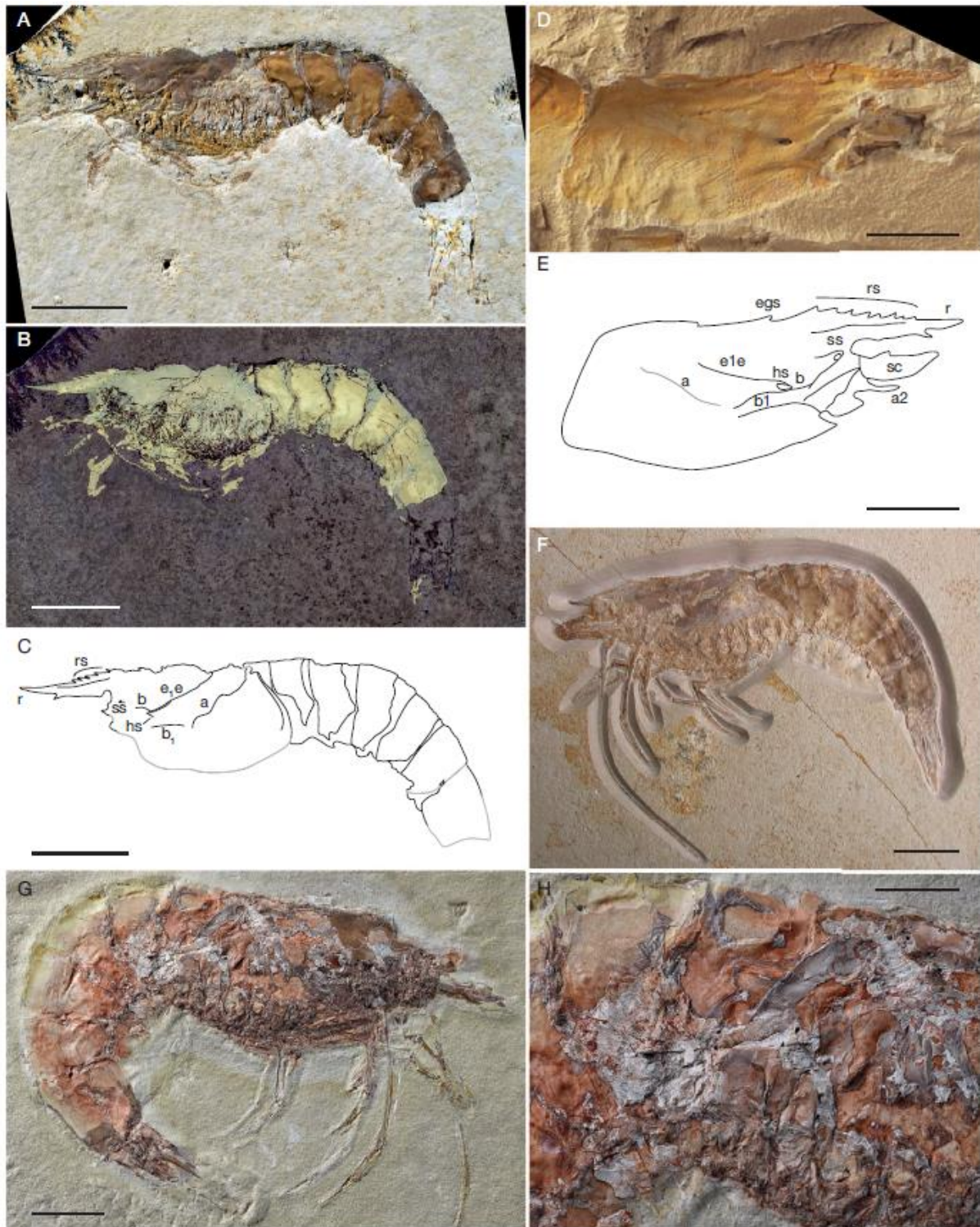


Fig. 3. — *Antrimpos speciosus* Münster, 1839: **A-C**, specimen MNHN.F.A33504 from Eichstätt: A, visible light; B, UV light; C, line drawing of the specimen; **D, E**, specimen CM-33420 likely coming from Solnhofen (Robalino *et al.* 2016); D, visible light; E, interpretation of the carapace; **F**, specimen from Solnhofen (illustrated in Schweigert 2015: fig. 568; private collection of Roger Frattigiani); **G, H**, specimen MNHN.F.A33519 from Solnhofen; G, full view of the specimen; H, close-up of muscle fibers. Scale bars: A-C, F, G: 2 cm; D, E, H, 1

cm. Abbreviations: a, branchiocardiac groove; a2, antenna; b, antennal groove; b1, hepatic groove; e1e, cervical groove; egs, epigastric spine; hs, hepatic spine; r, rostrum; rs, rostral spines; sc, scaphocerite; ss, supraorbital spine; Grey line of drawing, hypothesized delimitation. Photographs: L. Cazes (except D: M. McNaugher and F: G. Schweigert). Line drawing: G.P. Odin.

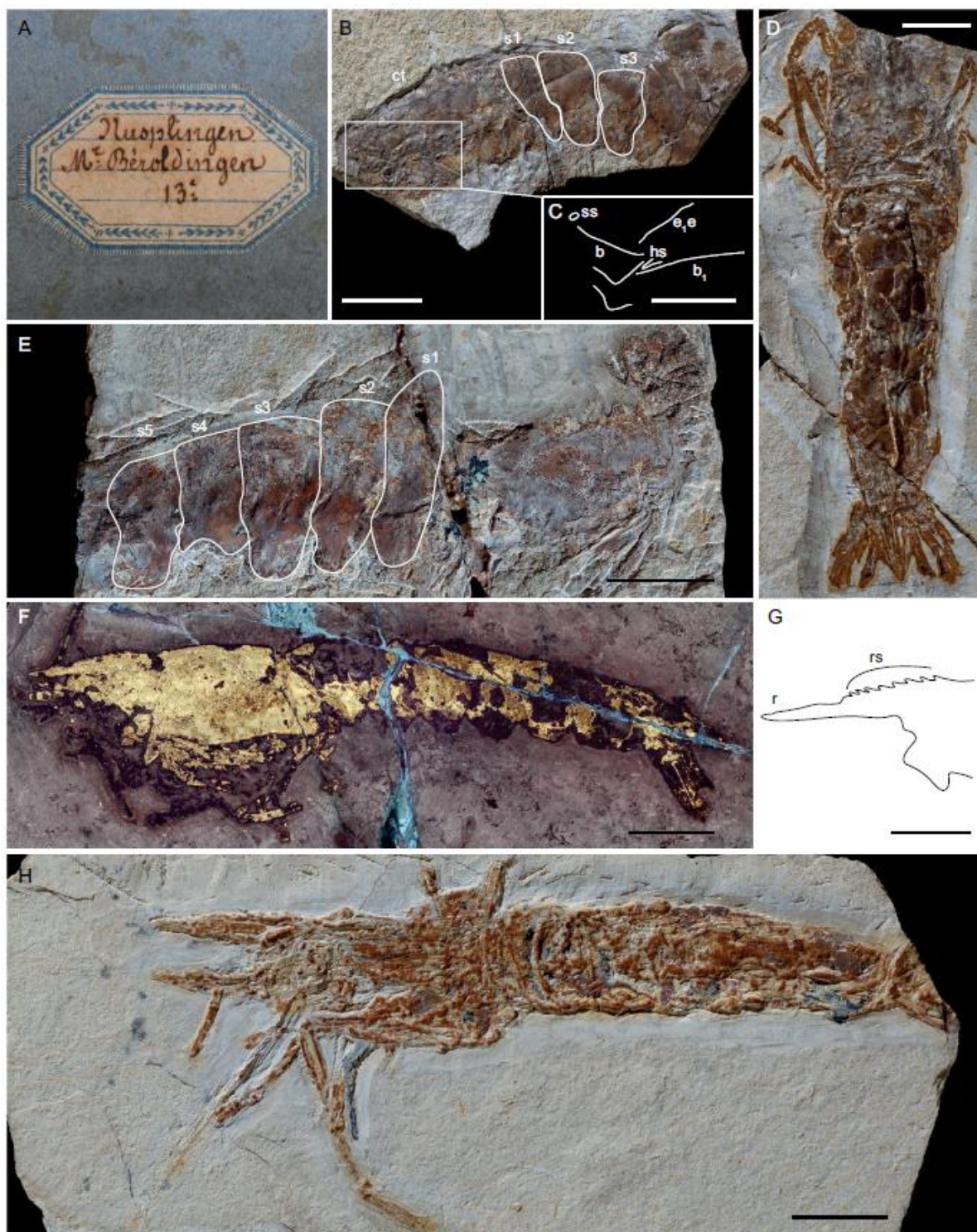


Fig. 4. — *Antrimpos undenarius* Münster, 1839 from Nusplingen, housed at the MNHN: **A**, picture of the old label; **B**, **C**, specimen MNHN.F.A49615; **B**, natural light picture; **C**, line-drawing of the grooves; **D**, specimen MNHN.F.A49610; **E**, specimen MNHN.F.A49622; **F**, **G**, specimen MNHN.F.A49608; **F**, UV picture; **G**, line-drawing of the rostrum; **H**, specimen MNHN.F.A49624. Scale bars: **B**-**F**, **H**, 1 cm; **G**, 2 cm. Abbreviations: **b**, antennal groove; **b₁**, hepatic groove; **ct**, cephalothorax; **e₁e₁**, cervical groove; **hs**, hepatic spine; **r**, rostrum; **rs**, rostral spines; **s1**-**s5**, pleonal somites; **ss**, supraorbital spine. Photographs: L. Cazes (except **A**: G. P. Odin). Line drawing: G. P. Odin.

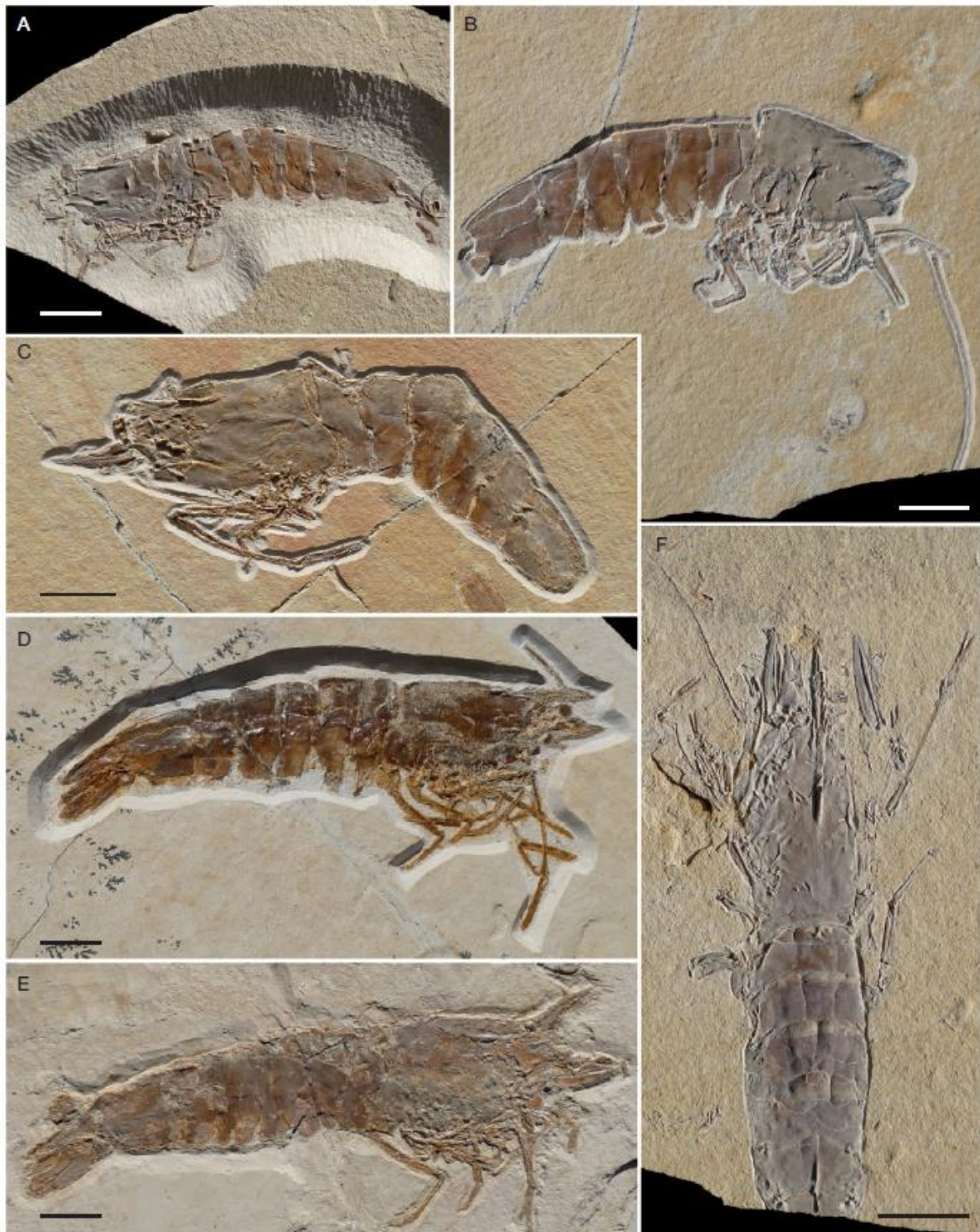


Fig. 5 — *Antrimpos undenarius* Münster, 1839 from Nusplingen, housed at the SMNS. **A**, specimen SMNS 80480. **B**, specimen SMNS 80481. **C**, specimen SMNS 80482. **D**, specimen SMNS 80483. **E**, specimen SMNS 24228. **F**, specimen SMNS 66122. Scale bars: A-F: 2 cm. Photographs: G. Schweigert.

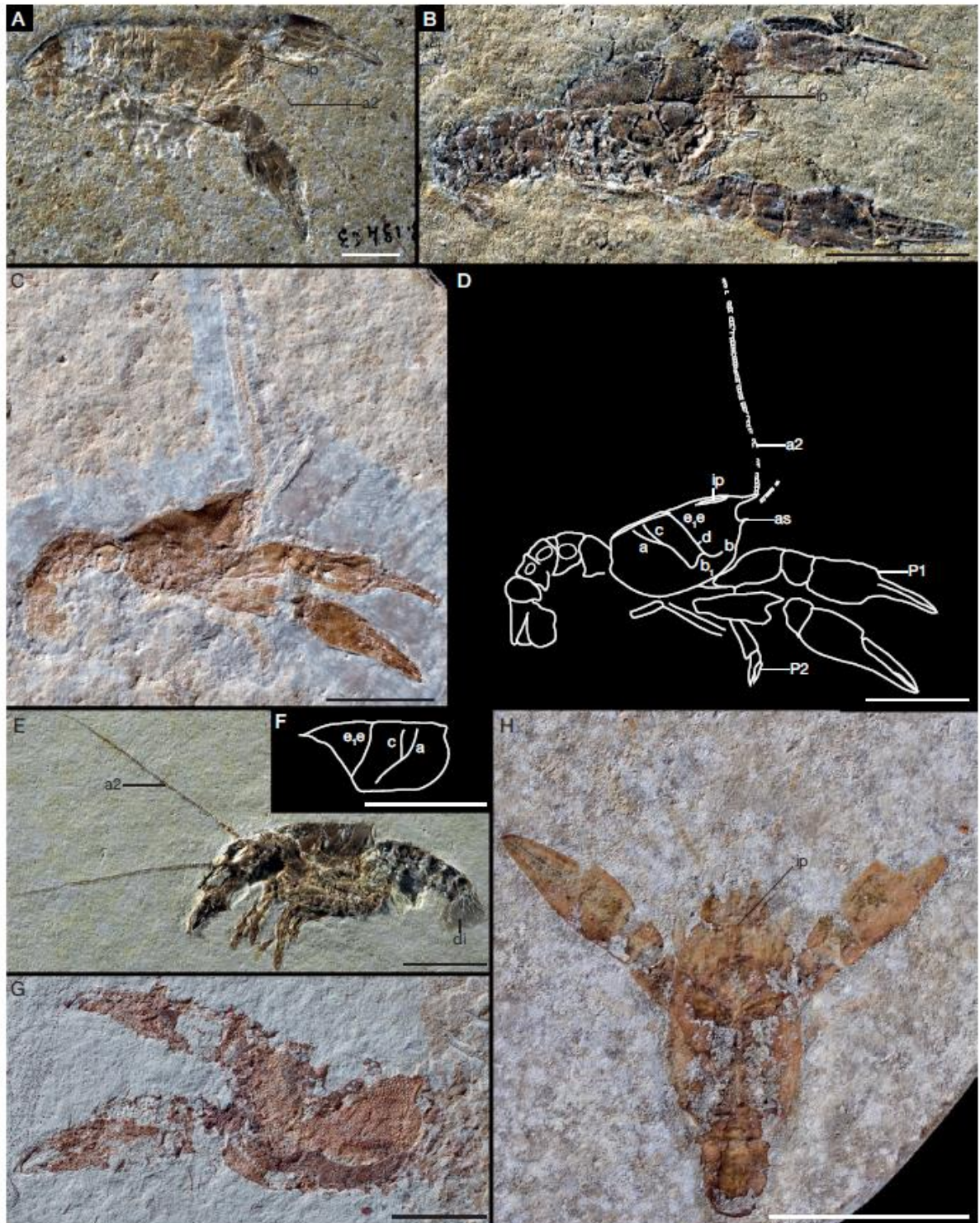


Fig. 6 — *Eryma modestiforme* (Schlotheim, 1822) from the Late Jurassic Solnhofen Lithographic Limestones (Bavaria, Germany). **A**, specimen MNHN.F.B13463 from Solnhofen; **B**, specimen MNHN.F.A33507 from Solnhofen; **C**, **D**, specimen MNHN.F.A70905 (unknown locality): general view (**C**) and line drawing (**D**); **E**, **F**, specimen MNHN.F.B13452 from Solnhofen: general view (**E**) and line drawing of the carapace (**F**); **G**, specimen MNHN.F.A70906 from Painten; **H**, specimen MNHN.F.A32408 from Eichstätt. Scale bars: 1 cm, except **H**: 0.5 cm. Abbreviations: a: branchiocardiac groove; as: antennal spine; a2: antenna; b: antennal groove; b₁: hepatic groove; c: postcervical groove; d: gastro-

orbital groove; di: diaeresis; e₁e: cervical groove; ip: intercalated plate; P1-2: periopods 1-2.
Preparation: Y. Despres (C). Photographs: C. Lemzaouda (A-B, E), L. Cazes (C, G-H). Line
drawing: J. Devillez.

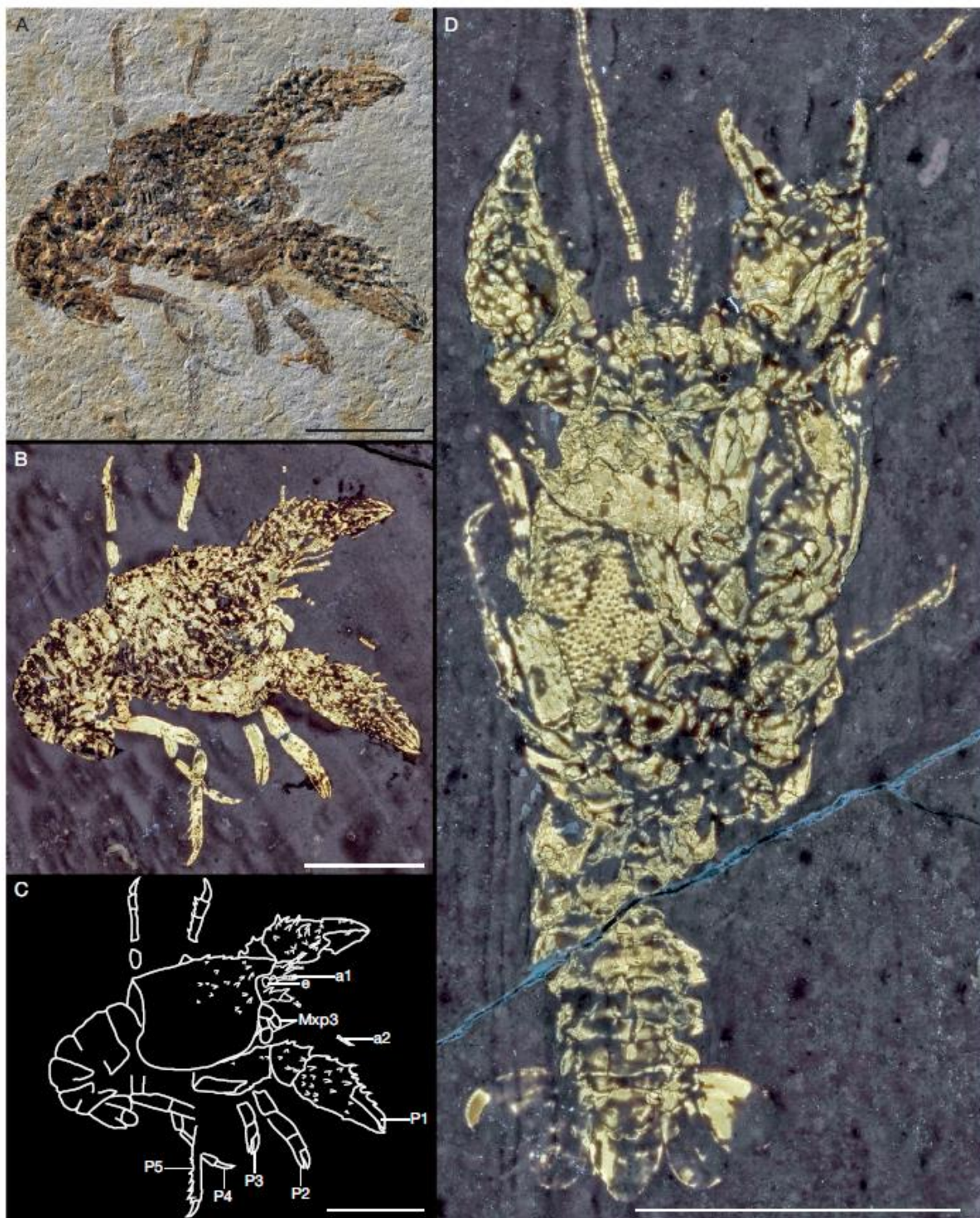


Fig. 7 — Other Erymoidea from the Late Jurassic Solnhofen Lithographic Limestones (Bavaria, Germany). A-C, specimen MNHN.GG.2004/8245 of *Palaeastacus fuciformis* (Schlotheim, 1822) from Solnhofen: specimen in natural light (A), specimen in UV light (B) and line drawing (C); D, specimen MNHN.F.B13445 of *Pustulina minuta* (Schlotheim, 1822) from Solnhofen in UV light. Scale bars: 1 cm, except D: 0.5 cm. Abbreviations: a1: antennule; a2: antenna; e: eye; Mxp3: third maxillipeds; P1-5: periopods 1 to 5. Photographs: L. Cazes. Line drawing: J. Devillez.

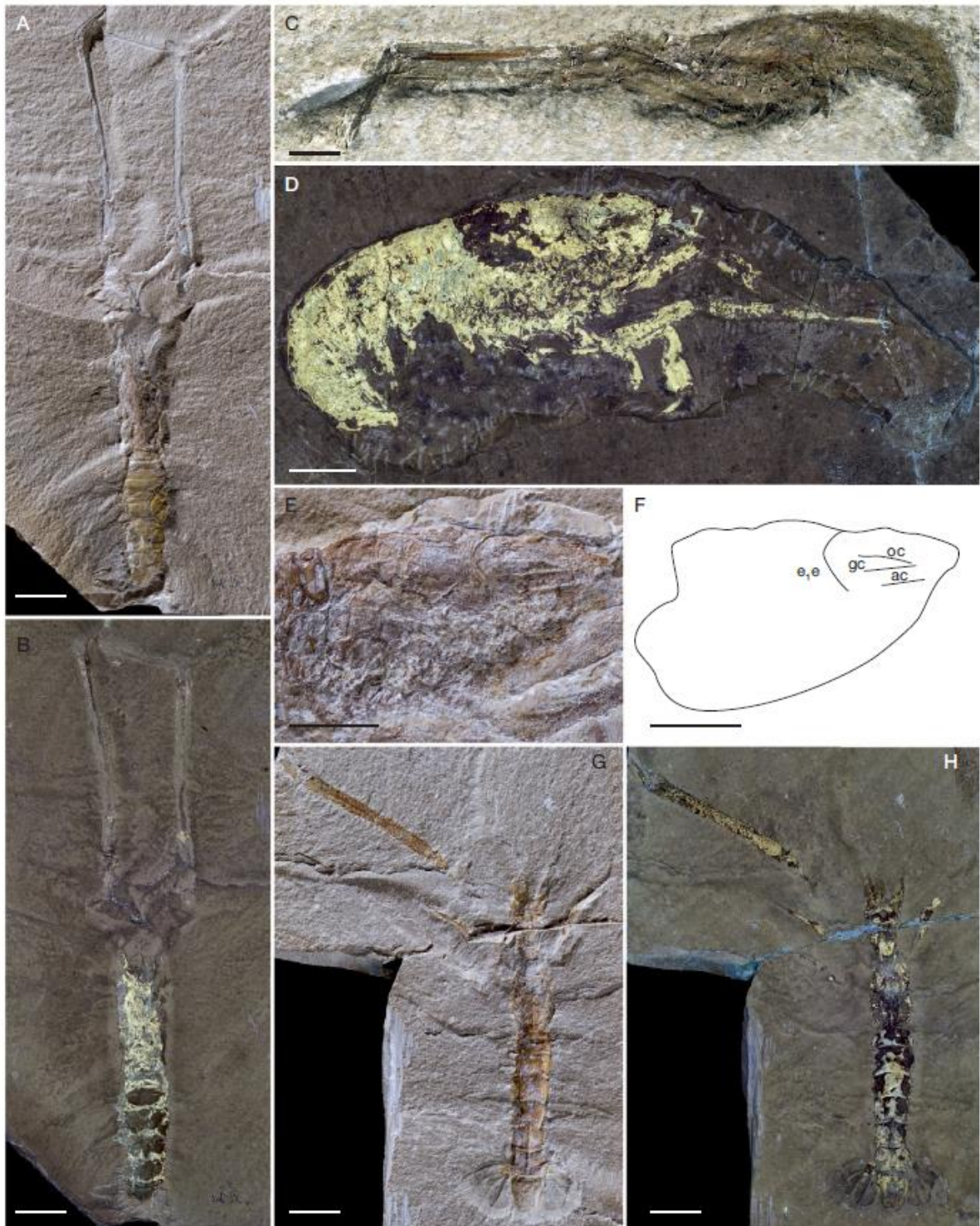


Fig. 8 — *Mecochirus longimanatus* (Schlotheim, 1820). **A-B**, specimen MNHN.F.33537, **A**: specimen in natural light, **B**: specimen in UV light; **C**, specimen MNHN.F.B13457; **D-F**, specimen MNHN.F.A70929, **D**: general view in UV light, **E**: view of the carapace in natural light and **F**: line drawing of the carapace; **G-H**, specimen MNHN.F.A33539, **G**: specimen in natural light, **H**: specimen in UV light. Scale bars: 1 cm. Abbreviations: ac = antennal carina, e,e = cervical groove, gc = gastro-orbital carina, oc = orbital carina. Photographs: L. Cazes. Line drawing: G.P. Odin.

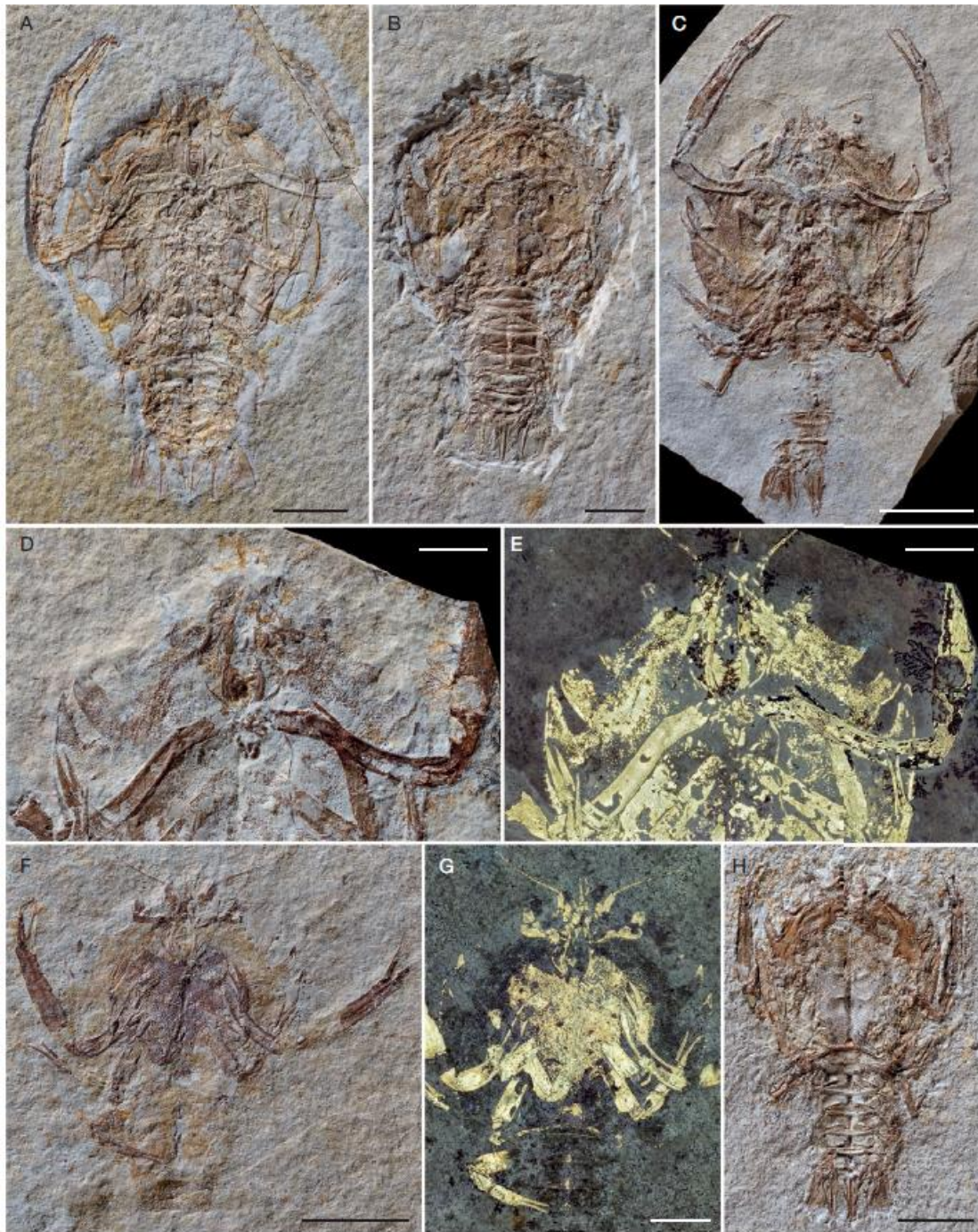


Fig. 9 — **A**, *Cycleryon propinquus* (Schlotheim, 1822): specimen MNHN.F.B13436 from Solnhofen; **B-H**, *Eryon cuvieri* Desmarest, 1817: **B**, specimen MNHN.F.A33501 from Solnhofen; **C**, specimen MNHN.GG.2004/8218 from Solnhofen area. This specimen was referred to as coming from Pappenheim. Since there are no Solnhofen Lithographic Limestones there, while many traders lived there, this specimen was probably purchased in Pappenheim. **D-E**, specimen MNHN.GG.2004/8220 from Solnhofen, natural light (**D**) and UV light (**E**); **F-G**, specimen MNHN.F.A33545 from Solnhofen, natural light (**F**) and UV light (**G**); **H**, specimen MNHN.F.B13439 from unknown locality. Scale bars: A, C, F, H: 2 cm; B, D, E, F: 1 cm. Photographs: L. Cazes.

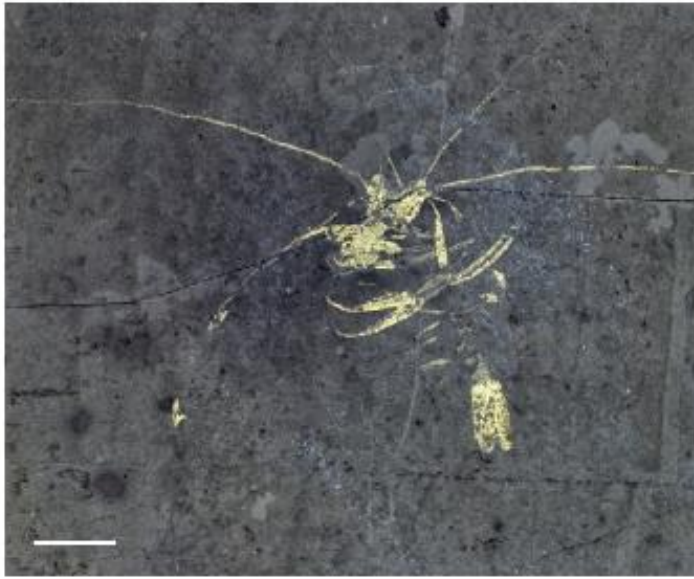


Fig. 10 — *Elder ungulatus* (Münster, 1839). Specimen MNHN.F.A33549 under UV light. Scale bar: 1 cm. Photograph: L. Cazes.



Fig. 11 — *Mesolimulus walchii* (Desmarest, 1817). **A**, specimen MNHN.F.B13432 **B**, specimen MNHN.F.B13433. Scale bar: 1 cm. Photographs: L. Cazes.