



## DIVERSITY AND PALAEOECOLOGY OF THE ENIGMATIC GENUS *KNEBELIA* (EUCRUSTACEA, DECAPODA, ERYONIDAE) FROM UPPER JURASSIC PLATTENKALKS IN SOUTHERN GERMANY

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Typescript received 7 March 2013; accepted in revised form 24 June 2013

**Abstract:** For a long time, the genus *Knebelia* Van Straelen, 1922 has comprised two species of eryonid lobster, *K. bilobata* (Münster, 1839) and *K. schuberti* (Meyer, 1836), both recorded exclusively from Late Jurassic Lagerstätten in southern Germany. Recently, the latter has been suggested to represent a juvenile individual of *Cycleryon propinquus* (Schlotheim, 1822). A re-examination of the type and new material has led to our rejection of that interpretation and confirmation of assignment of this species to *Knebelia*. Two specimens, both possessing short frontal lobes, from plattenkalks at Nusplingen (late Kimmeridgian) and at Solnhofen (early Tithonian), respectively, are here assigned to a

new species, *K. totoroï* sp. nov. This new species and a review of *K. bilobata* have furnished new insights into the origin and function of the frontal lobes, which are expansions articulated to the front of the carapace. They probably functioned as rudders facilitating 'tail-flip swimming' as observed in the paddle-like antennae of extant scyllarids (Eucrustacea, Decapoda, Scyllaridae). The rudder-like lobes identified in *Knebelia* may therefore represent a case of convergent evolution.

**Key words:** polychelidan lobsters, lithographic limestones, Lagerstätten, Kimmeridgian, Tithonian, palaeoecology.

THE Upper Jurassic plattenkalks in southern Germany comprise a wide array of Konservat-Lagerstätten deposited in small restricted lagoons near the Kimmeridgian–Tithonian boundary (Fig. 1). These Lagerstätten are often lumped as 'Solnhofen Lithographic Limestones' (Garassino and Schweigert 2006). They are renowned for their exceptionally preserved fossils including many delicate organisms such as articulated vertebrates, echinoderms, insects, jellyfish and eucrustaceans. For a review, reference is made to Frickhinger (1994, 1999; references therein). Among the decapod crustaceans are diverse polychelidan lobsters that have been assigned by Garassino and Schweigert (2006) and Audo *et al.* (2013a) to the families Eryonidae Haan, 1841 (seven species), Coleiidae Van Straelen, 1925 (one species) and the genus *Palaeopentacheles* Knebel, 1907 (one species). All these taxa have well-developed eyes and are associated with both shallow-water and terrestrial organisms. Extant representatives of the Polychelida, however, are blind and restricted to deep-water environments

(Galil 2000). Among eryonids, *Knebelia bilobata* probably ranks among the more enigmatic species. It is rather rare and typically possesses a pair of frontal lobes whose unique structure was interpreted by Knebel (1907), who considered them to be an anterior portion of the carapace, while Van Straelen (1925) thought that they were a pair of flattened antennae similar to those of scyllarids.

The aim of the present study was to review the genus *Knebelia* and describe a new species based upon new specimens recorded from the Solnhofen and Eichstätt (early Tithonian, Bavaria) and Nusplingen (late Kimmeridgian, Baden-Württemberg) Lagerstätten. Our observations on *Knebelia* present new insights into the origin and function of the peculiar frontal lobes, and new palaeoecological implications are put forward.

*Institutional abbreviations.* BSPG, Bayerische Staatssammlung für Paläontologie und Geologie (Munich, Germany); FSL, Université Claude Bernard Lyon 1 (Villeurbanne, France); JME, Jura-Museum

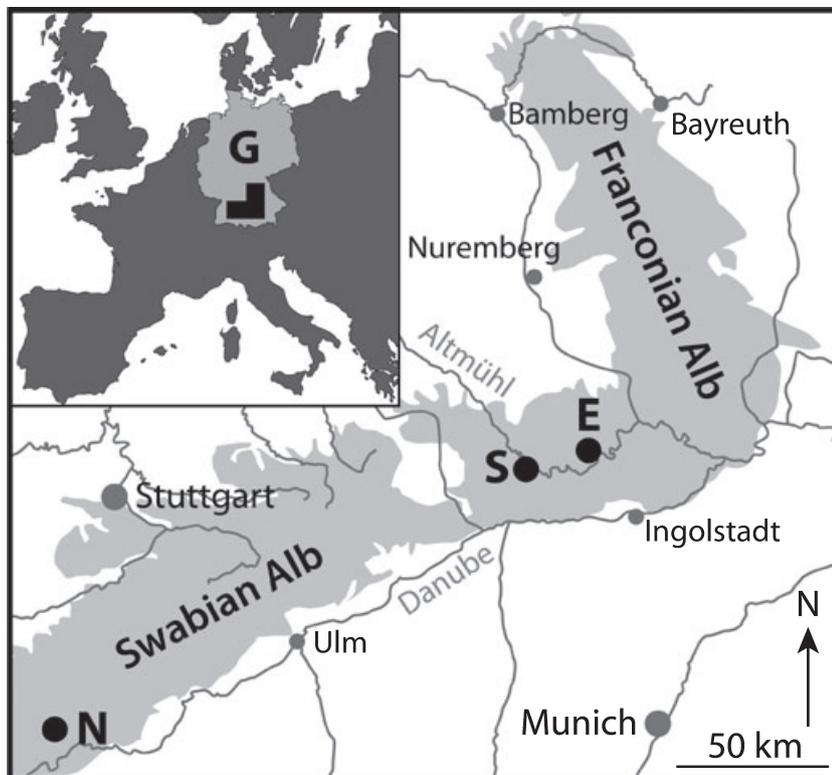
(Eichstätt, Germany); MHN, Musée des Confluences (Lyon, France); MNHN.F, Collection de Paléontologie du Muséum national d'Histoire naturelle (Paris, France); NHM, The Natural History Museum (London, UK); SMCU, Sedgwick Museum of Earth Sciences, Cambridge University (Cambridge, UK); SMF, Senckenberg Naturmuseum (Frankfurt am Main, Germany); SMNS, Staatliches Museum für Naturkunde (Stuttgart, Germany).

## GEOLOGICAL SETTINGS

### *Solnhofen lithographic limestones*

These strata constitute a world-famous Fossilagerstätte of Late Jurassic age in Bavaria, comprising laminated or thin-bedded, very pure limestones with intercalated thin marly layers, which occur especially in the vicinity of the village of Solnhofen and the town of Eichstätt. In the past, they have been quarried mainly for lithographic stone and roof tiles, but nowadays they are used as wall and paving tiles or for cement production. During their exploitation, thousands of excellently preserved fossils, including the ancient bird *Archaeopteryx lithographica* Meyer, 1861, have been recovered and have found their way to numerous palaeontological collections across the world. They are also illustrated in many popular science books (Frickhinger 1994, 1999). Numerous environmental models have been suggested for the formation of these

limestones; for an overview, reference is made to, for example, Barthel *et al.* (1990), Viohl (1994, 1998) and Keupp *et al.* (2007). In general, the Solnhofen Lithographic Limestones are almost devoid of bioturbation, and because of their excellent preservation, it is assumed that a fully marine environment existed, albeit with stagnant conditions due to a depletion of oxygen at least at the sea floor. Bedding planes often show typical structures related to microbial mats, and biostratinomy occasionally points to rapid sedimentation (Keupp *et al.* 2007). It seems that most of these limestones were laid down in moderately deep (<200 m) lagoonal settings situated along the northern Tethyan shelf. A serious problem, however, is that such environmental models need to explain observations from different localities. Historically, localities have often been simplified as 'Solnhofen', but fossils labelled 'Solnhofen' may in fact have come from the Eichstätt area or elsewhere and may even be of varying ages (Schweigert 2007b). The classic early Tithonian Solnhofen Limestone, the 'Oberer Schiefer Member' of Solnhofen and Langenaltheim, is quarried west of Solnhofen. This unit has a thickness of 20–50 m (Meyer and Schmidt-Kaler 1994). Hitherto, only a few attempts have been made to differentiate the various localities; for the Solnhofen area (*sensu stricto*), only Walther (1904) provided a faunal list. Contrary to what might be expected on the basis of museum collections, fossils are extremely rare in the field, except for mass occurrences of the tiny



**FIG. 1.** Geological map of southern Germany, with grey areas corresponding to the Upper Jurassic of the Swabian and Franconian albs. Abbreviations: E, Eichstätt Lagerstätte; G, Germany; N, Nusplingen Lagerstätte; S, Solnhofen Lagerstätte.

planktonic crinoid *Saccocoma tenella* (Goldfuss, 1831), which is the most typical fossil of the Solnhofen Lithographic Limestones. Occasionally, small bony fish occur in mass mortality assemblages. Numerous decapod crustaceans have been recorded (e.g. Garassino and Schweigert 2006; Charbonnier and Garassino 2012; references therein). The lithographic limestones in the Solnhofen–Langenaltheim area have yielded prawns such as *Antrimpos speciosus* Münster, 1839, *Aeger spinipes* (Desmarest, 1817) and *Acanthochirana cordata* (Münster, 1839), as well as lobsters including *Mecochirus longimanatus* (Schlottheim, 1820), *Glyphea pseudoscyllarus* (Schlottheim, 1822), *Palaeastacus fuciformis* (Schlottheim, 1822), *Eryma modestiforme* (Schlottheim, 1822), *Pustulina minuta* (Schlottheim, 1822) and numerous eryonoids. The last-named are represented by *Cycleryon propinquus*, *Cycleryon orbiculatus* (Münster, 1839), *Eryon cuvieri* Desmarest, 1817 (of which *E. arctiformis* is a synonym; see Charbonnier *et al.* 2012), *K. bilobata*, *K. schuberti* and *K. totoroi* sp. nov., the paratype of which is described below. Additional arthropods of the Solnhofen Lithographic Limestones in their type area are thylacocephaleans (genus *Clausocaris* Polz, 1989) and stomatopods (genus *Sculda* Münster, 1840). Despite the rarity of autochthonous benthic organisms in the Solnhofen–Langenaltheim area, several decapods did leave trackways or traces of moulting on bedding planes (Schweigert 2007a).

#### Nusplingen Plattenkalk

Also known as ‘Nusplingen Lithographic Limestone’, this unit constitutes another fossil Lagerstätte similar to the early Tithonian Solnhofen Lithographic Limestones and is situated in the western part of the Swabian Alb, about 12 km north of the Danube River Valley on top of the Westerberg hill, west of Nusplingen. It is the sole occurrence of fossiliferous laminated limestones in the Swabian Upper Jurassic. These strata (between 10.5 and 17.0 m in thickness) were deposited in an anoxic to dysoxic environment in a lagoon about 80–100 m in depth, surrounded by siliceous sponge/microbial mounds and shallower areas. Some of the mounds were tectonically uplifted above sea level to produce small islands. In contrast to Solnhofen, the Nusplingen lagoon had a more pelagic setting, far away from larger continental areas such as the Rhenish and Bohemian massifs to the north and south-east, respectively.

Based on ammonite faunas, the Nusplingen Plattenkalk is of late Kimmeridgian age and thus approximately 0.5 myr older than the Solnhofen limestones (Schweigert 1998, 2007b). Within the succession, several turbidites with graded bedding and a few thicker bioturbated beds are intercalated, indicative of periodic improvements in

oxygenation. The turbidites yield angular lithoclasts and other components such as calcareous ooids, sponge spicules and sponges, and even some fragments of hermatypic corals from shallower areas surrounding the lagoon. For detailed sections, reference is made to Dietl *et al.* (1998) and Bantel *et al.* (1999). General overviews of this fossil site are those of Dietl and Schweigert (2001a, b, 2004, 2011) and Schweigert *et al.* (2012); a list of older publications can be found in Schweigert (1997).

The Nusplingen Lithographic Limestone is well exposed at two small quarries (Nusplingen and Egesheim). New excavations by the Staatliches Museum für Naturkunde, Stuttgart (SMNS) at these localities have provided a wealth of new data on sedimentology, palaeoecology, taphonomy and biostratigraphy, as well as the overall fossil content of this unit. Since 1993 more than 8000 fossils have been recovered, comprising in excess of 400 taxa, many of them new. Decapod crustaceans, in particular shrimps and prawns, as well as erymid and polychelid lobsters, are common in the basal and middle beds of the Nusplingen Plattenkalk, and many of them are well preserved. Others are incomplete moults or show signs of predation (Schweigert and Dietl 1999; Schweigert *et al.* 2000; Schweigert 2001a, b). In contrast to the Solnhofen limestones, juvenile stages or larvae are absent. In total, about 20 decapod crustacean species have been recorded (Dietl and Schweigert 2011).

## MATERIAL AND METHODS

The present study is based upon ten specimens of *K. bilobata* (BSPG AS VI 39, BSPG AS VI 509, BSPG AS VII 752–754, JME-SOS 6864, JME-SOS 6866, JME-SOS 7817, NHM In.28964 and SMNS 70044), 32 specimens of *K. schuberti* (SMF X/m 73, JME-SOS 35–37, JME-SOS 6838–6842, JME-SOS 6846, JME-SOS 6848–6849, JME-SOS 6853, JME-SOS 6856–6858, JME-SOS 6860, SMNS 67806, BSPG 1972 I 95, BSPG AS VII 755 (syntype of *Eryon ovatus* Münster, 1839), BSPG AS VII 757, MNHL-20272104, MNHN.F.A33550, SMF X/m 144–146, NHM.41982 (two specimens in the same lot), NHM.44826, NHM.44827, NHM.44829 and SMCU F11402 (syntype of *E. ovatus*), as well as two specimens of *K. totoroi* sp. nov. (SMNS 67916 and BSPG AS VI 509). Specimens were studied using a stereo dissection microscope with an attached camera lucida device. Line drawings were prepared by the first author. One specimen was documented with the aid of composite fluorescence microscopy (Fig. 8A; Haug *et al.* 2008, 2009) on a Zeiss Axioscope 2 equipped with an Axiocam. Images were processed with CombineZM and Photoshop CS3. Some specimens were documented with a macrofluorescence setup (Fig. 6B; Haug *et al.* 2011a), with a Canon Rebel

T3i and an MP-E 65 mm macro lens. Images were processed as described in Haug and Haug (2011). Anatomical observations are summarized in Audo *et al.* (2013b).

A statistical study has been conducted to evaluate the ‘tail-flip swimming’ efficiency of *K. bilobata*, which is reported to have been equipped with an enormous tail fan (Van Straelen 1925). The main purpose has been to test statistically Van Straelen’s hypothesis by comparing tail fin *versus* carapace proportions in that species as well as in other eryonids. The result of these tests is used as a proxy in order to infer the ‘tail-flip swimming’ capabilities of *K. bilobata*. Similar analyses of extant species have proved valuable to inferences of variations in swimming capabilities during growth (Sardà *et al.* 1995).

The statistical study has been based on measurements of the uropodal exopods and carapaces of *K. bilobata* and other eryonids from the Upper Jurassic plattenkalks of Germany and France (Table 1). All measurements, based on photographs, were taken using the free software IMAGEJ (Schneider *et al.* 2012) and were rounded to the closest tenth of a millimetre. The length of the uropodal exopod (UL) is measured longitudinally from the distal margin to the articulation with the basipodite. The total length of the carapace (CL<sub>max</sub>) is measured parallel to the body axis from the most anterior to the most posterior point (Fig. 2B); thus, CL<sub>max</sub> includes the entire length of the frontal lobe in *K. bilobata*.

The ratio UL/CL<sub>max</sub> has been calculated for 8 specimens of *K. bilobata*, 17 of *E. cuvieri*, 5 of *Cycleryon elongatus*, 7 of *C. orbiculatus*, 16 of *C. propinquus* and 3 of *Soleryon amicalis* Audo, Charbonnier, Schweigert and Saint Martin, 2013a (Table 1). Each series of ratios constitutes a sample which is first tested for normality with a Shapiro–Wilk test. Samples following a normal law are compared with *K. bilobata* sample using a Welch two-sample unilateral test and the others using a unilateral Wilcoxon test (nonparametric equivalent of the Welch test). These tests were performed using the free software R (<http://www.R-project.org>).

To avoid unnecessary discussions of the rank of suprageneric taxa, we here follow Scholtz and Richter (1995) and do not indicate suprageneric ranks.

## SYSTEMATIC PALAEOONTOLOGY

MALACOSTRACA Latreille, 1802  
 DECAPODA Latreille, 1802  
 PLEOCYEMATA Burkenroad, 1963  
 REPTANTIA Bouvier, 1917  
 POLYCHELIDA Scholtz and Richter, 1995  
 ERYONIDAE Haan, 1841  
 Genus KNEBELIA Van Straelen, 1922

- 1839 *Eryon* Desmarest (*pars*); Münster, p. 11, pl. 6, figs 3–5.  
 1862 *Eryon* Desmarest (*pars*); Oppel, p. 17, pl. 3, fig. 2; pl. 18, fig. 5.  
 1907 *Münsteria* Knebel, p. 222 (*non Münsteria* J. A. Eudes-Deslongchamps, 1835).  
 1922 *Knebelia* Van Straelen, p. 982.  
 1969 *Knebelia* Van Straelen; Glaessner, p. R470; fig. 274 (1).

*Type species.* *Eryon bilobatus* Münster, 1839, by monotypy.

*Diagnosis.* Carapace rounded, longer than wide in dorsal view (emended after Knebel 1907; Van Straelen 1925; Glaessner 1969); frontal margin framed by a pair of frontal lobes; posterolateral angle rounded and expanded posteriorly; lateral margin with very small spines; shallow cervical and postcervical incisions; shallow cervical and postcervical grooves; postcervical groove curving forwards before cutting median line; second to sixth pleomeres with tergum bearing one shallow anterior transverse groove, one deep posterior transverse groove and an axial carina.

*Included species.* *Knebelia bilobata*, *K. schuberti* and *K. totoroï* sp. nov.

*Taxonomic remarks.* According to Knebel (1907), Van Straelen (1925), Glaessner (1969) and Ahyong (2009), *Knebelia* can be assigned to the Eryonidae because it lacks a diaeresis on the uropodal exopod, the pleon is distinctly narrower than the carapace, and the carapace is not confluent with the pleon in outline. We concur with such an assignment. Our redescription of the type species, *K. bilobata*, and the examination of *K. totoroï* sp. nov. have led to the recognition of cervical, postcervical and branchiocardiac grooves and shallow cervical and postcervical incisions. None of these characters were mentioned by previous authors whose descriptions mostly relied on the illustration supplied by Oppel (1862, pl. 3, fig. 2), which lacks fine details. Moreover, the carapace grooves identified in *Knebelia* are generally very faint among eryonids, having been recorded solely in *Soleryon* Audo, Charbonnier, Schweigert and Saint Martin (2013a), yet being well-marked among members of the families Coleiidae Van Straelen, 1925, Tetrachelidae Beurlen, 1930 and Polychelidae Wood-Mason, 1874.

### *Knebelia bilobata* (Münster, 1839) Figures 2–3

- 1839 *Eryon bilobatus* Münster, p. 11, pl. 6, figs 3–5.  
 1841 *Eryon bilobatus* Münster; Haan, p. 149.  
 1846 *Eryon bilobatus* Münster; Pictet, p. 31.  
 1858 *Eryon bilobatus* Münster; Bronn, p. 25.

**TABLE 1.** Length measurements (in mm) of total carapace ( $CL_{max}$ ) and uropodal exopod (UL) in adult specimens of *Knebelia bilobata* and other eryonids.

Sample	Species	$CL_{max}$	UL	UL/ $CL_{max}$
BSPG AS VI 39 (Lectotype)	<i>Knebelia bilobata</i>	46.1	11.5	0.2495
BSPG AS VII 752	<i>Knebelia bilobata</i>	15.9	4.6	0.2893
BSPG AS VII 753	<i>Knebelia bilobata</i>	49	11.7	0.2388
BSPG AS VII 754	<i>Knebelia bilobata</i>	43.1	11.3	0.2622
BSPG AS VI 509	<i>Knebelia bilobata</i>	48.3	12.9	0.2671
JME-SOS 6864	<i>Knebelia bilobata</i>	40	9.9	0.2475
JME-SOS 7817	<i>Knebelia bilobata</i>	39	10.1	0.2590
NHM.In.28964	<i>Knebelia bilobata</i>	44	11.6	0.2636
MNHN.F.A32407 (Lectotype)	<i>Eryon cuvieri</i>	50.5	9.7	0.1921
MNHN.F.A33501	<i>Eryon cuvieri</i>	33	6.5	0.1970
MNHN.F.A33520	<i>Eryon cuvieri</i>	30.6	5.9	0.1928
MNHN.F.A33518	<i>Eryon cuvieri</i>	63.4	21.4	0.3375
MNHN.F.B13439	<i>Eryon cuvieri</i>	42	8.6	0.2048
BSPG 1972 V	<i>Eryon cuvieri</i>	45	9.2	0.2044
BSPG A 17	<i>Eryon cuvieri</i>	38.3	9.2	0.2402
BSPG AS I 1556	<i>Eryon cuvieri</i>	30.7	5.3	0.1726
BSPG AS VI 41	<i>Eryon cuvieri</i>	54.6	10	0.1832
BSPG AS VII 764	<i>Eryon cuvieri</i>	57.7	14.4	0.2496
BSPG AS VII 766	<i>Eryon cuvieri</i>	47.3	9.5	0.2008
BSPG AS VII 1432	<i>Eryon cuvieri</i>	67.1	12.6	0.1878
BSPG (without number)	<i>Eryon cuvieri</i>	52.3	10.5	0.2008
BSPG 1990 XVIII 292	<i>Eryon cuvieri</i>	58	11.9	0.2052
JME-SOS 3674	<i>Eryon cuvieri</i>	53.5	11.7	0.2187
JME-SOS 6801	<i>Eryon cuvieri</i>	47.4	10.8	0.2278
JME-SOS 6818	<i>Eryon cuvieri</i>	35	6.8	0.1943
JME-SOS 7618	<i>Eryon cuvieri</i>	46.6	9.2	0.1974
BSPG 1990 XVIII 50	<i>Cycleryon elongatus</i>	23.9	4.9	0.2050
BSPG AS I 939	<i>Cycleryon elongatus</i>	41.4	10.6	0.2560
BSPG AS VI 43	<i>Cycleryon elongatus</i>	43.3	10.9	0.2517
BSPG AS VII 761 (Lectotype)	<i>Cycleryon elongatus</i>	41.5	10.7	0.2578
JME-SOS 38	<i>Cycleryon elongatus</i>	27.8	8.8	0.3165
SMCU.FI1408	<i>Cycleryon orbiculatus</i>	33	7.8	0.2364
BSPG AS I 990	<i>Cycleryon orbiculatus</i>	30	7	0.2333
BSPG AS VII 760	<i>Cycleryon orbiculatus</i>	37.4	6.8	0.1818
BSPG AS VII 762	<i>Cycleryon orbiculatus</i>	16.5	3.4	0.2061
BSPG (without number)	<i>Cycleryon orbiculatus</i>	31.4	7.1	0.2261
BSPG (without number)	<i>Cycleryon orbiculatus</i>	34.9	7.1	0.2034
BSPG (without number)	<i>Cycleryon orbiculatus</i>	26.4	6.8	0.2576
BSPG 1922 I 35	<i>Cycleryon propinquus</i> ♂	84	20.3	0.2417
BSPG 1968 I 14	<i>Cycleryon propinquus</i> ♂	73.3	17	0.2319
BSPG 1988 I 84	<i>Cycleryon propinquus</i> ♂	78	18	0.2308
BSPG AS V 31	<i>Cycleryon propinquus</i> ♂	67.7	15.6	0.2304
BSPG AS VI 42	<i>Cycleryon propinquus</i> ♂	57.2	13.3	0.2325
BSPG AS VII 758	<i>Cycleryon propinquus</i> ♂	82.6	19.9	0.2409
BSPG (without number)	<i>Cycleryon propinquus</i> ♂	30.4	5.7	0.1875
BSPG (without number)	<i>Cycleryon propinquus</i> ♂	73	17	0.2329
BSPG (without number)	<i>Cycleryon propinquus</i> ♂	57.4	10.1	0.1760
JME-SOS 59	<i>Cycleryon propinquus</i> ♂	47.8	9.9	0.2071
MNHN.F.B13436	<i>Cycleryon propinquus</i> ♂	58.4	13.3	0.2277
MNHN.Gg.2004/8071	<i>Cycleryon propinquus</i> ♂	60.5	15.1	0.2496
BSPG AS VII 765	<i>Cycleryon propinquus</i> ♂	66	15.2	0.2303
BSPG 1977 XIX 28	<i>Cycleryon propinquus</i> ♀	77.2	19.6	0.2539
BSPG AS VI 40	<i>Cycleryon propinquus</i> ♀	74	17.5	0.2365

TABLE 1. (Continued)

Sample	Species	CL <sub>max</sub>	UL	UL/CL <sub>max</sub>
BSPG AS I 982	<i>Cycleryon propinquus</i> ♀	52	12.5	0.2404
MNHL.20271902/20015598 (Holotype)	<i>Soleryon amicalis</i>	72.5	16	0.2207
MNHL.20015596 (Paratype)	<i>Soleryon amicalis</i>	79.5	15.4	0.1937
MNHL.20150479/20015597 (Paratype)	<i>Soleryon amicalis</i>	80.7	17.1	0.2119

- 1862 *Eryon bilobatus* Münster; Oppel, p. 16, pl. 3, fig. 2.  
 1866 *Eryon bilobatus* Münster; Woodward, p. 501.  
 1881 *Eryon bilobatus* Münster; Woodward, p. 529.  
 1883 *Eryon bilobatus* Münster; Morière, p. 119.  
 1904 *Eryon bilobatus* Münster; Peiser, p. 32.  
 1907 *Münsteria bilobata* (Münster); Knebel, p. 223.  
 1911 *Eryon bilobatus* Münster; Woodward, p. 307.  
 1922 *Knebelia bilobata* (Münster); Van Straelen, p. 983.  
 1924 *Eryon bilobatus* Münster; Balss, p. 175.  
 1925 *Knebelia bilobata* (Münster); Van Straelen, p. 121.  
 1928 *Knebelia bilobata* (Münster); Beurlen, pl. 8, fig. 6.  
 1929 *Knebelia bilobata* (Münster); Glaessner, p. 227.  
 1967 *Knebelia bilobata* (Münster); Secrétan, p. 175, fig. 9.  
 1969 *Knebelia bilobata* (Münster); Glaessner, p. R470, fig. 274(1).  
 2006 *Knebelia bilobata* (Münster); Garassino and Schweigert, p. 31, fig. 11(2); pl. 8; pl. 17, figs 3–4.  
 2009 *Knebelia bilobatus* (Münster); Ahyong, p. 372.  
 2010 *Knebelia bilobata* (Münster); Schweitzer *et al.*, p. 43.

*Lectotype.* BSPG AS VI 39 (Fig. 2A–B).

*Paralectotypes.* BSPG AS VI 509, BSPG AS VII 752–754. Münster (1839) did not list specimens on the basis of which he described the present species. All specimens contained in Häberlein's Collection (now at BSPG) that were probably used by Münster (1839) are here considered to be part of the original type material.

*Type locality and level.* Solnhofen, Bavaria (southern Germany), Solnhofen Platy Limestones.

*Stratigraphic age.* Early Tithonian (Hybonotum Zone, Rueppellianus Subzone; Schweigert 2007b).

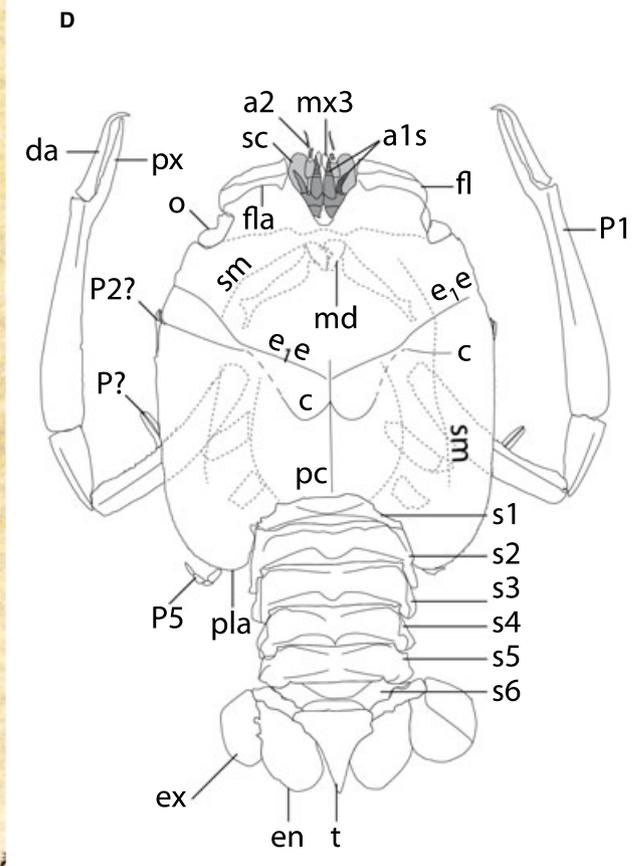
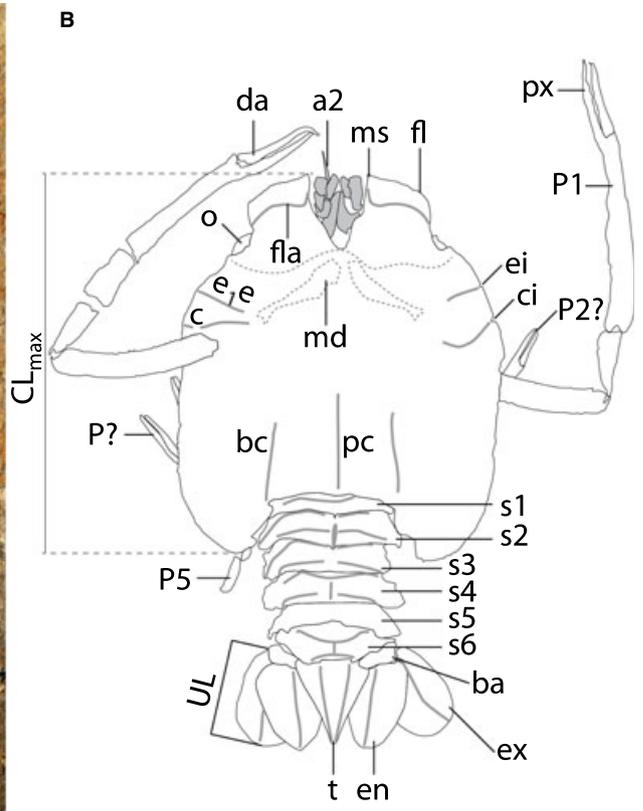
*Additional material.* In addition to the type material, five new specimens are herein considered: JME-SOS 6864, JME-SOS 6866, JME-SOS 7817, NHM In.28964 and SMNS 70044.

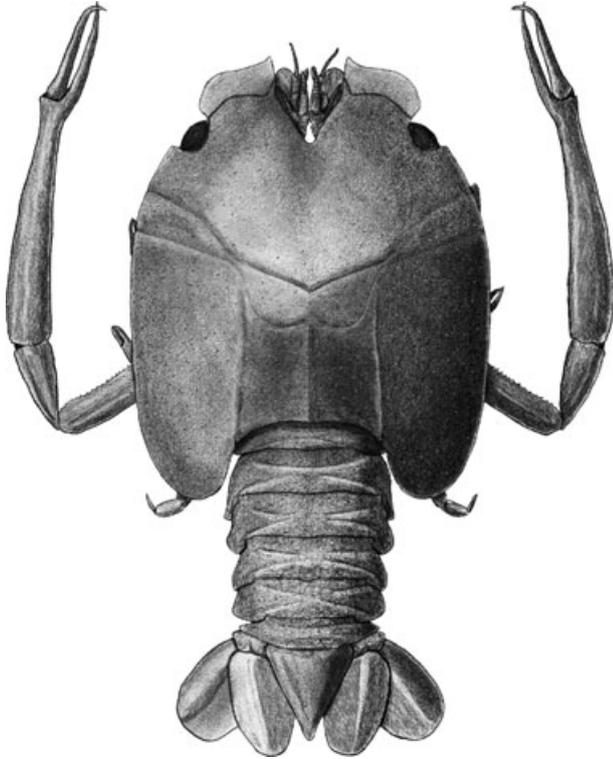
*Occurrence.* Solnhofen Basin (early Tithonian, Hybonotum Zone, Rueppellianus Subzone): Solnhofen (type locality), Hummelberg near Mörsheim; Eichstätt Basin (early Tithonian, Hybonotum Zone, Riedense Subzone): Eichstätt, Blumenberg.

*Diagnosis.* Dorsoventrally flattened carapace, subrectangular in dorsal view; narrow and very concave frontal margin framed by a pair of frontal lobes; large subtriangular frontal lobes with an anterior mesial spine; very small triangular cervical and postcervical incisions; very shallow cervical and postcervical grooves.

*Description.* Dorsoventrally flattened carapace, subrectangular in dorsal view; narrow, very concave, finely tuberculated frontal margin, framed by a pair of frontal lobes; very concave posterior margin; posterolateral angle rounded and expanded posteriorly; lateral margin bearing very small spines, with ocular, cervical and postcervical incisions; large frontal lobe laterally limited by ocular incision and anterolateral angle; shallow, wide, rounded ocular incision, closed ventrally; very small triangular cervical and postcervical incisions opening in first half of lateral margin; shallow cervical groove curved posteriorly, straight between branchial carina and median line; cervical groove intercepting median line at angle of *c.* 65 degrees; shallow postcervical groove almost joining cervical groove near branchial carina, not visible on mesial side of branchial carina, shallow and curving forwards before cutting postcervical carina; faint branchial carina almost parallel to median line; faint postcervical carina; submarginal carina parallel to lateral margin, extending from anterior part of ventral margin to posterolateral angle. Pleon shorter and narrower than carapace; first pleomere (s1) shorter than others; second to fifth pleomeres (s2–s5) slightly decreasing in width

**FIG. 2.** *Knebelia bilobata* (Münster, 1839). A–B, lectotype, BSPG AS VI 39, dorsal view and line drawing, respectively. C–D, exceptionally preserved specimen, SMNS 70044, dorsal view and line drawing, respectively; note the deformed tail fan with abnormally short telson and uropods; the entire right uropodal exopod is broader than expected. Abbreviations: a1s, inner and outer flagella of antenna; a2, antenna; ba, uropodal basipodite; bc, branchial carina; c, postcervical groove; ci, postcervical incision; CL<sub>max</sub>, total length of carapace; da, dactylus; e1e, cervical groove; ei, cervical incision; en, uropodal endopod; ex, uropodal exopod; fl, frontal lobe; fla, frontal lobe articulation; md, mandible; ms, mesial spine; mx3, third maxilliped; o, eye; P1–P5, pereopods 1 to 5; P?, indeterminate pereopod; pc, postcervical carina; pla, posterolateral angle; px, pollex; s1–s6, pleomeres 1 to 6; sc, scaphocerite; sm, submarginal carina; t, telson; UL, length of uropodal exopod. Scale bars represent 20 mm. Illustrations by D. Audo (A) and R. Frattigiani (C).





**FIG. 3.** Reconstruction of *Knebelia bilobata* (Münster, 1839). Illustration by D. Audo.

posteriorly; sixth pleomere (s6) slightly longer than others; s1–s6 with terga bearing a pair of transverse grooves converging medially, anterior one being faint and posterior one deep; s1–s5 with subrectangular terga; s6 with subtrapezoidal tergum; s2–s6 with faint axial carina and subtriangular tergopleura (part of terga folded laterally); s6 with elongate tergopleuron; lateral margin of s2–s5 tergopleura with small anterior process and small posterior axial notch at fold separating tergopleura from terga; subtriangular telson with pair of longitudinal carinae. Large eye slightly bulging out of ocular incision, ommatidia not preserved; short antennula slightly jutting out space between frontal lobes, with two slightly unequal flagella; antenna with short peduncle bearing flagellum and ovoid scaphocerite; mandible incisor process forming sharp triangular teeth of uneven size. Third maxilliped with stout ovoid dactylus; chelate first to fourth pereiopods (P1–

P4); achelate fifth pereiopod (P5) in preserved specimen, sexual dimorphism cannot be assessed; elongate P1, larger than others; P1 merus fringed anteriorly by row of spines; subtriangular P1 carpus; elongate P1 palm distally narrowing before dactylus insertion; slightly curved P1 pollex; P1 dactylus strongly curved distally. Pleopods 1–5 unknown due to preservation; large uropod consisting of stout basipodite, carrying very rounded exopod and pleopod, both strengthened by longitudinal carina. Ornament: very thin carapace, dorsally covered by very small tubercles.

*Linear morphometry.* Van Straelen (1925) noted that the tail fan of *K. bilobata* was proportionally larger than those of most other eryonids. Our statistical analysis of the ratio in different eryonid species yielded the following results (Table 2, Fig. 4): (1) the mean ratio  $UL/CL_{max}$  in *K. bilobata* is significantly larger than that in *E. cuvieri*, *Cycleryon orbiculatus*, *C. propinquus* (male and female morphotypes) and *Soleryon amicalis*. However, it is not significantly larger than that in *Cycleryon elongatus*. In conclusion, among eryonids, *K. bilobata* has one of the larger, or even the largest,  $UL/CL_{max}$  ratios. In other words, its uropodal exopods are proportionally longer than those of other eryonids.

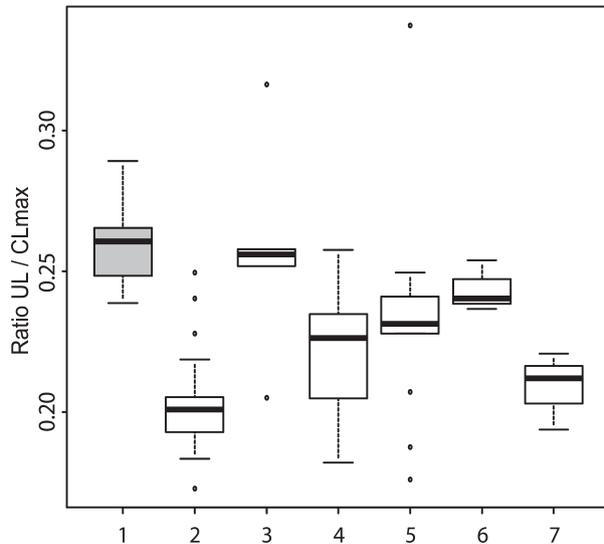
*Knebelia schuberti* (Meyer, 1836)

Figures 5, 6A–B, 7–8

- 1836 *Eryon Schuberti* Meyer, p. 271, pl. 12, figs 3, 6.  
 1838 *Eryon Schuberti* Meyer; Lamarck, p. 377.  
 1839 *Eryon ovatus* Münster, p. 11, pl. 7, figs 2–3.  
 1839 *Eryon Schuberti* Meyer; Münster, p. 13.  
 1841 *Eryon ovatus* Münster; Haan, p. 149.  
 1841 *Eryon Schuberti* Meyer; Haan, p. 149.  
 1846 *Eryon Schuberti* Meyer; Pictet, p. 31.  
 1846 *Eryon ovatus* Münster; Pictet, p. 31.  
 1856 *Eryon Schuberti* Meyer; Meyer, p. 44.  
 1862 *Eryon Schuberti* Meyer; Oppel, p. 18, pl. 3, fig. 5.  
 1866 *Eryon Schuberti* Meyer; Woodward, p. 501.  
 1881 *Eryon Schuberti* Meyer; Woodward, p. 529.  
 1904 *Eryon Schuberti* Meyer; Peiser, p. 34.  
 1907 *Eryon Schuberti* Meyer; Knebel, p. 219.  
 1911 *Eryon Schuberti* Meyer; Woodward, p. 307.  
 1924 *Eryon Schuberti* Meyer; Balss, p. 175.  
 1925 *Knebelia Schuberti* (Meyer); Van Straelen, p. 123.

**TABLE 2.** Results of statistical tests comparing the mean ratio  $UL/CL_{max}$  in *Knebelia bilobata* to that in other eryonids.

Species	Mean $UL/CL_{max}$	Statistic test	Degree of freedom	p-Value	Mean ratio of <i>Knebelia bilobata</i> is
<i>Knebelia bilobata</i>	0.2596	–	–	–	–
<i>Eryon cuvieri</i>	0.2041	Welch test	17.642	$2.61 \times 10^{-7}$	Significantly higher
<i>Cycleryon elongatus</i>	0.2574	Welch test	4.76	0.4556	Not significantly higher
<i>Cycleryon orbiculatus</i>	0.2207	Welch test	9.641	0.0028	Significantly higher
<i>Cycleryon propinquus</i> ♂	0.2326	Wilcoxon test	N/A	0.0011	Significantly higher
<i>Cycleryon propinquus</i> ♀	0.2436	Welch test	6.414	0.0376	Significantly higher
<i>Soleryon amicalis</i>	0.2088	Welch test	4.045	0.0030	Significantly higher



**FIG. 4.** Ratio of uropodal exopod length to carapace length of several eryonid morphotypes compared with that of *Knebelia bilobata*. 1, *Knebelia bilobata*; 2, *Eryon cuvieri*; 3, *Cycleryon elongatus*; 4, *Cycleryon orbiculatus*; 5, *Cycleryon propinquus* (male); 6, *Cycleryon propinquus* (female); 7, *Soleryon amicalis*.

- 1929 *Knebelia Schuberti* (Meyer); Glaessner, p. 228.
- 2006 *Cycleryon propinquus* (Schlotheim) (*pro parte*); Garassino and Schweigert, p. 24.
- 2010 *Cycleryon propinquus* (Schlotheim) (*pro parte*); Schweitzer *et al.*, p. 43.

*Holotype, by monotypy.* SMF X/m 73 (Fig. 5).

*Type locality and level.* Solnhofen, Bavaria (southern Germany), Solnhofen Platy Limestones.

*Stratigraphic age.* Early Tithonian (Hybonotum Zone, Rueppellianus Subzone; see Schweigert 2007b).

*Additional material.* In addition to the holotype, the following specimens have been studied: JME-SOS 35–37, JME-SOS 6838–6839, JME-SOS 6840 (Fig. 6A), JME-SOS 6841–6842, JME-SOS 6846, JME-SOS 6848–6849, JME-SOS 6853, JME-SOS 6856–6858, JME-SOS 6860, BSPG 1972 I 95, BSPG AS VII 751, BSPG AS VII 756–757, SMF X/m 144–146, FSL 170858, MNHN.F.A33550 (Fig. 6B), MNHL-20272104, SMNS 67806 (Fig. 8), NHM.41982 (two specimens in the same lot), NHM 44826–44827, NHM 44829; syntypes of *Eryon ovatus*: BSPG AS VII 755 (illustrated by Münster 1839, pl. 7, fig. 2; see Fig. 7A) and SMCU F11402 (illustrated by Münster 1839, pl. 7, fig. 3; see Fig. 7B).

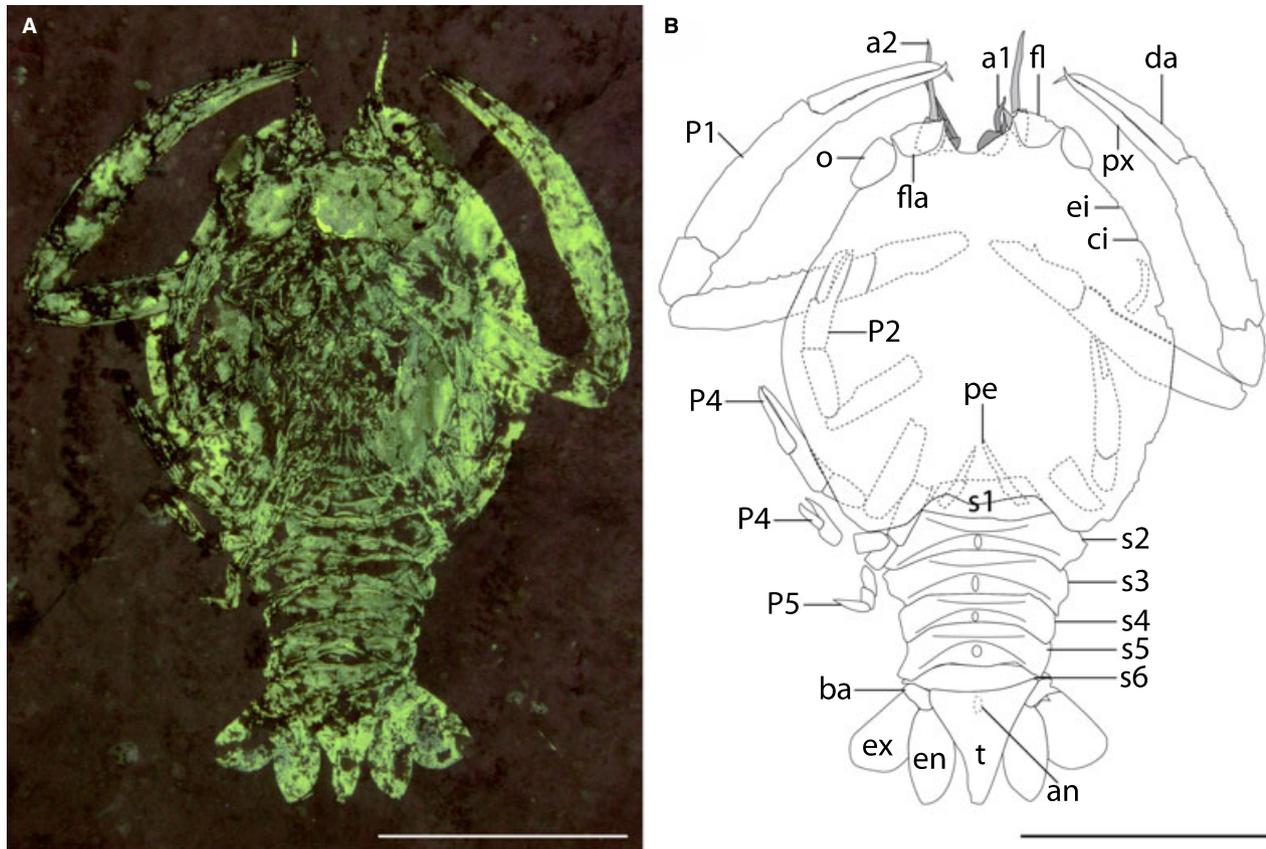
*Occurrence.* Solnhofen Basin (early Tithonian, Hybonotum Zone, Rueppellianus Subzone): Solnhofen (type locality). Eichstätt Basin (early Tithonian, Hybonotum Zone, Riedense Subzone): Eichstätt, Blumenberg, Workerszell and Schernfeld.

*Diagnosis.* Dorsoventrally flattened carapace, ovoid in dorsal view; very concave, angular frontal margin

framed by a pair of frontal lobes; ovoid frontal lobes with an anterior mesial spine; slightly concave posterior margin; very small triangular cervical and postcervical incisions.

*Description.* Dorsoventrally flattened carapace, ovoid in dorsal view; very concave, angular, finely spinose frontal margin, framed by a pair of frontal lobes; slightly concave posterior margin; posterolateral angle rounded and expanded posteriorly; finely spinose lateral margin, with ocular, cervical and postcervical incisions; ovoid frontal lobe, laterally limited by ocular incision and anterolateral angle, with an anterior mesial spine; shallow, wide, rounded ocular incision; very small triangular cervical and postcervical incisions opening in first half of lateral margin; cervical groove shallow near lateral margin and median line, effaced elsewhere; cervical groove cutting median line at angle of c. 60 degrees; postcervical groove shallow near median line, effaced elsewhere; postcervical groove cutting postcervical carina at angle >90 degrees; well-marked branchial carina covered by row of small tubercles; postcervical carina with row of small tubercles on each side; submarginal carina parallel to lateral margin, stretching from anterior part of ventral margin to posterolateral angle. Pleon shorter and narrower than carapace; s1 shorter than others and mostly covered by carapace; s6 shorter than others; s2–s6 slightly decreasing in width posteriorly; s1–s6 with terga bearing well-marked carina and pair of transverse grooves converging medially, anterior one being very faint and posterior one deep; s1–s5 with subrectangular tergum; s6 with subtrapezoidal terga; subtriangular s2–s6 tergopleura; s6 with elongate tergopleuron; lateral margin of s2–s5 tergopleura with small anterior process and small posterior axial notch at fold separating tergopleura from terga; subtriangular telson with pair of longitudinal carinae. Large eye slightly bulging out of ocular incision, ommatidia not preserved; short antennula slightly jutting out space between frontal lobes; antenna with short peduncle bearing flagellum; scaphocerite absent; chelate P1–P4; achelate P5 in preserved specimen, sexual dimorphism cannot be assessed; elongate P1, larger than others; P1 merus fringed anteriorly by row of spines; subtriangular P1 carpus; elongate P1 palm with serrated outer margin; slightly curved P1 pollex; P1 dactylus strongly curved distally with serrated outer margin; occlusal margin of P1 dactylus smooth in males, with two strong spines in females. Pleopods 1 to 5 unknown due to preservation; large uropod consisting of stout basipodite carrying long, petaloid exopod and long, pyriform endopod. Exoskeleton smooth.

*Taxonomic remarks.* Garassino and Schweigert (2006, p. 25) considered *K. schuberti* to represent a juvenile growth stage of *C. propinquus*, arguing that it ‘resembles juveniles of *C. propinquus*’. Haug *et al.* (2011b) subscribed to that interpretation and postulated that *K. schuberti* might represent a megalopa larva (*sensu* Williamson 1969). It should be noted that those authors based their observations on two specimens of probably immature *Cycleryon* sp. (compare Haug *et al.* 2011b, fig. 2), not on actual examples of *K. schuberti*. We disagree with their conclusion and note that, in contrast to juvenile specimens of



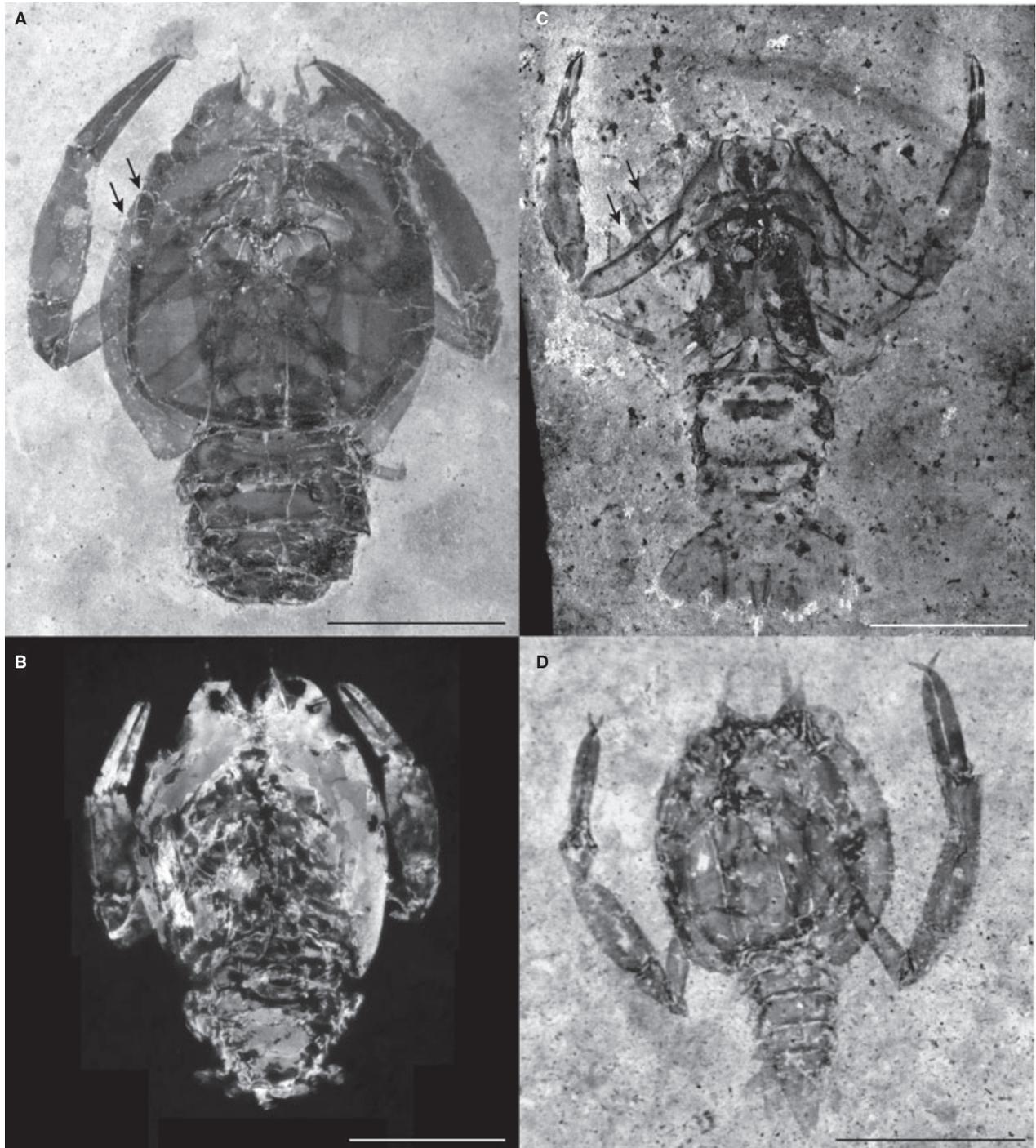
**FIG. 5.** Holotype of *Knebelia schuberti* (Meyer, 1836), SMF X/m 73. A, under UV light. B, line drawing. Abbreviations: a1, antennula; a2, antenna; an, anus; ba, uropodal basipodite; ci, postcervical incision; da, dactylus; ei, cervical incision; en, uropodal endopod; ex, uropodal exopod; fl, frontal lobe; fla, frontal lobe articulation; o, eye; P1–P5, pereopods 1 to 5; pe, petasma; px, pollex; s1–s6, pleomeres 1 to 6; t, telson. Scale bars represent 10 mm. Illustration by J. Anger.

*Cycleryon* sp. which have in their early development deep cervical and postcervical incisions (see Fig. 6C), those incisions are barely visible in *K. schuberti*. In addition, the latter species displays frontal lobes that are typical of *Knebelia*, while none are visible in either juvenile or adult *Cycleryon*, while the frontal margin in *K. schuberti* is distinctly concave and angular, unlike that of juveniles of *Cycleryon* sp. Moreover, the P1 chela in *K. schuberti* is more curved and shows a slight constriction near the insertion of the dactylus, contrary to juveniles of *Cycleryon* sp. *Knebelia schuberti* also superficially resembles juvenile *Palaeopentacheles* sp. (Fig. 6D), which is often erroneously identified as *K. schuberti* in collections; it differs from that in having lobes and a narrower frontal margin, a shorter P1, and in lacking spines between the tergopleura and terga on the pleon. Moreover, the P1 pollex is less curved.

We agree with Van Straelen (1925) in assigning *Eryon schuberti* to the genus *Knebelia*, on the basis of the peculiar frontal lobes, the ovoid carapace outline, the shallow cervical and postcervical incisions, s2–s6 terga with trans-

verse grooves (faint anteriorly and deep posterior) and curved P1 claws. *Knebelia schuberti* differs from *K. bilobata* *K. totoroï* sp. nov. by the rounded articulation of the frontal lobe, a carapace that covers most of s1, and a short s6. *Knebelia schuberti* also differs from *K. bilobata* in its wider frontal margin and more rounded lateral margins. It can be differentiated from *K. totoroï* sp. nov. by its larger frontal lobes and a more concave frontal margin.

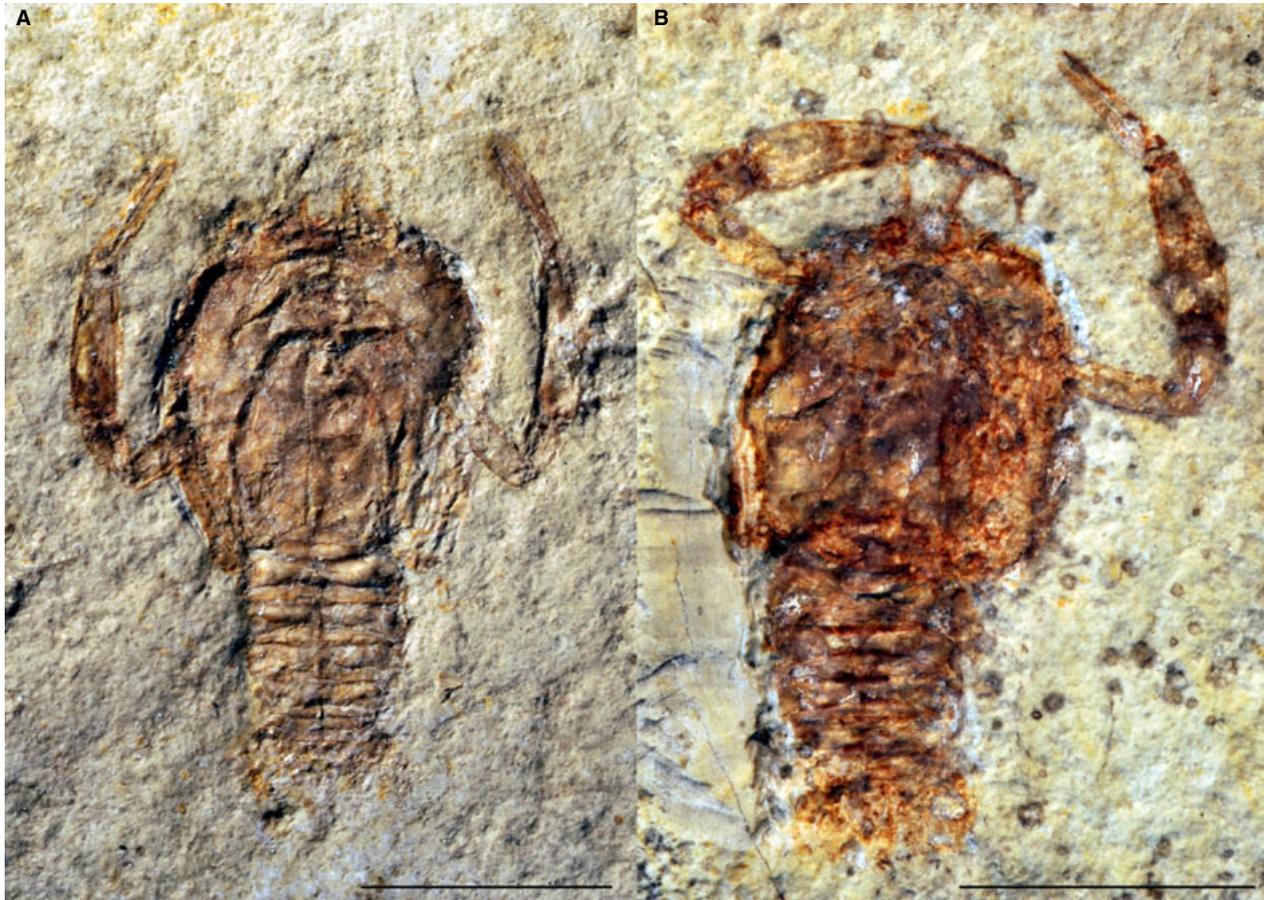
Oppel (1862) identified one of the two syntypes (Münster 1839, pl. 7, fig. 2) of *Eryon ovatus* as *K. schuberti*. He was uncertain about the identification of the other syntype (Münster 1839, pl. 7, fig. 3), but considered *Eryon ovatus* to be synonymous with *K. schuberti*. This view was adopted by Knebel (1907), Van Straelen (1925) and Glaessner (1929). A re-examination of the type material of *E. ovatus* has allowed us to observe that both syntypes actually display diagnostic characters of *K. schuberti*, that is, a curved and elongate P1 chela, a very concave frontal margin forming an angle and a slightly concave posterior margin that covers the anterior part of the first



**FIG. 6.** Small eryonoids from southern Germany: *Knebelia schuberti*, JME-SOS 6840, in natural light (A) and MNHN.F.A33550, fluorescence in green light (B); *Cycleryon* sp., JME-SOS 6862 (C); *Palaeopentacheles* sp., JME-SOS 6850 (D). Arrows highlight the cervical and postcervical incisions. Scale bars represent 5 mm (A, C–D) and 10 mm (C). Illustrations by D. Audo (A, C–D) and by J. T. Haug and C. Haug (B).

pleomere (Fig. 7A–B). Thus, we concur with Oppel (1862), Knebel (1907), Van Straelen (1925) and Glaessner (1929) that *E. ovatus* is a junior synonym of *K. schuberti*.

*Sexual dimorphism.* Two specimens, JME-SOS 6840 (Fig. 6A) and SMNS 67806 (Fig. 8), have two spines on the occlusal margin of the P1 dactylus, unlike other specimens in which this occlusal margin is smooth. The



**FIG. 7.** Syntypes of *Eryon ovatus* Münster, 1839, syntype BSPG AS VII 755, as illustrated by Münster (1839, pl. 7, fig. 2) (A); syntype SMCU F11402, as illustrated by Münster (1839, pl. 7, fig. 3) (B). Scale bars represent 10 mm. Illustrations courtesy of BSPG (A); copyright Sedgwick Museum of Earth Sciences, Cambridge (UK) (B).

holotype, in which the P1 dactylus is smooth, preserves a petasma and thus is a male. These characteristics can be compared with *C. propinquus*, in which the female morphotype (formerly described as *C. spinimanus* Germar, 1827) possesses a P1 dactylus with spines on the occlusal margin, while this margin is smooth in the male morphotype (Schweigert 2001a). Thus, it appears probable that this difference, similar to *C. propinquus*, is an expression of sexual dimorphism.

**Ontogeny.** In the sample studied,  $CL_{max}$  varies between 7.2 and 17.5 mm, the holotype being the largest specimen. The ratio length of P1 propodus and  $CL_{max}$  is similar for all specimens (Table 3, Fig. 9). Taking into account the wide size variation, it seems probable that these specimens represent an ontogenetic series. The small size of *K. schuberti* might indicate it to be a juvenile of another species, for example of *K. bilobata*. This hypothesis cannot be tested, however, because we have no specimen of intermediate size between the largest *K. schuberti* ( $CL_{max} = 17.5$  mm) and the smallest *K. bilobata*

( $CL_{max} = 40.7$  mm). Of note is that no ontogenetic trend in *K. schuberti* could be identified to support such a hypothesis. Rather, the species may be paedomorphic.

*Knebelia totoro* Audo, Schweigert and Charbonnier sp.  
nov.

Figure 10

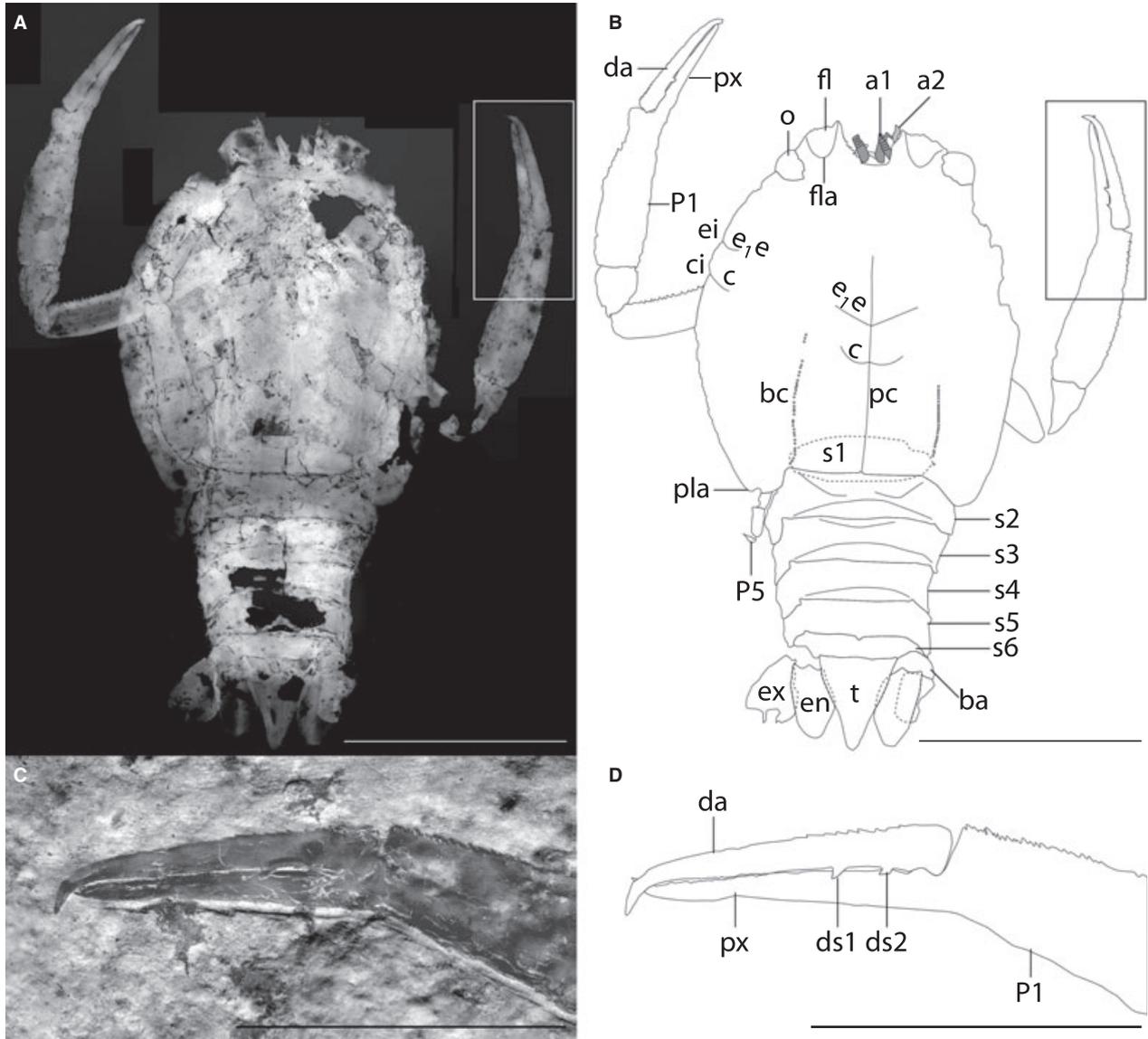
2012 *Knebelia*; Schweigert et al., p. 62, fig. 5.

LSID. urn:lsid:zoobank.org:act: DD0922F0-EE92-4B05-88EE-54052507D206.

**Derivation of name.** An allusion to the outline of carapace and scaphocerites, which is reminiscent of the silhouette of the fictional character Totoro in the 1988 film 'My Neighbor Totoro'.

**Holotype.** SMNS 67916 (Fig. 10A–B).

**Paratype.** BSPG AS VI 509 (Häberlein Collection; Fig. 10C–D).



**FIG. 8.** Sample of *Knebelia schuberti*, SMNS 67806, with two spines on the occlusal margin of P1 dactylus. A–B, complete specimen, dorsal view, fluorescence in green light and line drawing, respectively. C–D, close-up showing spines on the occlusal margin of P1 dactylus and line drawing, respectively. Abbreviations: a1, antennula; a2, antennae; ba, uropodal basipodite; bc, branchial carina; c, postcervical groove; ci, postcervical incision; da, dactylus; ds1, distal dactylus spine; ds2, proximal dactylus spine; e<sub>1</sub>e, cervical groove; ei, cervical incision; en, uropodal endopod; ex, uropodal exopod; fl, frontal lobe; fla, frontal lobe articulation; o, eye; P1, P5, pereopods 1, 5; pc, postcervical carina; pla, posterolateral angle; px, pollex; s1–s6, pleomeres 1 to 6; t, telson. Scale bars represent 10 mm (A–B) and 5 mm (C–D). Illustrations by J. T. Haug and C. Haug.

*Type locality and level.* Nusplingen Lagerstätte, Baden-Württemberg, southern Germany; Nusplingen Plattenkalk.

*Stratigraphic age.* Late Kimmeridgian (Beckeri Zone, Ulmense Subzone; after Schweigert 2007b).

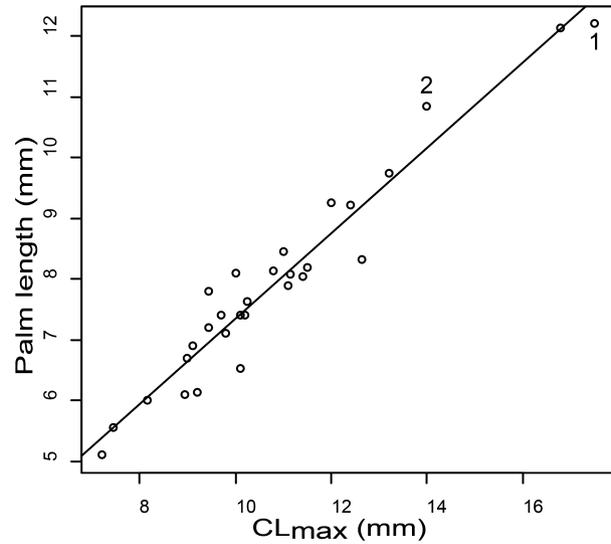
*Occurrence.* Nusplingen (type locality; see above) and Solnhofen (early Tithonian, Hybonotum Zone, Rueppellianus Subzone).

*Diagnosis.* Dorsoventrally flattened carapace, ovoid in dorsal view; broad and concave frontal margin framed by pair of frontal lobes; frontal lobes with mesial spine on their anterior margin; narrow, subtriangular, frontal lobes with anterior mesial spine; small triangular cervical incision; small triangular postcervical incision deeper than cervical; well-marked cervical, postcervical, branchiocardiac and inferior grooves.

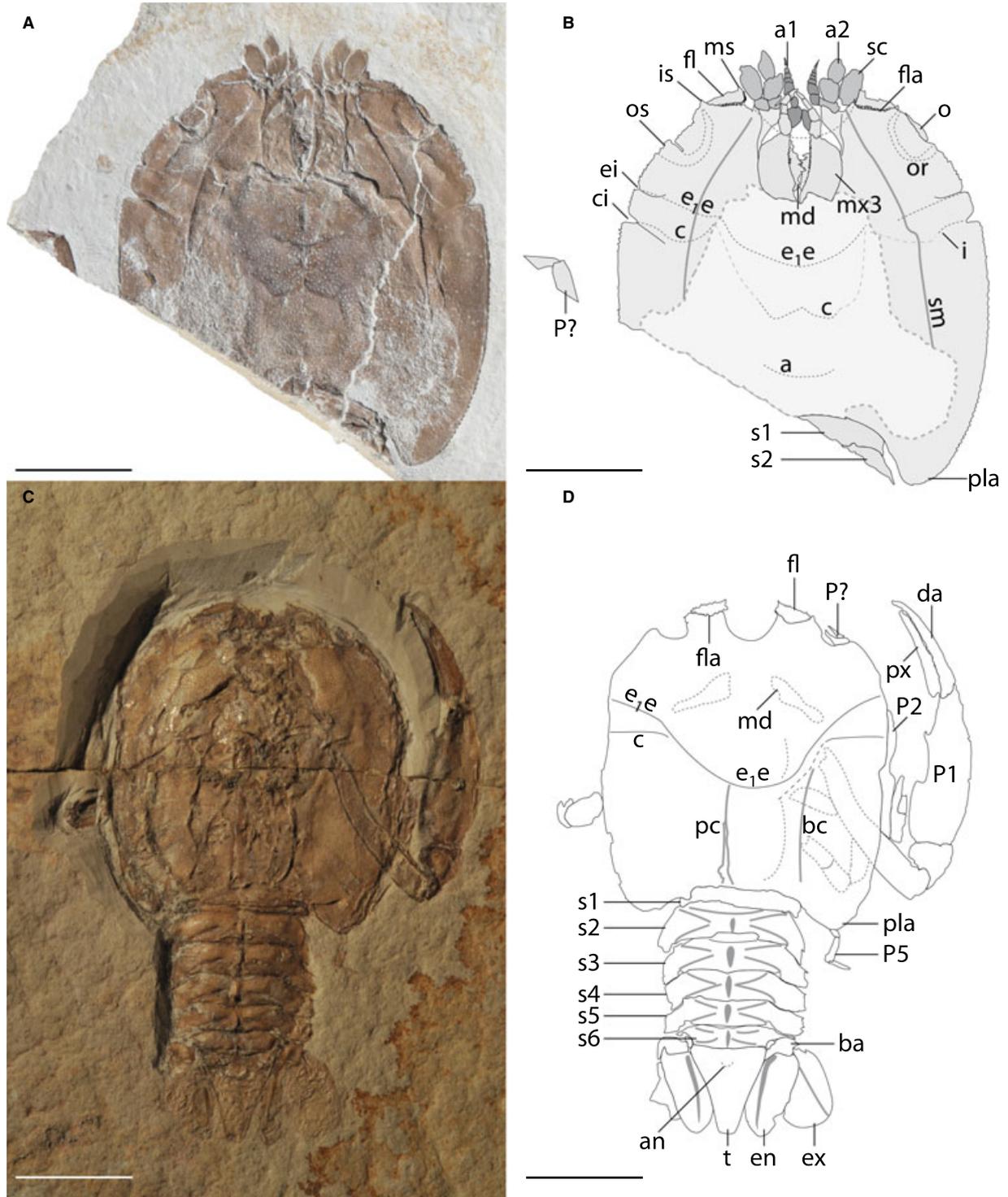
**TABLE 3.** Measurements (in mm) of total carapace length and length of P1 propodus of *Knebelia schuberti*.

Repository number	CL <sub>max</sub>	P1 Propodus length			CL <sub>max</sub> /Prop
		Left	Right	Mean	
SMF X/m 73 (Holotype)	17.5	12.05	12.35	12.2	1.43442623
JME-SOS 35	7.45	5.5	5.6	5.55	1.34234234
JME-SOS 36	12.4	9.15	9.3	9.225	1.34417344
JME-SOS 37	11.5	8.24	8.14	8.19	1.4041514
JME-SOS 6838	9.8	7.1	7.1	7.1	1.38028169
JME-SOS 6839	8.15	na	6	6	1.35833333
JME-SOS 6840	10.8	8.05	8.2	8.125	1.32923077
JME-SOS 6841	7.2	5.2	5	5.1	1.41176471
JME-SOS 6842	10	8.1	na	8.1	1.2345679
JME-SOS 6846	9.1	6.9	6.9	6.9	1.31884058
JME-SOS 6848	10.2	7.4	na	7.4	1.37837838
JME-SOS 6849	9.7	7.4	na	7.4	1.31081081
JME-SOS 6853	9.45	7.3	7.1	7.2	1.3125
JME-SOS 6856	9.45	7.8	na	7.8	1.21153846
JME-SOS 6857	9.21	6.21	6.05	6.13	1.50244698
JME-SOS 6858	11	8.45	na	8.45	1.30177515
JME-SOS 6860	13.2	9.5	10	9.75	1.35384615
SMNS 67806	16.8	12.05	12.2	12.125	1.38556701
SMF X/m 145	8.95	6.1	na	6.1	1.46721311
SMF X/m 146	12.65	8.45	8.2	8.325	1.51951952
FSL 170858	10.25	7.55	7.7	7.625	1.3442623
MNHN.F.A33550	10.1	6.5	6.55	6.525	1.54789272
MNHL.20272104	11.1	na	7.9	7.9	1.40506329
NHM.41982	12	9.35	9.15	9.25	1.2972973
NHM.41982	10.1	7.4	7.4	7.4	1.36486486
NHM.44826	11.15	7.8	8.35	8.075	1.38080495
NHM.44827	9	6.7	na	6.7	1.34328358
NHM.44829	11.4	na	8.05	8.05	1.41614907
BSPG AS VII 755 ( <i>Eryon ovatus</i> holotype)	14	10.6	11.1	10.85	1.29032258

**Description.** Dorsoventrally flattened carapace, ovoid in dorsal view; broad and concave frontal margin framed by pair of narrow frontal lobes; ornament of frontal margin not preserved; very concave posterior margin; posterolateral angle rounded and expanded posteriorly; finely spinose lateral margin with ocular, cervical and postcervical incisions; narrow, subtriangular frontal lobe, laterally limited by ocular incision and anterolateral angle, with one anterior mesial spine and serrated posterior margin; hemicircular ocular incision, dorsally strengthened by carina and ventrally closed, limited by one inner and one outer spine; cervical and postcervical incisions opening in first half of lateral margin; small triangular cervical incision; small triangular post-cervical incision deeper than cervical one; cervical groove curved posteriorly, intercepting median line at angle of *c.* 90 degrees in middle of carapace and extending on pterygostomian flap through cervical incision; postcervical groove effaced on mesial side of branchial carina, well-marked elsewhere; postcervical groove almost joining cervical groove near branchial carina, shallow and curving forwards before cutting postcervical carina;

**FIG. 9.** Scatter plot of P1 propodus length as a function of total carapace length (CL<sub>max</sub>). 1, Holotype of *Knebelia schuberti* (SMF X/m 73); 2, syntype of *Eryon ovatus* (BSPG AS VII 755).

shallow branchiocardiac groove, cutting postcervical carina near posterior margin of carapace; straight inferior groove, crossing pterygostomian flap transversally and joining postcervical groove through postcervical incision; branchial carina faint; submarginal carina parallel to lateral margin, extending from anterior part of ventral margin to posterolateral angle. Pleon shorter and narrower than carapace; s1 shorter than others; s2–s5 of similar width; s6 shorter than others; s2–s6 terga bearing axial carina and pair of transverse grooves converging medially, anterior one being faint and posterior one deep; subtrapezoidal s6 tergum; subquadrate s2–s5 tergopleura; elongate s6 tergopleuron; lateral margin of s2–s5 tergopleura with small anterior process and small posterior axial notch at fold separating tergopleura from terga; subtriangular telson with rounded distal extremity. Large eye slightly bulging out of ocular incision, quadratic ommatidia; antennula with short and wide peduncle bearing thick inner flagellum abruptly tapering distally (outer flagellum not preserved); antenna consisting of (1) wide peduncle composed of stout basipodite divided by deep longitudinal furrow and first two stout articles of antennal endopod, (2) flagellum corresponding to distal part of endopod, (3) ovoid scaphocerite covered by scattered tubercles and with serrated distal margin, corresponding to exopod; mandible incisor process forming sharp triangular teeth of uneven size. Third maxilliped composed of subrectangular ischium with crista dentata and series of four articles; P1 elongate, chelate, larger than others; strong and elongate P1 propodus, elliptical in outline; P1 merus anteriorly smooth; P1 carpus subtriangular; P1 chela with slightly curved dactylus and pollex, occlusal margins bearing small tubercles. Pleopods 1–5 unknown due to preservation; large uropod consisting of stout basipodite; pyriform uropodal endopod, strengthened by wide longitudinal carina; large, ovoid uropodal exopod, without diaeresis, strengthened by weak longitudinal carina delimiting fusiform area with outer margin. Ornament: dorsal surface of carapace, pleon and P1 covered by small pits; pterygostomian flap covered by small tubercles.



**FIG. 10.** *Knebelia totoroi* sp. nov. A–B, holotype, SMNS 67916, ventral view showing imprint of dorsal grooves and line drawing, respectively. C–D, paratype, BSPG AS VI 509, dorsal view and line drawing, respectively (D). Abbreviations: a, branchiocardiac groove; a1, antennula; a2, antenna; an, anus; ba, uropodal basipodite; bc, branchial carina; c, postcervical groove; ci, postcervical incision; da, dactylus; e<sub>1</sub>e, cervical groove; ei, cervical incision; en, uropodal endopod; ex, uropodal exopod; fl, frontal lobe; fla, frontal lobe articulation; i, inferior groove; is, inner spine of ocular incision; md, mandible; ms, mesial spine; mx3, third maxilliped; o, eye; or, ocular incision carina; os, outer spine of ocular incision; P1–P5, pereiopods 1 to 5; P?, indeterminate pereiopod; pc, postcervical carina; pla, posterolateral angle; px, pollex; s1–s6, pleomeres 1 to 6; t, telson. Scale bars represent 20 mm (A–B) and 10 mm (C–D). Illustrations by G. Schweigert (A) and D. Audo (C).

*Remarks.* The paratype of *K. totoroi* sp. nov. probably represents a more juvenile stage, as it is more than twice smaller than the holotype and the ocular incisions also open more forwardly than in the latter. This difference, however, seems to result from the poorer preparation of the paratype, which is otherwise similar to the holotype.

*Taxonomic remarks.* The new species is assigned to *Knebelia* on the basis of the peculiar frontal lobes, the ovoid carapace, the shallow cervical and postcervical incisions and the s2–s6 terga with two transverse grooves, one faint anterior and one deep posterior, plus an axial carina. *Knebelia totoroi* sp. nov. differs from *K. bilobata* and *K. schuberti* by having a wider and shallower frontal margin and well-marked cephalothoracic grooves.

## DISCUSSION

### *Functional morphology and palaeoecology*

The shovel-shaped frontal lobes of *Knebelia* are unique among polychelidan lobsters. These frontal lobes were called ‘breite Lappen’ by Oppel (1862, pp. 16–17) and Knebel (1907, p. 222). In his work, Oppel (1862) described the lobes on a specimen which lacked antennae. Both authors considered the breite Lappen to be part of the carapace. Van Straelen (1925, p. 122) considered them to be similar to the flattened antennae of slipper lobsters (Scyllaridae). We agree that these lobes are morphologically close to the antennae in scyllarids, but the origin of these structures is clearly different. Indeed, well-preserved specimens of *K. bilobata*, *K. schuberti* and the holotype of *K. totoroi* sp. nov. clearly show the presence of both antennae and frontal lobes (see Figs 2, 5, 6A, 10A–B). The coexistence of these structures invalidates Van Straelen’s hypothesis and confirms Oppel’s and Knebel’s views in that these frontal lobes are true expansions of the carapace.

In *K. bilobata* and *K. totoroi* sp. nov., the frontal lobes are separated from the remainder of the carapace by a dorsal carina and a ventral groove that mark the position of an articulation. The presence of such an articulation crossing the shield is unusual among crustaceans, yet not unique. Examples can be found in the early crustacean *Martinssonella elongata* Müller and Walossek, 1986, in the diminutive mystacocarids (Olesen 2001, fig. A4), as well as in different malacostracans. Richter and Scholtz (2001) even considered a moveable rostral structure to be part of the ground pattern of Malacostraca, as modern phyllocarids and most known hoplocarids (including modern mantis shrimp; Schram and Horner 1978; Haug *et al.* 2012) possess such a structure. Yet, the moveable rostrum in phyllocarids does not necessarily represent a ground-pattern feature of the

group, and the function and structure of the rostrum in phyllocarids and hoplocarids differ significantly. Therefore, the moveable rostrum most likely evolved independently in the two lineages. An anterior set-off region of the shield (although unclear if it is moveable) can also be found in spelaeogriphacean and mictacean peracarids (Boxshall 1999; Gutu 2001). Among decapods, the rhynchocentid shrimp (Caridea) have an articulated rostrum (Bauer 2004). However, the occurrence of articulated frontal lobes is unique to *Knebelia*.

Even if of different evolutionary origins, these articulated lobes may be compared with the paddle-like antennae of scyllarid lobsters in terms of function. Indeed, both these structures are articulated, thus probably share similar functions that would likely be the outcome of convergent evolution. According to Spanier and Weihs (1992) and Lavalli *et al.* (2007), the flattened antennae in scyllarids are used to protect the antennules against predator attacks, to lift and turn upside down an opponent during agonistic intraspecific behaviour, as well as to act as a rudder during ‘tail-flip swimming’. The frontal lobes in *K. bilobata* are large enough to have performed the same roles as the flattened antennae of scyllarids. The frontal lobes in *K. totoroi* sp. nov. are narrower and too small to have been useful in the protection of antennules and antennae or in agonistic behaviour. Finally, in both species, the main, and more obvious, function of the articulated frontal lobes probably was to act as a rudder during ‘tail-flip swimming’. Moreover, the dorsoventrally flattened body and the absence of a rostrum in *Knebelia* are very close to the picture seen in scyllarid lobsters. These common anatomical features suggest similar constraints for ‘tail-flip swimming’ and may explain the convergent evolution of rudder-like structures in both *Knebelia* and scyllarids. In addition, in comparison with other eryonids, *K. bilobata* has a thinner carapace and longer uropodal exopods (Fig. 4), suggesting that it was probably a good swimmer, propelled by powerful tail-flip strokes.

In conclusion, current evidence indicates that the primary role of the frontal lobes in *Knebelia* was very likely to act as a rudder, enhancing a ‘tail-flip’ swimming mode.

### *Eryonid diversity and disparity*

The putative specific life habits of species of *Knebelia* also have an impact on our concept of eryonid diversity. Ten species of eryonid are known from the Jurassic lithographic limestones of southern Germany, which leads to the question how these species could co-exist, because they would have exploited different resources, habitats and, more generally, differed to some extent in their ecology. Species of *Knebelia* apparently had modes of life

different to other eryonids, which allowed them to exploit other resources (habitat, food source) and tactics to evade predators.

The fact that, as an adaptation to such specific life habits, the carapace was thinner compared with most other eryonids and that adult morphology appears to have been reached at a relatively small size (at least for *K. schuberti*) might indicate the paedomorphic nature of *Knebelia*. Earlier ontogenetic stages are often less sclerotized than later ones; an easy way to evolve a thinner carapace is simply to terminate the ontogenetic process of sclerotizing the dorsal hard parts early. This would be in congruence with an early stop to differentiation, leading to early completion of final (adult) morphology. To understand such possible heterochronic evolutionary shifts better, small-sized specimens of eryonids need to be reassessed in detail. In many cases, they would appear to represent *Knebelia*, while numerous examples appear to be *Palaeopentacheles*, and a few specimens can be clearly identified as *Cycleryon*. Thus, small-sized specimens could entirely represent juveniles of previously named species, but it is also possible that an even greater diversity could be represented among the smaller eryonids. Whatever the outcome may be, the fact that there are now three species of *Knebelia* clearly documents eryonid diversity during the Late Jurassic.

**Acknowledgements.** We thank Martin Nose (Bayerische Staatssammlung für Paläontologie und Geologie, Munich), Martina Kölbl-Ebert (Jura-Museum, Eichstätt), Claire Mellish (The Natural History Museum, London) and Matthew Riley (Sedgwick Museum, Cambridge) for access to collections in their care, Christian Neumann (Museum für Naturkunde, Berlin) for assisting in our search for the original syntypes of *Knebelia bilobata*, Uwe Eller (Dümpelfeld) for preparing the holotype of *K. totoroï* sp. nov., Charlene Letenneur (MNHN) for advice on the reconstruction of *K. bilobata* (Fig. 3), Roger Frattigiani (Laichingen) for donation of wonderfully preserved specimens of *K. bilobata* and *K. schuberti* to the Staatliches Museum für Naturkunde (Stuttgart) for the present study, Stefan Liebau (University of Ulm) for long-standing support, Alessandro Garassino, Rodney Feldmann and John W. M. Jagt for useful comments on an earlier version of the typescript, and Martin Simpson (University of Southampton) for polishing our English. This is a contribution to the UMR CNRS 7207 Centre de Recherche sur la Paléobiodiversité et les Paléoenvironnements and to the Département Histoire de la Terre of the Muséum national d'Histoire naturelle, Paris. Joachim T. Haug was funded by the Alexander von Humboldt Foundation (Feodor Lynen Return Fellowship), while Carolin Haug was supported by the German Academic Exchange Service (DAAD) with a return fellowship. Joachim T. Haug is currently funded by the German Research Foundation (DFG) in the project 'Palaeo-Evo-Devo of Malacostraca' under HA 6300/3-1. Part of the cooperation of the present study was made possible by a grant from the European Commission's (FP 6) Integrated Infrastructure Initiative programme SYNTHESYS

(FR-TAF 2590) to Joachim T. Haug. Joachim T. Haug and Carolin Haug are grateful to their host Steffen Harzsch (Greifswald) and his working group.

*Editor.* John W. M. Jagt

## DATA ARCHIVING STATEMENT

Data for this study are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.72mn4>

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