Diversity of chondrostean fish *Coccolepis* from the Late Jurassic Solnhofen Archipelago, Southern Germany

ADRIANA LÓPEZ-ARBARELLO and MARTIN EBERT


Late Jurassic marine vertebrates are extraordinarily well preserved in several Plattenkalk Lagerstätten in central Europe. Among them, the Solnhofen Archipelago has yielded the very rare fish *Coccolepis bucklandi*, which was the first fossil chondrostean to be found in sediments younger than the Triassic. The type specimen of this species was lost, but it was rediscovered recently, prompting the alpha taxonomic revision of this iconic fish. A new species *Coccolepis solnhofensis* has been identified among the specimens referred to *C. bucklandi*. The two species differ in the distinctive distribution of scutes and fringing fulcra. Based on the available evidence, *C. bucklandi* is restricted to the Eichstätt Basin and the *Lithacoceras eigeltingense*  Β Horizon of the *Lithacoceras riedense* Subzone (*Hybonoticeras hybonotum* Zone), and *C. solnhofensis* sp. nov. is limited to the Solnhofen Basin and the slightly younger *Subplanites rueppellianus* Subzone (*Hybonoticeras hybonotum* Zone). Therefore, the two species are geographically and stratigraphically separated. The diagnosis of *Coccolepis* is improved with the addition of new characters, and the genus is here restricted to the two early Tithonian species from the Solnhofen Archipelago. Among the four species previously described or referred to *Coccolepis*, the generic assignment of “*Coccolepis* australis” and “*Coccolepis* liassica” remains unclear. *Sunolepis yumenensis* is here returned to its original genus, and the new combination *Condorlepis woodwardi* is proposed for this Early Cretaceous coccolepidid from Australia.

Key words: Actinopterygii, Coccolepididae, Chondrostei, Mesozoic, Jurassic, Tithonian, Solnhofen, Plattenkalk, Lagerstätte.

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Introduction

In the Late Jurassic, large carbonate platforms formed the northern shore of the Tethyan Ocean producing very rich ecosystems which are preserved in different Plattenkalk Lagerstätten in central Europe (Keupp et al. 2007; Fig. 1A). Among them are the famous lithographic limestone of the southern Franconia Alp in Bavaria. The fine-grained limestone beds of southern Bavaria were deposited within small to medium-sized depressions (Keupp et al. 2007). The Solnhofen Basin is only one among more than twelve different known depocenters (Fig. 1B), which together represent an evolving fossil archipelago spanning c. 3.5 Ma from the late Kimmeridgian to the early Tithonian (Tischlinger and Schweigert 2020). Over the last decades, the recognition of the complex spatial and temporal structure of this fossil archipelago has led researchers to refer to these deposits as the “Solnhofen Archipelago” and to emphasize the distinction of its different components (e.g., Rauhut et al. 2017). However, the early literature of the 19th century as well as the information in collection catalogues and archives of that time are usually vague concerning the precise locality for collection of the fossil specimens. Many historical specimens registered as originating from Solnhofen actually derive from depocenters other than the Solnhofen Basin (e.g., Moser et al. 2017). This lack of accuracy regarding the provenance of numerous fossils, including many type specimens collected over more than 200 years, makes it diffi-
cult to reconstruct the composition of the individual faunas corresponding to the different basins within the Solnhofen Archipelago. These difficulties become critical when trying to understand the dynamic of the Solnhofen Archipelago through space and time.

Moreover, several type specimens have been lost over the centuries, which makes the alpha taxonomic work extremely problematic. As an example, the holotype of the actinopterygian *Coccolepis bucklandi* Agassiz, 1843, has been considered lost (Hilton et al. 2004). When Louis Agassiz described the species, the type and only known specimen was part of William Buckland’s collection in Oxford, UK. Wagner (1863) roughly mentioned that the specimen was kept in England and Woodward (1891) indicated that it was in the Oxford Museum. However, according to the head curator Eliza Howlett (personal communication, June 2019), although there is a catalogue record for the holotype of *Coccolepis bucklandi*, the specimen has never been found in the Earth Collections of the Oxford University Museum of Natural History. Following the comment of Agassiz “I have received in communication from Dr. Buckland a small fish (j’ai reçu en communication de la part de M. le Dr Buckland un petit poisson)” (Agassiz 1843: 300), Laure Bapst and one of the authors (ME) were able to locate the specimen in the palaeontological collection of the Museum d’Histoire Naturelle in Neuchâtel, Switzerland (Fig. 2; Ebert et al. 2021).
Coccolepis bucklandi has been an iconic taxon because it was the first discovery of a non-neopterygian actinopterygian fossil in sediments younger than the Triassic (Agassiz 1843; Wagner 1863). Berg (1940) proposed the family Coccolepidae (original spelling Coccolepidae) to include this and other morphologically similar Mesozoic species. Initially classified in the unnatural palaeonisciform group, coccolepidids are currently referred to the Chondrostei (Acipenseriformes and their fossil relatives) (Hilton et al. 2004; López-Arbarello et al. 2013). Although a phylogenetic study is still necessary to confirm this referral as well as the monophyly of Coccolepididae, the strong morphological resemblance displayed by coccolepidid species between each other, and the lack of other potentially closely related lineages in the Jurassic and Cretaceous indirectly support these hypotheses.

Besides a very conservative morphology, the endo- and exoskeleton of coccolepidids are generally poorly ossified. Therefore, the preservation of coccolepidid fossils is usually poor or incomplete, making the low-level taxonomic work extremely difficult. Among the coccolepidid species currently accepted as valid, most of them were originally described as species of *Coccolepis* (Table 1). The relatively recent revision of several of these *Coccolepis* species led to their referral to the genus *Morrolepis* Kirkland, 1998 (Skrzycka 2014), and the erection of the genera Condorlepis López-Arbarello, Sferco, and Rauhut, 2013, and Barbalepis Olive, Taverne, and López-Arbarello, 2019. Most of the coccolepidid species have been found in freshwater environments, being *C. bucklandi* and “Coccolepis” liassica Woodward, 1890 (Lower Jurassic of Dorset in England), the only strictly marine members of the group (Olive et al. 2019).

Although *Coccolepis bucklandi* has been studied and described in detail relatively recently by Hilton et al. (2004), they were not able to examine the holotype and their work is exclusively based on five specimens referred to this species. Our detailed examination of the newly located holotype and the recognition of some significant morphological variation among the specimens referred to this species, triggered a new taxonomic study of this iconic taxon from the Solnhofen Archipelago.

### Institutional abbreviations
- JME, Jura-Museum Eichstätt, Germany; MACN, Museo Argentino de Ciencias Naturales, Ciudad Autónoma de Buenos Aires, Argentina; MCZ, Museum of Comparative Zoology (Harvard University), Cambridge, USA; MHN, Museum d’Histoire Naturelle in Neuchâtel, Switzerland; MMG-NSD, Museum für Mineralogie und Geologie, Senckenberg Naturkundliche Sammlungen Dresden, Germany; MPEF-PV, vertebrate paleontology collection of the Museo Paleontológico Egidio Feruglio, Trelew, Argentina; SNSB-BSPG, Bayerische Staatsammlung für Paläontologie und Geologie, Munich, Germany.

### Other abbreviations
- TL, total length.

### Nomenclatural acts
This published work and the nomenclatural acts it contains, have been registered in ZooBank: urn:lsid:zoobank.org:pub:3A157948-1BCF-4ABB-9261-562077788582

### Material and methods

The specimens were studied under stereomicroscopes Leica Wild PZO 20138 and Leica Wild M80. The line art images were made with an Intuos Pro PTH-651 Wacom tablet and the software Affinity Designer 1.8.6. Photographs were taken with a Nikon D7000 digital camera equipped with a Nikon AF-S micro 60 mm objective and a Jenoptik digital camera ProRes C5 attached to the stereomicroscope. The fossils were examined and photographed under white and ultraviolet (UV) light (Krantz UV Lamp I 361).

Anatomical comparisons are based on published literature and high-quality photographs and notes taken by one of the authors (ALA) during direct observation of the following specimens: *Condorlepis groeberi*: MACN 14434 (lectotype), MACN 14433, 14432, 18630A, 18551, 18552, 18553, 18561, 18562, 18575; MPEF-PV 1496-5A, 1556-6, 1731, 1732, 1733, 1766, 1767, 3958, 10504–10507; *Morrolepis schaefferi*: MWC 5305, 5306, 5307.

The signs attached to the entries in the synonymy list follow Matthews (1973). The size of the specimens is indicated through their total length (TL).

### Table 1. Taxonomic status of the species currently classified in Coccolepididae.

<table>
<thead>
<tr>
<th>Original binomen</th>
<th>Generic assignment herein</th>
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<tr>
<td><em>Coccolepis bucklandi</em> Agassiz, 1843</td>
<td><em>Coccolepis</em> Agassiz, 1843</td>
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<tr>
<td><em>Coccolepis solnhofensis</em> sp. nov.</td>
<td><em>Coccolepis</em> Agassiz, 1843</td>
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<tr>
<td><em>Coccolepis liassica</em> Woodward, 1890</td>
<td>uncertain</td>
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<tr>
<td><em>Coccolepis andrewsi</em> Woodward, 1911</td>
<td><em>Morrolepis</em> Kirkland, 1998</td>
</tr>
<tr>
<td><em>Coccolepis australis</em> Woodward, 1895</td>
<td>uncertain</td>
</tr>
<tr>
<td><em>Coccolepis macroptera</em> Traquair, 1911</td>
<td><em>Barbalepis</em> Olive, Taverne, and López-Arbarello, 2019</td>
</tr>
<tr>
<td><em>Coccolepis aniscowitchi</em> Gorizdro-Kulczycka, 1926</td>
<td><em>Morrolepis</em> Kirkland, 1998</td>
</tr>
<tr>
<td><em>Oligopleurus groeberi</em> Bordas, 1943</td>
<td><em>Condorlepis</em> López-Arbarello, Sferco, and Rauhut, 2013</td>
</tr>
<tr>
<td><em>Plesiococcolepis hunanensis</em> Wang, 1977</td>
<td><em>Plesiococcolepis</em> Wang, 1977</td>
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<tr>
<td><em>Sunolepis yumenensis</em> Liu, 1957</td>
<td><em>Sunolepis</em> Liu, 1957</td>
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Systematic palaeontology

Actinopterygii Cope, 1887
Chondrostei Müller, 1845
Coccolepididae Berg, 1940 sensu Hilton et al. 2004
Genus Coccolepis Agassiz, 1843

Type species: Coccolepis bucklandi Agassiz, 1843; Solnhofen Lagerstätte, Bavaria, Germany; lower Tithonian, Upper Jurassic.

Included species: Coccolepis solnhofensis sp. nov. Other species previously assigned to Coccolepis are now excluded from this genus (see Discussion).

Emended diagnosis.—Modified from Hilton et al. (2004) and López-Arbarello et al. (2013). Coccolepidid fish, with the following combination of characters: dermal bones of the skull roof, scales, and fin rays ornamented with mostly regularly arranged sharply pointed, posteriorly directed denticles; opercle is larger than subopercle; lower jaw extremely slender and short, about half the length of the maxilla; single row of large conical teeth on the lower jaw; dorsal fin origin anterior to origin of pelvic fins; large dorsal and pectoral fins, with 41–49 and more than 30 fin rays, respectively.

Coccolepis bucklandi Agassiz, 1843

Figs. 2–4A, 5A.

1843 Coccolepis bucklandi Agassiz, 1843: 300 (vol. 2), pl. 36, figs. 6, 7.
1881 Coccolepis bucklandi Agassiz, 1843; Vetter 1881: 37–42, pl. 1: 2.
1992 Coccolepis bucklandi Agassiz, 1843; Lambers 1992: 288, pl.1: A.
1995 Coccolepis bucklandi Agassiz, 1843; Frickhinger 1995: figure on p. 298.
1999 Coccolepis bucklandi Agassiz, 1843; Lambers 1999: 270, fig. 1.
2015 Coccolepis bucklandi Agassiz, 1843; Schultze and Arratia 2015: 369–370, figs. 723, 726.

Holotype: MHNN-FOS 361 (Fig. 2). Nearly complete fish in lateral view, missing a portion of its tail and the anteriormost part of the cra-
nium (approximately 75 mm total length). The Neuchâtel specimen has been identified with confidence as the missing type specimen (Ebert et al. 2021). The shape of the fish and the preserved bones and scales are at the finest detail consistent with Agassiz’ illustration and description of the type specimen.

Type locality: The provenance of the holotype is indicated as “Solnhofen” (written Solenhofen; see Ebert et al. 2021). However, the indication “Solnhofen” in historical labels from the 19th Century usually vaguely refers to the whole complex of basins within the Solnhofen Archipelago (e.g., Moser et al. 2017). Based on indirect evidence, MHNN FOS 361 most probably comes from one of the localities within the Eichstått Basin (see Discussion).

Type horizon: Hybonoticeras hybonotum Zone, Altmühltal Formation, lower Tithonian, Upper Jurassic (Tischlinger and Schweigert 2020).

Material.—Type material and JME-SOS3445 from Blumenberg (Fig. 3A), JME-SOS3382 from Workerszell (Fig. 3B), and JME-SOS2340 from Schernfeld, all three localities within the Eichstått Basin; MMG-SNSD BaJ 1845, Eichstått. All from the Lithacoceras eigeltingense B Horizon of the Lithacoceras riedense Subzone (Altmühltal Formation, Hybonoticeras hybonotum Zone).

Diagnosis.—Species of Coccolepis differing from the other species of the genus in the following characters: three dis-
tinct preanal scutes; fringing fulcra on pectoral, pelvic and caudal fins; numerous ventral caudal fringing fulcra.

**Remarks.**—According Article 73 of the International Code of Zoological Nomenclature (ICZN 1999), the single specimen figured and described by Agassiz (1843), i.e., the MHNN-FOS 361, when creating the nominal taxon *Coccolepis bucklandi* is the name-bearing type of this species. Considering the original type specimen lost, Hilton et al. (2004) designated the SNSB-BSPG 1904 I 19 as the neotype of *C. bucklandi*. After relocating the original type specimen, according to Article 75.8 of the ICZN, the rediscovered MHNN-FOS 361 becomes the name-bearing type of *Coccolepis bucklandi* Agassiz, 1843, and the neotype proposed by Hilton et al. (2004) is set aside.

**Stratigraphic and geographic range.**—Although the precise provenance of the holotype is unknown, all the other specimens referred to *Coccolepis bucklandi* were collected from localities within the Eichstätt Basin of the Solnhofen beds of the Solnhofen basin correspond to the Lagerstätte, Bavaria, Germany. The limestone beds of the Solnhofen basin correspond to the Subplanites rueppellianus Subzone, upper Hybonoticeras hybonotum Zone of the Altmühl Formation, lower Tithonian, Upper Jurassic (Fig. 1C) (Tischlinger and Schweigert 2020).

**Discussion**

The rediscovery of the name-bearing type specimen (MHNN-FOS 361) of *Coccolepis bucklandi* and the discovery of several morphological differences between JME-SOS3445 and other specimens referred to this species (Ebert et al. 2021) prompted the thorough revision of the fossils referred to this taxon. Consequently, two well-defined morphotypes were identified, which are, as far as can be determined, not only geographically, but also stratigraphically separated. One of the two morphotypes matches the morphology of MHNN-FOS 361 and, thus, corresponds to *C. bucklandi* Agassiz, 1843. The second morphotype is regarded as a new taxon.

**Anatomical comparison**

The morphology of the two species *Coccolepis bucklandi* and *C. solnhofensis* sp. nov. is very similar and mostly agree with the detailed description by Hilton et al. (2004). Therefore, we will only discuss the discovered differences between the two taxa and add a few new observations. Meristic information for all the studied specimens is provided in Ebert et al. (2021: table 1).

**Skull.**—Hilton et al. (2004) described the lower jaw as very slender and long, interpreting the jaw in MCZ VPF-5293 of *C. bucklandi* as broken. However, we disagree with their observation. The lower jaw in MCZ VPF-5293 (Hilton et al. 2004: fig. 6A) is complete or nearly complete, as it is in all the other specimens in which it is exposed (the holotype MHNN-FOS 361, JME-SOS2340, MMG-SNSD BaJ 1845 of *C. bucklandi*, and SNSB-BSPG 1895 I 44 of *C. solnhofensis* sp. nov.). Therefore, differing from other coccolepidid taxa, the lower jaw in the two species of *Coccolepis* is extremely slender and very short, about half the length of the maxilla.

The gular plate is not preserved in the specimens studied by Hilton et al. (2004), but it is well preserved, displaced and well exposed in internal view in JME-SOS3445 of *C. bucklandi* (Fig. 3A). The general shape of the median gular is oval, narrowing posteriorly, so that the anterior border is broader than the posterior, deeply convex border. The exposed surface of the gular plate is ornamented with several denticles which can be distinguished through the thin laminar bone. A V-shaped canal or groove is preserved,
exiting at the anterolateral corners of the plate indicating the presence of a gular sensory canal or pit line which was possibly connected with the mandibular sensory canal.

**Fins.**—The pectoral fins are located lateroventrally in all coccolepidid fishes. Therefore, the total number of fin rays is difficult to assert and only possible to evaluate in ventrally or lateroventrally exposed specimens. JME-SOS3445 of *C. bucklandi* is preserved in ventral view and both pectoral fins are well exposed (Fig. 3A). They consist of 36 or 37 fin rays and two basal fulcra. In the same specimen, approximately 17 small fringing fulcra are fused to the basal fulcra and attached to the marginal ray. All fringing fulcra have nearly the same size and at least the more proximal ones have an elongated patch of ganoin. The right pectoral fin in the acid prepared SNSB-BSPG AS I 1328 of *C. solnhofensis* sp. nov. is well exposed, including 33 lepidotrichia and a similar condition of the fringing fulcra. Hilton et al. (2004) described this structure as a pectoral spine formed by the fusion of fringing fulcra (Hilton et al. 2004: figs. 12A). Although this pectoral spine is relatively larger in SNSB-BSPG AS I 1328 (TL ~90 mm) than in JME-SOS3445 (TL ~120 mm), the organ is formed by the fusion of basal and fringing fulcra and, thus, equivalent in both specimens. The difference in the relative size might be due to ontogeny.

According to Hilton et al. (2004) fringing fulcra are absent on the pelvic fins and we confirm this condition in *C. solnhofensis* sp. nov. (Hilton et al. 2004: fig. 12B). However, differing from this species, JME-SOS3445 of *C. bucklandi* preserves at least three fringing fulcra on the marginal rays of the right pelvic fin (Fig. 4A1).

Hilton et al. (2004) did not notice the very few and slender fringing fulcra on the ventral marginal ray of the caudal fin of the holotype SNSB-BSPG 1904 I 19 and SNSB-BSPG 1986 XV 112 and SNSB-BSPG AS I 1328 of *C. solnhofensis* sp. nov. These fringing fulcra are mainly formed by the terminal segments of the marginal rays or a marginal branching of these rays (Fig. 4B). The ventral caudal fringing fulcra in *C. bucklandi* are formed not only by those terminal segments, but there are several additional fulcra laying on the marginal rays between those terminal segments (Fig. 4A2).

As a result, the ventral caudal fringing fulcra are significantly more numerous in this species; JME-SOS3445 preserves approximately 12 fringing fulcra along the ventral caudal ray.

All paired and median fin rays in the two species of *Coccolepis* are evenly joined, including the basal segment, the lepidotrichia are only very distally branched and they apparently divide only once.

**Scales.**—In both *Coccolepis* species, the body is covered with amioid elasmoid scales, and the axial lobe of the tail is flanked by rhomboid scales as described by Hilton et al. (2004). There is no significant difference between the species concerning these features. Differences between the taxa reside in the presence of in three preanal scutes in *C. bucklandi*, and a single predorsal scute *C. solnhofensis* sp. nov.
We have observed at least one preanal scute or clear remains of these scutes in all of the specimens representing this species, in which the area is preserved. In contrast, after a careful examination of the five specimens of *C. solnhofensis* sp. nov., we found no evidence of similar scutes. There are distinct preanal scales, however, which are preserved only in the holotype SNSB-BSPG 1904 I 19 (Fig. 5B) and in SNSB-BSPG AS I 1328. These preanal scales are identical to the adjacent amioid scales covering the body, but they are strongly mineralized. Preanal scutes or modified scales are related to gonopodial-like structures and modified anal fins and thus associated with potential sexual dimorphism in several early actinopterygians (e.g., Bürgin 1990; Lombardo 1999; Sun et al. 2012; Xu et al. 2016). Male and female individuals cannot be distinguished in the small samples representing *C. bucklandi* and *C. solnhofensis* sp. nov. because, when preserved, the presence of preanal scutes or modified preanal scales has a uniform distribution within each association, which is coincident with the distribution of the other diagnostic features. Still, sexual dimorphism can also be related to these preanal structures in *C. bucklandi* and *C. solnhofensis* sp. nov., a hypothesis that deserves further investigation.

Hilton et al. (2004) described a single basal fulcrum at the origin of the dorsal fin in the holotype of *C. solnhofensis* sp. nov. (SNSB-BSPG 1904 I 19). Additionally, we found a single scute preceding the dorsal fin in SNSB-BSPG 1986 XV 112 (Fig. 5C) and SNSB-BSPG 1895 I 44 of this species. No evidence of a predorsal scute have been observed in any of the specimens representing *C. bucklandi*.

**Distribution**

Among the specimens representing *Coccolepis bucklandi*, the precise provenance is only known for the three specimens in the Jura-Museum Eichstätt: Schernfeld (JME-SOS2340), Workerszell (JME-SOS3382), and Blumenberg (JME-SOS3445). These localities are within the Eichstätt Basin and dated in the *Lithacoceras eigeltingense* β Horizon of the *L. riedense* Subzone (Altmühltal Formation, *Hybonoticeras hybonotum* Zone) (Tischlinger and Schweigert 2020). The locality of the specimen in Dresden (MMG-SNSD BaJ 1845) is only indicated as Eichstätt, but according to Vetter (1881) it was collected in one of the quarries around the village of Obereichstätt, which is also referred to the *L. eigeltingense* β Horizon. Although the provenance of the holotype MNHN-FOS 361 is vaguely indicated as “Solnhofen”, the lithology of the rock containing the specimen matches the sediments from the quarries within the Eichstätt depocenter. Therefore, it is likely that the distribution of the species *C. bucklandi* is limited to the Eichstätt Basin and the *L. eigeltingense* β Horizon.

On the other hand, the SNSB-BSPG 1895 I 44 of *Coccolepis solnhofensis* sp. nov. was collected in the locality of Hummelberg near Solnhofen, well within the Solnhofen Basin. The limestone beds of Solnhofen sensu stricto correspond to the *Subplanites rueppelianus* Subzone (Altmühltal Formation, *Hybonoticeras hybonotum* Zone)
and Schweigert 2020. The provenance of the other three specimens of *C. solnhofensis* sp. nov. is only indicated as “Solnhofen” (SNSB-BSPG AS I 1328, SNSB-BSPG 1986 XVI 112) or “Lithographische Schiefer Solnhofen” (= lithographic limestone Solnhofen, holotype SNSB-BSPG 1904 I 19), but it is possible that *C. solnhofensis* sp. nov. is limited to the Solnhofen Basin, which is slightly younger than the Eichstätt Basin (Tischlinger and Schweigert 2020).

Although the potential geographic and stratigraphic separation of the two species of *Coccolepis* should be confirmed by further studies when more specimens are available and possibly through detailed lithographic analyses, their potential endemism is a valid hypothesis.

### Species excluded from *Coccolepis*

The taxonomy of several species previously referred to *Coccolepis* has been revised recently resulting in their referral to the coccolepidid genus *Morrolepis* (Skrzycka 2014) or the erection of new genera (López-Arbarello et al. 2013; Olive et al. 2019). Other species previously referred to *Coccolepis*, “Coccolepis” *liassica* Woodward, 1890, Lower Jurassic, Dorset, England; “C.” *australis* Woodward, 1895, Upper Jurassic, Talbragar, New South Wales, Australia; “C.” *yumenensis* (Liu 1957), Upper Jurassic or Lower Cretaceous, Yumen, Gansu Province, China; and “C.” *woodwardi* Waldman, 1971", Lower Cretaceous, Koonwarra, Victoria, Australia, are here excluded from the genus because they do not present the combination of features given in the emended diagnosis.

Differing from *Coccolepis* the skull bones of “C.” *liassica* are covered with ganoin and the ornamentation consists of coarse tubercles which sometimes merge producing rugae, there is a double row of teeth on the lower jaw, the dorsal and pectoral fins are significantly smaller, including only 20–25 dorsal and 18–20 pectoral fin rays, the lower jaw is notably more robust and larger, as long or longer than the maxilla (Gardiner 1960). “C.” *woodwardi* resembles “C.” *liassica* and differs from *Coccolepis* in the following features: opercle smaller than subopercle, double row of teeth on the lower jaw, small pectoral fins with 18 rays (Waldman 1971). The lower jaw of “C.” *yumenensis* is described as robust, with a double row of teeth, the opercle is smaller than the subopercle and the origin of the dorsal fin is located posterior to the insertion of the pelvic fins (Liu 1957). The more poorly known “C.” *australis* differs from *Coccolepis* in the relative position of the pelvic fins, which are closer to the pectoral fins, inserting well anterior to the origin of the dorsal fin (Woodward 1895; Waldman 1971).

Considering the differences mentioned above and pending a thorough revision of these four species, *Sunolepis yumenensis* Liu, 1957, most probably represents its own genus, as originally described (Table 1). As already indicated by Olive et al. (2019), “Coccolepis” *woodwardi* resembles *Condorlepis groeberi* (Bordas, 1943) very closely, including the following diagnostic features of this genus: subopercle and branchiostegals ornamented with low concentric striae; supracleithrum longer than cleithrum; small, oval postcleithrum; fringing fulcra present in caudal fin only. Accordingly, the species *Coccolepis woodwardi* Waldman, 1971, is here tentatively referred to *Condorlepis* López-Arbarello, Sferco, and Rauhut, 2013 (Table 1). “Coccolepis” *australis* is too poorly known to make any inference about its possible generic assignment, and “C.” *liassica* might represent a new genus.

### Conclusions

The relocation of the holotype of *Coccolepis bucklandii* triggered the alpha taxonomic revision of this early Tithonian (Late Jurassic) species. As a result, the species *C. solnhofensis* sp. nov. has been identified among the specimens referred to *C. bucklandii*. The two species of *Coccolepis* are ostensibly geographically and stratigraphically separated. As far as we can be certain about the provenance of some of the specimens, *C. bucklandii* is limited to the Eichstätt Basin and the *Lithacoceras eigeltingense* B Horizon of the *L. riedense* Subzone (Altmißhalt Formation, *Hybonoticeras hybonotum* Zone; Tischlinger and Schweigert 2020). Similarly, *C. solnhofensis* sp. nov. is limited to the Solnhofen Basin and the slightly younger *Subplanites rueppelliannus* Subzone (Altmißhalt Formation, *Hybonoticeras hybonotum* Zone; Tischlinger and Schweigert 2020).

The distinction of the new species of *Coccolepis* and the comparative anatomical analysis led to the improvement of the diagnosis of this genus with the addition of new characters. Consequently, four species previously described or referred to *Coccolepis* are here excluded from the genus. The generic assignment of two of these species, “C.” *australis* and “C.” *liassica*, remains unclear. *Sunolepis yumenensis* Liu, 1957, is here returned to its original genus, and the new combination *Condorlepis woodwardi* (Waldman, 1971), is proposed for this Early Cretaceous coccolepidid from Australia.

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