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Roveacrinida (Crinoidea) from Late Triassic (early Carnian) black shales of Southwest China

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Abstract Rich material of a tiny pelagic roveacrinid from the lower member of the Carnian Xiaowa Formation, Guanling area (Guizhou Province, Southwest China), is described. The remains are assigned to a distinct species, *Osteocrinus sinensis* n. sp. The species is characterised by an aboral element of variable length, a radial circlet forming a small cup and unusually long arms with hollow brachials grouped in pairs. This morphology is unique among crinoids. The remains settled partly articulated on the seafloor. Coprolites comprised of roveacrinid remains and apparently produced by ammonites are common, corroborating a pelagic lifestyle of the roveacrinids. An overview of previously described species of *Osteocrinus* is given; the present material contributes recognising variability and growth stages of the partly insufficiently known forms.

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Dedicated to the memory of Edith Kristan-Tollmann (1934–1995) for her pioneering research on planktonic crinoids from the Triassic Tethys.

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Introduction

Roveacrinida are small, stalkless and mostly pelagic crinoids that first appeared during the Middle Triassic of the Tethys realm. They are grouped in four families: the exclusively Triassic Axicrinidae (containing only the genus *Axicrinus*) and Somphocrinidae, the Jurassic Saccocomidae and the Cretaceous Roveacrinidae (Hess 2010; Hess in Hess and Messing 2011; Hess 2015a). Descended from presumably sessile ancestors (*Axicrinus*), the pelagic Somphocrinidae radiated extensively during the early Carnian. It may not be a coincidence that the first members of the calcareous nannoplankton, minute phytoplanktonic organisms representing the lowest member of the food chain, appeared around this time (Bown et al. 2004). The second major roveacrinid radiation took place during the Late Jurassic with the Saccocomidae, starting with the presumably benthic *Crassicoma* during the Kimmeridgian and reaching its acme during the early Tithonian with the large, spectacular *Saccocoma tenella* (Hess 2002, 2015b; Hess and Etter 2011). *S. tenella* occurs in the Solnhofen Limestone, partly comprised of coccolithophores on which the crinoids probably fed. The third major radiation included the Roveacrinidae and lasted from the middle (Albian) into the late (Cenomanian) Cretaceous (Hess 2015a). During this time, sediments were commonly deposited as chalk, consisting largely of the remains of coccolithophores. Each of the three major radiations produced distinctive forms (see Hess 2015a, Fig. 20). The Somphocrinidae have a spine-like aboral element attached to a simple radial circlet (cup); the brachials may have spines and tend to be elongate. The cups of the Saccocomidae are simple bowls, with or without processes; the brachials commonly have lateral flanges or wings. The Roveacrinidae include forms with widely different, at times

bizarre looking cups with lateral processes and wings; the brachials may have flanges or spines and are elongate in one species. A distinctive character of the Roveacrinida is a strongly sloping cryptosynarthry between the two primibrachials that also occurs between lower secundibrachials. Most forms have a delicate skeleton with processes and wings to facilitate floating. Members of the Triassic genus *Osteocrinus* (type *Osteocrinus rectus*, Somphocrinidae) and the Cretaceous *Roveacrinus pyramidalis* (Roveacrinidae) differ from all other Roveacrinida by rod-shaped brachials devoid of food grooves (Kristan-Tollmann 1970; Hess 2015a).

Recently, remains of partly articulated somphocrinids were discovered in Late Triassic (Carnian) black shales, the "Guanling Biota" of Guanling County (Guizhou Province, Southwest China). This Lagerstätte has furnished spectacular, intact colonies of the pseudopelagic *Traumatocrinus* and many articulated vertebrate remains (Wang et al. 2008; Figs. 1, 2). The roveacrinids were described by Wang et al. (2007) who assigned them to *Osteocrinus* cf. *virgatus* Kristan-Tollmann and *O. spinosus* Kristan-Tollmann. Wang et al. (2008) assigned them to *Osteocrinus* sp. Except for the much larger Upper Jurassic *Saccocoma tenella* from southern Germany and the Middle Cretaceous *Poecilocrinus* (Hess 2015a), the Chinese somphocrinid is the only form known from at least partly articulated specimens. Their detailed examination and comparison with other Triassic somphocrinids are presented with the intention of improving our knowledge of these earliest pelagic crinoids (Hagdorn 2011). The first Roveacrinida are known from mass occurrences of *Osteocrinus* during the late Ladinian, and their ancestry is unknown. Several *Osteocrinus* species appear during the early Carnian in the Cassian Formation. They occur together with *Axicrinus*, a form with distinct basals and a sloping cryptosynarthry between the primibrachials and the first and second secundibrachials. Such morphology is considered basic to Roveacrinida (Hess in Hess and Messing 2011). In contrast, isolated echinoderm remains from the EarlyTriassic Vardebukta Formation of Svalbard assigned to *Somphocrinus* and *Osteocrinus* by Salamon et al. (2015) are definitely not roveacrinids.

Osteocrinus in the Late Triassic world

The genus *Osteocrinus* was established by Kristan-Tollmann in 1970 while studying mass occurrences of planktonic microcrinoids in late Ladinian/early Carnian beds, widely distributed in the Tethys. She called these occurrences "*Osteocrinus* Facies" and compared them to the Late Jurassic "*Saccocoma* Facies", also called "*Lombardia* Facies" (see Hess 2002). Earlier, Peck (1948) had established the genus *Somphocrinus* from the Carnian of Mexico; the corresponding species, *S. mexicanus*, is the only one in this genus and has also been described from various other localities. *Osteocrinus*, *Somphocrinus* and the less well-known *Ossicrinus* Kristan-Tollmann (1970) constitute the family Somphocrinidae Peck in Rasmussen (1978). A revised diagnosis is given by Hess in Hess and Messing (2011).
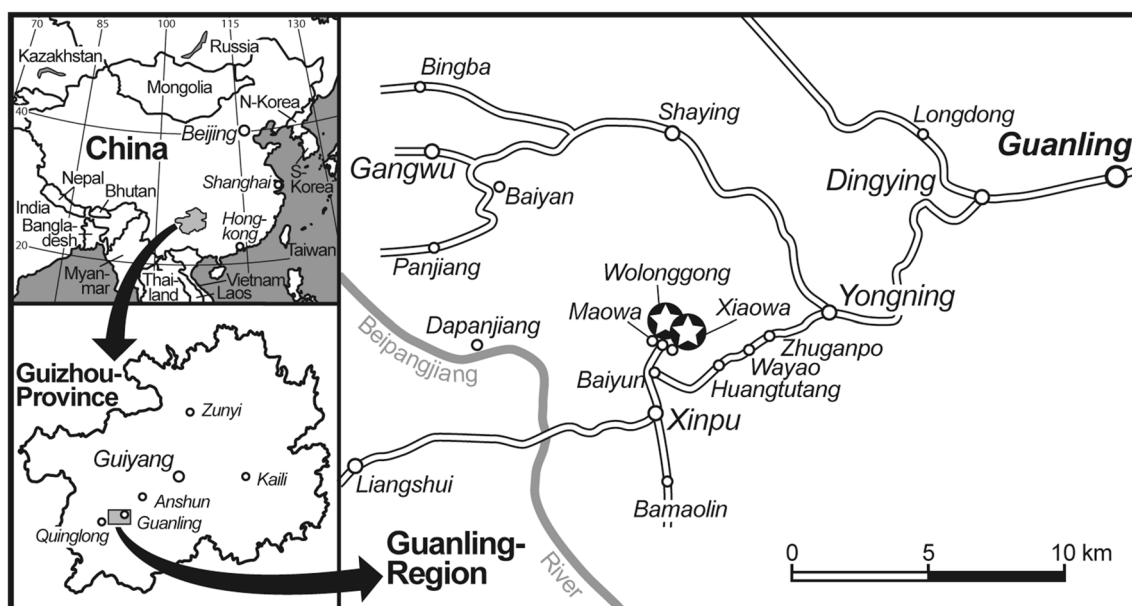

Fig. 1 Geography of the Guanling area with positions of main sites; the described material comes from Xiaowa Village and Wolonggong (after Wang et al. 2008)

Fig. 2 Stratigraphy and conodont zonation of the Middle and Upper Triassic in southwest Guizhou. The beds with *Osteocrinus* are in the upper unit of the Lower Xiaowa Formation containing the Lagerstätte (after Wang et al. 2008)
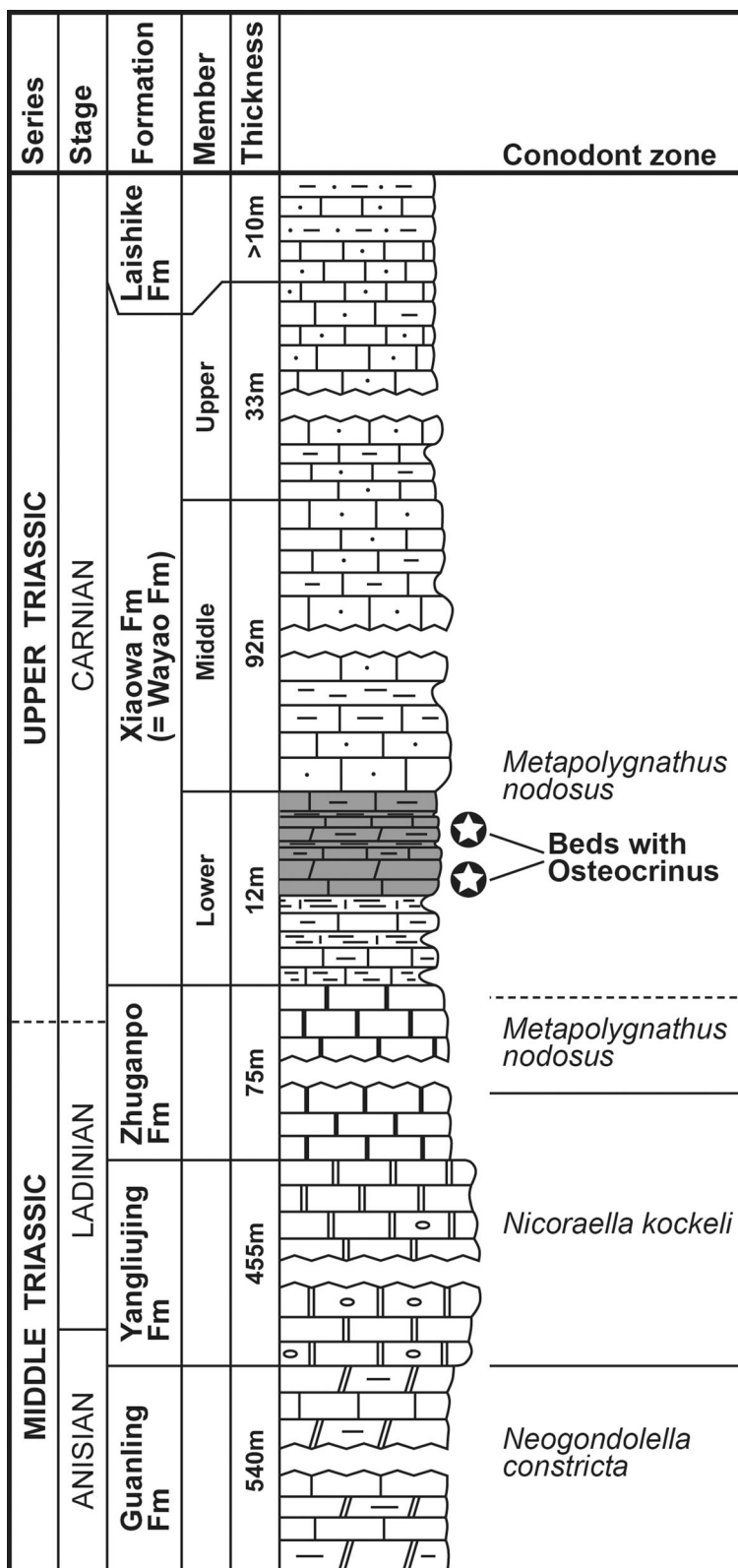
The type species of *Osteocrinus*, *O. rectus* (Frizzell & Exline 1955), was originally described as holothurian sclerites. In her original paper, Kristan Tollmann (1970) established seven species or subspecies: *O. rectus rectus*, *O. rectus goestlingensis*, *O. acus*, *O. rimosus*, *O. spinosus*, and *O. virgatus* from Alpine Europe. In later papers Kristan-

Tollmann (in Kristan-Tollmann and Krystyn 1975; Kristan-Tollmann 1991) described two additional species, *O. saklibelensis* from the early Carnian of Turkey and *O. aghdarbandensis* from the latest Ladinian of Iran; these strata also furnished *O. saklibelensis* and remains of *Traumatocrinus caudex* (Dittmar). Whether the Chinese *Traumatocrinus* belongs to the same species has yet to be ascertained (see Hagdorn and Wang 2015). Reconstructions of Kristan-Tollmann's species are shown in Fig. 3 (Kristan-Tollmann 1977, 1991; Kristan-Tollmann in Kristan-Tollmann and Krystyn 1975). It may well be that *O. aghdarbandensis* is a juvenile of *O. saklibelensis*. Additional species of the genus were proposed by Mostler (1972) on the basis of aboral elements only, illustrated by drawings. These are: *O. acanthicus*, *O. hessi*, *O. longispinosus*, *O. planus*, *O. squamosus*, and *O. sulcatus*. Simms (1990) questioned the status of many somphocrinid species, because some were based on corroded material or were insufficiently described. The status of these species is discussed in the next section, in the context found in the Chinese material.

Remains of *Osteocrinus* were considered to be useful index fossils across the Tethys Ocean (Kristan-Tollmann 1970; Donofrio and Mostler 1975; Bizzarini et al. 1989; Laghi and Rechichi 1999); however, their usefulness is hampered by the difficulties of distinguishing individual species. They may form high concentration constituting up to two-thirds of sediment by volume in the Carnian Hallstatt limestone (Mostler 1972, p. 714). Kozur and Mostler (1971) found such mass occurrences in the basal Longobardian (late Ladinian) of the Balaton area of Hungary. Oravecz-Scheffer (1979) described remains from three lower Carnian (Julian) sites of the central Transdanubian Mountains of western Hungary; she identified the following species: *Osteocrinus rectus*, *O. rimosus*, *O. spinosus*, and *O. virgatus*. Bizzarini et al. (1989) described and figured well-preserved aboral elements of *Osteocrinus rectus*, *O. hessi*, *O. virgatus* and *O. spinosus* from the Cassian Formation (Longobardian to Julian) of the Dolomites; a radial circlet with attached aboral element of *O. virgatus* was also figured. Laghi and Rechichi (1999) sampled the Stuores Wiesen/Prati di Stuores section (now GSSP of the Ladinian–Carnian boundary; Gaetani 2009) bed by bed and recorded five species of *Osteocrinus* out of 11 species of microcrinoids. *Osteocrinus rectus, O. goestlingensis*, and *O. saklibelensis*, are long-ranging species that occur in the *Osteocrinus* facies from the late Ladinian *regoledanus* Subzone to the early Carnian *aon* Subzone, with *O. rectus* being the most abundant species in each of the samples. An *Osteocrinus* species appears only immediately below the Ladinian/Carnian boundary. *Osteocrinus acus* disappeared before the end of the earliest Carnian *Daxatina* cf. *canadensis* Subzone.

The Chinese material was described by Wang et al. (2007; Hagdorn is mentioned as co-author, but did not contribute to this publication) who assigned them to *Osteocrinus* cf. *virgatus* Kristan-Tollmann (with short aboral element) and *O. spinosus* Kristan-Tollmann (with long aboral element). However, the morphology of the Chinese *Osteocrinus* specimens differs in many aspects from other forms not considered by the authors at that time. Furthermore, in the English abstract Wang et al. (2007) "concluded with confidence that *Osteocrinus* and *Saccocoma* have similar lifestyle because they are similar in morphology". In fact, the Chinese specimens (herein assigned to *Osteocrinus sinensis* n. sp.) have a most peculiar and unexpected morphology, especially their hollow brachials, that is quite different from *Saccocoma* and invites a discussion of its lifestyle and the environmental conditions that we offer below. No other species of Roveacrinida with hollow brachials has ever been found, be it a somphocrinid from the Triassic, a saccocomid from the Jurassic, or a roveacrinid from the Cretaceous.

Overview of *Osteocrinus* species

Simms (1990) published a list of somphocrinid species established previously, and was the first to doubt the status of many of these. For example, he considered some of the taxa discussed by Donofrio and Mostler (1975) to represent ontogenetic stages, a conclusion we question. In particular, Simms considered short aboral elements to be earlier ontogenetic stages of adults with longer elements.

Species proposed by Kristan-Tollmann (see Fig. 3) (Modified after Kristan-Tollmann 1970, 1991; and Kristan-Tollmann in Kristan-Tollmann and Krystyn 1975)

Osteocrinus rectus (Frizzell and Exline 1955), the type species of the genus, is also the best known to date. The two subspecies, *O. rectus rectus* (Fig. 3a) and *O. rectus goestlingensis* Kristan-Tollmann (1970) (Fig. 3b) occur at the same localities and are distinguished mainly by differences in length of the aboral element; for details see Kristan-Tollmann (1970) and Kristan-Tollmann in Kristan-Tollmann and Krystyn (1975). The difference between the subspecies is considered here within the morphological range of the species. The two aboral elements figured by Bizzarini et al. (pl. 3, fig. 3, 7) and described as *Osteocrinus rectus* fall in the range of Kristan-Tollmann's specimens. Unique to *O. rectus* are terminal brachials resembling palm trees and called "Palmalia" by Kristan-
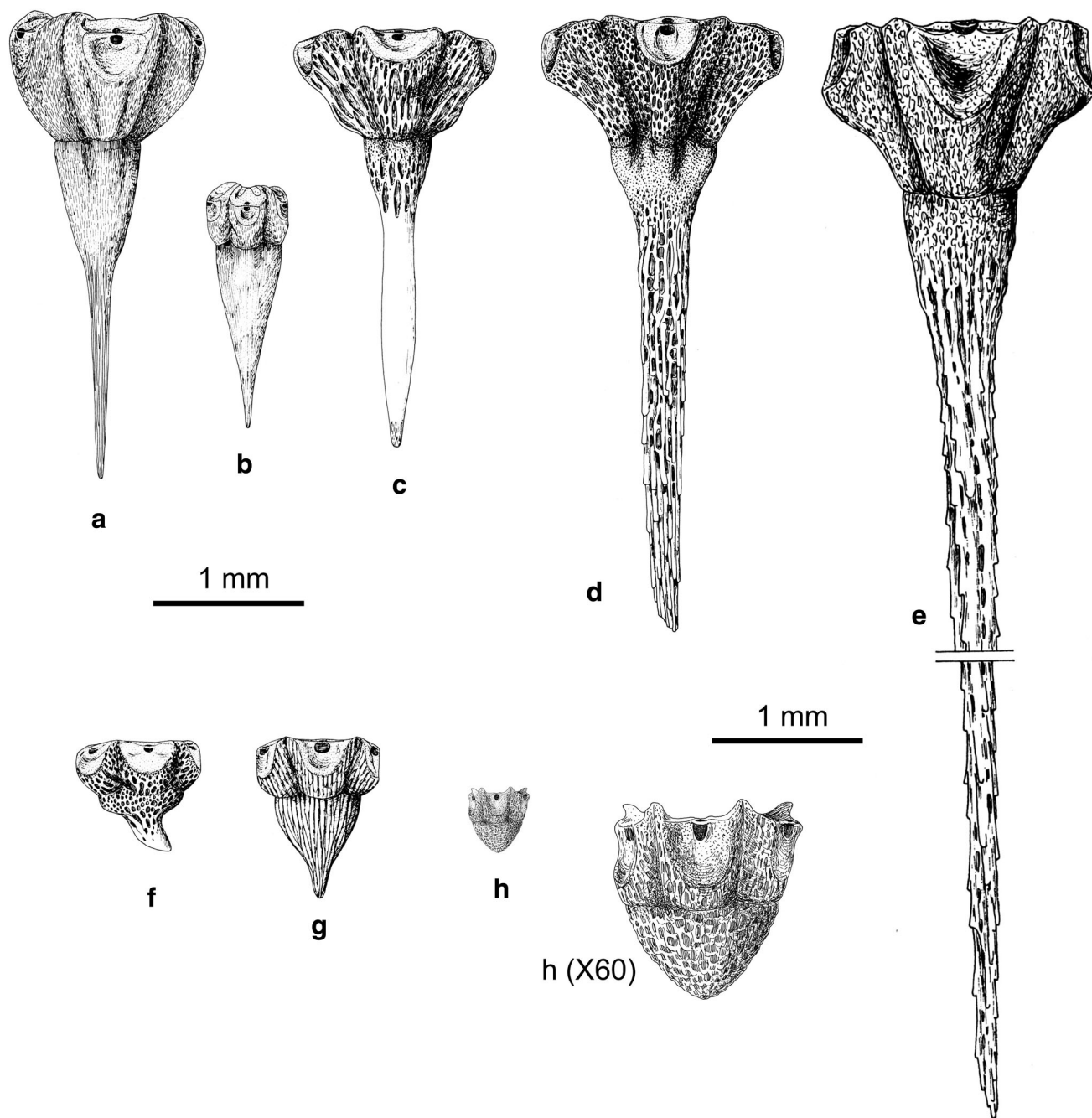
Fig. 3 Reconstruction of species proposed by Kristan-Tollmann (1970: **a–d**, **f–g**; 1991: **h**) and Kristan-Tollmann in Kristan-Tollmann and Krystyn (1975: **e**). Figured is the radial circlet (cup) with attached aboral element ("centrodorsal"). **a** *Osteocrinus rectus rectus* (Frizzell & Exline); **b** *O. rectus goestlingensis* K-T; **c** *O. acus* K-T; **d** *O. spinosus* K-T; **e** *O. saklibelensis* K-T; **f** *O. rimosus* K-T; **g** *O. virgatus* K-T; **h** *O. aghdarbandensis* K-T. After Kristan-Tollmann (1977). *Note* In this paper the author figured *O. saklibelensis* as smaller species (1977, figs. 1, 6). However, in the original paper (Kristan-Tollmann in Kristan-Tollmann and Krystyn 1975, fig. 30) the author's reconstruction is much larger, with a cup diameter of 1.8 mm and an aboral element length of 10 mm or more. We have chosen the larger specimen

Tollmann and Tollmann (1983, pl. 10, figs. 1–3), see also Hess in Hess and Messing (2011, fig. 109, *3f*). *O. rectus* is found near the Ladinian/Carnian boundary and has been recorded from the *regoledanus* Subzone through the *aon* Subzone. It is a widely distributed Tethyan species.

Osteocrinus acus Kristan-Tollmann (1970) (Fig. 3c). The species is characterised by a needle-shaped aboral element. Toward the upper end, the stereom is coarsely meshed at first and then becomes finer near the facet to the radial circlet. The radials are sculptured similar to the

coarse part of the aboral element. The aboral ligament fossa is restricted to the upper third of the surface and has a distinct pit; the muscle fossae are triangular and extend downward onto the adoral side. In the Cassian Formation *O. acus* appears immediately below the Ladinian/Carnian boundary and its last appearance is in the upper *Daxatina* cf. *canadensis* Subzone (Laghi and Rechichi 1999).

Osteocrinus rimosus Kristan-Tollmann (1970) (Fig. 3f). The species has a compact and short aboral element that commonly is a short, bent spine. The radial circlet is wider than high, compact, with a semi-circular aboral ligament fossa and a small pit. Both ossicle types have a pitted surface.

Osteocrinus spinosus Kristan-Tollmann (1970) (Fig. 3d). The two primibrachials on this species are connected by a strongly sloping cryptosynarthry; the first primibrachial has a widened base that is offset from the slender shaft (Kristan-Tollmann 1970, fig. 11). Most of the aboral element is covered by distinct anastomosing ribs; the uppermost part is finely granulated (Kristan-Tollmann 1970, fig. 10). On their inner side, the radials resemble those of *O. acus* but are less ornamented. Part of an aboral element figured by Bizzarini et al. (1989, pl. 3, fig. 5) agrees well with Kristan-Tollmann's figures.

Osteocrinus virgatus Kristan-Tollmann (1970) (Fig. 3g). This species is characterised by a compact, funnel-shaped aboral element. The radials are compact and bulging, the aboral ligament fossa is large. The aboral element and the radials are ornamented by fine longitudinal ribs. Bizzarini et al. (1989, pl. 2, figs. 1–2) figured an aboral element with the same characters and an element attached to the radial circlet from the *austriacum* Subzone of the Cassian Formation of the Dolomites (Fig. 5a–b).

Osteocrinus saklibelensis Kristan-Tollmann in Kristan-Tollmann and Krystyn (1975) (Fig. 3e). The aboral element is very long, gradually diminishing in diameter. The radials are high and narrow in the lower part; the aboral ligament fossa is nearly triangular. The brachials are long and thin, with adoral spines near the muscular facets, the adoral groove is reduced to small pits.

Osteocrinus aghdarbandensis Kristan-Tollmann (1991) (Fig. 3h). The aboral element is very small, compact and short. The radials are nearly rectangular in outline; the aboral ligament fossa is large and occupies most of the aboral surface. The first primibrachial has a broadened base. The very small specimens may represent juveniles of *O. saklibelensis*.

Species proposed by Mostler (1972) (see Figs. 4, 5)

Figure 4 is copied from Mostler (1972), Fig. 5 from Bizzarini et al. (1989). Mostler's specimens were isolated from acid-dissolved limestone and may be corroded. The well-preserved specimens of Bizzarini et al. (1989) were processed from marly sediments.

Osteocrinus squamosus Mostler (1972) (Fig. 4a). The aboral element is rather short, with cone-shaped upper part ornamented with scales; the lower part has a triangular end with short spines. Note: mistyped as *O. squanosus* in the original figure caption.

Osteocrinus longispinosus Mostler (1972) (Fig. 4b). The aboral element is very long, with a short, funnel-shaped and strongly ornamented upper part; the lower part shows three furrows widening to a blunt end.

Osteocrinus hessi Mostler (1972) (Fig. 4c). The nearly hemispherical, upper part of the aboral element is strongly demarcated from the distal part, ornamented slightly in weak spines. Bizzarini et al. (1989) figured three aboral elements from the Julian part of the Cassian Formation (*aonoides* and *austriacum* Subzones) agreeing well with this diagnosis (Fig. 5c–e).

Osteocrinus acanthicus Mostler (1972) (Fig. 4d). The aboral element is long and slender, the upper part is high ovate, and the lower part has a triangular end with short spines. Radials are unknown.

Osteocrinus sulcatus Mostler (1972) (Fig. 4e). The aboral element is long, with wide funnel-shaped and ornamented upper part; the lower part has three furrows and a weakly serrated tip. The radial is triangular and coarsely ornamented in aboral (exterior) view, and the upper ends are prolonged to wings.

Osteocrinus planus Mostler (1972) (Fig. 4f). The aboral element has a wide, disk-shaped upper part, strongly demarcated from a short lower part with long spines and oval pores.

Discussion

The previously described species may be grouped according to overall shape of the aboral element as follows. (1) Compact forms with a short aboral element (*O. rimosus*, *O. virgatus*). (2) Forms with a long aboral element, upper part broad and demarcated from spine-like lower part (*O. hessi*, *O. planus*). (3) Forms with a long aboral element gradually diminishing in diameter distally (*O. rectus*, *O. acus*, *O. acanthicus*, *O. sulcatus*). Ornamentation may help to confirm the diagnosis. *O. virgatus* has fine anastomosing ribs on the radials and the aboral element. *O. rimosus* has a pitted surface on the radials and the aboral element. The presence of furrows on long aboral elements (*O. longispinosus*, *O. acanthicus*, *O. squamosus*) appears less distinctive as seen in the Chinese material. To what extent the species established by Mostler (1972) are distinct must remain open until better material becomes available, preferably from marly sediments to exclude artefacts related to acid preparation. Taking
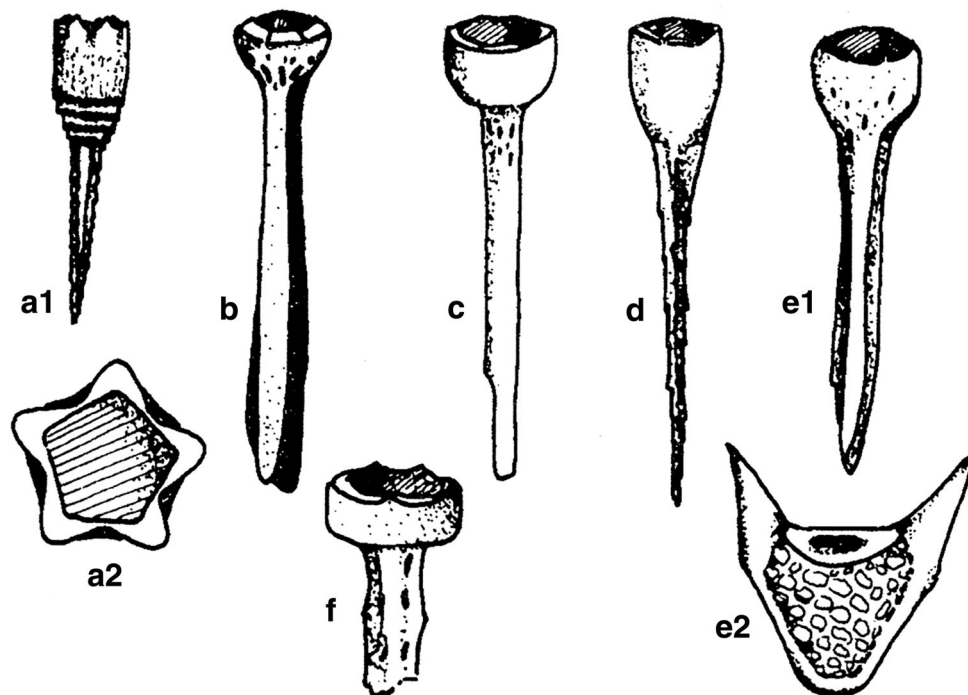
Fig. 4 New *Osteocrinus* species proposed by Mostler (1972), with stratotype and type locality; for the range of the different species see Donofrio and Mostler (1975). **a** *O. squamosus* Mostler, Hallstätter Kalk (Carnian, Julian), Sommeraukogel, Salzkammergut; **a1** aboral element lateral, **a2** upper (adoral) view of aboral element. **b** *O. longispinosus* M., aboral element; Hallstätter Kalk (Carnian, Tuvalian), Sommeraukogel, Salzkammergut. **c** *O. hessi* M., aboral element; Hallstätterkalk (Julian), Teltschen Alpe, Salzkammergut. **d** *O. acanthicus* M., aboral element; Hallstätterkalk (Carnian, Tuvalian), Millibrunnkogel, Salzkammergut. **e** *O. sulcatus* M., Hallstätter Kalk (Carnian, Julian), Sommeraukogel, Salzkammergut, **e1** aboral element lateral, **e2** aboral (exterior) view of radial. **f** *O. planus* M., aboral element; Hallstätter Kalk (Carnian, Julian), Sommeraukogel, Salzkammergut. The figured aboral elements are holotypes; the author indicates that the species will be treated in more detail in a later paper which never appeared. A scale is lacking and repositories are not mentioned

growth changes into account the following species may represent ontogenetic stages. *O. goestlingensis* is a juvenile of *O. rectus*; this is corroborated by the co-occurrence in the Cassian Formation (Laghi and Rechichi 1999). *O. aghdarbandensis* probably is a juvenile of *O. saklibelensis*. The overview discusses that a number of species are well enough defined to be useful for future studies. They include most of Kristan-Tollmann's species and one or two of Mostler's species with a widened upper part of the aboral element (*O. hessi*, *O. planus*).

Geological setting, materials and methods, terminology used

The tiny fossils were detected due to their whitish-pale colour on weathered slabs of black bituminous shales on the waste tips of quarries run for excavation of marine reptiles and *Traumatocrinus* colonies in the Xiaowa Formation of Guanling County. Major localities are in the vicinity of the hill of Wolonggong (Fig. 1), where the Guanling National Geopark and Museum has been built. Most of the figured and described specimens come from Xiaowa Village (Figs. 6, 7, 8, 9, 10, 11, 12, 13, 14, 15a–c, e–k; MHI inventory number 1879; coordinates 25° 5́316.5 N; 105° 2́558.1 E), and a few additional specimens are from Wolonggong (Figs. 15d, l, 17, 18; MHI inventory number 2137; 25°53′20.04 N; 105° 25′29.9 E). The precise position of the specimens in the section could not be located, but their origin from the black shales of the Lower Xiaowa Formation is certain (Wang et al. 2008, p. 42; fig. 2). As indicated by abundant ammonoids in the black shales and in limestone nodules of its Lower Member, the Xiaowa Formation belongs to the *Trachyceras multituberculatum* Zone of early Carnian age (Wang et al. 2008). This is confirmed by bed-by-bed ammonoid sampling conducted by Zou et al. (2015). According to these authors, the top of the underlying Zhuganpo Member is of earliest Carnian age (*Trachyceras* beds), and at the base of the Wayao Member (=Xiaowa Formation) is the first appearance of *Trachyceras multituberculatum*, the index species of the *multituberculatum* Zone. This regional Guizhou ammonoid biozone is regarded to be
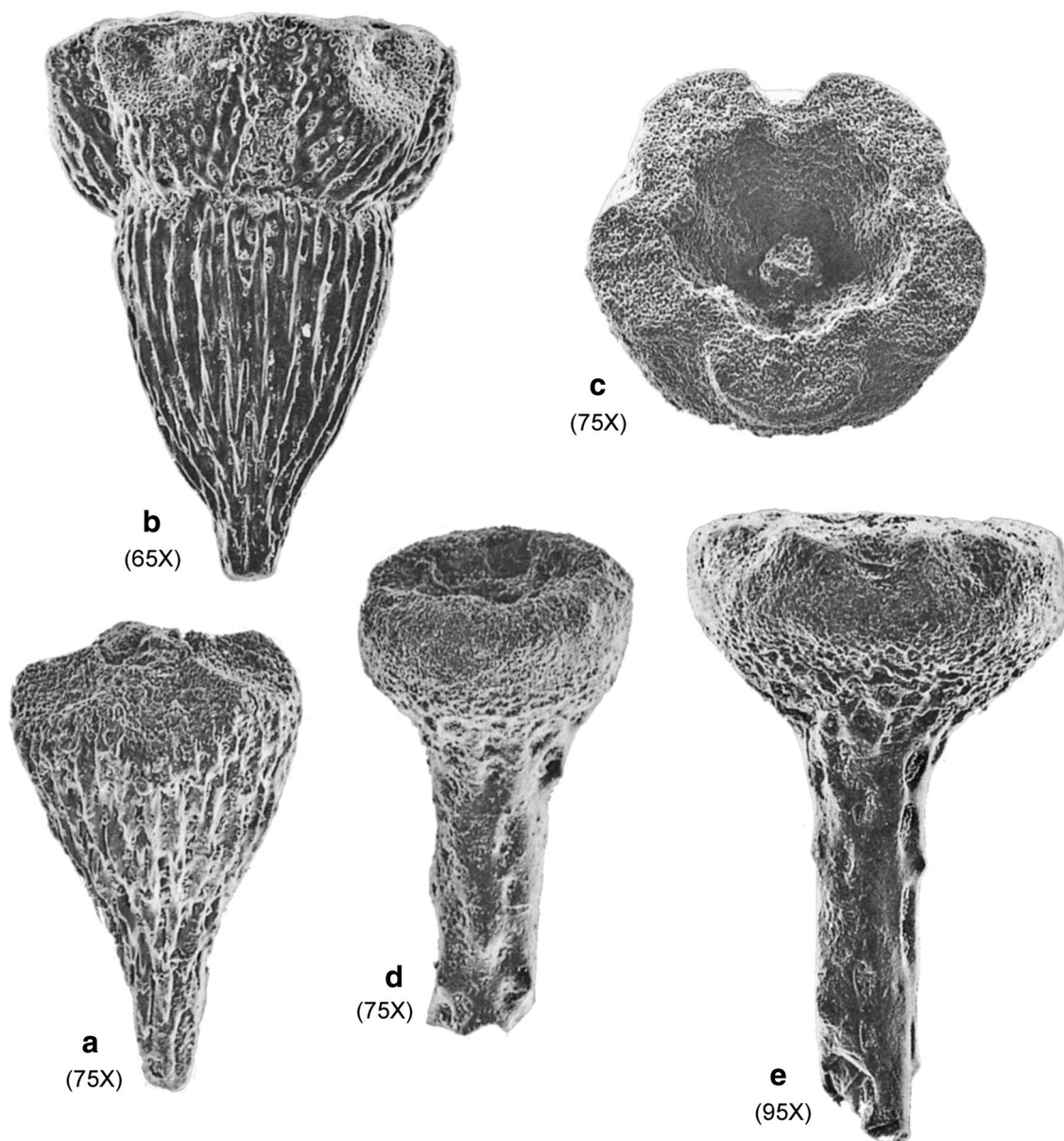
Fig. 5 Remains of *Osteocrinus* species copied from Bizzarini et al. (1989), Lower Carnian Cassian Formation (Julian) of the Dolomite area (exact location not given). **a**, **b** *Osteocrinus virgatus* Kristan-Tollmann; **a** aboral element, **b** radial circlet with attached aboral element. **c–e** *Osteocrinus hessi* Mostler; **c** adoral (*upper*) view of aboral element. **d** Oblique lateral view of partly broken aboral element. **e** Lateral view of partly broken aboral element

isochronous with the *aon* Zone of the western Tethys (Zou et al. 2015).

One largely articulated and several semi-articulated specimens include the aboral element, radial circlet (cup) and part of the arms, but most specimens occur as single elements or brachial pairs. The delicate ossicles are difficult to extract from the bituminous black shale and difficult to clean from sediment particles, making the study of isolated elements by SEM photography unrewarding. This is also true of the ligamentary facets which lack any distinctive character. The best preserved specimens are from

Fig. 6 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, marl- ▶ stone bed, Xiaowa Village. Holotype, MHI 1879/1/2. ae = aboral element; R = radial circlet; IBr1 = first primibrachial; IBr2 = second, axillary primibrachial; IIBr1 first secundibrachial. Note short adoral spine on first primibrachial (*inset*, *arrow*). *Scales* 1 mm

weathered slabs and stand out against the surface due to their pale colour, making them suitable for light microscopy. On some of the slabs the ossicles occur in more than one bedding plane, but only those on weathered surfaces are well enough produced.
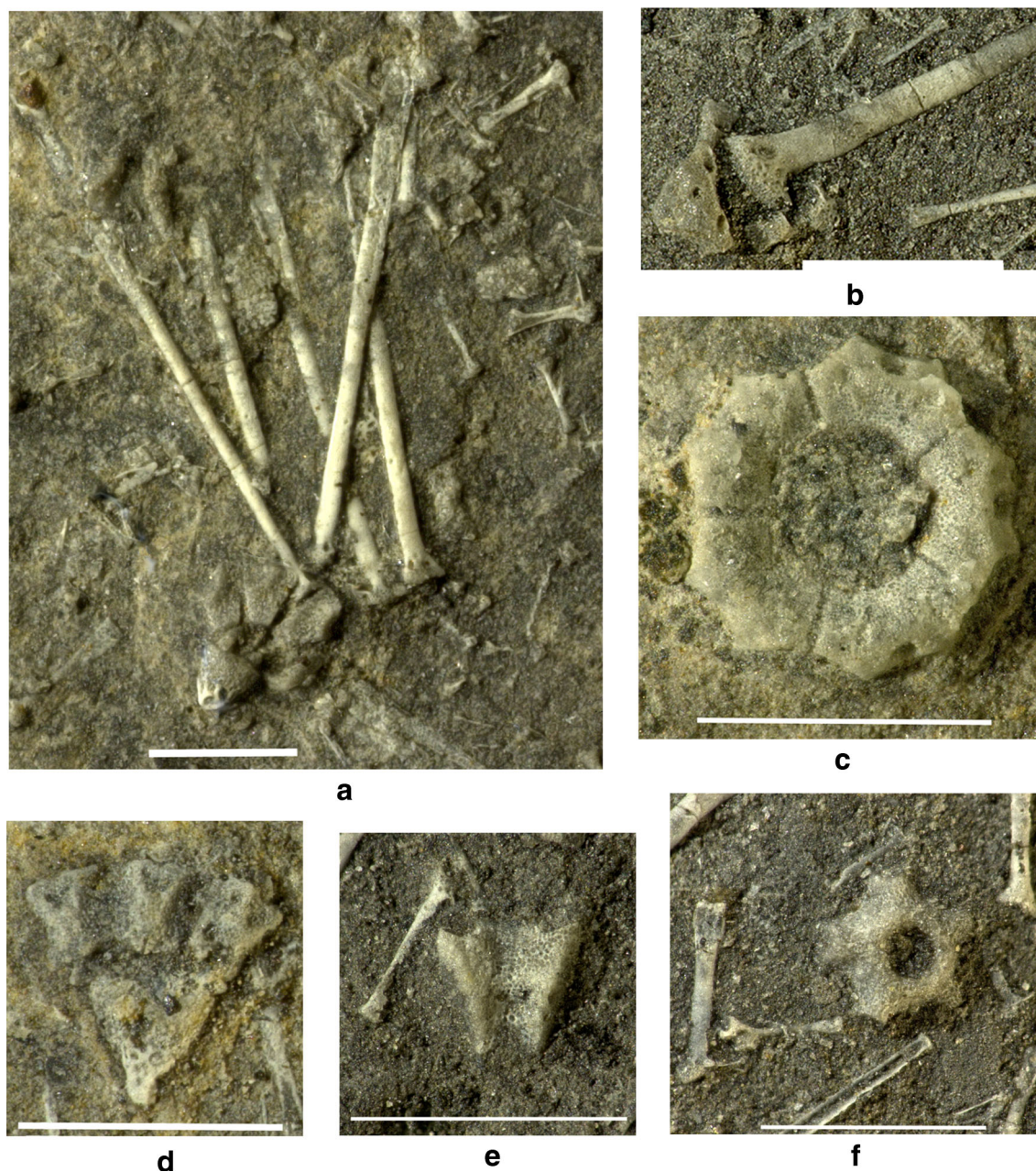
Fig. 7 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, marlstone bed (**a**, **c**), shale (**b**, **d**–**f**) Xiaowa Village. **a** Disarticulated radial circlet with aboral element and first primibrachials, MHI 1879/2/1. **b** Lateral view of aboral element and radial circlet with single first primibrachial, MHI 1879/6/3. **c** Adoral view of radial circlet, paratype, MHI 1879/1/8. **d** Aboral element with three radials, MHI 1879/12/1. **e** Interior view of radial, MHI 1879/7/1. **f** Aboral view of radial circlet, MHI 1879/11/3. *Scales* 1 mm

The photographs of specimens on the slabs were made at the Naturhistorisches Museum Basel using a Keyence VHX 2000 (20-200) digital microscope. The SEM micrographs of isolated crinoid ossicles were made at the Zentrum für Mikroskopie of the University of Basel, using a Philips XL30 ESEM and gold-coated samples ("Basel"), and at the Institute of Palaeontology of the University of Bonn ("Bonn").

Terminology of the *Treatise* (Hess and Messing 2011) and of other publications has been modified in the present paper as follows. The cup is comprised of radials only so that we prefer *radial circlet*. "Theca" (German Theka) was used by Kristan-Tollmann (1970, 1977) for the combination of radial circlet plus aboral element. For the *aboral element* (aboral projection of the *Treatise*) the terms "centrodorsal" (pl. centrodorsalia) were used by Peck

(1948), Kristan-Tollmann (1970, 1977), Kristan-Tollmann in Kristan-Tollmann and Krystyn (1975), Mostler (1972); and "centrale" or "central" (pl. centralia) for the same element by Kristan-Tollmann (1988, 1991), Kristan-Tollmann and Tollmann (1983) and Kristan-Tollmann and Strele (1994). Kristan-Tollmann (1987) also used the term "dorsal spine". The term "centrodorsal" should be avoided to prevent confusion with the cirri-bearing element of comatulids. Dorsal spine (spina dorsale) was used by Bizzarini et al. (1989).

Repository of specimens: MHI = Muschelkalkmuseum Ingelfingen (Germany).

Taphonomy

The skeleton of *Osteocrinus* includes three major types; (1) the radial circlet (cup) comprised of five radials, (2) the aboral element (also called centrodorsal or centrale in the literature, see above) projecting from the radial circlet, and (3) the arms comprised of a seemingly large number of elongate brachials. Of these ossicle types all growth stages are present. More or less intact specimens with aboral element, radial circlet and proximal brachials articulated or closely associated are mostly preserved in lateral posture (Figs. 6, 7a). Mouth up position with brachials arranged radially is less common (Fig. 8e), but isolated radial circlets tend to be preserved in this way (Figs. 7c, 8f). Specimens with the apex of the short aboral element exposed and arms spread radially are exceptional (Fig. 8a); such preservation has been described as starburst up and mouth up by Baumiller et al. (2008). Also rare are specimens with the aboral element in lateral view and the radial circlet in oral view (Fig. 8c, d). The material contains a number of aboral elements of widely different size and length. Most of them are in lateral view; shorter ones may be preserved with their adoral (upper) side exposed. Radial circlets display their adoral (Figs. 7c, 8c–f) or aboral side (Fig. 7f); they are exceptionally preserved in lateral position. Isolated radials are preserved in an aboral (Fig. 15g) or adoral position (Fig. 7e). The bulk of the ossicles on the slabs are elongate, rod-shaped brachials. They are elliptical in cross section and are mostly preserved laterally. Articular facets are only exceptionally exposed. Rather dense aggregations are common, but preferred orientation is exceptional (Fig. 10; see also Wang et al. 2008, fig. 12A). In some cases, major parts of the arms are preserved as ring-like structure (Fig. 11a) or partly open rings. Angles are always between muscular facets, and articulations are opened adorally, characterised by adoral spines. Such preservation is caused by the decay of the adoral muscles leading to ligamentary recoil of the aboral ligament. Many brachials are preserved as straight pairs, still connected at

the ligamentary facets (Figs. 10, 12b). This also indicates that the ligamentary articulations were less prone to decay. During lifetime, the arms were movable only at the muscular facets; thus, half of the articulations were immovable. Both lateral and radial positions of the crown also occur among the huge *Traumatocrinus* colonies that are preserved together with *Osteocrinus* remains (Hagdorn and Wang 2015).

Because the stratigraphic position of the slabs in the quarry section is unknown, it cannot be determined whether the fossils occur on the upper or on the lower side of the slabs. In any case, the irregular distribution and rarity of preferred orientation, the presence of all growth stages, and the variable positions of the aboral elements and radial circlets suggest low deposition rates onto an anoxic bottom. Occasionally, fine-meshed sclerites attributable to a holothurian are preserved (Fig. 8c). The presence of coprolites comprised of *Osteocrinus* ossicles (Figs. 11a, b, 12a) indicates that the crinoids were preyed on in the upper water column, presumably by ammonites of which several species are present. Coprolites are also a common feature of the Tithonian Solnhofen Limestone (Hess 1999, 2015b; Keupp and Schweigert 2015). In comparison with the tiny *O. sinensis* n. sp., *Saccocoma tenella* is a giant. In addition, the Jurassic species is mostly preserved intact and mouth up, with the aboral side of the cup standing out from the underside of the slabs. Arms are commonly curled (Hess and Etter 2011). For this species, mass mortality is assumed in most cases. For *O. sinensis* n. sp. such a scenario is less likely, although a benthic habitat may be excluded in both cases.

Systematic palaeontology

Order Roveacrinida Sieverts-Doreck, 1953

Family Somphocrinidae Peck in Rasmussen (1978)

Genus *Osteocrinus* Kristan-Tollmann, 1970

Osteocrinus sinensis n. sp.

Material

The material is found in two types of lithology: slabs of shaly limestone overlain by one or possibly more thin layers of mudstone (Fig. 13) and in a larger number of fragile mudstones; it is from the latter that some elements were isolated for SEM photographs.

Holotype

Figure 6, MHI 1879/1/2. Xiaowa Village.

Paratypes Fig. 7c, MHI 1879/1/8; Fig. 8c, MHI 1879/1/3; Fig. 9g, MHI 1879/2/2; Fig. 11a, MHI 1879/1/1; Fig. 14c, MHI 1879/11/1. Xiaowa Village.

After the occurrence in Southwest China, the species has not been found in other parts of the Tethys so far.

Type locality and horizon

Xiaowa Village, Lower Xiaowa Formation.

Diagnosis

Small species. Aboral element variable in length, from short conical to long spine like; articulated to radial circlet by simple and thickened rim; fine-meshed near facet to radial circlet, coarsely meshed and becoming smooth distally, hollow. Radial circlet (cup) with protruding radial part which on its upper third has a nearly vertical, shallow aboral ligament fossa; axial canal and circular adoral muscle fossae on upward-directed adoral side. Radial cavity diameter about half of circlet diameter. First primibrachial long, with coarsely meshed proximal end and lateral openings near muscular facet and a pair of short adoral spines, ossicle widening distally in hollow shaft comprised of imperforate stereom and ending in widened part. Second primibrachial with similar length, proximal part widened to match first primibrachial, distal facet of holotype axillary for reception of two secundibrachials, no further arm branching; smaller or juvenile specimens apparently without arm branching; adoral spines present but short. Primibrachials joined by straight or weakly inclined synostosis; no strongly sloping cryptosynarthries throughout arms. Secundibrachials similar in shape to primibrachials except for the presence of a pair of prominent keeled adoral spines projecting from near the lateral openings; other end widened and articulated by slightly inclined or horizontal synostosis to adjoining element. Arms long, with brachials slowly diminishing in length and thickness; comprised throughout of brachial pairs alternatively joined by muscular and ligamentary facets. Brachials elliptical in section, hollow except in most proximal part, without open food grooves; shafts of imperforate material.

Description

Radial circlet

The circlet consists of five radials and is subpentagonal in outline, with protruding radial articular facets (Fig. 7c, f). The circlet is high in adults. Aborally, a central depression with a diameter of about a quarter of circlet diameter and surrounded by a rim connects to the aboral element. The adoral cavity is about half the diameter of the circlet (Fig. 7c); it is connected with the aboral element by a funnel-shaped opening (Fig. 7e). The articular facets of the radials are angularly bent at the transverse ridge. The aboral ligament fossa is vertical and shallow; it is roughly triangular and may cover nearly half the side, a pronounced

Fig. 8 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, limestone bed (**a–d**), shale (**e–f**) Xiaowa Village. **a** Aboral view of juvenile specimen with first primibrachials, short aboral element overlies radial circlet, MHI 1879/1/4. **b** Upper view of aboral element (partly hidden by sediment) and lateral view of small aboral element (upper right), MHI 1879/1/10. **c** Lateral view of aboral element with part of radial circlet exposed in adoral view showing articular facets and four first primibrachials, note holothurian sclerite on the circlet, paratype, MHI 1879/1/3. **d** Partly disarticulated radial circlet with short aboral element and some first primibrachials, MHI 1879/4/4. **e** Adoral view of small radial circlet with attached first primibrachials, MHI 1879/4/4. **f** Adoral view of radial circlet, note muscle fossae (arrows), MHI 1879/6/1. *Scales* 1 mm

pit is lacking (Figs. 7d, 15g). The axial canal and the two circular muscle fossae are situated on the upper, adoral and nearly horizontal side (Figs. 8f, 15h). The interarticular ligament fossae are indistinct. There is no sign of a tegmen.

Aboral element

In the literature, this ossicle has been referred to as centrodorsal that, together with the radial circlet, constitutes the theca (Kristan-Tollmann 1970, 1991; Bizzarini et al. 1989). But the origin of this ossicle is uncertain and we prefer the neutral term aboral element. The aboral elements vary widely in length regardless of the diameter of the uppermost, adoral part (Fig. 9). Because the upper, wide part is fine-meshed on top and coarsely meshed distally in all specimens, (Fig. 9g, i, l), we consider the differences in length to be intraspecific. This distal coarsening of the stereom is observed even in the smallest elements, forming a shallow cup (Fig. 15a, b). The elements grew aborally in long pillars of imperforate stereom surrounding a hollow space that may occur on the side (Fig. 9). Exceedingly long elements were not found articulated to radial circlets (Figs. 6, 7a, b, d, 8a, d, 9k); the longest element in contact with a radial circlet is twice as long as its upper diameter (Fig. 8c). The lack of long elements still attached to the radial circlet may be a taphonomic artefact. The material includes some very small elements (Fig. 15a, b). The shallow cups have a narrow rim; the stereom is finemeshed in the upper part and coarse-meshed toward the aboral apex. Such a structure is maintained during development (Figs. 9, 11a–d). Whether the aboral element resulted from the fusion of basals cannot be ascertained.

Primibrachials and brachials

Morphology of these elements is similar throughout the arms (Figs. 6, 10, 11). In the holotype the second primibrachial is axillary. However, in small specimens such brachials were not found, and axillaries are rare among the isolated ossicles. This suggests that most individuals had five unbranched arms. An articulated arm preserved in the
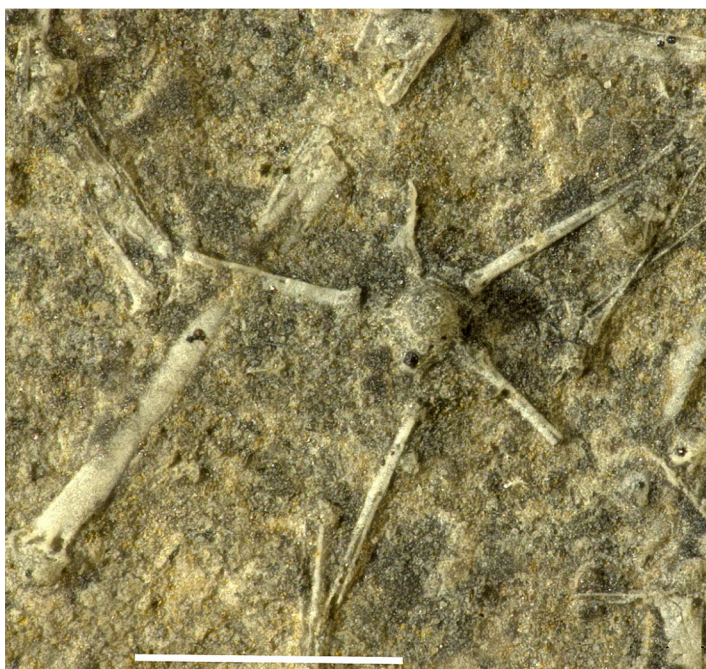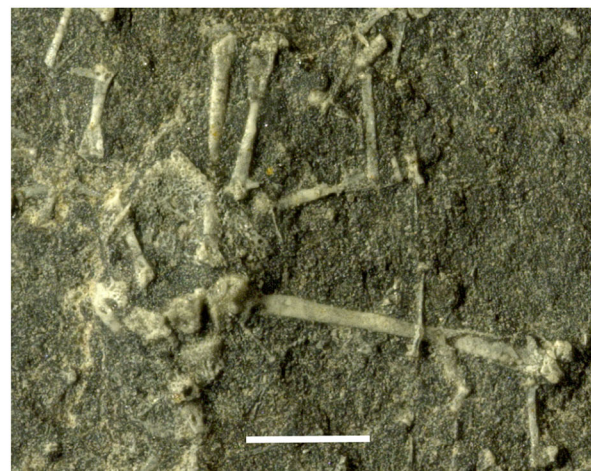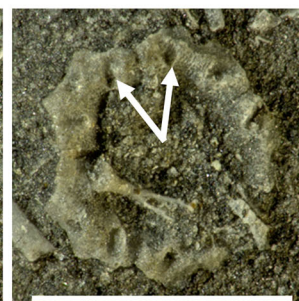
a

b

c

d

e

f

form of a circle (Fig. 11a) consists of 14 brachials that gradually diminish in length and width. Brachials are articulated by either muscular or synostosial facets. Facets are rarely exposed. Muscular facets have an aboral ligament fossa with a distinct pit and a pair of circular muscle fossae (Fig. 16d). Synostosial facets are indistinct (Fig. 15k); they are mostly straight but may be somewhat sloping in shorter brachials (Fig. 16a–c). The primibrachials carry a pair of short adoral spines (Fig. 6). Such spines are much more pronounced distally, reaching a length of three to four times the diameter of the shaft (Figs. 10, 11, 12). The spines are keeled and emanate from the part with the larger lateral openings (Fig. 16). The brachials are hollow through most of their length (Figs. 11b, c, 14c–e), and many brachials resemble crushed egg shells in their widening part extending to the ligamentary facet (Figs. 10, 11, 17). Along most of the shaft the stereom is imperforate (see Smith 1984, fig. 3.2). The shaft near the muscular facet has a pattern of lateral openings (Figs. 15l, 16, 17, 18), presumably to reduce weight or, perhaps, also to provide entry to the interior.

Remarks

The Chinese *Osteocrinus* represents the most complete material of this Triassic genus, and indeed of Somphocrinidae, discovered so far. The genus was proposed by Kristan-Tollmann (1970), and her diagnosis included characters of six species or subspecies, respectively. One of the main differences between the species/subspecies is the length of the aboral element. Short, conical aboral elements are found on specimens with low, wide radials; long and spine-like aboral elements on those with high and slender radials. A number of brachials of the type species, *Osteocrinus rectus rectus* (Frizzell and Exline), were figured by Kristan-Tollmann (1970, fig. 5). The brachials are long and slender; they bear a pair of keeled adoral spines, and the synostosial facets are hardly sloping in this species. However, all of these brachials are solid throughout, and the area near the facets has no openings. In addition, the spines are shorter and thicker than those found in the Chinese material. However, Kristan-Tollmann and Strele (1994, pl. 2, fig. 2) figured a secundibrachial with a long spine, comparable to the Chinese specimens; the find was named *Osteocrinus* sp. and is from the lower Carnian of the northern Calcareous Alps. Strongly sloping cryptosynarthrial facets between the primibrachials were described in another species, *O. spinosus* Kristan-Tollmann (1970, fig. 11), so that this character is not diagnostic of the genus. Kristan-Tollmann (1970, p. 785) mentioned the different articulation types: muscular between radial and first primibrachial, cryptosynarthrial between the two primibrachials, muscular between second primibrachial and first

Fig. 9 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, marl-▶ stone bed (**b–g**, **i**, **k**), shale (**a**, **h**, **j**, **l–m**), Xiaowa Village. The figure shows aboral elements of widely different length, the upper (proximal) part is largely identical. **a**, **c** Small elements with coarsely meshed spine, MHI 1879/9/2 and MHI 1879/4/2. **b** Element with straight furrow on spine, MHI 1879/4/3. **d** Long element showing walls of hollow spine, oblique aboral view of isolated radial at lower left, note secundibrachial with pair of adoral spines at right; MHI 1879/4/1. **e** Long element with coarsely meshed proximal part, pillars of aporous stereom distally broken into fragments; MHI 1879/5/1. **f** Long element with proximal furrow on spine, MHI 1879/3/1. **g** Long element with intact spine showing openings, paratype, MHI 1879/2/2. **h** Short element with coarsely meshed spine; note group of small, partly hollow secundibrachials; MHI 1879/1/7. **i** Compact conical element, MHI 1879/8/3. **j** Oblique adoral view of short element showing partly broken rim to radial circlet, MHI 1879/14/2. **k** Partly articulated specimen with conical aboral element (ae), radial circlet (rc) and first primibrachial (IBr1, at *left*), aboral view of radial circlet (rc) at lower right; MHI 1879/4/5. **l** Longer element with deep furrow on blunt spine, MHI 1879/8/1. **m** Small aboral element and three secundibrachials, MHI 1879/9/2. *Scales* 1 mm

secundibrachial, and so forth. She also mentioned certain differences between the brachials, such as length of the adoral extensions and ornamented ends which resemble that of the radial circlet. Length and ornamentation of the aboral element were considered of special importance for distinguishing species. The number of *Osteocrinus* species was further increased by Mostler (1972), Kristan-Tollmann in Kristan-Tollmann and Krystyn (1975), and Kristan-Tollmann (1991). Mostler's six new species are based on aboral elements only; and the corresponding figures are schematic, as noted by Kristan-Tollmann (1977). According to Kristan-Tollmann (1970, pl. 1) the different forms occur from the late Ladinian to the early Carnian, and regionally from the Alps to southern China and as far as Timor (Kristan-Tollmann 1988). Bizzarini et al. (1989) restricted the "*Osteocrinus* facies" of the Cassian Formation to the Carnian (Julian); according to Laghi and Rechichi (1999) this facies extends into the Ladinian part. According to Donofrio and Mostler (1975) and Kristan-Tollmann (1987) the most abundant species, *Osteocrinus rectus*, ranges stratigraphically from the Ladinian (Longobardian) to the Carnian (end of the Julian). However, Kristan-Tollmann (1988) mentioned that the species occurs from the Anisian to the Rhaetian.

The Chinese *Osteocrinus* material was not assigned to a species by Wang et al. (2008). In contrast, Wang et al. (2007) assigned specimens with short, cone-like aboral elements to *O.* cf. *virgatus* Kristan-Tollmann, and those with long, spine-like elements to *O. spinosus* Kristan-Tollmann. We disagree with the assignment of the Chinese material to two (or more) species because of the nearly identical structure of the different parts of the aboral element. Although the morphology of the Chinese specimens seems closest to *O. rectus* (including both subspecies, *rectus* with long aboral element and *goestlingensis* with a
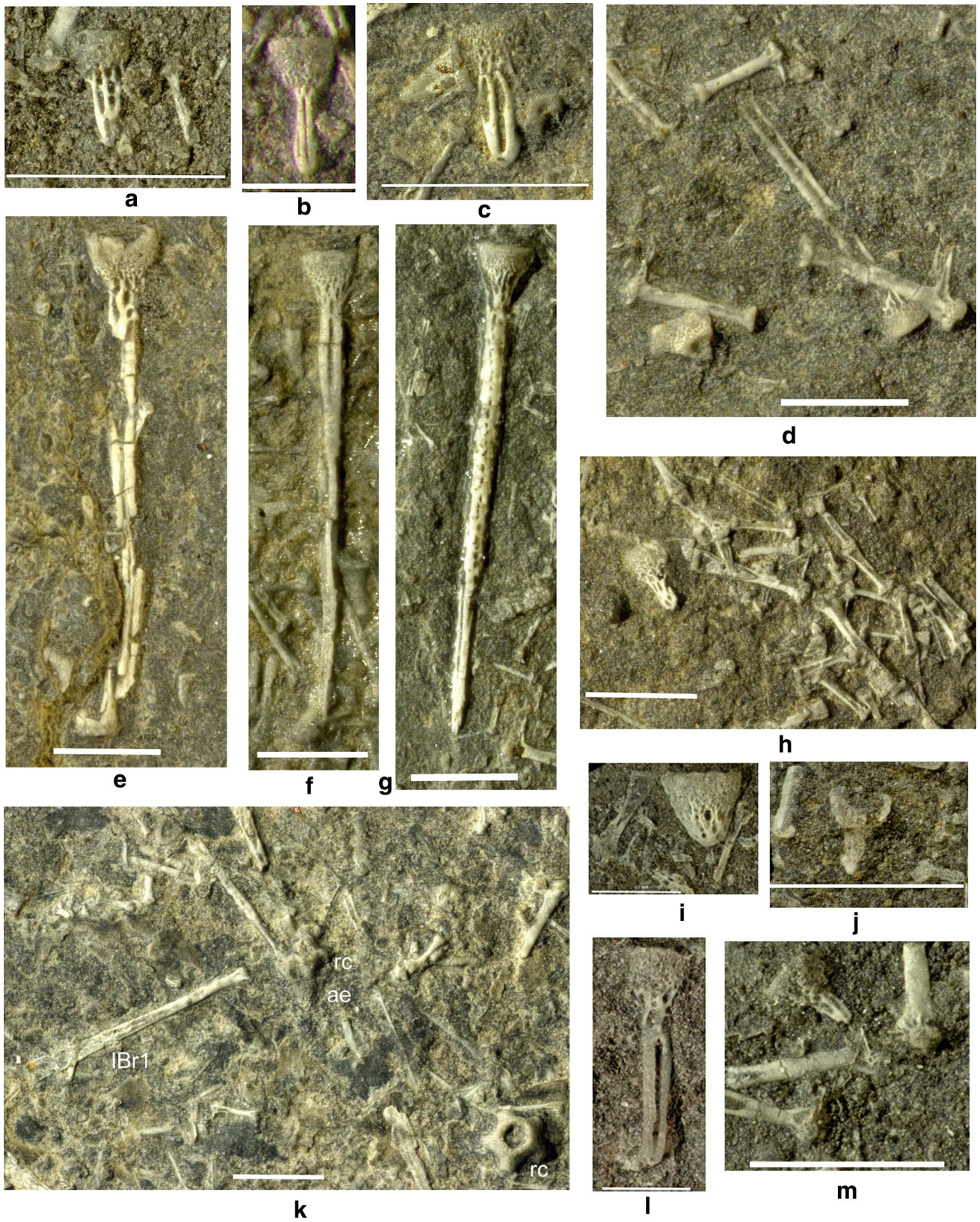
Fig. 10 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, marlstone bed, Xiaowa Village. Group of current-oriented secundibrachials and first primibrachial (at left), MHI 1879/13/1. *Scale* 1 mm

short element), it is a well-defined species of its own. Distinct features of *O. sinensis* n. sp. are the hollow brachials with openings near the muscular facet and the skeletal structure of the aboral element, be it short or long. The material suggests that mere length of aboral elements is not a suitable diagnostic feature for all species. However, ornamentation—if consistent—seems suitable for distinguishing different species (see section "Overview of *Osteocrinus* species"). Incidentally, the Late Triassic *Somphocrinus mexicanus* Peck also has aboral elements of different length (Peck 1948; pl. 20, figs. 12, 13, 15).

Ecology and functional morphology

The roveacrinids occur on several bedding planes of the black shales and are best seen when weathered out. Other fossils on the bedding planes containing the crinoids are rare. Bedding planes *without* crinoids may be covered with remains of halobiids and, less commonly, ammonoids. In the preferred taphonomic hypothesis of Wang et al. (2008) the marine reptiles, the halobiid bivalves and the

ammonoids inhabited poorly oxygenated surface waters over stagnant oxygen-deficient bottom water enriched in H_2S. Yet the majority of bivalve experts consider *Halobia* together with other thin-shelled black-shale bivalves as fully benthic (see McRoberts 2010 and references therein). Accumulations of *Halobia* shells would represent intermittent weak oxygenation episodes and colonisation of the seafloor by this opportunistic bivalve. Oxygen-depleted to fully anoxic/sulfidic conditions nevertheless persisted in one or more large depressions at the margin of the drowned Yangtze Platform (Wang et al. 2008, p. 57). Such a situation would also explain the apparently endemic nature of *O. sinensis* n. sp. The *Traumatocrinus* colonies attached to driftwood may have either lived in the region or drifted in. Where did *Osteocrinus* live and how did the remains reach the bottom? More or less intact specimens embedded with aboral element, radial circlet and proximal part of the crown and also partly articulated brachials suggest that *Osteocrinus* lived in the water column above and were not transported as far as driftwood might be. This is supported by coprolites largely comprised of broken *Osteocrinus* ossicles (Fig. 12a). The common occurrence of coprolites

Fig. 11 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, limestone bed, Xiaowa Village. **a** Ring of articulated secundibrachials with articulations, paratype; note coprolite at lower right, MHI 1879/1/1. **b** Secundibrachial with two adoral spines near lower facet, note corroded upper part exposing interior and coprolite to the left; MHI 1879/14/1. **c** Secundibrachial and conical aboral element (lower left), MHI 1879/4/7. *Scales* 1 mm

(*Lumbricaria*) comprised entirely of remains of *Saccocoma tenella* on the same bedding planes as the crinoids is convincing evidence that *Saccocoma* was preyed on in the upper, oxygenated water layers of the Late Jurassic Plattenkalk basins (Hess 2010, 2015b; Hess and Etter 2011). In this case, the predators are assumed to have been teuthoid

Fig. 12 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, marlstone bed, Xiaowa Village. **a** Coprolite comprised of *Osteocrinus* remains, MHI 1879/1/6. **b** Three articulated secundibrachials with collapsed shaft near synostosial facet, small secundibrachials from distal parts of the arms; MHI 1879/1/11. *Scales* 1 mm

cephalopods and ammonites (Schweigert and Dietl 1999). Ammonites are also assumed to have preyed on *Osteocrinus*. The *Osteocrinus* occurrence in the Triassic black shales of Southwest China and that of *Saccocoma* in the Jurassic Plattenkalk basins are the only occurrences with preservation of partly articulated or intact specimens belonging to a single species. In the Plattenkalk facies *Saccocoma tenella* commonly accumulated after mass mortality on sediment surfaces with microbial mats.

Subsequent rapid sedimentation of calcareous mud embedded the intact animals on the lower side of the overlying limestone bed (Hess 2015b). Such bedding obviously did not occur in the case of *Osteocrinus sinensis* n. sp., as documented by the more or less disarticulated specimens. At other localities several species of Roveacrinida commonly occur in great profusion. However, in those occurrences, specimens are generally disarticulated (Peck 1943), and partly articulated specimens are rare
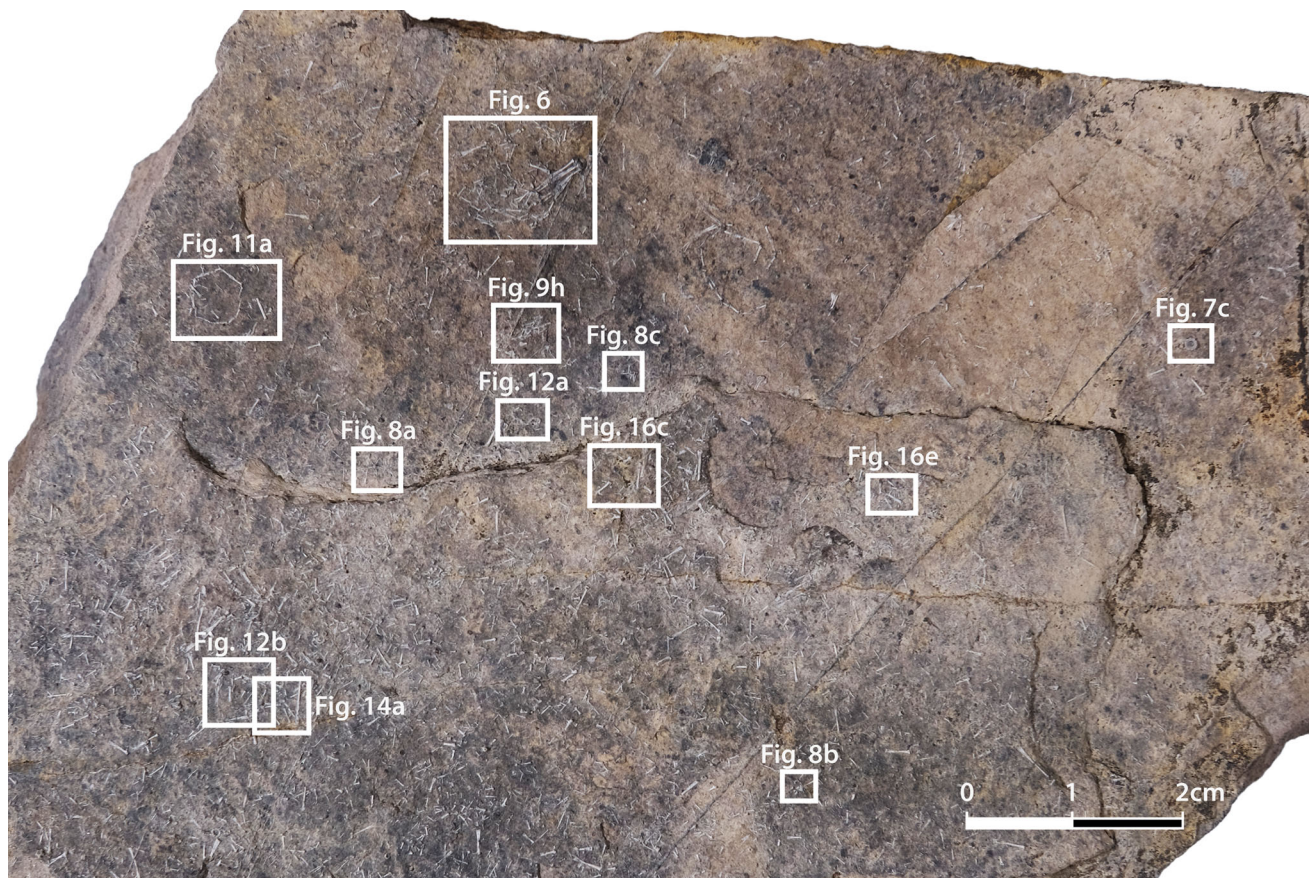
Fig. 13 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation. Partial view of marlstone slab with holotype (see Fig. 6). Numbers refer to figures

(Scott et al. 1977; Hess 2015a). These examples indicate life in oxygenated water above bioturbated bottoms.

Osteocrinus sinensis n. sp. is characterised by a small radial circlet bearing disproportionally long arms comprised of long brachials (Fig. 19). The radial circlet lacks any sign of an oral region covering the vital parts; such is also the case in other well-preserved Roveacrinida, e.g., *Saccocoma tenella* (Hess 2010, 2015b). The brachials are paired, with muscular articulations and synostoses alternating in regular fashion. Strongly sloping cryptosynarthries, as present in the Triassic *Osteocrinus spinosus*, the Axicrinidae, *Somphocrinus*, in the Jurassic Saccocomidae and the Cretaceous Roveacrinidae are absent; ligamentary articulations seem to be simple synostosial and are only slightly sloping. A distinct axial canal occurs only at the muscular facets which are thickened in a coarse-meshed end. Toward the other end with the ligamentary facet, the shaft is widened and commonly crushed on the slabs, indicating that it is hollow. The remains of all other *Osteocrinus* species were obtained from limestones by acid preparation (Mostler 1972; Kristan-

Tollmann and Krystyn 1975), or from marly sediments (Kristan-Tollmann 1987; Bizzarini et al. 1989), and one might argue that recrystallization filled any hollow space of the brachials in these occurrences. However, thin sections of limestone samples (Kristan-Tollmann 1970) and well-preserved specimens from marls indicate that this was not the case (see also Hess 2015a for the equally long and solid brachials of *Roveacrinus pyramidalis* Peck). The brachials of *Osteocrinus sinensis* n. sp. have a pair of adoral spines near the muscular facet, possibly a deterrent against predators. Brachial pairs still connected at the synostosial facets are rather common. Food grooves are not observed on brachials, making the uptake of food conjectural in the absence of a modern analogue. Prey capture by means of the arms, similar to the extant basket stars (see Stöhr et al. 2012) may be excluded because of the multitude of synostosial articulations and the long brachials, rendering the arm too stiff for curling and raptorial feeding.

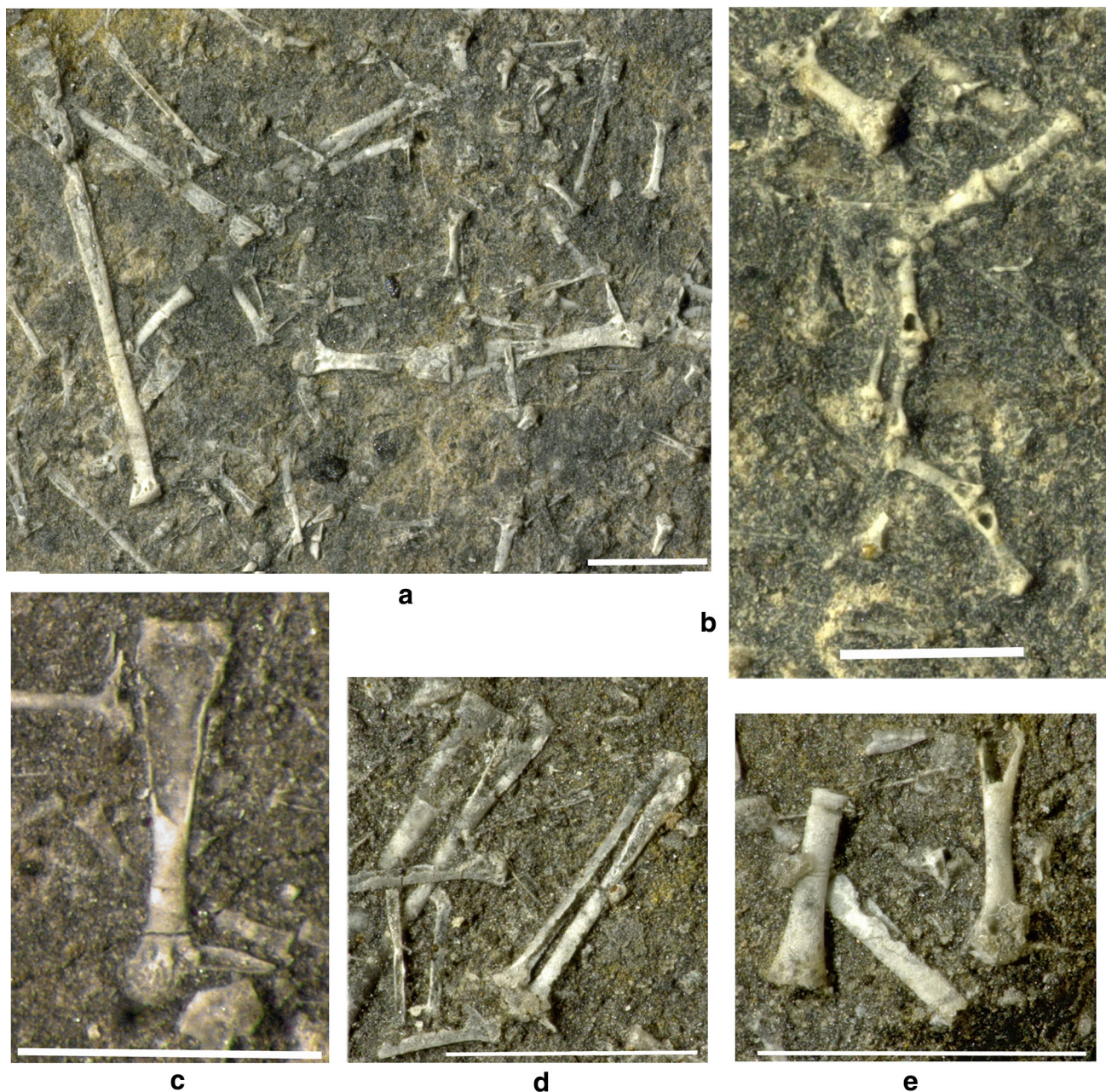One might speculate that nutrients of some kind could have entered the brachials via the openings near the

Fig. 14 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, marlstone bed (**a**, **b**, **d**, **e**), shale (**c**), Xiaowa Village. Partly weathered secundibrachials with hollow shafts (**a**–**e**) from different parts of the arms. **a** Secundibrachials and long first primibrachial with collapsed and partly weathered upper (distal) part at left, the proximal part of the primibrachial lacks adoral spines; MHI 1879/1/13. **b** Group of articulated secundibrachials with opening near the synostosial facet, MHI 1879/4/8. **c** Secundibrachial with thin wall below the straight synostosial facet, paratype, MHI 1879/11/1. **d** Juvenile or distal secundibrachials at lower left and pair of longer narrow secundibrachials at right, one of them with a hollow space extending from near the muscular facet at the bottom to the upper end, the other with collapsed upper part; MHI 1879/11/2. **e**. Three secundibrachials, two of them with damaged shaft; MHI 1879/9/1. *Scales* 1 mm

muscular facets (Fig. 15l). In contrast, the hollow part with its imperforate shell resembling a test tube might have harboured microorganisms or nannoplankton serving as nutrients. How these would have reached the mouth is enigmatic unless one assumes that they passed along the axial canal. Getting rid of the residues of digested calcareous nannoplankton would also be difficult to explain. At the present time there are no data available to test among these various hypotheses. An alternative and perhaps the most parsimonious explanation is that the animals
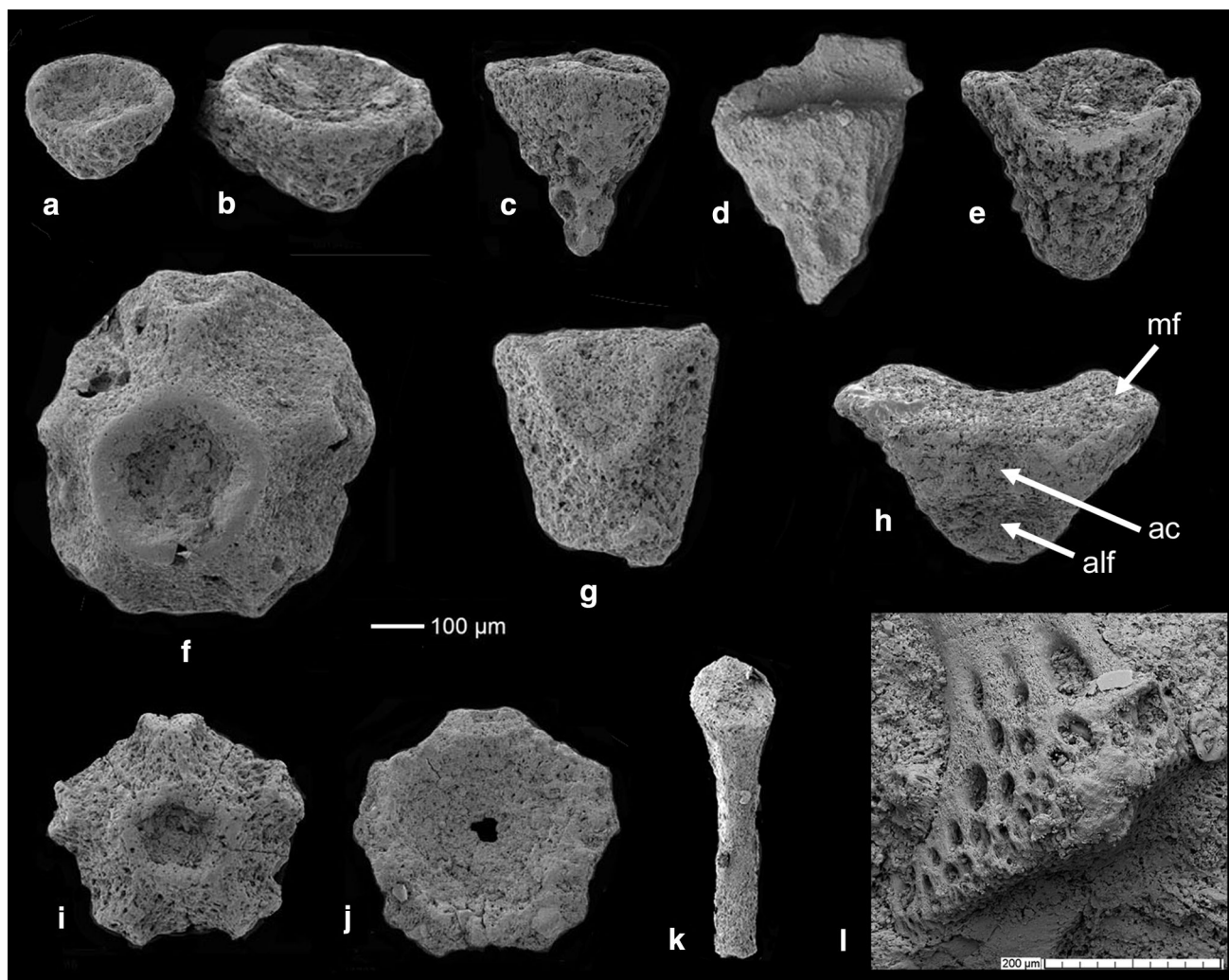
Fig. 15 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, Xiaowa Village (inventory number 1879) and Wolonggong (inventory number 2137). Elements isolated from shales. **a–e** Aboral elements of juvenile individuals; **a**, **b** oblique adoral (upper) view, MHI 1879/15/1, MHI 1879/15/2; **c–e** lateral view (rim partly broken in **e**), MHI 1879/15/3, MHI 2137/5/1, and MHI 1879/15/5. **f** Aboral view of radial circlet with facet to aboral element, MHI 1879/15/6. **g** Aboral (exterior) view of radial, MHI 1879/15/7. **h** Radial articular facet (*mf* muscle fossa, *ac* axial canal, *alf* aboral ligament fossa), MHI 1879/15/8. **i** Aboral view of small radial circlet, MHI 1879/15/9. **j** Adoral view of small radial circlet, 1879/15/10. **k** Synostosial facet of small secundibrachial, MHI 1879/15/11. **l** Coarsely meshed stereom and lateral openings of first primibrachial near proximal facet, MHI 2137/3/1. SEM photographs: **a–c**, **e–k**, Basel; **d**, **l**, Bonn

possessed food grooves, but that these left no visible impression on the ossicles. The radial circlet carries an aboral element whose length varies widely. Such variability in the same population is surprising. The role of the aboral element in the different *Osteocrinus* species has not been discussed in the literature. However, it is reasonable to assume that it may have kept the floating animal in a mouth up position and stabilised it in agitated water. Longer elements may also have served as deterrents to predators, perhaps similar to the adoral spines on the brachials. All these characters suggest that the animals were not active swimmers but rather floated most of the time.

Conclusions

The morphology of *Osteocrinus sinensis* n. sp. is unique among the pelagic Triassic Roveacrinida. This suggests that the species adapted to rather special local conditions and, thus, was endemic. It is tempting to explain the unusual morphology of *O. sinensis* as an adaptation to extreme environmental conditions. Yet the early Carnian was relatively cool and arid (Mueller et al. 2016a, b), and atmospheric oxygen values were higher than during the Early Jurassic (Berner et al. 2007). The almost lethal conditions with ocean surface temperatures of 40° C, extremely high
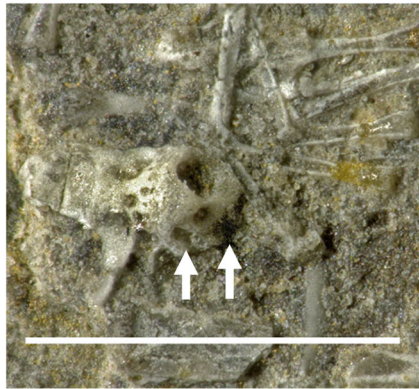
◀ **Fig. 16** *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, Xiaowa Village. Marlstone bed (**a**, **c–f**), shale (**b**). **a–c**, **e–f** Secundibrachials with mostly well-developed adoral spines near the spongy area at the muscular facet, MHI 1879/2/4, MHI 1879/6/4, MHI 1879/1/12, MHI 1879/1/9, MHI 1879/5/3; in **b** the two adoral spines are visible, MHI 1879/6/4. **d** Muscular articular facet of secundibrachial, arrows indicate muscle fossae below axial canal and large aboral ligament fossa, the adoral spines are also visible; MHI 1879/4/6. *Scales* 1 mm

atmospheric CO_2 and very low O_2 values that characterised the Triassic according to Ward and Kirschvink (2015) prevailed only during the Early Triassic (Preto et al. 2010; Winguth et al. 2015). A later environmental perturbation known as the Carnian Humid or Pluvial Phase (Mueller et al. 2016a, b) clearly postdates the occurrence of *O. sinensis* and of the spectacular, large pseudoplanktonic *Traumatocrinus* (Hagdorn and Wang 2015). Both *O. sinensis* and *Traumatocrinus* are derived from Ladinian ancestors without special adaptations. In the pseudo-planktonic *Traumatocrinus* the column is porous and by its flexibility plankton-rich layers could be reached. The crown has an extraordinarily dense pinnulation, optimised for plankton collection; and all muscular articulations were replaced by a special type of ligamentary articulation. *Traumatocrinus* was a passive floater making use of drift-wood. *O. sinensis* n. sp. must also have floated passively.

Fig. 17 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, Wolonggong. Brachials on a slab, MHI 2137/3/2. Note the different facets, one compact with coarsely meshed stereom (at right), the other fine-meshed near the facet (at left); the ossicles are collapsed at about half their length. Away from the facets the stereom is imperforate. The very short adoral spines suggest that the ossicles may be primibrachials. SEM photograph Bonn. *Scale* 1 mm
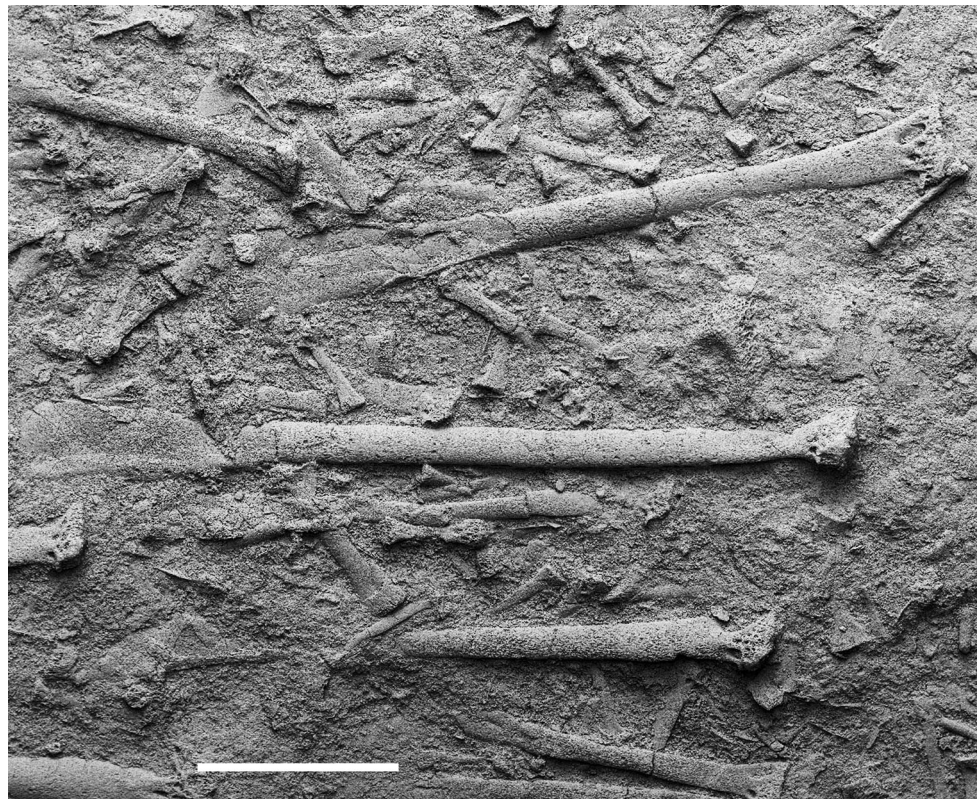
Fig. 18 *Osteocrinus sinensis* n. sp., Lower Xiaowa Formation, Wolonggong. Two short secundibrachials from median arm region articulated by synostosis, the upper is broken near the muscular facet, note adoral spine on the secundibrachial at the top; MHI 2137/2/1. SEM photograph Bonn
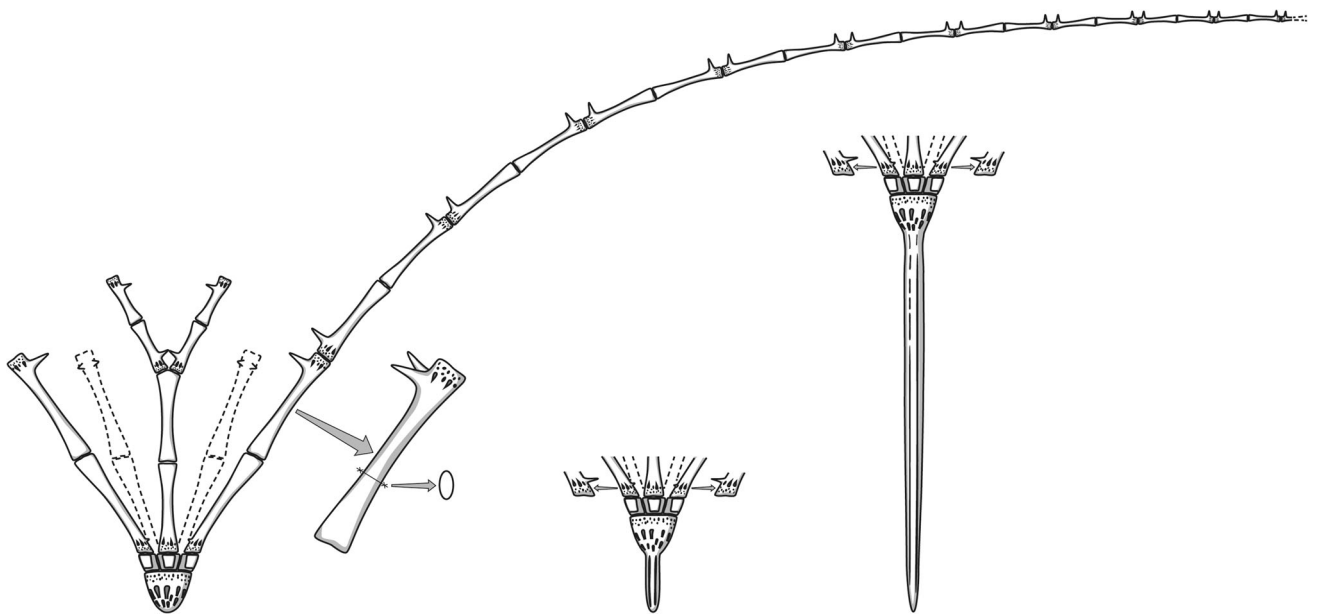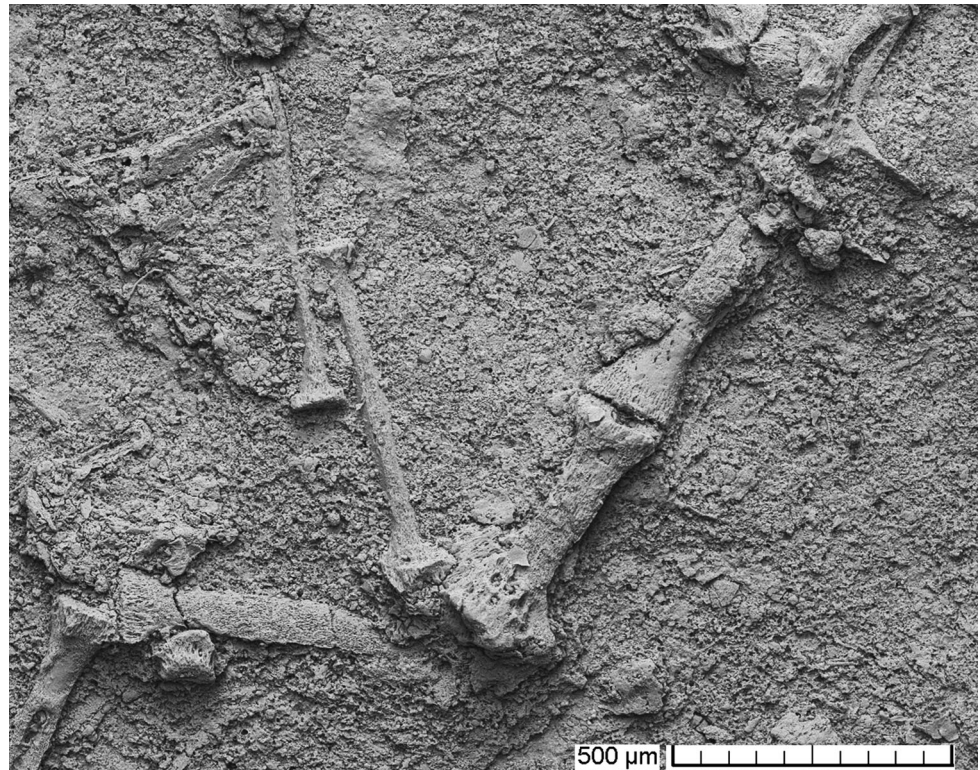

Fig. 19 Schematic reconstruction of *O. sinensis* n. sp. with three aboral elements of different length. The brachials are drawn in side view as they occur on the slabs, with only one of the pair of adoral spines visible in most cases. The main figure is drawn after the holotype (Fig. 6), with arms branching at the second primibrachial

Changing conditions in the Tethys at the end of the Julian stage seem to be responsible for the disappearance of both *Traumatocrinus* and most *Osteocrinus* species.

References

Baumiller, T., Gahn, F. J., Hess, H. & Messing, C. G. (2008). Taphonomy as an indicator of behavior among fossil crinoids. In Ausich, W. I., & Webster, G. (Ed.), *Echinoderm paleobiology* (pp. 7–20) Bloomington: Indiana University Press.

Berner, R. A., VandenBrooks, J. M., & Ward, P. D. (2007). Oxygen and evolution. *Science, 316,* 557–558.

Bizzarini, F., Laghi, G. F., Nicosia, U., & Russo, F. (1989). Distribuzione stratigraphica dei microcrinoidi (Echinodermata) nella formazione di S. Cassiano (Triassico superiore, Dolomiti): Studio preliminare. *Atti della Società dei Naturalisti e Matematici di Modena, 120,* 1–12.

Bown, P. R., Lees, J. A., & Young, J. R. (2004). Calcareous nannoplankton evolution and diversity through time. In H. R. Thierstein & J. R. Young (Eds.), *Coccolithophores—From molecular process to global impact* (pp. 481–508). Berlin: Springer.

Donofrio, D. A., & Mostler, H. (1975). Neue Schwebcrinoiden aus Hallstätter Kalken des Berchtesgadener Raumes. *Geologisch-Paläontologische Mitteilungen Innsbruck, 5,* 1–28.

Gaetani, M. (2009). GSSP of the Carnian stage defined. *Albertiana, 37,* 36–38.

Hagdorn, H. (2011). The Triassic—Crucial period of post-Palaeozoic crinoid diversification. *Swiss Journal of Palaeontology, 130,* 91–112.

Hagdorn, H., & Wang, X. (2015). The pseudoplanktonic crinoid *Traumatocrinus* from the Late Triassic of Southwest China—Morphology, ontogeny, taphonomy. *Palaeoworld, 24*(4), 479–496.

Hess, H. (1999). Upper Jurassic Solnhofen Plattenkalk of Bavaria, Germany. In H. Hess, W. I. Ausich, C. E. Brett, & M. J. Simms (Eds.), *Fossil crinoids* (pp. 214–224). Cambridge: Cambridge University Press.

Hess, H. (2002). Remains of Saccocomids (Crinoidea: Echinodermata) from the Upper Jurassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde, Serie B (Geologie und Paläontologie), 329,* 57.

Hess, H. (2010). *Paleoecology of pelagic crinoids.* Treatise Online No. 16, 33 pp.

Hess, H. (2015a). Roveacrinids (Crinoidea) from the mid-Cretaceous of Texas: Ontogeny, phylogeny, functional morphology and lifestyle. *Swiss Journal of Palaeontology, 134,* 77–107.

Hess, H. (2015b). Stachelhäuter, Seelilien. In G. Arratia, H.-P. Schultze, H. Tischlinger, & G. Viohl (Eds.), *Solnhofen, Ein Fenster in die Jurazeit* (pp. 299–307). München: Verlag Dr. Friedrich Pfeil.

Hess, H., & Etter, W. (2011). Life and death of *Saccocoma tenella* (Goldfuss). *Swiss Journal of Geosciences, 104*(Supplement 1), S99–S106.

Hess, H., & Messing, C. G. (2011). Treatise on Invertebrate Paleontology, Part T. In Ausich, W. I. (Ed.) *Echinodermata 2, Revised, Crinoidea* Vol. 3, 261 pp. The University of Kansas Paleontological Institute, Lawrence, Kansas.

Keupp, H., & Schweigert, G. (2015). Kopffüsser (Cephalopoda). In G. Arratia, H.-P. Schultze, H. Tischlinger, & G. Viohl (Eds.), *Solnhofen, Ein Fenster in die Jurazeit* (pp. 210–228). München: Verlag Dr. Friedrich Pfeil.

Kozur, H., & Mostler, H. (1971). Holothurien-Sklerite und Conodonten aus der Mittel- und Obertrias von Köveskal (Balatonhochland, Ungarn). *Geologisch-Paläontologische Mitteilungen Innsbruck, 1,* 1–36.

Kristan-Tollmann, E. (1970). Die Osteocrinusfazies, ein Leithorizont von Schwebcrinoiden im Oberladin—Unterkarn der Tethys. *Erdöl und Kohle, Erdgas, Petrochemie, 23,* 781–789.

Kristan-Tollmann, E. (1977). Zur Gattungsunterscheidung und Rekonstruktion der triadischen Schwebcrinoiden. *Paläontologische Zeitschrift, 51,* 185–198.

Kristan-Tollmann, E. (1987). Triassic of the Tethys and its relation with the Triassic of the Pacific Realm. In K. G. Mc Kenzie (Ed.), *Shallow Tethys 2* (pp. 169–186). Rotterdam: Balkema.

Kristan-Tollmann, E. (1988). Unexpected communities among the crinoids within the Triassic Tethys and Panthalassa. In R. D. Burke (Ed.), *Echinoderm Biology* (pp. 133–142). Rotterdam: Balkema.

Kristan-Tollmann, E. (1991). Echinoderms from the Middle Triassic Sina Formation (Aghdarband Group) in NE Iran. *Abhandlungen der geologischen Bundesanstalt Wien, 38,* 175–194.

Kristan-Tollmann, E., & Krystyn, L. (1975). Die Mikrofauna der ladinisch-karnischen Hallstätter Kalke von Saklibeli (Taurus-Gebirge, Türkei) I. Sitzungsberichte der Österr. Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse. *Abt I, 184,* 259–340.

Kristan-Tollmann, E., & Strele, K. (1994). *Die Crinoiden-Vergesellschaftung der unterkarnischen Münztaler Schichten der Mürzschlucht bei Frein (Steiermark, Österreich).* Jubiläumsschrift 20 Jahre Geologische Zusammenarbeit Österreich-Ungarn, 2, pp. 329–342. ISBN3-900312-92-3.

Kristan-Tollmann, E., & Tollmann, A. (1983). Überregionale Züge der Tethys in Schichtfolge und Fauna am Beispiel der Trias zwischen Europa und Fernost, speziell China. Schriftenreihen der Erdwissenschaftlichen Kommissionen, 5, pp. 177–230; Veröffentlichungen des Österreichischen Nationalkomitees für das International Geological Correlation Programme Project Nr. 73/I/4 (Triassic of the Tethys Realm).

Laghi, G. F., & Rechichi, M. (1999). Microcrinoids and holothurian sclerites. In Broglio Loriga, C., Cirilli, S., de Zanche, V., di Bari, D., Gianolla, P., Laghi, G. F., Lowrie, W., Manfrin, S., Mastandrea, A., Mietto, P., Muttoni, G., Neri, C., Posento, R., Rechichi, M., Rettori, R., & Roghi, G. (Eds.), *The Prati di Stuores/Stuores Wiesen Section (Dolomites, Italy): a candidate Global Stratotype Section and Point for the base of the Carnian stage.* Rivista Italiana di Paleontologia e Stratigrafia, 105, 61–63.

McRoberts, C. A. (2010). Biochronology of Triassic bivalves. In Lucas, S. G. (Ed.), *The Triassic Timescale* (pp. 201–219). Geological Society, London, Special Publications 334.

Mostler, H. (1972). Die stratigraphische Bedeutung von Crinoiden-, Echiniden- und Ophiuren-Skelettelementen in triassischen

Karbonatgesteinen. *Mitteilungen der Gesellschaft für Geologie- und Bergbaustudien in Österreich, 21*, 711–728.

Mueller, S., Hounslow, M. S., & Kürschner, W. M. (2016a). Integrated stratigraphy and palaeoclimate history of the Carnian Pluvial Event in the Boreal realm; new data from the Upper Triassic Kapp Toscana Group in Spitsbergen (Norway). *Journal of the Geological Society, 173*, 186–201.

Mueller, S., Krystyn, L., & Kürschner, W. M. (2016b). Climate variability during the Carnian pluvial phase—A quantitative palynological study of the Carnian sedimentary succession at Lunz am See, Northern Calcareous Alps, Austria. *Palaeogeography, Palaeoclimatology, Palaeoecology, 441*, 198–211.

Oravecz-Scheffer, A. (1979). Pelagikus crinoidea maradványok a dunántúli Triász képzödményekböl.—Földtani Közlöny. *Bulletin of the Hungarian Geological Survey, 109*, 75–100.

Peck, R. E. (1943). Lower Cretaceous crinoids from Texas. *Journal of Paleontoogy, 17*, 451–475.

Peck, R. E. (1948). A Triassic crinoid from Mexico. *Journal of Paleontology, 22*, 81–84.

Preto, N., Kustatscher, E., & Wignall, P. B. (2010). Triassic climates—State of the art and perspectives. *Palaeogeography, Palaeoclimatology, Palaeoecology, 290*, 1–10.

Rasmussen, H. W. (1978). Articulata. In R. C. Moore & C. Teichert (Eds.), *Treatise on invertebrate paleontology. Pt. T, Echinodermata 2*, Vol. 3, pp. T813–T928. Geological Society of America and University of Kansas Press.

Salamon, M., Gorzelak, P., Hanken, N.-M., Riise, H. E., & Ferré, B. (2015). Crinoids from Svalbard in the aftermath of the end-Permian mass extinction. *Polish Polar Research, 36*, 225–238.

Schweigert, G., & Dietl, G. (1999). Zur Erhaltung und Einbettung von Ammoniten im Nusplinger Plattenkalk (Oberjura, Südwestdeutschland). *Stuttgarter Beiträge zur Naturkunde, Serie B, 272*, 1–31.

Scott, R. W., Root, S. A., Tenery, J. H., & Nestell, M. (1977). Morphology of the cretaceous microcrinoid *Poecilocrinus* (Roveacrinidae). *Journal of Paleontology, 51*, 343–349.

Simms, M. J. (1990). Crinoid diversity and the Triassic/Jurassic Boundary. *Cahiers de l'Université Catholique de Lyon, Série Sciences, 3*, 67–77.

Smith, A. (1984). *Echinoid palaeobiology*. London: George Allen & Unwin.

Stöhr, S., O'Hara, T. D. & Thuy, B. (2012). Global diversity of brittle stars (Echinodermata, Ophiuroidea). *PLoS One, 7*(3), 1–14, e31940.

Wang, X., Bachmann, G. H., Hagdorn, H., Sander, P. M., Cuny, G., Chen, X., et al. (2008). The Late Triassic black shales of the Guanling Area (Guizhou Province, Southwestern China)—A Unique Marine Reptile and Pelagic Crinoid Fossil Lagerstätte. *Palaeontology, 51*, 27–61.

Wang, C., Wang, X., Hagdorn, H., Chen, X., & Chen, L. (2007). The first discovery of Triassic roveacrinids in China and its significance. *Acta Palaeontologica Sinica, 46*, 334–339. **(In Chinese with English Abstract.)**.

Ward, P., & Kirschvink, J. (2015). *A new history of life*. London: Bloomsbury.

Winguth, A. M. E., Shields, C. A., & Winguth, C. (2015). Transition into a Hothouse World at the Permian-Triassic boundary—A model study. *Palaeogeography, Palaeoclimatology, Palaeoecology, 440*, 316–327.

Zou, X., Balini, M., Jiang, D., Tintori, A., Zuo, Y., & Sun, Y. (2015). Ammonoids from the Zhuganpo Member of the Falang Formation at Nimaigu and their relevance for dating the Xingyi Fossil Lagerstätte (Late Ladinian, Guizhou, China). *Rivista Italiana di Paleontologia e Stratigraphia, 121*, 35–161.