

## Permian

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### PALAEOZOIC TWILIGHT

The Permian crinoids are the last to represent all four Palaeozoic subclasses – the Camerata, Flexibilia, Disparida and Cladida (see Simms & Sevastopulo 1993). With the extinction of 30 families, the Camerata, Flexibilia and Disparida disappeared altogether at or near the end of the Permian in the greatest extinction of all time. This crisis, 245 million years ago, nearly wiped out the crinoids as a whole (Figs. 3 and 61), but, fortunately, some survived to form in the Triassic the stem group of the articulate. Compared with older Palaeozoic systems, crinoids were fairly rare throughout most of the Permian, and assemblages, as described elsewhere in this book, are exceptional. However, because the Permian was a critical time in crinoid existence and evolution, a brief chapter on Permian crinoids is justified.

### CLASSIC CRINOID SITES IN TIMOR AND AUSTRALIA

Until World War Two, the most diverse and abundant Permian crinoid fauna known was the one from the Island of Timor in Indonesia. It was discovered, exploited and described by Johannes Wanner in a series of outstanding papers during the first half of the twentieth century. In one of his later monographs Wanner (1937) listed 320 species belonging to 100 genera, most of them

new and unique to Timor. The total fauna includes other echinoderms (echinoids and blastoids) as well as gastropods, bivalves, brachiopods and corals. On the basis of the massive skeleton of many of the forms, Wanner concluded that the animals lived in a warm, shallow and partly agitated sea. Their mode of preservation indicates a certain amount of transport before burial. The Timor crinoids, usually isolated cups, have a large variety of cladids and flexibles, but disparids and camerates are rare. Stem fragments of more than 10 mm diameter are common, whereas the cups, on which most species are based, show much smaller attachments for the stem. These cups are generally quite small, with a diameter of 1 or 2 cm, at the most. In addition, many of the Timor cladids exhibit evolutionary features that demonstrate a trend toward simplification of an earlier, more complex structure (Lane & Webster 1966). The suppression of one or two arms (*Indocrinus*, *Sundacrinus*, *Tibrachyocrinus*) is a significant feature among these Permian crinoids. Some have only one arm (Fig. 35), or the arms are completely absent. The reduction of arms goes hand in hand with a high variability and many (pathological?) deformations. A number of the crinoids have asymmetric cups. In the flexibles *Prophylocrinus* and *Proapsidocrinus*, the arms could be enclosed within prolonged radials, as in the Jurassic cyrtocrinids *Phyllocrinus* and *Apsidocrinus*; see Fig. 33 (Wanner 1924). In the cladid *Timorechinus*, the arms could be received between projecting ribs of the balloon-like anal sac. In the

strange, stemless genus *Timorocidaris* (first mistaken for an echinoid spine), the skeleton is reduced to a single, extremely variable piece that carried at the most three arms on a small neck. Even by Timor standards this crinoid was hugely successful, as judged by the incredible number of about 110,000 cups of the main species, *Timorocidaris sphaeracantha*, collected at Basleo (Wanner 1940). Such stemless and unattached crinoids with reduced arms are unknown from later strata (the unattached Middle Jurassic *Ailsacrinus* has well-developed arms; see Chapter 24), but in many respects the Timor crinoid fauna shows similarities to the cyrtocrinids from the Jurassic and Lower Cretaceous of Europe (see Chapter 3, section titled 'Mesozoic Cyrtocrinid Assemblages'). This raises some doubts as to the classification of the Timor crinoids as reef forms as postulated by Wanner (1924, 1940). However, Wanner (1924) also noted striking similarities with the Eifel region, where Middle Devonian crinoids thrived in forereef shelf areas.

The Upper Permian (most likely Guadalupian) age of the Timor crinoids (Erwin 1993) has been questioned

by Webster (1987, 1990) on the basis of the similarities between the Australian and the Timor crinoids. On Timor, the crinoids occur in yellowish to reddish mudstones, but also in tuffs and tuffaceous siltstones; these are interbedded with highly fossiliferous, partly crinoidal limestones. This so-called Maubisse Formation also includes basaltic rocks. These strata were displaced from the north to the present Timor area and may have been part of the West Australian geosyncline (Webster 1990). Accordingly, the crinoid-bearing beds of western and eastern Australia were deposited on the shelf at the southern margin of this sea (Fig. 175).

Of the roughly 100 crinoid species described from Australia, about half were from the eastern (including Tasmania) and half from the western part of the continent, with no species common to both regions. Because some crinoid genera occur in eastern and western Australia and some species are closely related, migration pathways around the northern margin or across the central interior of the continent must have been open during part of the Permian (Webster 1990). The Permian

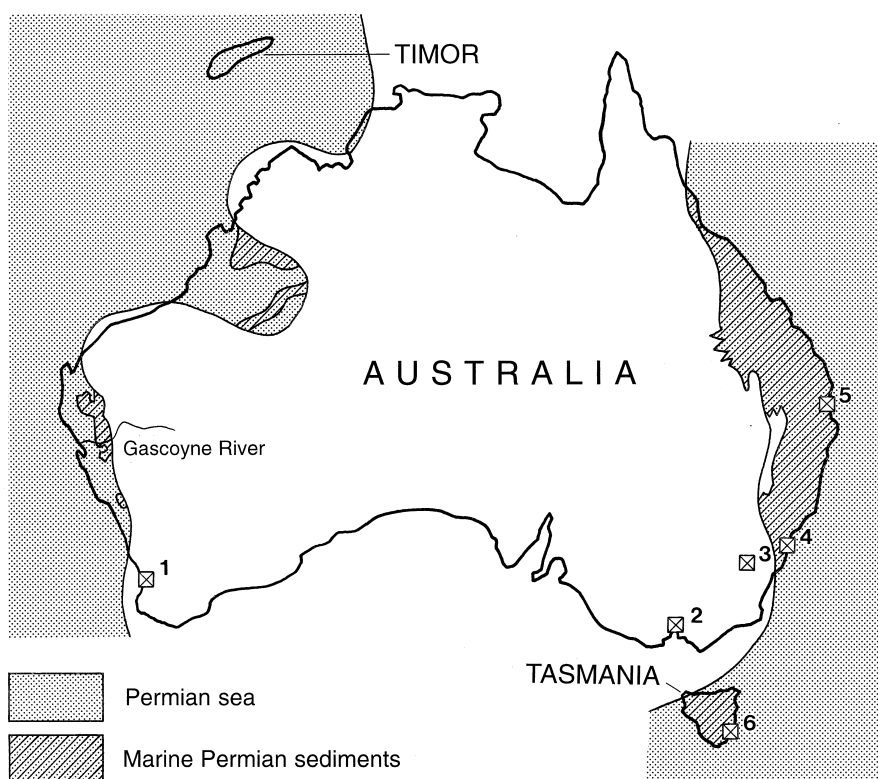


Fig. 175. Distribution of marine Permian rocks in Australia and extent of Permian Sea. (1) Perth; (2) Melbourne; (3) Canberra; (4) Sydney; (5) Brisbane; (6) Hobart. (After Teichert 1951; Willink 1979.)

strata of Australia are dominated by clastic sediments (sandstones, siltstones and shales) and limestones are rare. About half of the Australian Permian crinoids are from limestones or calcareous mudstones, and the other half from sandstones and siltstones. Many of the crinoids, embedded in fine-grained sandstones or mudstones with sandy layers, are preserved as iron oxide replacements of the original calcite. The crinoid faunas from Australia are the only cooler water faunas from the Palaeozoic and have a much lower diversity than the Timor crinoids. They include forms reaching a very large size, with specialized arm structures.

### CALCEOLISPONGIIDS: A PERMIAN SUCCESS STORY

The most outstanding forms of Australian crinoids are the calceolispongiids, the genera being *Calceolispongia* and *Jimbacrinus*. These are large dicyclic cladid crinoids with bulky, commonly spinose basals, slender stems and unbranched, uniserial arms. The amazing *Calceolispongia* is characterized in a number of species by strongly hypertrophic basal plates, which are drawn out into long, horn-shaped processes resembling slippers (hence the first part of the name of the genus, from the Latin *calceolus*) (Fig. 176). These plates were originally misinterpreted as sponge remains (hence the second part of the name). Wanner named this form *Dinocrinus* on the basis of some plates from Timor. This appropriate name was, however, proposed one year after the name '*Calceolispongia*' was assigned and is therefore a junior synonym. It is interesting that many of the eastern Australian species of this genus have no significant thickening of the basals (Willink 1979). Teichert (1949, p. 3) characterized this crinoid as follows: 'It is as if Nature had not been content with producing one of the oddest crinoids that ever existed: individuals of each species vied with each other to excel in oddities and individual peculiarities. This is all the more remarkable since the cup of *Calceolispongia* is of the simplest design; number and general size and arrangement of the cup plates never vary, and anomalies are rare. Yet the shape and ornamentation of individual plates is subject to variation without limit. As a result the degree of variability in general appearance of the cups is such as is rarely found and perhaps never surpassed in invertebrates.'

In western Australia, 13 species of *Calceolispongia* follow each other in a stratigraphic sequence of about 2,000 m of Artinskian strata, estimated by Teichert (1949) to be approximately 6 million years. During the

evolution of this genus, the basal plates increased in bulk 400 times. The last species of this phylogenetic series, *Calceolispongia robusta*, is a giant among crinoids, with a cup diameter of 130 mm (Fig. 176). With the exception of *Calceolispongia*, the western Australian crinoid fauna may be regarded as an extremely impoverished Timor assemblage. Well-preserved calcitic specimens of *Jimbacrinus bostocki* have been found in recent years in the Artinskian of the Gascoyne River in western Australia (Fig. 177), where they occur in a fine-grained sandstone. In more or less complete specimens, the stem is sharply bent just below the crown. Teichert, who figured one such specimen (1954, Pl. 13, Fig. 1), believed this to be the result of muscular contraction at the death of the animals. However, the stem of these crinoids may have been bent in life, with the stem as runner along the substrate. Bent-stem flexible crinoids

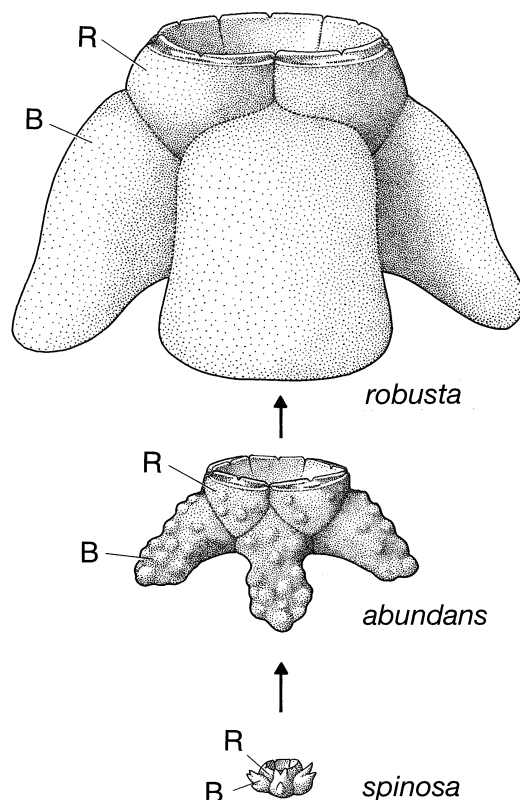


Fig. 176. Three examples of the size increase of Lower Permian *Calceolispongia* species in successive strata of western Australia. Side views of *C. spinosa* (Callytharra Series, Sakmarian), *C. abundans* (Middle Wandagee Series, Artinskian) and *C. robusta* (Upper Wandagee Series). Key: B, basals; R, radials. (After Teichert 1949.)  $\times 0.5$ .



Fig. 177. *Jimbacrinus bostocki*. Artinskian, Gascoyne River, western Australia. Note swollen basal plate with spine and enrolled atomous arms with uniserial, wedge-shaped brachials. (Hess Collection; photograph S. Dahint.)  $\times 1.6$ .

have been reported from the Lower Permian of Nevada (see the next section). The Early Permian (probably Artinskian) limestones of Callytharra Springs in western Australia have furnished a crinoid fauna composed of a range of species feeding at different levels. Unfortunately, the fossils occur mainly as disarticulated cups, with only a very few crowns (Webster 1987).

What could have been the reason for the excessive growth of the basals of many of these forms? It has been

suggested that the basals helped to stabilize the cup on the substrate and to lift the crown above the bottom. Teichert, who wrote a monograph on the genus *Calceolispongia* in 1949, thought that the stem was too weak to support the crown and may have been without any function. This may have been a reasonable possibility for species with very large basals such as *C. robusta*, but this theory is difficult to accept for the species with rather long stems and radicular cirri. Other possibilities have been discussed by Willink (1979), such as a baffle function of the protruding basals inducing an eddy effect in currents. Thickening of the basals may thus have been an adaptation to life in strong currents; as a matter of fact, most species with very large basals occur in sandstones (a common substrate for Australian crinoids) and are disarticulated, whereas species with less developed basals occur in mudstones and are commonly preserved completely. The articulations of the arms indicate that these could be coiled quite tightly, perhaps another adaptation to stronger currents, but they also conferred an advantage against predation (Fig. 177).

#### WIDE DISTRIBUTION OF THE REMAINS OF PERMIAN CRINOIDS

The best-known Permian crinoid faunas are those from Timor and Australia, but Permian crinoids have also been reported from North America, Bolivia, Europe (Sicily) and Tunisia, as well as from Russia (Urals), China, India and Thailand. The Russian crinoids form a link between Timor and North American faunas and contain advanced poteriocrines and indocrinids. A rich fauna of Lower Permian crinoids with 37 genera and 47 species, mostly cladids, has been described from southern Nevada (Lane & Webster 1966; Webster & Lane 1967). A number of these silicified fossils are preserved as more or less complete crowns and were collected from two biohermal lenses of coarse-grained, well-bedded, skeletal limestone composed mainly of disarticulated crinoids. This fauna is dominated by advanced poteriocrines, but the flexibles *Trampidocrinus* and *Nevadacrinus* with their wedge-shaped columnal beneath the crown appear to be an adaptation for a stem running along the substrate. Lane and Webster assumed that the rather robust Nevada crinoids adapted to life in agitated water.