# 15
# *Posidonia Shale: Germany's Jurassic Marine Park*

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THE LOWER JURASSIC POSIDONIA SHALE (*POSIDONIENschiefer*) of southern Germany and, especially, the Holzmaden region is one of the most celebrated of all Lagerstätten. This deposit has, in places, been quarried for centuries, and large numbers of splendidly preserved fossils have found their way into museums and private collections around the world. Since quarrying in the Holzmaden region continues, even today spectacular fossils are being uncovered. Famous finds include not only fully articulated marine reptiles and fish, but also articulated crinoids attached to logs and belemnites with preserved soft parts (Hauff and Hauff 1981; Seilacher 1990; Urlichs, Wild, and Ziegler 1994). The most frequently found fossils include, however, a variety of ammonites and bivalves, which can be found on almost every bedding plane. The black and laminated bituminous Posidonia Shale has long been treated as the prototype stagnation deposit (Seilacher 1982b; Seilacher, Reif, and Westphal 1985). This classification still holds true, although over the years it has become clear that there were several episodes with oxygenated bottom-waters (Röhl 1998; Röhl et al. 2001).

Quarrying in the Holzmaden region dates back for centuries. In fact, floor tiles coming from the Posidonia Shale can be found in the Hohenstaufen castle, built in the twelfth century (Seilacher 1990). Early attempts to distill oil from the highly bituminous black shales date back to the late sixteenth century (Seilacher 1990). Fossils have been found since that time (historical review in Urlichs, Wild, and Ziegler 1994). The first fundamental treatments of the Posidonia Shale and its fossils were published in the early nineteenth century by Schlotheim, Zieten, Quen-

sted, and Fraas (Riegraf, Werner, and Lörcher 1984; Seilacher 1990). The first comprehensive study of the Posidonia Shale of the Holzmaden region appeared in 1921 (Hauff 1921). Since then, many workers have studied various aspects of the paleontology, sedimentology, and geochemistry of this deposit. But even with such extensive examination, there is still some controversy about the exact nature of the paleoenvironmental conditions that existed during the deposition of this Lagerstätte and the mode of life of some fossil species.

## Geological Context

The lower Toarcian Posidonia Shale of southwestern Germany crops out in a southwest–northeast-trending belt extending from Waldshut to the Nördlinger Ries in the foreland of the Swabian Alb (Urlichs 1977; Riegraf, Werner, and Lörcher 1984; Urlichs, Wild, and Ziegler 1994) (Figure 15.1). In somewhat reduced thickness, the Posidonia Shale extends in the southwest into northern Switzerland (Riegraf 1985; Kuhn and Etter 1994) and in the northeast into the Franconian Alb (Urlichs 1971; Bandel and Knitter 1986). However, the best exposures can be found in quarries around the villages of Ohmden, Zell, Bad Boll, and, especially, Holzmaden (Figure 15.1), a place that is inextricably linked to this Lagerstätte (Hauff and Hauff 1981).

The Posidonia Shale of the Swabian Alb is a 6 to 14 m thick succession of dark gray to black bituminous shales with intercalated bituminous limestones (Riegraf, Werner, and Lörcher 1984) (Figure 15.2). It has long been recognized that each of the individual beds of the Posidonia Shale shows a distinct sedimentological, paleontological, and taphonomic signature. Successful attempts to correlate marker horizons over large geographic distances date back to the nineteenth century, and the first detailed lithostratigraphic subdivision of the Posidonia Shale was made by Quenstedt (1858), who labeled the lithostratigraphic units of the Jurassic of southern Germany with Greek letters; Schwarzer Jura ε ("epsilon") designates the Posidonia Shale. An even more detailed subdivision was established by Hauff (1921), and this lithostratigraphy is still in use (Riegraf, Werner, and Lörcher 1984; Riegraf 1985; Urlichs, Wild, and Ziegler 1994) (Figure 15.2). According to this subdivision, a lower (ε I), a middle (ε II), and an upper part (ε III) of the Posidonia Shale can be recognized, with each of the individual marker beds specifically named and numbered. On a regional scale where individual laminae can be traced over a distance of several kilometers, an even finer correlation is possible (Seilacher 1990).

The biostratigraphy of the Posidonia Shale is well established, by both ammonites (Riegraf, Werner, and Lörcher 1984) and microfossils (ostracodes, foraminifers) (Riegraf 1985). The lower boundary of the Posido-

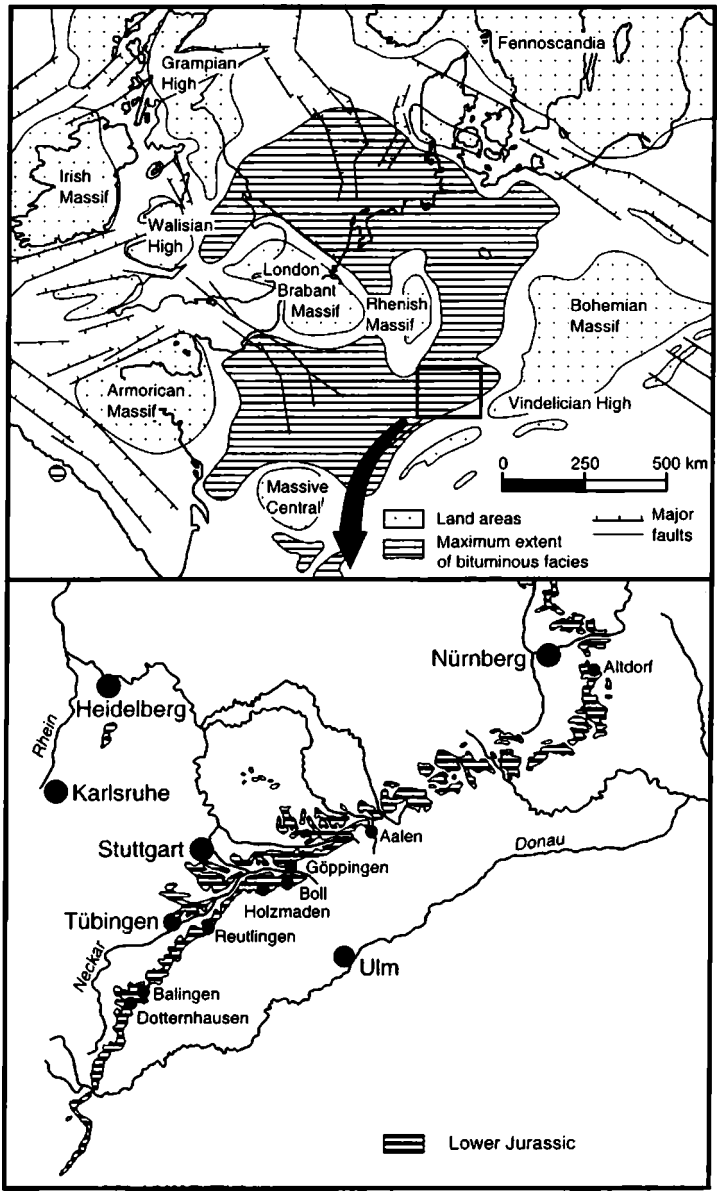


**FIGURE 15.1** Paleogeography during the early Toarcian (*top*) and location of outcrops (*bottom*). (Modified from Urlichs 1977 and Riegraf 1985)

nia Shale is drawn with the onset of the first bituminous horizons (>2 percent organic matter content) (Riegraf, Werner, and Lörcher 1985). In the Holzmaden region, the bituminous facies starts in the early *tenuicostatum* zone (lowermost Toarcian) (Figure 15.2), but toward both the southwest (northern Switzerland) and the northeast (Franconian

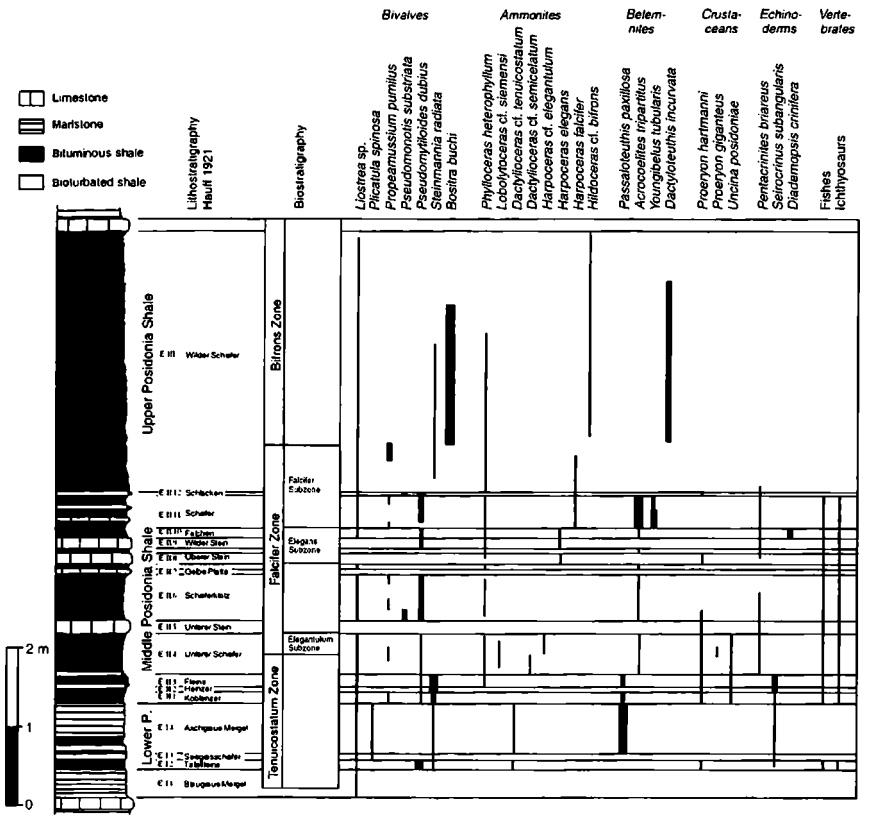


**FIGURE 15.2** Stratigraphic column with range of common fossils indicated. (Modified from Hauff and Hauff 1981, Riegraf 1985, and Urlichs, Wild, and Ziegler 1994)

Alb), the basal layers of the Posidonia Shale are missing and the lowermost bituminous horizons are dated as late *tenuicostatum* zone or even early *falciferum* zone (Urlichs 1977; Riegraf 1985; Kuhn and Etter 1994).

The upper boundary of the Posidonia Shale normally coincides with an erosive surface that truncates the bituminous facies (Riegraf, Werner, and Lörcher 1984). This truncation can reach down to the lower *bifrons* zone or even the upper *falciferum* zone (Riegraf, Werner, and Lörcher 1984; Riegraf 1985). Where the transition from lower to upper Toarcian is continuous, the youngest bituminous layers have been dated as belonging to the middle *bifrons* zone (Riegraf, Werner, and Lörcher 1984). The deposition of the Posidonia Shale in southern Germany, where it is not secondarily reduced by erosion, lasted for 2.5 to 3 Ma (Riegraf 1985). Assuming a compaction rate of the sediment of 1:20, an average accumulation rate of 10 cm of uncompacted sediment per 1 Ka has been calculated for the *falciferum* zone of Gomaringen (Riegraf 1985). In the Holzmaden region, the thickness of the Posidonia Shale is

more reduced, and accumulation rates are likely to be only half that value.

Apart from several bioturbated intervals, which are more prominently developed at the base and near the top of the sections, the whole sequence is finely laminated (Seilacher 1982b; Riegraf, Werner, and Lörcher 1984). The submillimetric laminations are an alternation of light-colored carbonate-rich laminae, consisting mainly of coccolith debris (especially *Schizosphaerella*), and darker laminae, consisting of clay minerals, organic material, and pyrite (Riegraf, Werner, and Lörcher 1984; Riegraf 1985). Besides these differences between individual laminae, there are major geochemical differences between calcareous beds and bituminous shales. As a general rule, the middle Posidonia Shale is more bituminous than the lower and upper parts of the sections (Urlichs, Wild, and Ziegler 1994).

The limestones consist of 60 to 80 weight percent (wt%) carbonate and 10 to 20 wt% clay minerals, mainly illite and muscovite, less commonly kaolinite, montmorillonite, and chlorite (Einsele and Mosebach 1955; Riegraf 1985). Quartz contributes around 5 wt%, pyrite adds 2 to 5 wt%, and the contents in organic material, mainly bitumen, have values of 3 to 7 wt% (exceptionally, more than 10 wt%) (Brockamp et al. 1944; Einsele and Mosebach 1955; Heller 1965; Riegraf 1985).

The bituminous shales, though, consist mainly of clay minerals (the same minerals found in the limestones), which account for up to 70 wt% (Einsele and Mosebach 1955). The carbonate content is usually less than 40 wt%, and quartz is present with up to 15 wt% (Einsele and Mosebach 1955; Riegraf 1985). Finely disseminated pyrite reaches values of 5 to 10 wt%, and organic carbon averages 4 to 10 wt%, although occasionally higher values (up to 12 wt%) have been observed (Einsele and Mosebach 1955). In certain layers, pyrite can occur abundantly in nodular or disk-shaped concretions.

## Paleoenvironmental Setting

The Posidonia Shale can be correlated with other organic-rich shales in Europe. The most prominent examples are the Jet Rock and Alum Shale in England (Hallam 1967; Morris 1979, 1980) and the Schistes Cartons in France (Thomas 1977), but contemporaneous epicontinental black shales are also known from northern Germany (Loh et al. 1986; Littke et al. 1991) and from boreholes in the Netherlands and the North Sea (Ziegler 1990) (Figure 15.1). In fact, organic-rich shales from the lower Toarcian, which were deposited in deeper-water settings in the Tethys, are also found in Austria, Italy, Switzerland, Hungary, Greece, and Tunisia (Jenkyns 1988). Even outside Europe, strata of early Toarcian age are not uncommonly organic-rich, and this was the reason to coin

the term *early Toarcian anoxic event* (Jenkyns 1988). The most widespread development of these black shales is in the *falciferum* zone (Jenkyns 1988), which corresponds to the middle Posidonia Shale.

The geological and paleontological documentation of the Posidonia Shale is probably more voluminous than that of any other Lagerstätten, but the environmental conditions during deposition of the Posidonia Shale have been a matter of debate for a long time. Early in the twentieth century, Pompeckj (1901) compared the sediments of the Posidonia Shale with those found today in the Black Sea. This was the first time that deposition of these laminated black shales was linked to anoxic bottom-water conditions. Ever since then, various workers have proposed different and sometimes conflicting scenarios for deposition of the Posidonia Shale.

The stagnant basin model introduced by Pompeckj (1901) has found many supporters during the history of research on the Posidonia Shale (Fischer 1961), and it is, with some modifications, still the most popular paleoenvironmental model (Seilacher 1982b, 1990; Seilacher, Reif, and Westphal 1985). There are, indeed, many indications that during deposition of the Posidonia Shale, the near-bottom environment was either anoxic or severely oxygen depleted. This evidence includes the preservation of laminations and the near absence of bioturbation, as well as the predominance of pelagic life forms among the fossils (Seilacher 1982b, 1990).

Another feature that is usually linked to severely oxygen-depleted environments is the preservation of high amounts of organic carbon. Indeed, apart from localized occurrences of Sinemurian oil-shales, the Posidonia Shale is the only sedimentary rock in southern Germany that shows values of total organic carbon (TOC) higher than 4 wt% (Riegraf, Werner, and Lörcher 1984). The high content of pyrite, mainly in the form of disseminated framboids, also supports a low-oxygen paleoenvironment (Brett and Baird 1986). In addition, the concentrations of iron and manganese in the Posidonia Shale are similar to those expected in anoxic basins (Veizer 1977).

A strict application of the stagnant basin model has been questioned by many paleontologists. The first to cite evidence against the Black Sea hypothesis was Beurlen (1925), who mentioned the occurrence of benthic crustaceans from the Posidonia Shale of Holzmaden. Since then, many workers have observed benthic life-forms, including bivalves, gastropods, crustaceans, and echinoderms (review in Riegraf, Werner, and Lörcher 1984). Additional evidence for benthic life comes from the presence of trace fossils (Brenner and Seilacher 1978) and autochthonous microfossils (Riegraf 1985). However, most of the authors reporting benthic life still maintain that during deposition of the Posidonia Shale, the bottom-waters were, as a rule, severely oxygen depleted or even anoxic.

Only brief oxygenation events allowed metazoan life-forms to colonize the seafloor (Brenner and Seilacher 1978; Röhl 1998).

A radically different view has been presented by Kauffman (1978, 1981), according to whom the water column was almost normally oxygenated throughout the early Toarcian. At or a few centimeters above the seafloor, however, an algal–fungal mat periodically developed, trapping anoxic water beneath it and allowing only benthic colonization of elevated shells that projected above it: the so-called ammonite shell surface community (Kauffman 1981). During times of stronger bottom currents, these mats may have been destroyed, allowing the colonization of the sediment surface and the bioturbation of sediment (Kauffman 1981). While many of Kauffman's observations are certainly valuable, they are not supported by sufficient data. In particular, his ammonite shell surface community probably represents ammonite shells that were overgrown while the shells were still afloat (Seilacher 1982a).

The current consensus is that the bottom-waters of the Posidonia Shale sea were severely oxygen depleted throughout the deposition of this formation, allowing the colonization of the seafloor by specialized or opportunistic taxa only at certain times. However, the mechanism that led to this unique and widespread deposition of black shales is still disputed. During early Toarcian times, southern Germany (as well as northern Switzerland, eastern France, northern Germany, and parts of England) was a basinal setting in an epicontinental seaway during a time of high sea-level stand (Riegraf 1985; Jenkyns 1988; Ziegler 1990). A highly structured bottom relief is evidenced by marked lateral variability in thickness of the Posidonia Shale (Riegraf, Werner, and Lörcher 1984; Riegraf 1985). Detrital material was shed mainly by the Bohemian Massif (Ziegler 1990). Bottom currents, which are not thought to be related to oxygenation events, followed the contours of the basins in a mainly south–north direction (Urlichs 1971; Brenner and Seilacher 1978).

Several models have been developed to explain the widespread occurrence of black shales and the exceptional preservation of fossils in this setting. The first is the classic stagnant basin model, involving salinity stratification. This explanation, which was favored by earlier authors, has recently been supported by palynologists who have observed that during deposition of the lowermost Posidonia Shale, a normal-marine phytoplankton association (consisting mainly of dinoflagellates, coccoliths, and acritarchs) was rather suddenly replaced by an assemblage dominated by prasinophytes (Loh et al. 1986; Prauss and Riegel 1989). This has been interpreted as the result of lowered salinity of surface water, produced by increasing river runoff. The same conclusion has been drawn by Brumsack (1988), who has documented high contents in manganese, lead, and cobalt in the Posidonia Shale, which, he believes, can have been derived only from enhanced river influx.

However, the salinity stratification model seems an unlikely explanation for the deposition of the Posidonia Shale for several reasons. First, apparently stenohaline pelagic organisms (radiolarians, cephalopods) occur throughout the sequence (Riegraf, Werner, and Lörcher 1984; Riegraf 1985). Second, geochemical tracers other than those cited by Brumsack (1988) seem to indicate normal-marine salinity (Küspert 1982). And third, the paleogeographic situation, which is known in detail (Ziegler 1990), does not seem to be appropriate for large-scale salinity stratification (Tyson and Pearson 1991).

A variation of the salinity stratification model has been proposed by Jordan (1974), according to whom a halocline developed not by high freshwater input (and hence a brackish surface layer), but by hypersaline bottom-waters produced by salt diapirism in northern Germany. However, corresponding diapirs are not known to have ascended during the early Toarcian in southern Germany, France, and England, and it seems very unlikely that enough hypersaline water could have been produced by this mechanism to cause such a large stratified body of water (Riegraf 1985).

A second model involving thermal stratification has been applied to the Posidonia Shale by Hallam (1987). While it is generally true that a thermally stratified water mass is less stable than a salinity stratified one, and is likely to experience seasonal mixing, a thermocline could be quite stable under equable climate (Hallam 1987). As has been pointed out, the irregular bottom topography of extensive shelf areas limited the amount of horizontal advection (Hallam and Bradshaw 1979; Hallam 1987). During the early stages of a transgression, the basinal settings of an epicontinental sea would have become deep enough to be situated beneath the thermocline. Black shales could thus have been formed in these stagnant water masses (Hallam and Bradshaw 1979). With further transgression, the expanded thermocline would have become less stable, and better circulation in the deeper, more extensive seas would have allowed more oxygenated water to enter the basins, leading to a complete mixing of the water column. This would have caused cessation of black shale formation (Hallam and Bradshaw 1979).

In its original formulation, this model also predicted the deposition of black shales during the early stages of regression, when water circulation was again restricted, but water depth of the depositional environment was still deep enough to be below the thermocline (Wignall and Hallam 1991). In a new variation of the theme, the expanding puddle model has been proposed, which incorporates additional sedimentological observations (Wignall and Hallam 1991). According to this model, black shales formed during the initial stages of transgressions in basinal settings, while land-derived sediment was trapped in newly formed estuaries. Indeed, the marginal areas of Posidonia Shale depo-

sition (Franconian Alb, northern Switzerland) show condensed deposits and hiatal surfaces at the base of the Posidonia Shale, as predicted by the model (Bandel and Knitter 1986; Kuhn and Etter 1994; Urlichs, Wild, and Ziegler 1994). With ongoing transgression, sediment influx would have been reestablished and the basin (through sediment input) would have become shallower, ending black shale formation (Wignall and Hallam 1991). This was, indeed, the case in southern Germany, with the termination of the bituminous facies occurring in the *bifrons* zone, which was the time of the highest sea-level stand (Wignall and Hallam 1991).

While the expanding puddle model explains many aspects of the deposition of the Posidonia Shale, it does not account for the synchronous occurrence of organic-rich shales in deep-marine settings (Jenkyns 1988). Therefore, a third model must be considered: the oxygen minimum zone model (OMZ). There is, indeed, good evidence that Tethyan mid-waters were oxygen depleted during the early Toarcian (Jenkyns 1988). This is supported not only by the widespread occurrence of organic-rich shales (Dercourt et al. 2000), but also by the analysis of carbon isotopes. Sediments of early Toarcian age in all parts of Europe show a pronounced positive carbon isotope excursion (Jenkyns 1988). This event can be dated as occurring in the *exaratum* subzone of the *falciferum* zone, and is interpreted as reflecting a time interval during which anormally high rates of production, sedimentation, and burial of organic carbon took place (Jenkyns 1988). Since organic matter is isotopically much lighter (much more enriched in $^{12}C$) than carbonate, removal of large amounts of organic material from the world's oceans would have left this carbon reservoir enriched in the heavier isotope $^{13}C$. Carbonate produced from this reservoir (e.g., coccoliths) would thus show a shift to very positive $\delta^{13}C$ values (Jenkyns 1988). In contrast, the very low $\delta^{13}C$ values of the organic carbon at the base of the Posidonia Shale are thought to reflect upwelling of isotopically light organic carbon during times of anoxic bottom-waters (Küspert 1982).

Various authors have proposed that during the early Toarcian transgression, waters from the Tethyan oxygen minimum zone entered the epicontinental seas of central and western Europe (Knitter 1983; Jenkyns 1988; consistent with paleocurrent measurements: Brenner and Seilacher 1978). Together with the presumably highly fertile surface waters on the shelf, the accumulation of black shales and the preservation of high amounts of organic material would, therefore, largely reflect abnormally high plankton productivity (Jenkyns 1988). While the OMZ model is supported by geochemical evidence, many sedimentological and stratigraphic features of the Posidonia Shale are better explained with a model involving a thermally stratified basin during the early stages of a transgression. At present, it seems best to allow for both mechanisms

to operate and to combine stratification (e.g., expanding puddle) with the OMZ model.

## Taphonomy

The Posidonia Shale of southern Germany is most famous for its rich yield of fully articulated vertebrates. Indeed, thousands of spectacularly preserved marine reptiles and fish have been collected, with occasional soft-part preservation. Although the number of vertebrate specimens now on display in museums around the world is indeed impressive, it must be noted that this large number of fossils is the result of intense sampling efforts over more than 200 years (Hauff and Hauff 1981; Seilacher 1990). While the density of vertebrate occurrences in the Holzmaden region may actually be higher than in the Posidonia Shale of adjacent regions (Hauff 1921; Hauff and Hauff 1981; but see Seilacher 1990, who considers a sampling bias), spectacular finds are rare. Based on reported numbers of recovered specimens, Hauff and Hauff (1981) estimated that, on average, 12 quarry workers would have to dig for a year to recover one fully articulated ichthyosaur. Partially disarticulated and incomplete specimens are more common and account for about 90 percent of the finds (Hauff and Hauff 1981).

For most people, the ichthyosaurs are most readily associated with the Posidonia Shale of Holzmaden. Since most of the information about soft-part morphology of ichthyosaurs comes from specimens of this Lagerstätte, they indeed deserve their own paragraph. More than 500 fully articulated specimens have been found (Hauff and Hauff 1981), and some of them show remarkable soft-part preservation. Most spectacular is the preservation of the skin, which allowed for the first detailed reconstruction of the body outline (Hauff and Hauff 1981) (Figure 15.3), with a large mid-dorsal fin and a shark-like caudal fin (with the vertebral column, however, projecting into the lower lobe). The authenticity of this skin preservation has been questioned, and the presence of a distinct body outline was attributed to forgery by clever preparators (Martill 1987a, 1987b). However, a detailed investigation of the microfacies and geochemistry of ichthyosaurs showing skin preservation has confirmed their authenticity (Keller 1992) and subsequent study of the skin has provided important paleobiological information (Lingham-Soliar 2001). Other remarkable features associated with ichthyosaurs are the preservation of embryos in the body cavity of female specimens (Hauff and Hauff 1981; Böttcher 1990; Urlichs, Wild, and Ziegler 1994) and of stomach contents, mainly belemnite hooks (Keller 1976; Böttcher 1989).

Other reptiles from the Posidonia Shale are also known from fully articulated specimens, but they are much rarer and do not show excep-

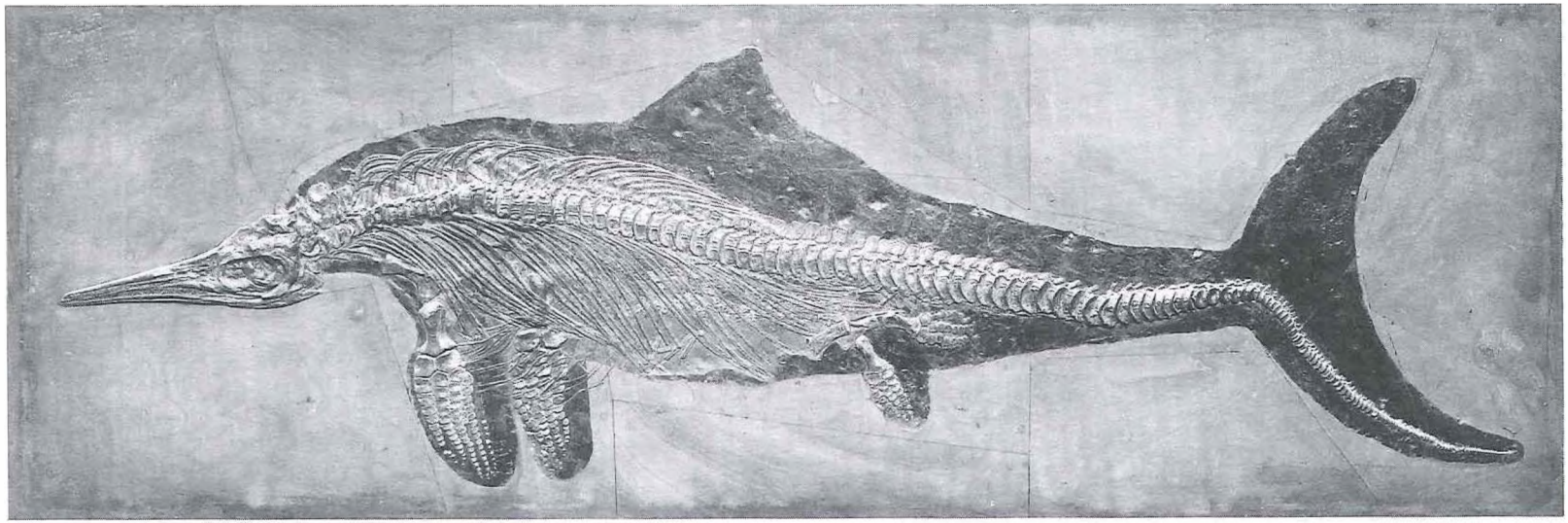

**FIGURE 15.3** Ichthyosaur *Stenopterygius* sp. with skin preservation. Length of specimen is 2.85 m. (Photo by H. Lumpe, courtesy of Staatliches Museum für Naturkunde, Stuttgart)

tional features such as skin preservation. Among the fish, however, which outnumber the reptiles by far, some specimens do show soft-part preservation. Preservation of the digestive tract (possibly phosphatized) is known from *Leptolepis* and *Pachycormus* (Hauff and Hauff 1981). Some sharks (*Hybodus*) and chimaeres (*Acanthorhina*) show preservation of the cartilaginous skeleton, parts of the skin, and stomach contents (Keller 1977; Urlichs, Wild, and Ziegler 1994). Again, incomplete specimens are much more common than fully articulated ones (Hauff and Hauff 1981).

Spectacular examples of exceptional preservation are also found among many invertebrates. Most notable is the crinoid *Seirocrinus subangularis,* which attained a column length of up to 20 m (Seilacher, Drozdzewski, and Haude 1968). Many perfectly preserved specimens have been found, and they are, unless broken, always attached to logs (Seilacher, Drozdzewski, and Haude 1968; Seilacher 1990) (Figure 15.4). Articulated specimens of other echinoderms are known as well (echinoids, asteroids, ophiuroids), but they are exceedingly rare (Seilacher 1990). The same is true for decapod crustaceans (Hauff and Hauff 1981; Seilacher 1990).

The Posidonia Shale of southern Germany is, furthermore, the only Lagerstätte that has yielded belemnites with preserved soft parts. The first of these specimens were described in 1976 (Wiesenauer 1976), but they turned out to be forgeries (Riegraf and Reitner 1979). Only a few years later, however, true soft-bodied belemnites were discovered, showing the presence of an ink sac and 10 arms with double rows of hooks (Reitner and Urlichs 1983; Riegraf and Hauff 1983) (Figure 15.5). All these specimens have a fractured alveolar region. This feature seems to be an integral part of soft-body preservation in belemnites and was the reason to formulate the cherry stone hypothesis (Wiesenauer 1976; Seilacher 1990). According to this theory, the major predators on belemnites (mainly ichthyosaurs) were selectively biting off the calcareous belemite rostra and spitting them out before swallowing the animal. Occasionally, an ichthyosaur would injure a belemnite without consuming the animal. After such an unsuccessful attempt, gas would be released from the phragmocone of a bitten specimen, which would then sink to the seafloor and be buried with attached soft parts. Specimens that died naturally would have floated long enough to disintegrate in the water column (Seilacher 1990).

Preservation of soft parts is also known in teuthoid cephalopods from the Posidonia Shale (Hauff and Hauff 1981; Riegraf, Werner, and Lörcher 1984), and in a few specimens of ammonites, preserved crop and stomach contents have been observed (Riegraf, Werner, and Lörcher 1984). However, the frequent preservation of aptychi in their body chambers indicates that many ammonites were embedded while the soft parts still held the jaws in position (Riegraf, Werner, and Lörcher 1984; Seilacher 1990). This is also indicated by the fact that the sediment

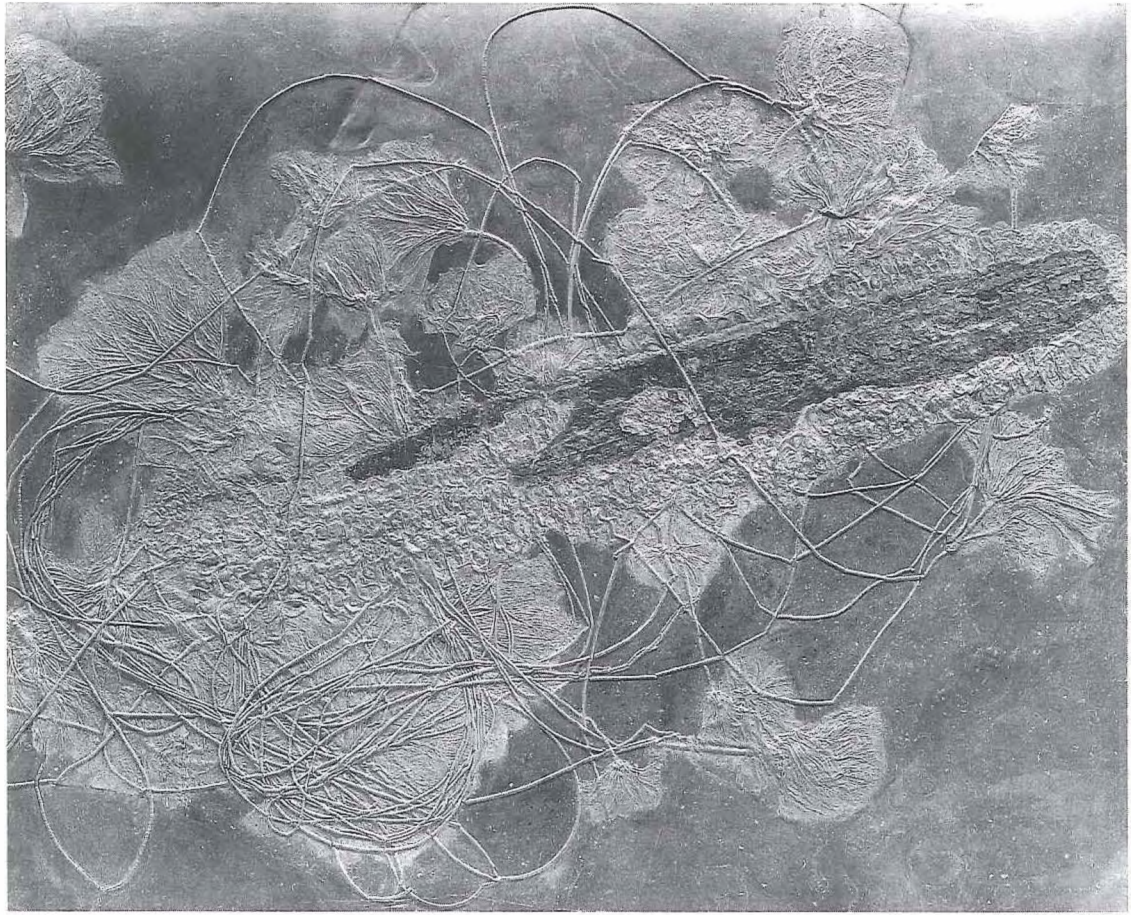

**FIGURE 15.4** Multiple specimens of the crinoid *Seirocrinus subangularis* attached to a log that is overgrown by the bivalve *Pseudomytiloides dubius*. Length of log is 2.4 m. (Photo by H. Lumpe, courtesy of Staatliches Museum für Naturkunde, Stuttgart)

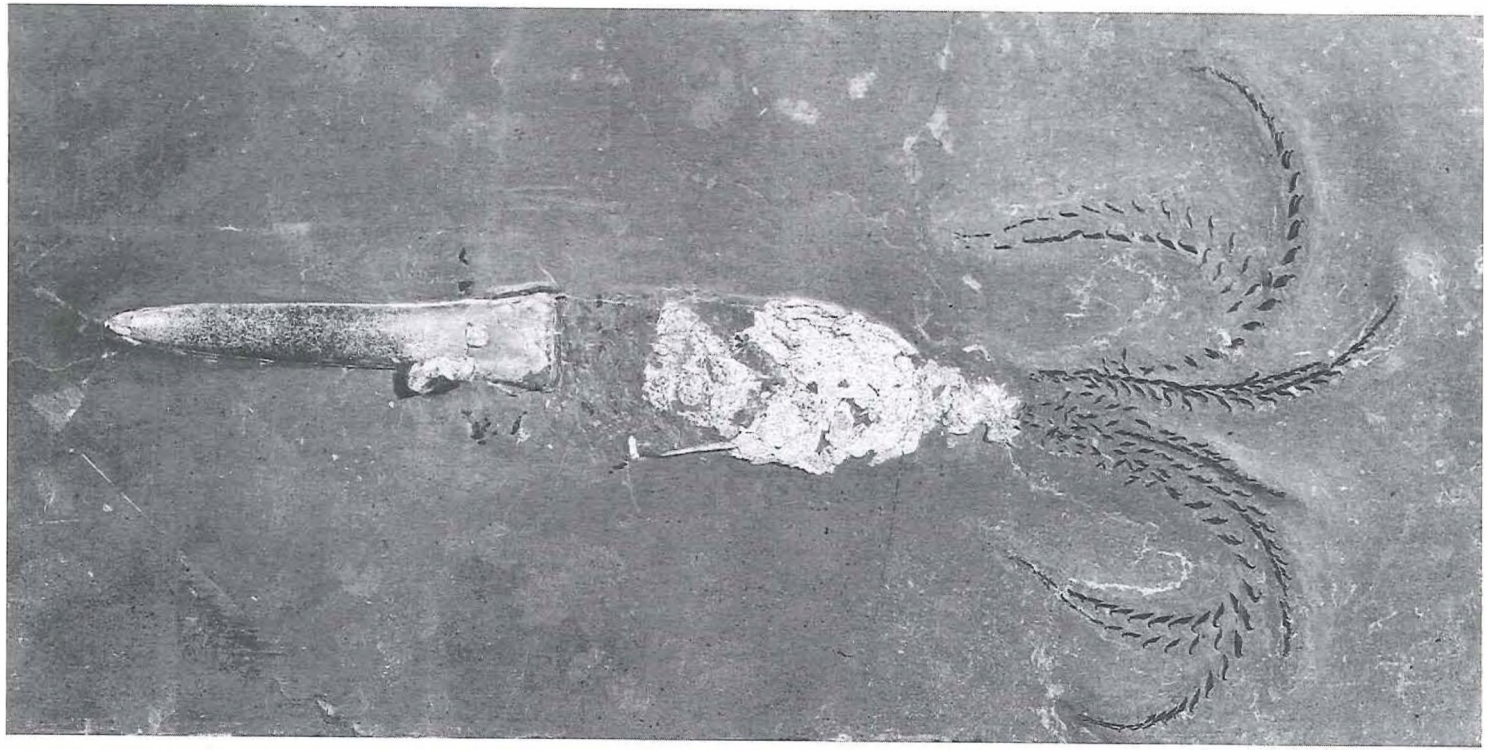

FIGURE 15.5 Belemnite *Passaloteuthis bisulcata* with soft parts. Length of rostrum is 11 cm. (Photo by H. Lumpe, courtesy of Staatliches Museum für Naturkunde, Stuttgart)

in the vicinity of ammonite body chambers contains organic matter contents, especially amino acids (Heller 1965). Among the other mollusc groups, soft-part preservation is not known, but at least one specimen of a bivalve (*Plagiostoma*) showing color preservation has been described (Riegraf, Werner, and Lörcher 1984). Worth mentioning also is the preservation of trace fossils in the Posidonia Shale. The rare bioturbation intervals show such a remarkable preservation of the lower tiers (frozen tiers) that this locality has even been called an Ichnofossil-Lagerstätte (Savrda and Bottjer 1989; for a discussion of trace fossils, see "Paleobiology and Paleoecology").

The exceptional preservation of fully articulated specimens, showing preserved soft parts in many cases, has long been explained by minimal decay under anoxic bottom-waters (Seilacher 1970; Seilacher, Reif, and Westphal 1985). Nektonic and pseudoplanktonic organisms would have, after death, sunk to the seafloor, where they were partially embedded in the very soft, soupy sediment. Under anoxic bottom-water conditions, decay was slow, and bioturbating and scavenging animals, which would normally disrupt multielement skeletons, were absent (Seilacher, Reif, and Westphal 1985). However, stagnation alone cannot explain the occurrence of articulated crinoids, because their skeletons would have disintegrated at the sediment surface within several hours to several days, even under anoxic conditions (Seilacher 1990). It is therefore believed that occasional sediment blanketing played an important role in the preservational history of such specimens (Brett and Seilacher 1991). That these sediment layers were thin is testified to by the fact that larger carcasses, which projected above the sediment–water interface, are better preserved on the underside than on their upper side, which is commonly partially disarticulated (Kauffman 1981).

Sediment was not invariably soupy throughout deposition of the Posidonia Shale. In some layers, drag and roll marks have been observed (Riegraf, Werner, and Lörcher 1984), and there is good evidence that microbial mats periodically covered the sediment surface, especially during deposition of the lower Posidonia Shale (Riegraf 1985). Whether these microbial mats played a crucial role in the preservation of fossils is not known at present.

The early diagenesis of Posidonia Shale fossils is characterized by strong compaction and dissolution of aragonite, but preservation of calcite, phosphate, and scleroproteins (and occasionally other tissues). The best clues for deciphering the early diagenetic history of the Posidonia Shale come from analysis of the ammonites (Seilacher et al. 1976). The Posidonia Shale ammonites show, unless they had a very rigid shell (*Dactylioceras*), a two-phase collapse (Seilacher et al. 1976). In the first stage, the body chamber collapsed, resulting in a fracture pattern. Later, the aragonitic shell started to dissolve, weakening the septal support of

the phragmocone. This part of the shell collapsed without fractures because only the organic periostracum was left, resulting in a so-called leaf-preservation (Seilacher et al. 1976). The calcitic aptychi, however, were not dissolved. This diagenetic sequence is modified in concretions and some bituminous limestone beds where ammonites (and other fossils) can be preserved uncompacted, and sometimes with their shell recrystallized to calcite (Riegraf, Werner, and Lörcher 1984).

## Paleobiology and Paleoecology

Fossils have long been considered the most useful tool for deciphering environmental conditions during deposition of the Posidonia Shale. At the same time, however, controversial interpretations of some species were the main reason for the different views that have been expressed on the origin of this Lagerstätte. While many macrofaunal species are clearly benthic and even more clearly pelagic, the life habits of some species are still debated. In addition to the large number of marine organisms, a few terrestrial species are also known from the Posidonia Shale. They include a few plant remains (cycads, ginkgos, conifers) (Hauff and Hauff 1981; Urlichs, Wild, and Ziegler 1994), rare pterosaurs (Wild 1975; Hauff and Hauff 1981; Seilacher 1990; Urlichs, Wild, and Ziegler 1994), and even rarer sphenodontid lizards and sauropod dinosaur remains (Wild 1978; Hauff and Hauff 1981; Urlichs, Wild, and Ziegler 1994). Although preserved in deposits at localities from the Franconian Alb and central eastern Germany, insects have not been found in the Posidonia Shale of the Swabian Alb (Urlichs, Wild, and Ziegler 1994).

### *Pelagic Organisms*

Most of the fossils that made the Posidonia Shale of Holzmaden famous are nektonic animals (Seilacher 1990; Urlichs, Wild, and Ziegler 1994). They include the well-known ichthyosaurs, of which around a dozen species have been described (Riegraf, Werner, and Lörcher 1984; Maisch 1998a; but see Maisch 1998b, who accepts only eight valid species), and which range in adult size from about 2 to 10 m (Hauff and Hauff 1981). Other pelagic reptiles include plesiosaurs (four species with only 12 specimens) and marine crocodiles (three species, including *Platysuchus multiscrobiculatus*) (Hauff and Hauff 1981; Riegraf, Werner, and Lörcher 1984) (Figure 15.6). The ichthyosaurs spent their whole life in the sea, as is obvious from their morphology and from the female specimens carrying embryos at the near-hatching stage and even giving birth (Hauff and Hauff 1981; Urlichs, Wild, and Ziegler 1994). The plesiosaurs were less perfectly adapted to a permanent life in the sea, and the crocodiles most probably spent some time on land (Seilacher 1990; Urlichs, Wild, and Ziegler 1994).

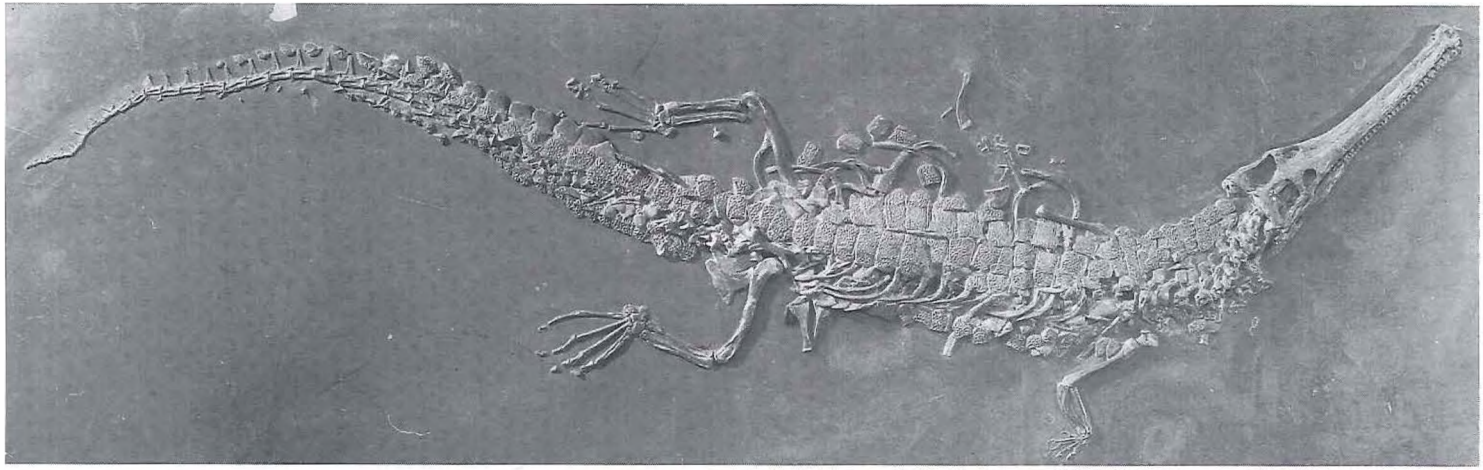

FIGURE 15.6 The marine crocodile *Platysuchus multiscrobiculatus*. Length of specimen is approximately 3 m. (Photo by H. Lumpe, courtesy of Staatliches Museum für Naturkunde, Stuttgart)

More than 20 species of bony fish have been described from the Posidonia Shale of southern Germany (Hauff and Hauff 1981; Riegraf, Werner, and Lörcher 1984). They range in size from only a few centimeters (*Leptolepis, Tetragonolepis*) to almost 3 m (*Chondrosteus, Ohmdenia*) (Hauff and Hauff 1981). Various taxonomic groups are present (Coelacanthidae: *Trachymetopon;* Teleostei: *Leptolepis, Pholidophorus;* Holostei: *Hypsocormus, Caturus, Pachycormus, Saurostomus, Euthynotus;* Subholostei: *Dapedium, Lepidotes, Tetragonolepis;* Chondrostei: *Ptycholepis, Saurorhynchus, Chondrosteus, Ohmdenia*), but all the species show morphologies of open- or shallow-water forms. Bottom-dwelling species seem to be absent (Aldinger 1965; Seilacher 1990; Urlichs, Wild, and Ziegler 1994). The same is true for the cartilaginous fishes (sharks and holocephalans), of which eight species are known (Riegraf, Werner, and Lörcher 1984).

Among the invertebrates, ammonites, squids, and belemnites are open-water swimmers (Seilacher 1990; Röhl 1998; but see Jäger and Fraaye 1997, who describe some ammonites of the genus *Harpoceras* with crustacean remains in their living chamber). However, some differences seem to exist in the mode of life of the various cephalopods. While the ammonites occur throughout the sections, belemnites are restricted to layers where ammonites are rare. Because these layers usually also contain some benthic bivalves, a nektobenthic mode of life was suggested for the belemnites (Röhl 1998). Besides the cephalopods, only rare specimens of a gooseneck barnacle (pseudoplanktonic scalpellid crustaceans) can be assigned, without doubt, to the pelagic realm (Seilacher 1990).

## *Benthic Organisms (Body Fossils)*

Although no bottom-dwelling vertebrates are known from the Posidonia Shale, some invertebrate species are indisputably benthic. Most of them are quite rare, but their articulated state of preservation indicates that they are autochthonous. These unquestionably benthic organisms are mostly restricted to certain horizons and are found mainly in the lowermost and in the upper part of the Posidonia Shale (Brenner and Seilacher 1978; Urlichs, Wild, and Ziegler 1994) (Figure 15.2). Members of the benthos include rare asteroids and ophiuroids (Riegraf, Werner, and Lörcher 1984; Seilacher 1990), diademoid echinoids (Urlichs, Wild, and Ziegler 1994), and holothurians (only isolated ossicles in microfossil samples) (Riegraf 1985). Although the rare decapod crustaceans (*Uncina, Proeryon, Coleia*) (Figure 15.7) have been treated by some authors as possibly allochthonous (Hauff and Hauff 1981; Seilacher, Reif, and Westphal 1985), they are now widely regarded as autochthonous benthic organisms of the Posidonia Shale basin (Seilacher 1990).

Unquestionable members of the benthos also include some rare brachiopods (*Lingula, "Rhynchonella," Spiriferina*), which occur only in beds

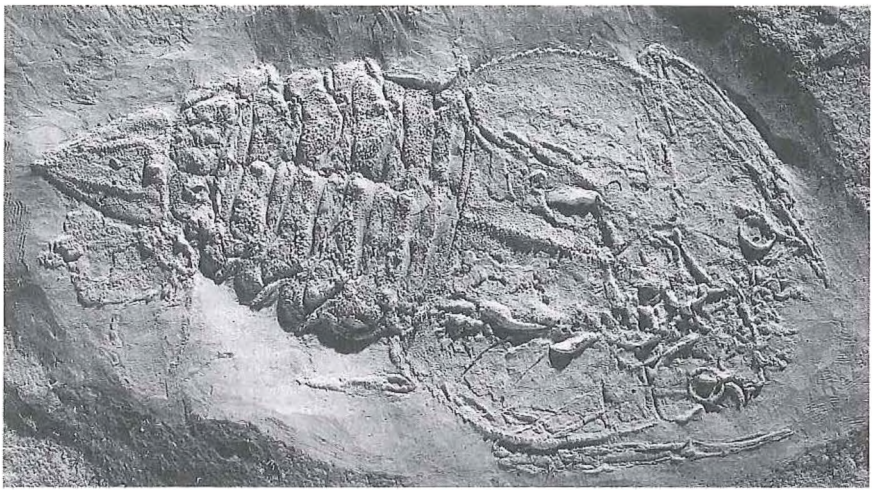

**FIGURE 15.7** Decapod crustacean *Proeryon macrophthalmus*. Length of specimen is 15 cm. (Photo by H. Lumpe, courtesy of Staatliches Museum für Naturkunde, Stuttgart)

with low organic carbon content (Hauff and Hauff 1981; Riegraf, Werner, and Lörcher 1984; Röhl 1998). Larger gastropods are exceedingly rare in the Posidonia Shale, and most of the eight species are known from only a few specimens (Riegraf, Werner, and Lörcher 1984). Among the bivalves, several genera were endobenthic (*Solemya, Mesomiltha, Goniomya*) or semi-infaunal (*Cucullaea, Pinna*). Although these bivalves (which occur only in beds with low organic carbon content) are rare and were considered by some to be transported (Riegraf 1977), their preservation suggests that they are autochthonous (Bandel and Knitter 1986).

The microfossils of the Posidonia Shale, which are difficult to isolate from the bituminous shales and limestones, have recently been documented comprehensively (Riegraf 1985). In the strongly bituminous layers, foraminifers are either absent or represented by only an assemblage of small, mostly unsculptured species. Ostracodes are exceedingly rare in bituminous shales (Riegraf 1985). However, only a few horizons have not yielded foraminifers (Riegraf 1985). In bioturbated layers, the foraminiferan assemblage is more diverse and contains larger species, and ostracodes, although always a minor component, are present (Riegraf 1985).

## *Trace Fossils*

Whereas the majority of the Posidonia Shale beds are finely laminated, as many as 14 bioturbated intervals containing a low-diversity assemblage of trace fossils were found throughout the sequence (Savrda and Bottjer 1989). The most common trace fossils are *Chondrites, Phymatoderma,* and

*Thalassinoides* (Savrda and Bottjer 1989), but in addition *Spongeliomorpha, Planolites,* and *Rhizocorallium* have been observed (Brenner and Seilacher 1978; Kauffman 1978, 1981). *Chondrites,* which usually occupies the lowermost tier, is interpreted to be produced by a worm-shaped animal living in symbiosis with sulfide-reducing bacteria (Fu 1991). *Phymatoderma* (formerly also known as *Chondrites*), on the contrary, was produced by a deposit feeder (Fu 1991). The bioturbated beds have been viewed as very short, one-phase benthic events (Brenner and Seilacher 1978). Whereas this seems to be true for thin horizons in the middle Posidonia Shale, thicker beds (*Seegrasschiefer*) found in the lower and uppermost part of the Posidonia Shale probably represented extended periods (several years) of bottom-water oxygenation (Savrda and Bottjer 1989).

## *Controversial Fossils (Pseudoplanktonic or Benthic)*

Apart from the vertebrate fauna, the Posidonia Shale of southern Germany is most famous for the occurrence of large articulated crinoids (Hauff and Hauff 1981; Seilacher 1990; Urlichs, Wild, and Ziegler 1994). Specimens of the crinoid *Seirocrinus subangularis* may reach a length of up to 20 m and are, unless broken free, always attached to fossil logs (Seilacher, Drozdzewski, and Haude 1968) (Figure 15.4). Detailed investigation of a single occurrence revealed that these crinoids were attached to the underside of the log and were therefore pseudoplanktonic (Seilacher, Drozdzewski, and Haude 1968). This view has been challenged by Rasmussen (1977) and Kauffman (1978, 1981), who argued that these crinoids colonized the upper side of the logs at the seafloor and thus were truly benthic. However, analysis of the functional morphology of the stem of *Seirocrinus* has shown that this species had adapted to a pendent lifestyle and was indeed pseudoplanktonic (Simms 1986).

Associated with crinoids and also frequently found attached to logs is the inoceramid bivalve *Pseudomytiloides dubius* (Hauff and Hauff 1981; Urlichs, Wild, and Ziegler 1994). This attachment, as well as their scattered occurrence throughout the sequence, points to a pseudoplanktonic lifestyle (Seilacher 1982b, 1990; Seilacher, Reif, and Westphal 1985). However, although *Pseudomytiloides* is one of the most common bivalves of the Posidonia Shale, wood fragments are much rarer (Kauffman 1981). Furthermore, wood remains do not always seem to be overgrown on their underside, as would be expected when colonized by a byssally attached pseudoplanktonic bivalve (Kauffman 1981). It thus seems possible that *Pseudomytiloides* was facultatively pseudoplanktonic and that many specimens lived benthically (Wignall and Simms 1990; Etter 1996; Röhl 1998).

Other byssally attached bivalve genera of the Posidonia Shale include *Gervillia, Pteria, Plagiostoma, Antiquilima, Oxytoma,* and *Pseudomonotis*

(Riegraf, Werner, and Lörcher 1984). Earlier authors have regarded all these species as pseudoplanktonic (Fischer 1961). Again, Kauffman (1978, 1981) challenged this view and assigned all those bivalves to an epibenthic lifestyle. Articulated shells of these bivalves always occur in association with ammonite shells (Kauffman 1981; Seilacher 1982a). While Kauffman believed that colonization took place on dead ammonite shells at the seafloor, it can be shown that these ammonite shells were colonized while still afloat and the bivalves were thus pseudoplanktonic (Seilacher 1982a). Ammonite shells are overgrown on both flanks, which becomes impossible once an ammonite shell is lying with one flank on the seafloor (Seilacher 1982a). A possible exception to the pseudoplanktonic lifestyle is *Pseudomonotis substriata,* which occurs at certain localities in large numbers in a bed of the uppermost middle Posidonia Shale (Hauff and Hauff 1981); this species may have been benthic.

A pseudoplanktonic lifestyle is even more obvious for the cemented bivalves (*Liostrea, Exogyra, Plicatula*), attached inarticulate brachiopods (*Discinisca*), and serpulid worms. Again, they are associated with ammonite shells or found as isolated upper valves (Hauff and Hauff 1981; Seilacher 1982a). The fact that available benthic substrates like vertebrate bones and belemnite rostra show no encrustation at all (Seilacher 1982a; only one oyster attached to an ichthyosaur bone, which was recently found; A. Seilacher, personal communication, 1996) strongly supports the view that these organisms were truly pseudoplanktonic.

The most common fossils of the Posidonia Shale are the bivalves, which gave this formation its name: the posidoniids (Seilacher 1990; Urlichs, Wild, and Ziegler 1994). Two species can be distinguished: *Steinmannia bronni* (formerly *Posidonia bronni* var. *magna*) and *Bositra buchi* (= *Posidonia bronni* var. *parva;* but see Röhl 1998, who argues that there is only one species, *Bositra buchi,* occurring in different sizes). These species have gained some celebrity because of their widespread occurrence in black shales and the highly controversial interpretation of their mode of life. Earlier authors regarded them as epibenthic, but with the advent of the idea that black shales formed under anoxic bottom-waters, they were mostly interpreted as pseudoplanktonic (historical review in Jefferies and Minton 1965). However, there is no trace of a byssal notch, and it is doubtful that these species could byssally attach to a hard substrate (Jefferies and Minton 1965). As a radical solution, a nektonic mode of life was proposed to explain their occurrence in black shales (Jefferies and Minton 1965).

The interpretation of these bivalves as pelagic organisms has recently been supported, but now as fully planktonic, huge larvae (Oschmann 1993, 1994). However, this seems unlikely for three reasons. First, the original shell was probably thicker than reported by Jefferies and Minton

(1965; Kauffman 1981), which would preclude a floating lifestyle. Second, these bivalves do show a clear facies distribution in the Posidonia Shale, with *Steinmannia* occurring only in the lower part, and *Bositra* only in particular laminae in the upper part of the sequence (Riegraf, Werner, and Lörcher 1984; Urlichs, Wild, and Ziegler 1994; Röhl 1998). Third, well-preserved bedding-plane associations of articulated *Bositra* shells do show a highly regular spatial distribution, which would be impossible to explain if these shells had rained from the upper part of the water column (Etter 1996). A benthic mode of life thus seems the most likely explanation (Kauffman 1981; Seilacher 1990; Urlichs, Wild, and Ziegler 1994). It has been suggested that *Bositra* was chemosymbiotic (Kauffman 1988; Seilacher 1990), but this is difficult to imagine for an epibenthic species that is also known from sediments deposited under fully oxygenated conditions (Jefferies and Minton 1965).

A last genus that needs to be mentioned is the tiny gastropod *Coelodiscus* (maximum shell diameter, 3 mm). Because this gastropod was found mainly in carbonate-rich layers and in concretions around ichthyosaurs (Urlichs, Wild, and Ziegler 1994), it was concluded that it was a benthic scavenger (Einsele and Mosebach 1955; Fischer 1961). However, this genus occurs in microfossil samples throughout the Posidonia Shale (Riegraf 1985), and because of the close resemblance of its shell to those of certain modern heteropods (planktonic carnivores), it was concluded that *Coelodiscus* was planktonic (Bandel and Hemleben 1986).

In sum, the large majority of Posidonia Shale fossils were pelagic organisms. Even if some of the taxa formerly assigned to a pseudoplanktonic lifestyle actually belonged to the benthos, benthic organisms are still confined to certain horizons in the Posidonia Shale and are almost absent in the middle Posidonia Shale (*falciferum* zone). The paleoecological analysis, therefore, strongly supports a modified stagnant basin model.

## Conclusions

The Posidonia Shale of southern Germany has probably received more scientific attention than any other Lagerstätte. This deposit is especially famous for its reptiles and fish and has yielded the best Jurassic marine vertebrate fauna of the world. It is from this Lagerstätte that we know about the actual body form of ichthyosaurs. The Posidonia Shale has also provided spectacularly preserved invertebrates, including fully articulated crinoids attached to logs, and the only belemnites showing soft-part preservation.

Although many features of this Lagerstätte have been studied thoroughly, there are still many controversies surrounding it. Strongly oxygen-depleted bottom-waters are indicated throughout the deposition

of the Posidonia Shale, but there is still dispute about the amount of oxygen present and the duration of anoxic intervals. Although there is also some controversy about the exact nature of the depositional environment, a modified stagnant basin model is supported by the paleontological evidence. Whereas some of the fossils formerly considered as pseudoplanktonic or nektonic may actually represent benthic organisms, pelagic taxa are still predominant. Furthermore, benthic species preferentially occur in the lowermost and in the upper Posidonia Shale, and are considered to have been deposited under somewhat less severely oxygen-depleted bottom-waters.

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