Chapter 16
Deformities in the Late Callovian (Late Middle Jurassic) Ammonite Fauna from Saratov, Russia

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1 Introduction

Like other molluscs, every ammonite carries a record of its ontogeny and, commonly, its death, in its shell. Traumatic life events such as bites, diseases, epizoa, and diet all left evidence in the shell as scars, blisters, disfigurations, holes, nicks, crushing, attachments, and abnormalities, along with slow, rapid, stunted, or enlarged growth. If an ammonite survived bites due to predation, its shell documented the damage. Often, the cause and stage of life when that injury happened can, at times, be interpreted and diagnosed. If an ammonite did not survive the attack, its shell

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commonly exhibits holes or missing portions. If most of the ammonite was consumed, only parts, pieces, or fragments of the shell will be found.

In the case of severe, sublethal bites, injuries to ammonite shells are expressed as conspicuous scars, blisters, or uneven growth. Deep bites to the body chamber sometimes resulted in the mantle rupturing out beyond the confines of the shell. Some of the fragmented shell that originally covered that area could be resorbed, and new shell was often secreted to patch the ruptured area. Deep bites to the mantle are expressed in the form of long scars, irregular apertures, deep-healed gouges, or displaced shell fragments molded back into the shell. If the ammonite was subjected to only minor attacks (nicks and bites to the aperture at some point in life), proof of these injuries are usually shown as interruptions or slight distortions in the normal shell structure. Sometimes, this shell damage can be distinguished as interruptions in the ribbing, rib displacement, irregular shell growth, small scars, or even as repeated "check marks" in the shell.

The presence of epizoa also can disfigure the shell. Commonly, these animals were serpulids, brachiopods, limpets, bryozoans, oysters, pelecypods, etc. Davis et al. (1999) noted that attachments of epizoa rarely occurred on living ammonites. Seilacher (1982) observed that it was quite common for epizoa to attach themselves to empty ammonite conchs as they floated in the sea or lay on the sea floor. Normally, epizoa did little to no obvious damage to living ammonites, merely etching the surface and perhaps causing little more than an inconvenience to the ammonite. In rare instances, epizoa were overgrown by the ammonite, and deformation occurred to the ammonite shell.

There have been numerous papers on the deformations of ammonite shells due to epizoa, most notably Hölder (1956), Hengsbach (1996), Maeda and Seilacher (1996), Davis et al. (1999), Checa et al. (2002), and Keupp (1996, 2000, 2005). Hölder (1956, 1973) assigned a complex series of "forma" names to identify the different types of pathologies present in ammonite shells and Hengsbach (1996) provided a nearly complete list of different types of "forma" names for each pathological deformation. Davis et al. (1999) tried to tackle the complex details and terminology, coining the new term "epicole" for any organism that spends its life attached to a hard surface, be it living, dead, or inorganic. Checa et al. (2002) described the complex deformities associated with epizoa attached to an ever-growing ammonite, and attempted to understand the growth patterns of the ammonite in response to these attached organisms. H. Keupp has spent the last several decades collecting and publishing on as many different ammonite pathologies as possible, while trying to establish the different ways that ammonites survived and adapted to other organisms that bit, damaged, and formed encrustations.

Large collections of ammonites from a single horizon or, perhaps, a single locality, can provide much information on the life habits, growth, predation, and even death of the ammonites. Individual growth, dimorphism, predation incidence, and interactions with other species can also be assessed. The study of large collections of a single ammonite species allows us to elucidate the life and death of these animals.

The upper Callovian *Quenstedtoceras (Lamberticeras) lamberti* Zone (Upper Jurassic), exposed in the Dubki Quarry near Saratov, Russia, has preserved a large number of unusually deformed ammonites. An unknown percentage of these ammonites were subjected to normal predation, with many of them preserving healed defects and scars in their shell. Along with healed predation, many of these ammonites also exhibit some unusual malformations. It seems that while the ammonites were living, tiny organisms attached themselves to some of the shells and began to grow. Probably, by the time the ammonites discovered something was growing on their shells, it was already too late to remove the epizoa. Because the ammonites continued to grow with these epizoa attached, their shell grew over and around their "guests." This commonly resulted in extreme shell disfigurement for the ammonites and death for the epizoa. Because this is such a large and unique collection of pathological specimens from one site, this paper will describe and illustrate most of the types of pathologic distortions in the species *Quenstedtoceras* (*Lamberticeras*) *lamberti* Sowerby, 1819, and make some interpretations as to why and how these abnormalities occurred.

2 Material

The *Quenstedtoceras* (L.) *lamberti* Zone lies in the uppermost upper Callovian of the Upper Jurassic. The fauna from this zone was deposited in clays and marls in the central portion of the Russian Platform (Meledina, 1988). The *Q*. (L.) *lamberti* Zone directly overlies the *Peltoceras athleta* Zone, corresponding to the western European ammonite zones (Meledina, 1988). The ammonite fauna in the *Q*. (L.) *lamberti* Zone is also quite similar to that of the stratotype described from Europe. In addition to *Quenstedtoceras*, other ammonite genera in the Dubki Quarry include *Eboraciceras*, *Grossouvria*, *Hecticoceras*, *Kosmoceras*, *Peltoceras*, *Prorsiceras*, *Cadoceras*, and *Rursiceras* (?). Further information on the geology of the area can be found in Aleksejev and Repin (1986).

Residing within the collections of the Black Hills Museum of Natural History and Black Hills Institute of Geological Research, Hill City, South Dakota, are approximately 1,100 ammonite specimens collected from the Dubki Quarry, a commercial clay quarry and brickyard, near Saratov, Russia. These collections contain nearly 1,000 specimens of *Quenstedtoceras* (Lamberticeras) *lamberti* and 100 mixed specimens of *Eboraciceras*, *Peltoceras*, *Kosmoceras, Grossouvria*, *Prorsiceras*, *Cadoceras*, and *Rursiceras* all collected from the same zone during 2001 and 2002. There are 167 specimens of *Q*. (*L.*) *lamberti* and 89 specimens of other ammonite genera that exhibit a wide range of healed injuries due mostly to predation. A total of 655 specimens of *Q*. (*L.*) *lamberti* display very unusual deformed growth of the shell (15 of these also exhibit healed predation scars and are included in the above count). There are 48 *Q*. (*L.*) *lamberti* with an unusual distortion, where the ammonite grew in a tilted manner due to an unknown cause. A total of 43 *Q*. (*L.*) *lamberti* exhibit small depressions in the venter, believed to be due to the attachment of

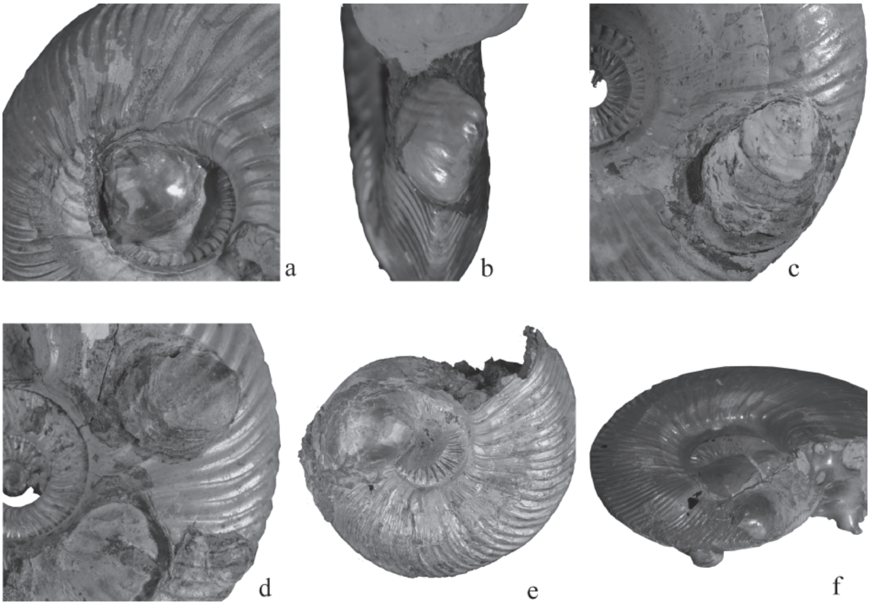

Fig. 16.1 *(a)* Placunopsis *(9 × 10 mm) on umbilicus of* Quenstedtoceras (L.) lamberti *(BHI-5360). (b)* Placunopsis *(7 × 9.7 mm) on venter of* Q. (L.) lamberti *(BHI-5345). (c) Ostrea (?) (15 × 19.8 mm) on flank of* Q. (L.) lamberti *(BHI-5336). (d) Ostrea (19.5 × 19.5 mm) on flank of* Q. (L.) lamberti *(BHI-5469). (e)* Placunopsis *(11.5 × 15 mm) on* Q. (L.) lamberti *(BHI-5306). (f) Four* Placunopsis *(largest 12.5 mm; smallest 8.3 × 10 mm) on flank, venter, and umbilicus of* Q. (L.) lamberti *(BHI-5340).*

epizoa on the venter or the result of a healed bite. Only 95 specimens of *Q*. (*L*.) *lamberti* in this collection exhibit little to no shell deformation.

While about 25% of these ammonites display healed, predatory scarring, 60% exhibit some very unusual and grotesque abnormalities from a nonpredatory source. These bizarre deformities appear to be the result of an infestation of immature bivalves attached to the shell of the ammonite. Originally, the author believed the epizoa were articulate brachiopods; however, H. Feldman (2005, personal communication) confirmed that they were not brachiopods, but rather bivalves. D. Seilacher finally identified the majority of the epizoa as the bivalve *Placunopsis* along with some minor *Ostrea* (2005, personal communication).

Although this collection contains eight different genera of ammonites with healed injuries, only *Quenstedtoceras* (*L*.) *lamberti* seems to have been utilized as a host for this infestation of epizoa. It appears that, in most cases, the epizoa were not removed by the ammonites and, as a result, the ammonites grew over and/or around their “guests.” Some bivalves grew quite large relative to the size of their ammonite hosts, and this resulted in some very bizarre and erratic deformities to

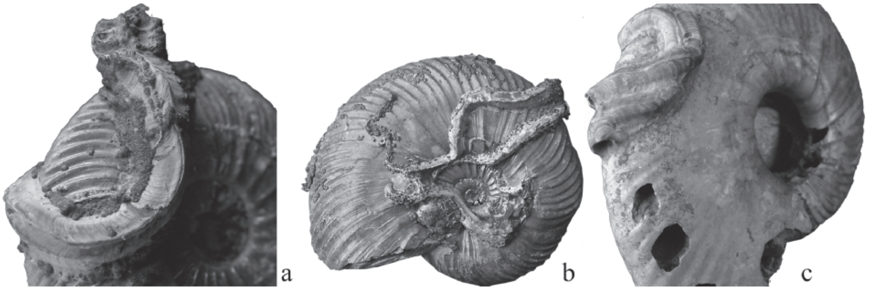

Fig. 16.2 *(a) Serpula on flank and venter of* Quenstedtoceras (L.) lamberti *(BHI-5440) (x1). (b) Serpulids lying across umbilicus, flank, and venter of* Q. (L.) lamberti *(BHI-5442) (x0.7). (c) Serpulids crossing over the venter of* Q. (L.) lamberti *(BHI-5597) (x1).*

the ammonites. The ammonite shell became further distorted when the animal tried to compensate for the additional weight and uneven distribution of the bivalves.

It is unknown why the bivalves attached themselves to the ammonites. It is possible that *Quenstedtoceras* (*L.*) *lamberti* were being used as carriers by the bivalves to migrate into other areas of the sea, as documented by Allen (1937) for extant articulate brachiopods attached on mobile gastropods and scallops. The ammonite fauna from the Dubki Quarry was collected in marl or clay (material suitable for making bricks). Deposition of these clay particles suggests a calm, deep marine environment (Reineck and Singh, 1980). The ammonite specimens contain a great deal of pyrite filling and replacement in the phragomocone, indicating that they were buried in a reducing or oxygen-deficient environment (Reineck and Singh, 1980). Because the ammonites would have been unable to survive in this low oxygen environment, they must have been living in the water column, well above the bottom, although (to my knowledge) there has not yet been any isotopic studies of *Quenstedtoceras* (L.) *lamberti* to determine what water depth they inhabited. They were most likely active swimmers, though it is not known how well they were able to swim.

As stated before, approximately one thousand ammonite specimens from the Dubki Quarry were used in this study. That is a small portion of the total number of ammonites collected from this site to date. S. Baskakov (personal communication, February, 2003) estimated that between 50,000 and 70,000 ammonite specimens were collected from this locality by the Spring of 2003, and thousands more since then. These numbers represent a very small percentage of the ammonites originally deposited in this particular stratum, as large excavations have previously taken place in the quarry to mine the clay (and the ammonites) for the production of industrial bricks. Of all the genera of ammonites identified from this locality, only *Quenstedtoceras* (*L.*) *lamberti* exhibits deformations due to attached epizoa, while all species from the locality exhibit sublethal pathological scarring due to bites or predation.

It is interesting to note that there are no complete or even nearly complete specimens of *Quenstedtoceras* (*L.*) *lamberti* in this entire collection. All of the specimens from this site consist primarily of phragmocones; partial body chambers

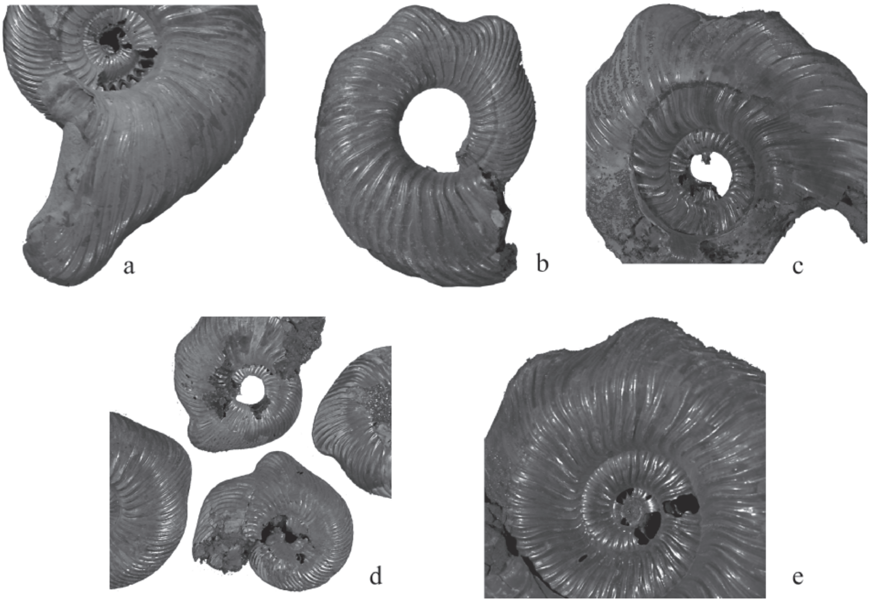

Fig. 16.3 *(a) Protuberance extruding from venter of* Quenstedtoceras (L.) lamberti *(BHI-5379) (x1). (b) Two small swellings on the venter of* Q. (L.) lamberti *(BHI-5380) (x0.9). (c) Protuberances extruding from the venter of* Q. (L.) lamberti *(BHI-5372) (x1). (d) Protuberances extruding from the venter of several* Q. (L.) lamberti *specimens (BHI-5366 left, BHI-5367 top, BHI-5335 right, BHI-5374 bottom) (x0.5). (e) Flattened swellings on the venter of* Q. (L.) lamberti *(BHI-5391) (x1.5).*

are rare. Apparently, either the body chambers were not filled with a stable enough host material, or postmortem predation did away with the body chambers before preservation. The large numbers of *Q.* (*L.*) *lamberti* from this site most likely represent mass spawning deaths over several years or generations. This is one of the largest known collections of a single ammonite species from a single site with such a large percentage of deformities resulting from the infestation of epizoa. All of the ammonites illustrated in this paper reside in the collection of the Black Hills Museum of Natural History, 117 Main St., Hill City, South Dakota and are identified by the prefix BHI.

3 Previous Reports of Epizoa on Ammonites

Reports of epizoa on ammonites are not something new; over the last 50 years there have been scores of papers. It is not rare or unusual to find epizoa attached to ammonite shells, but often they are overlooked. Discovering epizoa on ammonites is often dependant on the ammonite species as well as how much of the host rock is saved with the ammonite. Because certain ammonite species are rarely found with epizoa, we can assume that these species were either not suitable hosts or that they may have been able to keep themselves much cleaner than other species. In the case of saving the host rock with the fossil, many fossil preparators often remove all matrix from ammonites during preparation. Because epizoa (and the ammonite shell) are often weathered or textured on their outer surface, they stick to the rock when the ammonite is cleaned. In these cases, saving the host rock and looking at the outer surface of the ammonites can often result in the discovery of epizoa attached to the ammonite shells. Below (listed by date) are some cases of epizoa on ammonites that are important to this study.

Seilacher (1960) reported on the encrustation of a Late Cretaceous ammonite *Buchiceras* by oysters [for further discussion about this example, see Keupp et al. (1999) and Seilacher and Keupp (2000)]. The oysters attached to the ammonite during life, encrusting the flanks, the umbilicus, and the venter. The oysters on the lower flanks and venter grew quite large with respect to the ammonite, several nearly one-fourth to one-third the diameter of the ammonite. Seilacher used the oysters to determine the orientation of the swimming ammonite. Based on the encrustation, he concluded that *Buchiceras* was neither a crawler nor a rapid swimmer, but rather a slow floater that swam near the ocean floor.

Meischner (1968) described an adult *Ceratites* (Triassic) encrusted with *Placunopsis ostracina*, on the flanks, umbilicus, and venter. He determined that swarms of larval *Placunopsis* had settled on the ammonite several times during the life of the animal. Based on the different phases of *Placunopsis* settlements on the ammonite shell, he concluded that these attachments occurred over four annual periods, meaning that the last whorl of the ammonite was formed within four years.

Cope (1968) determined that the oyster distribution on some Kimmeridgian ammonites from Dorset was most likely a postmortem attachment. These ammonites were nearly completely encrusted on the side facing up, and relatively free from oysters on the side facing down, in contact with the sediments.

Seilacher (1982) analyzed the orientations and patterns of overgrowth of oysters, serpulids, bryozoans, and articulate brachiopods on ammonites from the Posidonia Shale of Holzmaden. The importance of this study is that it indicated that many of the epizoa were attached while the host (ammonite) was still alive.

Keupp (1996) illustrated some specimens of *Pavlovia* preserved without epizoa that exhibit distortions similar to some of the pathologies present in *Quenstedtoceras* from the Dubki Quarry. Keupp (1984, 2000: 126) later illustrated several extreme umbilical and dorsal distortions in *Pavlovia* and attributed them to parasites and brachiopods that had attached to the venter of the still-growing ammonites (the epizoa were no longer attached).

Kase et al. (1998) illustrated a specimen of *Placenticeras* from South Dakota with 102 limpets (*Acmaea occidentalis*) attached to both flanks of the ammonite. They concluded that the limpets either attached themselves to a floating shell or to a live ammonite. I have observed hundreds of specimens of *Placenticeras* with attached limpets and know that many of the limpets were attached during the lifetime of the ammonites because the limpets are frequently found under the overlying whorls. Shell distortion from infestation of the epizoa has not been recognized in any of these specimens. Limpet-like or oyster-like animals have been found under some layers of shell near the aperture of a large specimen of *Baculites grandis* (BHI 5502), indicating that they too attached during life.

Davis et al. (1999) tried to cover the many different forms of epizoa on shelled cephalopods. Their study surveyed the evidence of epizoa in many Paleozoic ammonoids from Morocco and Texas illustrating many of the different forms of attachment. They attempted to bring together the records of such epizoa along with the many different manners and places of attachment, whether on living or empty shells. They found that epizoa on Paleozoic ammonites was less common than on co-occurring nautiloids, but that differences could have been due to collector or preparator bias. They concluded that not enough data have been acquired yet to determine the distribution and evolution of epizoa on ammonites through time and that more data were needed.

Checa et al. (2002) illustrated many shell deformations caused by epizoa and listed this type of malformation in 16 Jurassic ammonite genera from Eurasia. They described the action taken by the ammonite to grow over the epizoa and listed two different coiling patterns that ammonites used as they continued their growth: zigzag and trochospiral. Zigzag was defined as a lateral deviation of the whorl with an epizoön more or less centered on the venter of the underlying whorl. Trochospiral was defined as a displacement in whorl growth to counterbalance the weight of the ever-enlarging epizoön upon the ammonite's center of gravity.

There has also been one paper written on the pathologies in *Quenstedtoceras* from the Dubki Quarry. Keupp (2005) published on some of the healed predations and deformations due to epizoa from this site. He noted that "parasites" caused much of these very bizarre deformities, and figured several specimens with these malformations. His publication showed many of the types and forms of grotesque deformities that this study also shows.

4 Terminology

Finding the correct terminology for the epizoa attached to living animals has been a difficult task. Following the presentation "Symbiotic deformities in the Late Callovian fauna from Saratov, Russia," at the Sixth International Cephalopod Symposium, held in Fayetteville, Arkansas, 2004, a discussion ensued on the proper use of terminology regarding the word "symbiont." G. Westermann (personal communication, September, 2004), argued that the term symbiont was improper, and should not be used to describe the attached organisms on *Quenstedtoceras* (*L.*) *lamberti*, while others argued in favor of this usage. There has been a host of terms that ammonite biologists have used when referring to attached "guests" on "host" ammonites, such as epibionts, epizoa, epizoans, epifauna, parasites, etc. (see Davis et al., 1999).

One of the goals of this study is to find the proper terminology to describe the ammonite and the attached bivalve (*Placunopsis*). Both were alive at the same time, neither feeding on the other nor needing the other to survive. The bivalves attached

Fig. 16.4 *(a)* Placunopsis *(7 × 9 mm) on the venter of* Quenstedtoceras (L.) lamberti *(BHI-5345). (b)* Placunopsis *(2.5 × 3 mm) on the flank and venter of* Q. (L.) lamberti *(BHI-5598). (c) Ventral swellings on* Q. (L.) lamberti *with* Placunopsis *(8 mm across) near the umbilicus (BHI-5354).*

themselves to only a small percentage of ammonites, yet the bivalves did not need to live on ammonites to survive. Both the host and the guest were ultimately harmed in different ways from this uncommon union, and it appears that neither one benefited, though one of them may have. This relationship has previously had little written about it.

Grier and Burk (1992) described symbiosis as “living together,” along with “an interaction that brings animals of different species into close relationships throughout much or all of their lives, particularly commensalism, mutualism, and various forms of parasitism.” The biological definition of symbiosis in the Oxford English Dictionary is an “Association of two different organisms (usually two plants, or an animal and a plant) which live attached to each other, or one as a tenant of the other, and contribute to each other’s support. Also more widely, any intimate association of two or more different organisms, whether mutually beneficial or not.” Parker (1994) described symbiosis as the interrelationship between two different organisms where the relationship is neither harmful nor beneficial. For the general definition of symbiosis, the term symbiont would work, but because both were ultimately harmed in the union, symbiosis is not the proper term.

Nor was this a commensal union. Parker (1994) described as commensal when animals or plants live with other animals or plants for support, or sometimes for mutual advantage, but not as parasites. Both the ammonite and the bivalves certainly lived together in a nonparasitic relationship, but it appears that there was neither any mutual advantage nor a single advantage for either animal.

Grier and Burk (1992) used the term amensalism for an encounter that results in harm or loss to one of the species while not affecting the other. Since both were ultimately harmed, by either deformation or death, this term does not seem to be quite correct either.

Among “ammonitologists,” the terms epizoa (plural) and epizoön (single) (Davis et al., 1999) are frequently used, but for most epizoa, there is either no harm to the coexisting animals or the damage done to each other is usually negligible to nonexistent. Grier and Burk (1992) described epizoa as simply animals that live on other animals; but epizoa as described by Parker (1994) are any of various parasitic animals that live externally upon the bodies of other animals. Davis et al. (1999) proposed the term "epicole" for an organism that might live on a hard substrate or any empty shell or even a shell still occupied by its maker.

Grier and Burk (1992) described a defensive interaction as one "where one or both of the participants stand to lose, including amensalism and competition…. Both sides actually lose when one or both are defensive, even if they both survive." It appears that, in many ways, this was a defensive interaction between the two participants. The ammonites became greatly deformed, and most of the bivalves were buried under the ammonite shell; thus, it appears that neither one was a winner.

Normally, the choice for the correct terminology is simple, such as in the case for animals attached after death (epibionts in the act of epibiosis), or more commonly, if the attached animal was a parasite. R. A. Davis (2005, personal communication) noted how there seems to be a problem with finding the one word that best describes this relationship between the host and the "guest." The proper terminology is difficult to ascertain for this most unusual relationship because both organisms lost due to their ultimate connection. J. Grier (2005, personal communication) recommended against using the term symbiosis, and stated that the term epizoa are correct but it may carry inadvertent connotations. He suggested that maybe a new term should be coined, or maybe not use any terminology at all.

R. A. Davis (2005, personal communication) advised that the relationship should be called "epizoism" and the "guest" should be referred to as an epizoön (single) or epizoa (plural), but only if it could be demonstrated that the "guest" was attached to the "host" while the "host" was still alive. To prove that the "host" was alive while the "guest" was attached and to prove that the deformities were caused from this relationship is the basis for this study. Davis' suggested terminology will be used, but sparingly. There appears to be a need to coin a term for the unique relationship between the animals discussed in this paper, but that will be left to those more knowledgeable on the subject than the author.

5 Epizoa

D. Seilacher (2005, personal communication) tentatively identified the majority of the epizoa attached to the ammonite shell as *Placunopsis*, with occasionally some *Ostrea* (Fig. 1). *Placunopsis* were living, attached "guests" that seem to have interacted only with *Quenstedtoceras* (*L.*) *lamberti*, while leaving the other ammonite species in the zone alone. Seilacher (1960) referred to *Placunopsis* as a false oyster, based on the attachment of the right valve rather than the left valve, as in true oysters (such as *Ostrea*). In *Placunopsis*, the lower valve is flat, the upper valve is rounded, and the ornamentation is barely visible. Sometimes the shell structure seems to mimic the ornamentation of *Q.* (*L.*) *lamberti*, perhaps because the ammonite grew over the bivalves while they were still living and growing.

Placunopsis found at the Dubki Quarry seem to have been almost a plague on *Quenstedtoceras* (*L.*) *lamberti*, and are inferred to be the cause of shell deformations

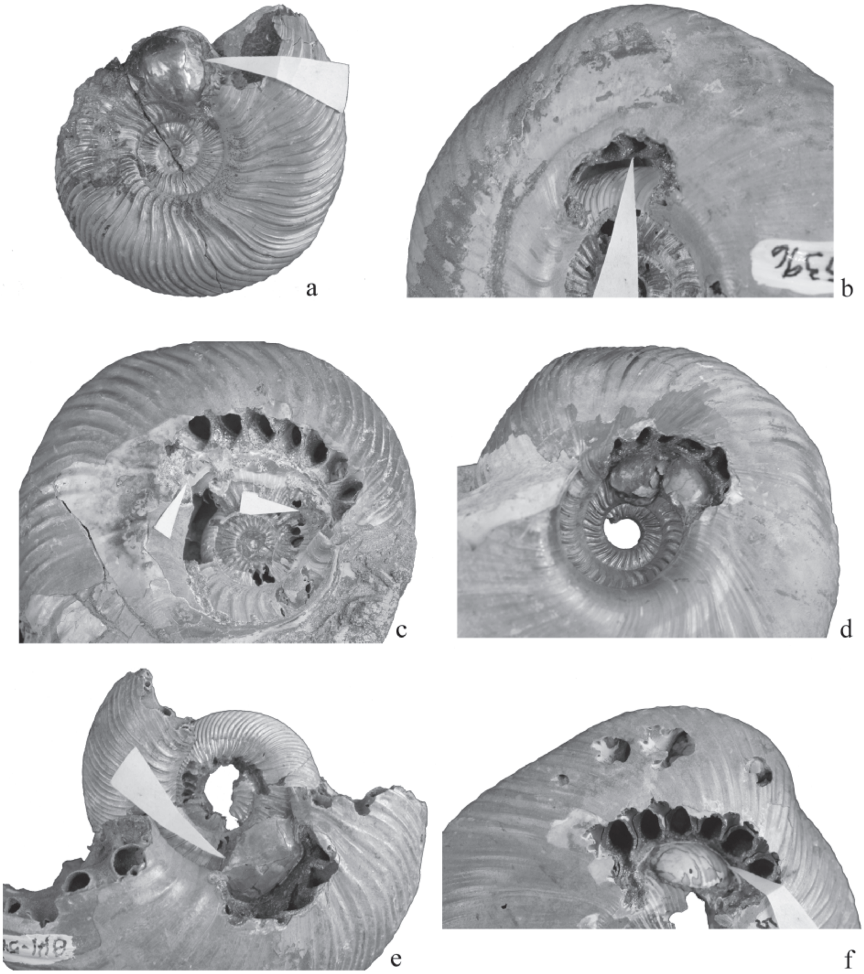

Fig. 16.5 *(a)* Placunopsis *(10 × 11 mm) exposed on* Quenstedtoceras (L.) lamberti *(BHI-5352). (b) Epizoa are missing in exposed void on the venter of* Q. (L.) lamberti *(BHI-5396) (x1). (c) Two small* Placunopsis *(6 mm across) on* Q. (L.) lamberti *(BHI-6000). (d) Two large* Placunopsis *(5 × 7 mm and 6 × 9 mm) on* Q. (L.) lamberti *(BHI-5357). (e)* Placunopsis *(10 × 15 mm) exposed on* Quenstedtoceras (L.) lamberti *(BHI-5470). (f)* Placunopsis *(10.5 × 15 mm) exposed on ventrolateral shoulder of* Q. (L.) lamberti *(BHI-5383).*

in more than 700 specimens in our collections, although the overall percentage is unknown. By comparison, *Ostrea* were found on only eight specimens. While most *Placunopsis* are assumed to be juveniles, some seem to have approached adult size. Attached *Placunopsis* (that were able to be measured on *Q.* (*L.*) *lamberti*) range in size from 2.5 × 3 mm (Fig. 16.4b) to 16 × 18.5 mm (Figs. 16.1, 16.4b, 16.5). Most attached *Placunopsis* are probably smaller than 2 mm, but, if they are, they tend to be destroyed during preparation.

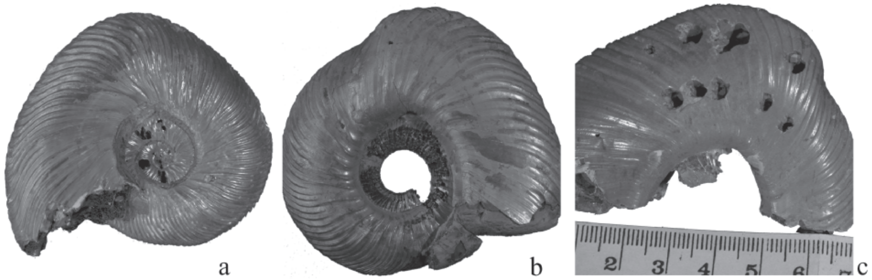

Fig. 16.6 *(a) "Hunchback" deformity on* Quenstedtoceras (L.) lamberti *(BHI-5376) (x0.8). (b) "Hunchback" effect on the venter of* Q. (L.) lamberti *(BHI-5342) (x0.6). (c) Typical "hunchback" on the venter of* Q. (L.) lamberti *(BHI-5383) (x0.7). Note that this is the same specimen as Fig. 5b, but before preparation.*

Fifteen *Quenstedtoceras* (*L.*) *lamberti* have serpulid worm tubes attached to them. Some of the worm tubes appear to have also grown on the ammonites while the ammonites were still alive (Fig. 16.2). Two specimens have large worm tubes that grew on both flanks and across the venter. There are no shell deformities observed resulting from worm-tube attachment, so even though some of the worms grew in a manner that suggests that the ammonites were alive, their attachment to empty ammonite shells could still be a possibility. There are no other types of epizoa detected on *Q*. (*L.*) *lamberti* or any other ammonite genus.

Schindewolf (1936) illustrated four specimens of *Arietites* and *Schlotheimia* from the Jurassic with individual worm tubes (serpulids) growing from one side of the venter to the other. These worms grew larger as the ammonite grew, and their placement on the ammonite shell was determined by how the ammonite shell rotated as the serpulid grew. Landman et al. (1987) observed serpulids, bryozoans, barnacles, and scyphozoans all attached on living *Nautilus*. If present-day serpulids and other epizoa can attach to living *Nautilus*, it is probable that, in the past, serpulids and other epizoa could and did attach to living ammonites (at least in some species).

6 Deformities Caused by Epizoa

The shells of *Quenstedtoceras* (*L.*) *lamberti* contain numerous and bizarre deformities that are attributed to the placement and size of attached epizoa. The pathologies all seem due to *Placunopsis*. In the entire collection of ammonites from Saratov (978 specimens of *Q*. (*L.*) *lamberti*), only 8 specimens have *Ostrea* attached and 15 have serpulids attached. Of the remaining 955 specimens of *Q*. (*L.*) *lamberti*, 655 or 67% of them have deformities known to be caused by *Placunopsis*, and another 101 or 10% are suspected of deformities caused by epizoa. *Placunopsis* attached themselves to the venter, flank, and umbilicus of *Quenstedtoceras*, and sometimes in multiple locations. Within this collection, 4 *Quenstedtoceras* have four *Placunopsis* attached, 12 have three attached, and 38 have two attached. Of these 54 specimens, 17 *Placunopsis* are attached to the flank and venter or flank and umbilicus.

It is known that these epizoa were attached to living ammonites because most of the shell malformations, with the exception of sublethal injuries, were caused by the ammonite growing over the attached organism. In some instances, it also appears that the ammonite grew over the epizoön, but the epizoön somehow dislodged itself, leaving a deformed shell (Fig. 16.5b–f). It is also certain that the epizoa attached when they were still planktonic and then grew. Descriptive names for the location of the deformities will be used in this study, and the causes of the deformities will be discussed. Previously assigned "forma" names are referenced for each deformity, but because there are several types of causes for many of the different "forma," I have chosen not to use this terminology to name the pathology.

6.1 Ventral Attachments

The venter and ventrolateral shoulder of the ammonite are the most common places of attachment of *Placunopsis* on *Quenstedtoceras* (*L.*) *lamberti*. Of 655 known deformities caused by epizoa, 582 or nearly 89% have epizoa attached to the venter or on the ventrolateral shoulder. Obviously, the venter was a more ideal location for attachment without initial discovery, but it was not too favorable for *Placunopsis*. Checa et al. (2002) described ventral deformations on other Jurassic ammonites caused by similar epizoa, and the compensatory growth that was probably undertaken by the ammonites.

6.1.1 Protuberances

Deformity. This deformity is defined as consisting of one or more protuberances on the venter. These protuberances on the ammonite are generally thin, flattened swellings and/or elongated shapes (Figs. 16.3a–c, 16.4a–b). Keupp (2005: Fig. 16.7) illustrated a specimen of *Quenstedtoceras* (*L.*) *lamberti* from the Dubki Quarry with this same deformity. Similar appearing deformities, although caused by bites, were described by Keupp (1976) as *forma inflata* and Kröger (2000) as *forma augata*. Keupp (1976) showed identical multiple ventral protuberances on *Amoeboceras alternans*, which may or may not be due to epicoles. The deformities described as *forma inflata* by Keupp (1996, 2000) and Hengsbach (1996) were not caused by the ammonite growing over an attached epizoön, but rather were the results of bites that had caused a rupture of the mantle, similar to bites seen in scaphites from the US Western Interior (N. L. Larson, 2003).

Cause. This bizarre deformity occurred when a single or several *Placunopsis* attached onto the ammonite venter (Fig. 16.4c). Abnormalities of the ammonite occurred when the shell grew around and over the epizoön attached to the venter, leaving a large, flat, rounded protrusion. The ventral placement of the epizoön caused an unusual deformation to the ammonite and must have been quite terrible for the attached "guest" as well. Because the ammonite grew its shell completely over the epizoön, the epizoön must have died from starvation or suffocation.

Several specimens were taken apart to expose the attached epizoa (Fig. 16.5b–f). While some specimens revealed small and deformed bivalves, most of the bivalves were not very deformed. This additional weight (on the venter) also upset the center of gravity and caused the ammonite to grow off "normal" (Fig. 16.9a), generally resulting in the venter veering off from a straight line, or zigzag as described by Checa et al. (2002).

6.1.2 Hunchbacks

Deformity. A wide, low, broad, sometimes elongated distortion on the venter, which gives the ammonite the appearance of a "hunchback" (Fig. 16.6a–c). Checa et al. (2002) illustrated several deformities caused by epizoa and coined the term zigzag to describe the resulting ammonite growth in relation to the epizoa.

Keupp (2000: 126) illustrated a similar deformity in a specimen of *Pavlovia* sp. cf. *P. iatriensis* from Russia and showed the way that this ammonite shell was

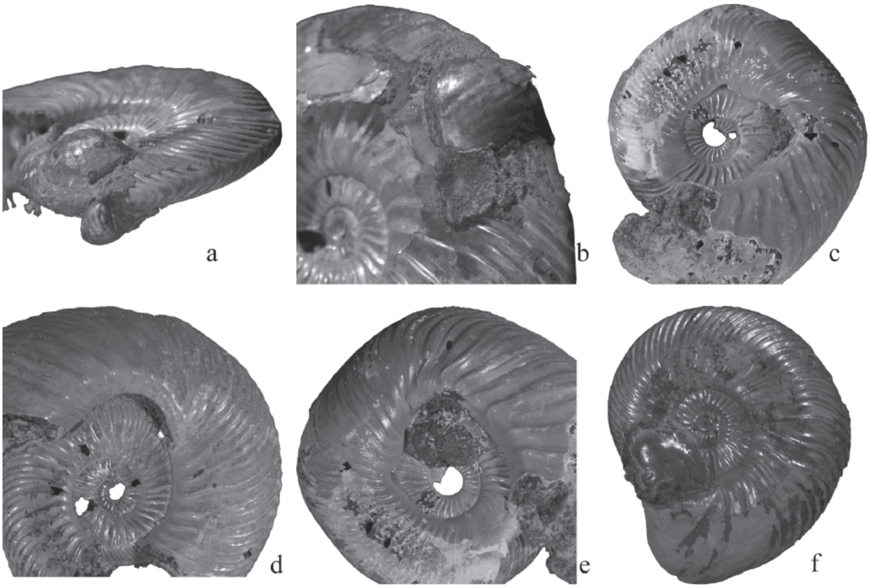

Fig. 16.7 *(a) Two* Placunopsis *(7 × 8.8mm and 11 × 13mm) on flank and venter of* Quenstedtoceras (L.) lamberti *(BHI-5362). (b) Close-up of* Placunopsis *(7 × 8.8mm) (BHI-5362). (c) The effect of a* Placunopsis *on the venter of* Q. (L.) lamberti; *note the place of attachment to the right of the umbilicus (BHI-5382) (x0.6). (d)* Q. (L.) lamberti *with the "hunchback" effect*, Placunopsis *missing (BHI-5370) (x0.8). (e)* Q. (L.) lamberti *with the "hunchback" deformity*, Placunopsis *(10 × 11mm) on flank and the venter (BHI-5307). (f)* Q. (L.) lamberti *with the "hunchback" deformity*, Placunopsis *(9 × 11mm) still attached (BHI-5349).*

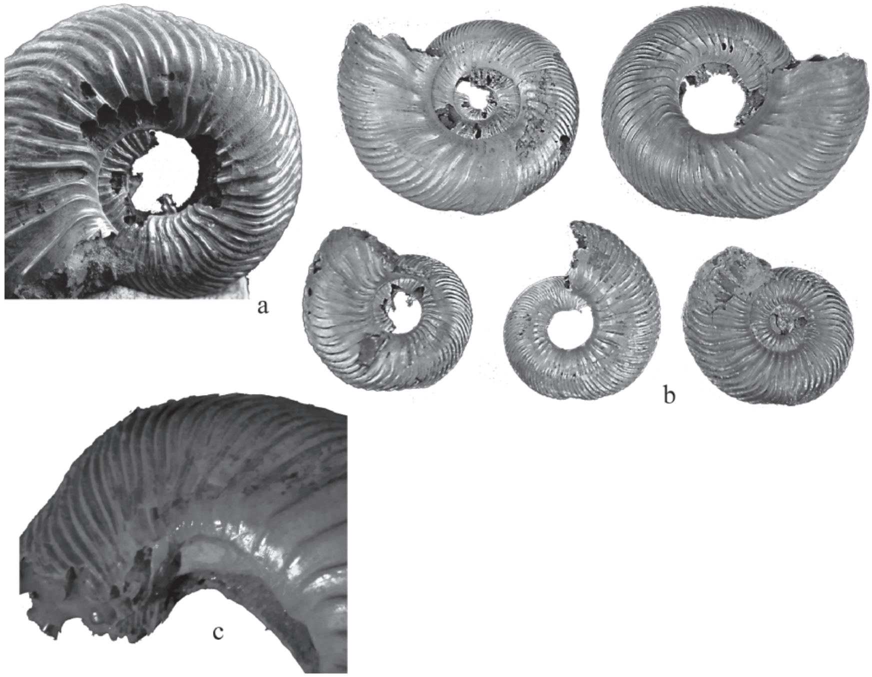

Fig. 16.8 *(a) Ventral "depression" on* Quenstedtoceras (L.) lamberti *(BHI-5454) (x1). (b) Several specimens of* Q. (L.) lamberti *showing the ventral "depression" (x0.8). (c) Note the ventral "depression" on* Q. (L.) lamberti *and the place where the* Placunopsis *rested on the venter to cause the deformity (BHI-5378) (x1.5).*

deformed as it grew over an attached epizoön. Kröger (2000) described this deformation as *forma augata* and similar specimens from the Dubki Quarry were figured by Keupp (2005: Fig. 16.3).

Cause. This is the result of a larger epizoön attached to the venter, and perhaps, partially to the flank (Figs. 163.5b, 16.5d, 16.5f, 16.7a–f). The attached *Placunopsis* seemed to have grown in size before the ammonite grew over it, thus making this deformation quite different from the previous description. The placement and large size of the pelecypod resulted in a deformity that resembles *kyphosis*, which according to Webster's New World Dictionary (Guralnik, 1986) means "a hump, to bend or arch, an abnormal curvature of the spine resulting in a hump or hump-back." This could not have been advantageous to either life form, the epizoön dying either before or after the ammonite shell grew over it, and the ammonite shell becoming disfigured in the process.

6.1.3 Depressions

Deformity. A deformity appearing as a depression or dip on the venter (Fig. 16.8a–b). Landman and Waage (1986) illustrated several specimens of *Hoploscaphites nicolletii* with similar ventral depressions. They referred to this as a “stretch pathology” related to the growth of the ammonite as it rapidly reached maturity. The depressions in *Quenstedtoceras* are not the same, because these dips or depressions occur far back on the phragmocone, whereas in *H. nicolletii*, they tend to occur on the shaft of the body chamber. This was not related to a bite or a disease, even though it is similar in appearance to what was figured by Keupp (1977) as *forma aegra aptycha*.

Cause. This deformity is the result of a very small bivalve attached to the venter (Fig. 16.8c), as described in the previous descriptions but with a slightly different distortion. The ammonite added extra shell and grew evenly over the small animal attached to the venter. The continued growth of the ammonite shell then rebounded, leaving a slight depression on the ammonite venter.

6.2 Flank Attachments

Of 655 known deformities caused by epizoa, 61 or about 10% have epizoa attached to the flank. This number is somewhat significantly lower than ventral attachments yet still a much larger place for attachments than the umbilical placements.

Deformity. Bivalves attached to the flanks caused the ammonite to suffer a crooked and twisted venter that deviates from the center (Fig. 16.9a–c). This is similar in appearance to the human deformity called “scoliosis,” which means “a lateral curvature of the spine.” Ammonite shell distortions, mainly the result of

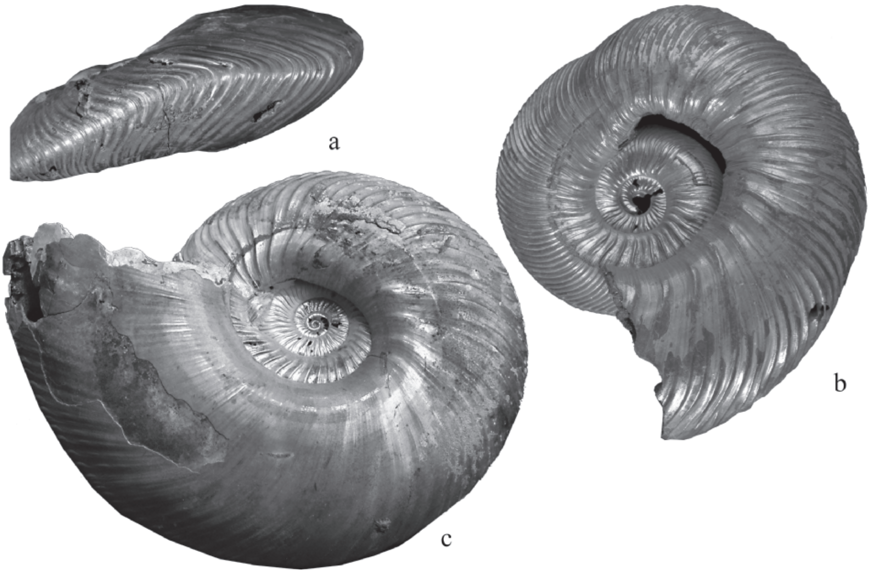

Fig. 16.9 *(a) Curvature of the venter on* Quenstedtoceras (L.) lamberti *(BHI-5384) (x1). (b) Severely deformed* Q. (L.) lamberti, *resulting from attached epizoa (BHI-5338) (x1). (c) Another severely deformed and twisted* Q. (L.) lamberti *(BHI-5466) (x0.8).*

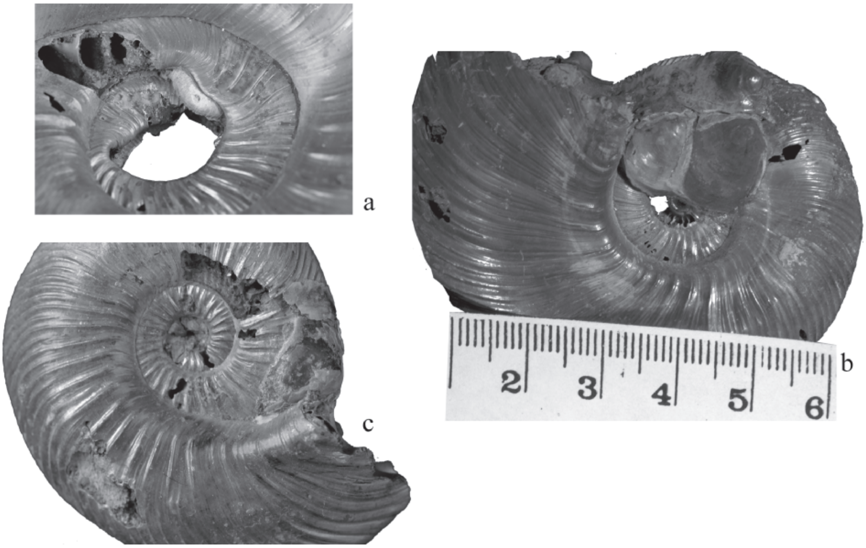

Fig. 16.10 *(a)* Placunopsis *(?) (7.5 mm across) near umbilicus of* Quenstedtoceras (L.) lamberti *(BHI-5613). (b)* Placunopsis *on flank and venter of* Q. (L.) lamberti *(BHI-5340). (c)* Placunopsis *(9.5 × 13.7 mm) on flank and venter of* Q. (L.) lamberti *(BHI-5305).*

healed bites, resembling the deformities seen from the Dubki Quarry have been described as *forma undatecarinata* by Heller (1958), and illustrated by Hengsbach (1979: Fig. 16.8b), and as *forma aegra undatispirata* by Keupp and Ilg (1992) and Keupp (1995, 1996, 2000). Landman and Waage (1986) referred to a similarly twisted venter as "Morton's syndrome," although they did not believe the deformity was caused by an injury. Those ammonites described as having "Morton's syndrome" most likely suffered from unsuccessful predation early in their life.

Cause. Checa et al. (2002) described this deformity as "zigzag." This deformity occurred when the epizoön attached itself to the flank of the ammonite (Fig. 16.10a–c). Depending upon the size and number of animals that attached to the shell, this regularly resulted in grotesque and monstrous deformities. Sometimes there were many of these pelecypods, and commonly they grew quite large on the flanks of the ammonites. In attempting to cover the epizoa, the ammonite had to deal with the ever enlarging and uneven weight distribution caused by the size of these epizoa and its own malformed shell growth. As a result, the ammonite became twisted, with an extremely crooked venter that bent to one side and sometimes back again (Fig. 16.10b, c).

6.3 Umbilical Attachments

Of 655 known deformities caused by epizoa, only 12 or a little more than 1% have epizoa attached on or near the umbilicus. In one-half of these specimens there are more than one *Placunopsis* attached to the ammonite. As evidenced by the low

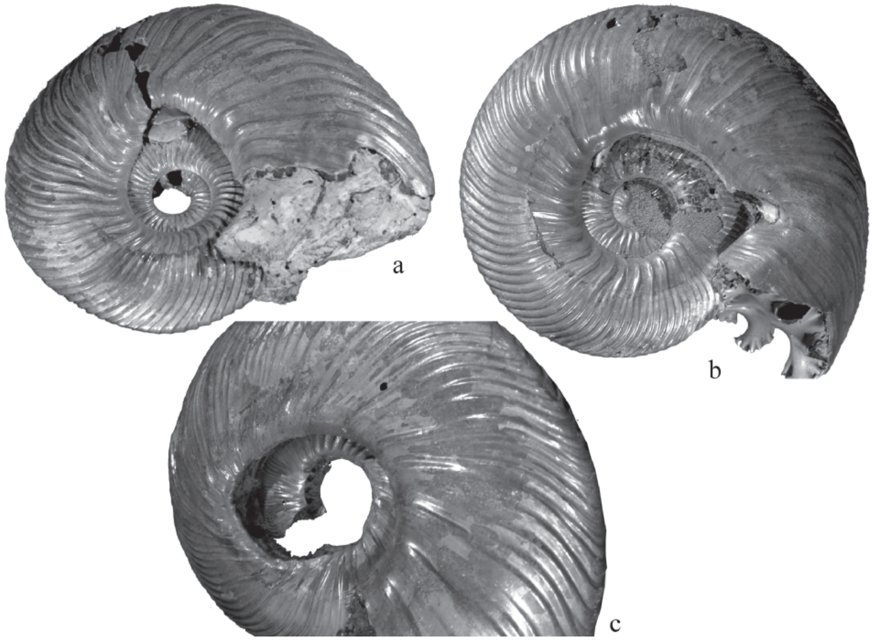

Fig. 16.11 *(a)* Placunopsis *(9.5 mm) near umbilicus of* Quenstedtoceras (L.) lamberti *causing "hunchback" and "depression" deformations (BHI-5346). (b)* Placunopsis *near the umbilicus and on the venter of* Q. (L.) lamberti *caused the deep depression in the dorsum (BHI-5353) (x1). (c)* Q. (L.) lamberti *with the epizoön gone; note the deformation near the umbilicus (BHI-5397) (x1.2).*

numbers, this is the most unusual place for attachment, yet the most easily to see and distinguish.

Deformity. One or more epizoa attached near the umbilicus of the ammonite (Fig. 16.11a–c). This phenomenon has also been described as occurring in *Pavlovia* (well illustrated by Keupp, 1996), although there are no illustrations with the epizoön attached. Keupp and Ilg (1992) referred to this deformity as *forma aegra undatispirata*.

Cause. Newly hatched *Placunopsis* attached themselves in or around the umbilicus of the ammonite and then continued to grow (Fig. 16.12a–f). It may have been impossible for the ammonite to remove epizoa from this location. This point of attachment, of all places, was probably the best for the *Placunopsis* and the least disfiguring for the ammonite. The bivalve was able to survive for a longer time, and, if there were multiple epizoa (Fig. 16.10b), they may have been able to spawn and colonize new areas of the ocean; this could account for different sizes of *Placunopsis* on the ammonites. *Placunopsis* may have been able to "infect" other ammonites after they released their spat (as in living bivalves) into the currents and thus onto other ammonites.

The umbilical attachment site was not too bad for the ammonite. It had an easier time compensating for the additional weight of the epizoön, and its shell growth did not become as contorted as in some of the other attachment places. As seen in Fig. 16.12b–f, there is still considerable distortion around the umbilicus, some on the flanks, and occasionally on the venter, as a result of epizoa attached near the umbilicus.

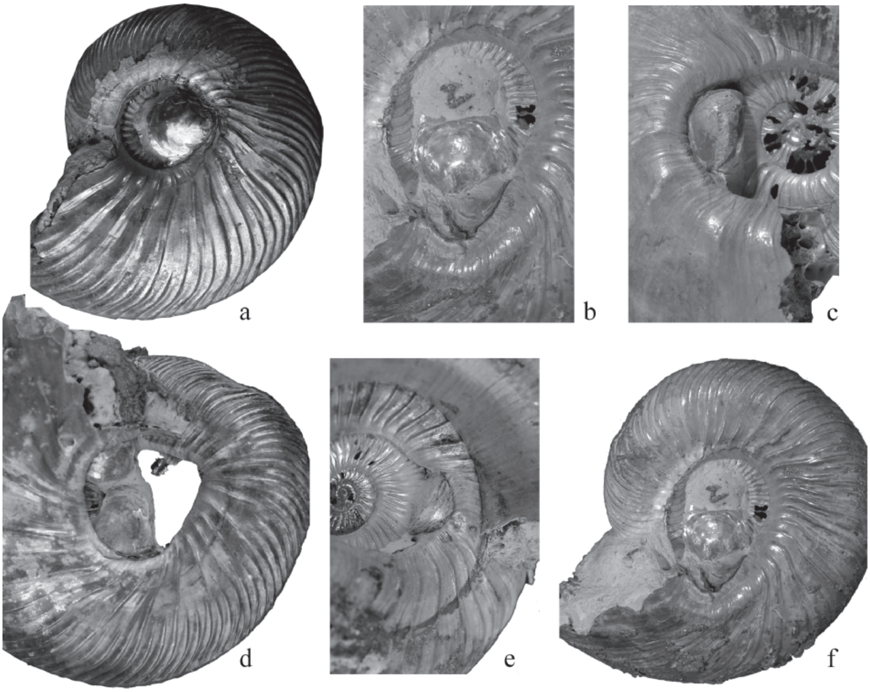

Fig. 16.12 *(a)* Placunopsis *(8.3 × 9.7 mm) attached on the umbilicus of* Quenstedtoceras (L.) lamberti *(BHI-5360). (b)* Placunopsis *(10.5 mm across) attached on the umbilicus of* Q. (L.) lamberti *(BHI-5343). (c)* Placunopsis *(9.7 mm across) attached near the umbilicus of* Q. (L.) lamberti *(BHI-5488). (d) Two* Placunopsis *(large one 7.1 × 9.5 mm) attached near the umbilicus of* Q. (L.) lamberti *(BHI-5467). (e)* Placunopsis *(5 mm across) attached near the umbilicus of* Q. (L.) lamberti *(BHI-5466). (f) Two* Placunopsis *(large one 10 × 10.7 mm) attached near the umbilicus of* Q. (L.) lamberti *causing deformities to the dorsum (BHI-5343).*

7 Healed Shell Fractures

Nonlethal injuries are observed in specimens of all ammonite species from the Dubki Quarry. These injuries have been interpreted as originating as bites or some other form of damage to the ammonite shell or mantle. These pathologies occur as irregularities of the shell in the form of ruptures, scars, wrinkles, folds, scratches, and displaced ribs. They prove that not only did the ammonites have to contend with the infestation of epizoa, but they also had to survive attacks from a variety of predators such as fish, reptiles, and other cephalopods (animals commonly cited as modern cephalopod predators). The injuries in this fauna are all consistent with healed paleopathologies as seen in many publications (for example, Landman and Waage, 1986; Bond and Saunders, 1989; Keupp, 1976, 1996, 2000; Hengsbach 1996; and others).

Hengsbach (1996) listed a fairly complete summary of most of the previous work on pathological ammonites. His use of the German *forma* and *aegra* names to describe the healed ammonite pathologies was not new, but rather a comprehensive overview of the previous work done by so many paleopathologists. The terms *forma* meaning "form" and *aegra* meaning "sick," though appropriate, are very confusing when used in conjunction with the healed wounds found on pathological ammonites. I have chosen to use other names for these injuries, while maintaining the original references for the *forma* names.

Kröger (2002) showed several examples of nonlethal injuries in ammonites. He noted six different types of breakage and repair to the ammonite shell and assigned names from medical terminology. He documented the high incidence of injuries in the genus *Quenstedtoceras*, among many other genera. But because all of the specimens utilized in his paper were from the collection of H. Keupp, who selectively collects such specimens, there was naturally a high incidence of pathological ammonites. Kröger's study dealt with the percentage of different types of sublethal predation, and the most common breakage to the shell. The most common breakage or injury is damage to the aperture of the ammonite. Only a small percentage of shell damage appears as a deeper injury to the flank or venter.

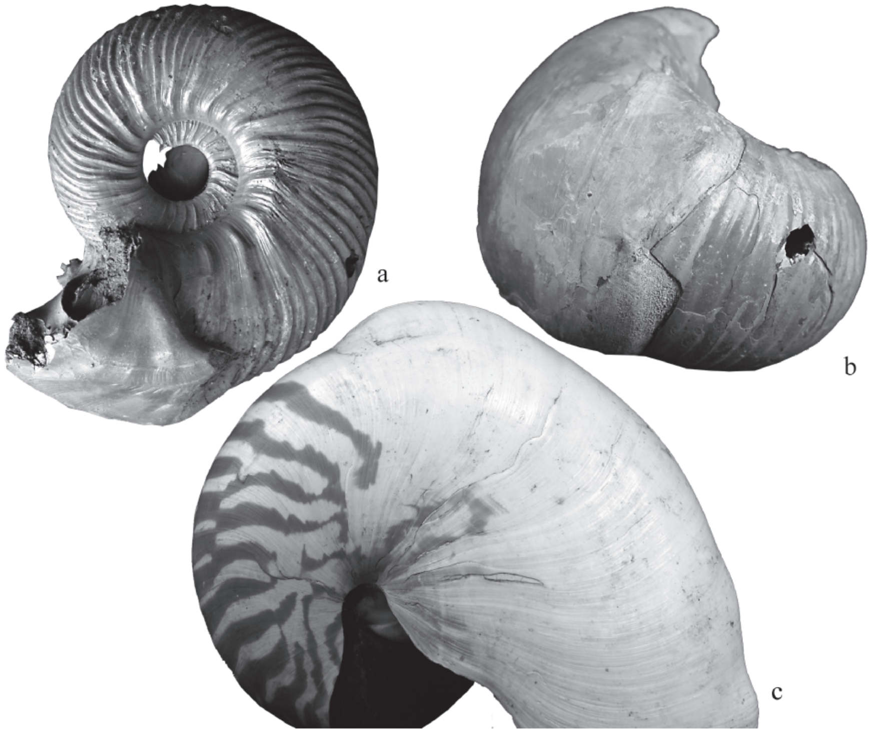

Fig. 16.13 *(a)* Quenstedtoceras (L.) lamberti *showing large-repaired rupture (BHI-5424) (x0.8). (b)* Eboraciceras *showing large-repaired rupture and shell regrowth (BHI-5499) (x0.8). (c) Recent* Nautilus *showing a healed rupture (BHI-5603) (x0.35).*

The percentage of sublethal injuries (as well as deformities caused by epizoa) in the fauna from the Dubki Quarry is difficult to calculate. The specimens used in this study were chosen out of perhaps ten to twenty thousand, or more. Bond and Saunders (1989) reported a 15% incidence of shell injury and repair among Late Mississippian ammonites from the Imo Formation of northwest Arkansas. P. L. Larson (1984) reported that the number of pathological specimens in the family Scaphitidae from the Fox Hills Formation ranged from 15% (*Hoploscaphites nicolletii* Range Zone) to 46.7% (*Jeletzkytes nebrascensis* Range Zone). Landman and Waage (1986) noticed a 10% incidence of shell abnormalities from the *Hoploscaphites nicolletii* Zone and 25–40% from the *Jeletzkytes nebrascensis* Zone based on their ammonite collection. Judging from the thousands of specimens seen and reported from the Saratov locality, it is estimated that perhaps only 10% of the Saratov fauna had any sort of deformities resulting from healed fractures or attached bivalves.

There are several different pathologies that occurred in all ammonite species, as a result of survived predatory attacks. The following list includes some of the different forms of scarring in the ammonites that have been found at the Dubki Quarry.

7.1 Ruptures

Deformity. This deformity is observed as a small or large unornamented swelling of the shell, emanating from one small area (Fig. 16.13a, b). The protrusion is generally round to oblong, and extends away from the rest of the shell. It was described as *forma inflata* by Keupp (1976) and illustrated by Keupp (1995, 1996, 2000), Hengsbach (1996), and N. L. Larson (2003).

Cause. This deformed, bulbous protrusion from the shell is probably the result of a bite through some portion of the body chamber (from fish, reptile, crustacean, or cephalopod) and a subsequent rupture of the mantle through the broken shell (N. L Larson, 2003). As is common in all animals that receive an injury, the ammonite would most likely have tried to immediately repair the rupture or wound. This repair usually resulted in a lack of ornamentation, or a smooth, rounded shell at the point of injury. A similar type of deformity has also been observed in extant *Nautilus* (Fig. 16.13c).

7.2 Rib Displacement

Deformity. A displacement to the sculpture of the ammonite shell, resulting in the conspicuous displacement of the ribs (Fig. 16.14a–c), classified by Hengsbach (1979) as *forma aegra syncosta*, and illustrated by Keupp (1973), Landman and Waage (1986), and Bond and Saunders (1989).

Cause. Most likely, the result of a bite that caused fracturing and displacement of the shell. This deformity has also been observed in present-day *Nautilus* (see Ward, 1987).

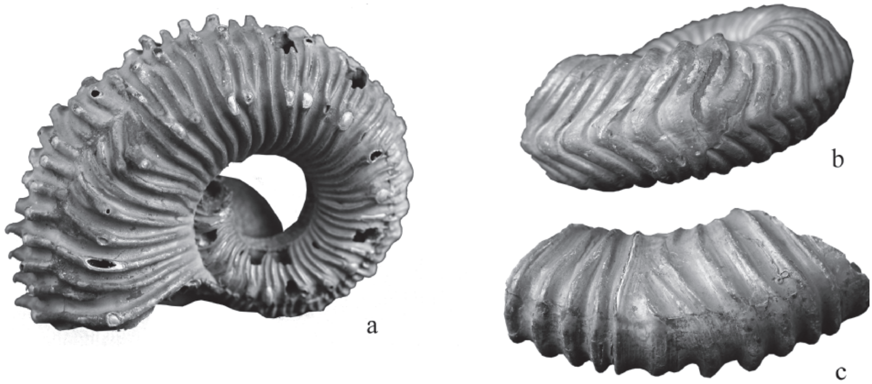

Fig. 16.14 *(a)* Kosmoceras, *injury showing rib displacement (BHI-5599) (x1). (b)* Prorsiceras *with an injury, showing displacement on the venter (BHI-5602) (x1.2). (c)* Rurciceras *(?) showing damage to the venter (BHI-5601) (x1).*

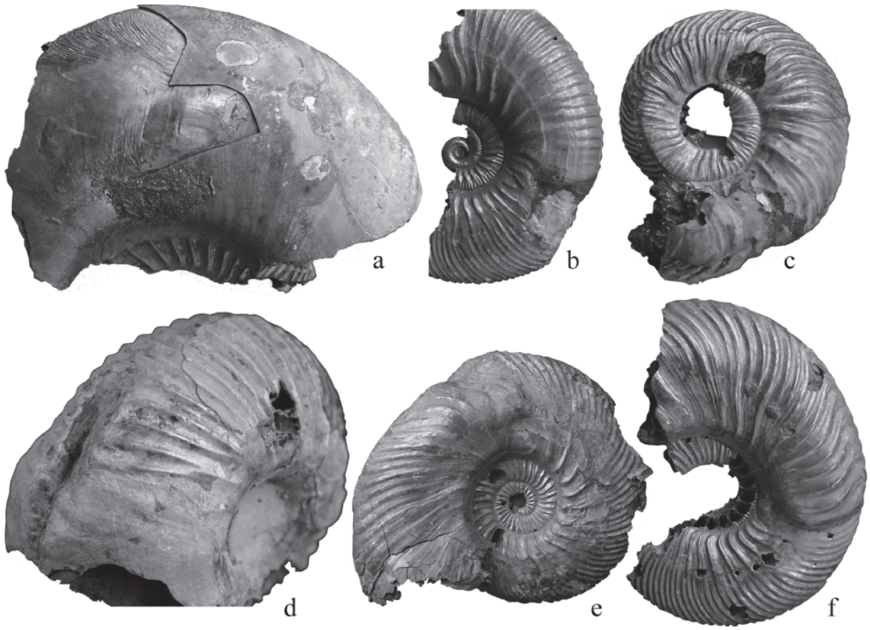

Fig. 16.15 *(a)* Quenstedtoceras (L.) lamberti *with repaired injury (BHI-5415) (x1). (b)* Grossouvria *with repaired bite (BHI-5427) (x1). (c)* Q. (L.) lamberti *showing deformed whorl from a bite (BHI-5426) (x1). (d)* Eboraciceras *showing a deep groove and healed shell (BHI-5608) (x0.8). (e)* Q. (L.) lamberti *with displaced shell (BHI-5432) (x0.7). (f)* Q. (L.) lamberti *showing healed injury as rib repair (BHI-5434) (x0.9).*

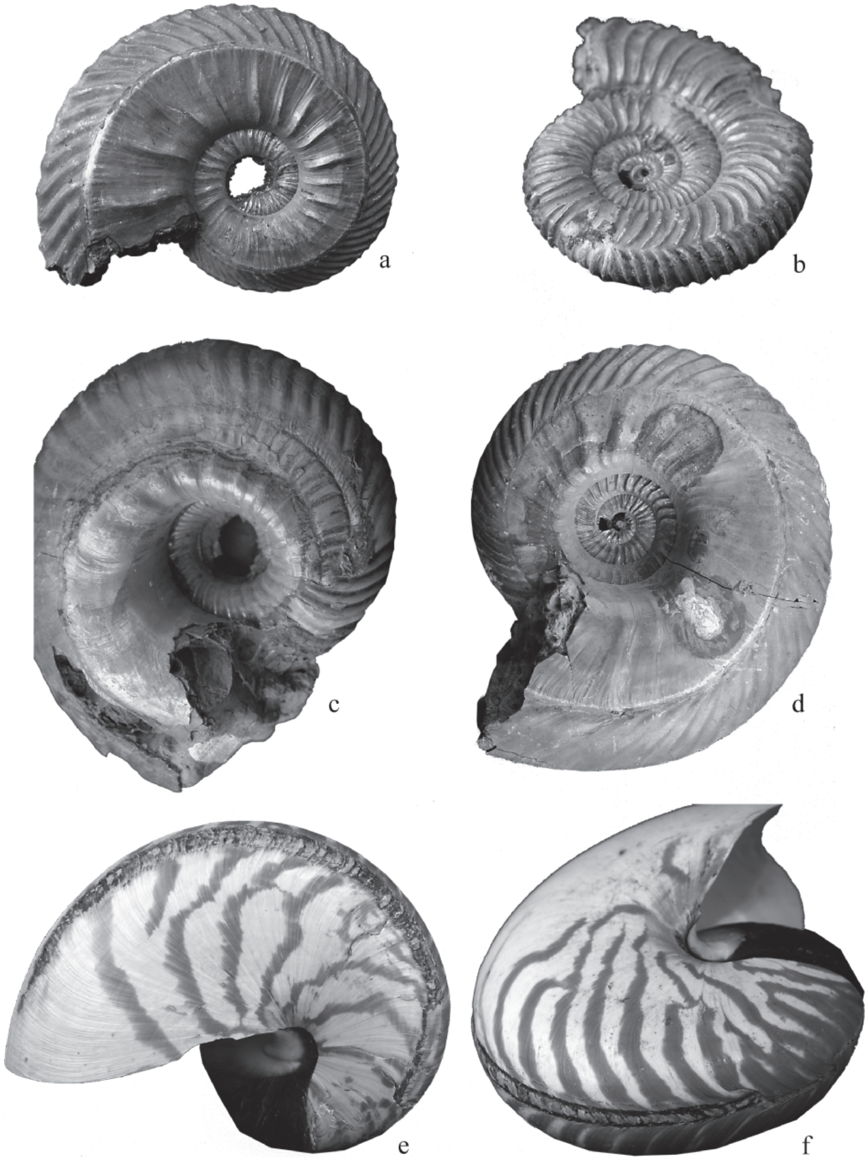

Fig. 16.16 *(a)* Quenstedtoceras (L.) lamberti, *showing "spiral" scarring (BHI-5420) (x1). (b)* Peltoceras*, with rib displacement at the point of injury (BHI-5610) (x1.2). (c)* Q. (L.) lamberti *with a spiral scar along with scars from previously attached epizoa (BHI-5609) (x1.2). (d)* Cadoceras *exhibiting a healed groove with rib displacement at the point of injury (BHI-5604) (x0.8). (e) Recent* Nautilus *showing similar scarring from a healed bite (BHI-5611) (x0.3). (f) Recent* Nautilus *showing "spiral" scarring, and the point of injury (BHI-5612) (x0.2).*

7.3 Scars

Deformity. There are two types of deformities seen on either the flank or the venter, which are the results of a deep bite. One is characterized by the appearance of a large healed injury, regularly seen as a deep depression, remodeled and sculpted, devoid of normal ornamentation, and frequently with portions of the shell completely missing (Fig. 16.15a–f). Similar scarring was described as *forma aegra aptycha* by Keupp (1977) and illustrated by Bond and Saunders (1989).

The second deformity is typified by a long, shallow to deep depression that follows the spiral growth of the ammonite shell (Fig. 16.16a–d). This type of injury was classified by Hölder (1956) as *forma aegra verticata* and figured by Keupp (1979, 1985). This type of scarring was also labeled by P. L. Larson (1984) and Landman and Waage (1986) as a "spiral furrow."

Cause. Both of these depressed scars are the result of severe bites or injuries to the body chamber and mantle during life. The first deformity resulted in the loss of some of the mantle, and as the ammonite attempted to heal the bite, it grew a smooth shell covering the bitten region. Because there was flesh and shell lost in the bite, there is a depression left that never grew back to the original form. If there is no ornament, this indicates that the injury happened somewhere behind the mantle margin, because only the lip of the mantle can create ribbing and ornament. If there is ornament, this indicates that the injury happened near or at the aperture, and that the ammonite managed to create new shell material with its damaged mantle.

The depressed line of scarring is the result of an injury to the lip (or edge) of the mantle in a still-growing ammonite. This type of injury resulted in a damaged and disfigured mantle that would have continued to produce a scarred shell throughout the lifetime of the ammonite, because some portion of the mantle was severely damaged. This type of deformity also has been observed in extant *Nautilus* (Fig. 16.16e, f).

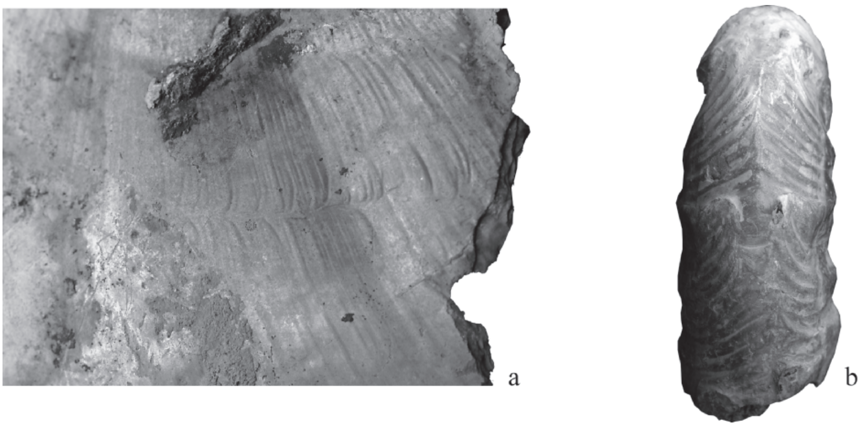

Fig. 16.17 *(a)* Quenstedtoceras (L.) lamberti *with small "nibble" (BHI-5614) (x2). (b)* Grossouvria *(?) with scarring on the venter (BHI-5605) (x1).*

7.4 Scratches

Deformity. This obscure deformity is commonly observed as a scratch on the shell of the ammonite (Fig. 16.17a–b). It may appear in the form of shallow and minute scars that parallel the growth of the ammonite, are restricted to one small area, or are at different angles to the growth. This type of injury has been referred to as "parvus-type" by Kröger (2002), and similar, nonlethal deformities were illustrated by Bond and Saunders (1989).

Cause. Injuries resulting from perhaps a bite or a nibble from another ammonite or an interaction with some other animal. Similar shell damage has been observed to have taken place between breeding pairs of present-day *Nautilus* (see Ward, 1987).

8 Distorted Shapes of Unknown Origin

Deformity. Webster's New World Dictionary (Guralnik, 1986) describes "anamorphism," as "an abnormal change of form which gives the appearance of a different species." The overall shape of the ammonite has become distorted with more shell growth on one side of the ammonite than on the other (Fig. 16.18a–c), making it look quite different when comparing both sides. The venter is commonly shifted to one side, so that one side is generally rounded with both sets of ventral tubercles, whereas the other side is commonly flat. This distortion, which can be viewed by

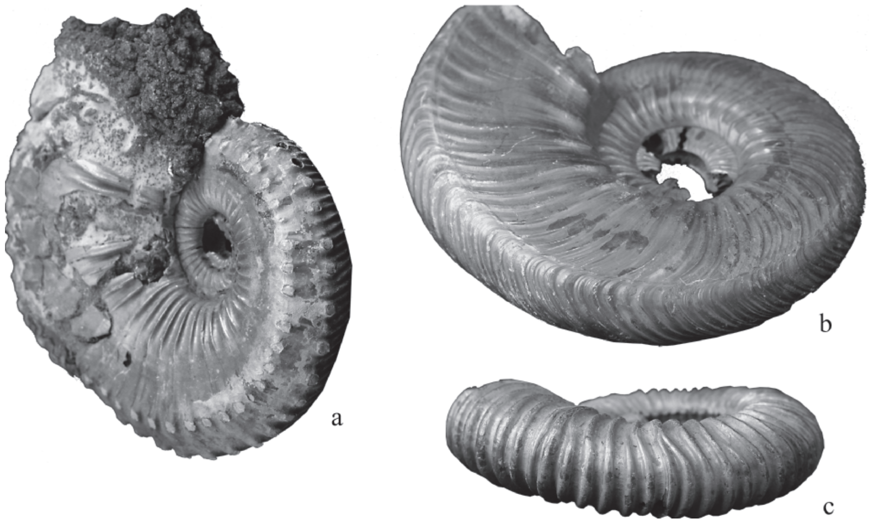

Fig. 16.18 *(a)* Kosmoceras *with nonsymetrical venter (BHI-5607) (x1.2). (b) Trochospiral* Quenstedtoceras (L.) lamberti *"flattened" on one side, round on the other (BHI-5436) (x1). (c)* Rurciceras *(?) with a bent and curved venter (BHI-5606) (x1).*

comparing one side of the ammonite to the other, was described as "forma cacoptycha" by Lange (1941) and illustrated by Keupp (1977, 1984, 2000), and Hengsbach (1996). Kröger (2002) described similar deformities in other ammonites calling them "Harpoceras-type", while Landman and Waage (1986) described this deformity as simply "local asymmetry." Checa et al. (2002) called the deformity "trochospiral growth," attributing the distortions to attachments of epizoa, which caused the ammonites to grow off center.

Cause. It is unknown, in any of the ammonites from this site, whether this distortion is the result of an attached, small organism (such as an epizoön) on the outer flank near the venter in an early growth stage of the ammonite, or the result of a nonlethal bite that damaged the mantle early in life, causing the ammonite to grow in a crooked or asymmetrical manner. Both possibilities are an option because this distortion is commonly observed in *Quenstedtoceras* (*L.*) *lamberti* from the Saratov site. Checa et al. (2002) attributed similar distortions to the attachment of epizoa during an early stage of life, causing tilting or trochospiral growth. Landman and Waage (1986) noted similar distortions in Maastrichtian scaphites from the Western Interior, which have never been reported to have deformities caused by epizoa but have a high percentage of healed bites (P. L. Larson, 1984; Landman and Waage, 1986; N. L. Larson, 2003).

This type of trochospiral growth is known to occur in ammonites of nearly all species, including those from the Late Cretaceous families Scaphitidae, Placenticeratidae, and Sphenodiscidae, and within these Late Cretaceous genera, the cause appears to be from a nonlethal bite earlier in life. This is theorized because attachments of epizoa on scaphites are still unknown. Keupp (1976: Fig. 16.4) noted a similar distortion in *Pleuroceras* and interpreted it as a healed bite.

9 Discussion

Allen (1937) described articulate brachiopods attached to gastropods and scallops and postulated that the molluscs were being used as carriers for the migration of brachiopods into different areas of the sea. Logan et al. (1975) reported on unusual attachments of brachiopods on the surfaces of present-day scallops. These brachiopods were also apparently using the scallops for transportation to different portions of the sea. It is postulated that *Placunopsis* may have inadvertently colonized other areas of the Callovian Sea by attaching themselves to *Quenstedtoceras* (*L.*) *lamberti* and moving with the shoal. The bivalves likely attached themselves to *Q.* (*L.*) *lamberti* while still in the larval stage and grew in place. *Placunopsis* could later release their hold on the ammonites or release their spat while still on the ammonites. This could introduce new settlements of *Placunopsis* into many different areas. Judging by the percentage of distorted ammonites that grew over the epizoa, it appears that perhaps only a small percentage of these *Placunopsis* were successful in further colonization of the sea.

Whether feeding on the waste of the ammonite, or just hitching a ride, as the pelecypod grew, it became so firmly attached, that the ammonite could not dislodge it from the shell once the pelecypod was finally large enough to be a nuisance. Because of the need to increase the size of the shell, both from the additional weight of its growing body and from the increasing weight of the pelecypod, it became necessary to grow over and around the epizoön. In the process, the ammonite shell commonly became grotesquely deformed. Occasionally, the pelecypod is missing from under the ammonite shell (as seen in Fig. 16.5b), even though there is a hole where it used to be. Was the pelecypod able to dislodge itself and move on, or was it somehow dislodged or removed later? Whatever the case, most pelecypods were buried during the construction of the ammonite shell and were unable to escape. The pelecypods must have succumbed to a slow death, unable to escape while the ammonite covered them. The ammonites, which were permanently disfigured, must have had a difficult time swimming properly and because of their grotesque deformities, they may have been less desirable sexually.

There is abundant literature written on pathological ammonites. Yet throughout all of this literature, this widespread ammonite–epizoa relationship is unusual. Hopefully, one day the significance of this relationship may be further explained.

10 Conclusions

The "guest" (*Placunopsis*) was probably planktonic when it attached to the "host" (*Quenstedtoceras* (*L.*) *lamberti*), and in many cases, both were alive at the time of their union. Neither organism needed the other, nor did they live parasitically with each other. For the most part, the "guest" was completely or mostly buried under the shell of the "host." This relationship was not beneficial to either organism, unless the bivalve had reached maturation and was able to spawn. It appears that this may have happened, though it cannot be proved. In this example, the bivalve spat, or offspring, would have been introduced to other parts of the ocean; thus, the "guest" could have benefited. The ammonite host seems never to have benefited; usually, its shell was grotesquely deformed, and its ability to swim and reproduce may have been greatly compromised.

Epizoa did not commonly attach themselves to living ammonites. Davis et al. (1999) pointed out that even in large collections, the attachment of epizoa on ammonites is rare. So why did these ammonites become the hosts of these epizoa? R. A. Davis (2005, personal communication) pointed out to the author that "the ammonoids provided a hard substrate to which the young pelecypods could and did attach." These ammonites happened to be in the wrong place at the wrong time, and something in their anatomy made them suitable for the *Placunopsis* to attach to without being removed. The ribbing on *Quenstedtoceras* (*L.*) *lamberti* is similar to that of other species of ammonites that are found in the same zone. The size of the ammonites did not seem to matter; *Placunopsis* infestation occurred on all parts and on all sizes of *Q.* (*L.*) *lamberti*, yet on no other species.

Why was the pelecypod successful in attaching itself to *Quenstedtoceras* (*L.*) *lamberti*, while leaving the other species of ammonites in the sea alone? The ribbed shell of *Quenstedtoceras* is consistent with the ribbed shells of other genera found in the deposit. There appears to be no noticeable size difference or any other physical shell difference that would favor one species while leaving the others alone. It must be that either the swimming patterns of *Q*. (*L.*) *lamberti* were much different from other ammonite species, or they were unable to clean themselves as efficiently as other ammonites could. The arms of *Q*. (*L.*) *lamberti* could have been much shorter or quite different from those of other species, because they were apparently unable to remove the intruders. Because *Q*. (*L.*) *lamberti* are found in much greater abundance than any of the other ammonite species, they must have lived in much larger shoals, so that there were more of them "hanging around" when the planktonic *Placunopsis* were in the currents looking for a place to attach. *Q*. (*L.*) *lamberti* just happened to be available when they were needed the most.

Of the 655 specimens of *Quenstedtoceras* (*L.*) *lamberti* that were confirmed to have *Placunopsis* attachments, nearly 89% of the *Placunopsis* were attached on or near the venter of the ammonites. A total of 10% had attachments midflank and only a little more than 1% had umbilical attachments. That figure is significant. It seems that *Q*. (*L.*) *lamberti* were unable to remove many epizoa from their venter. Perhaps the venter was out of their line of sight, or maybe even out-of-reach for them. It could have had something to do with their sharp, ribbed keel as well.

The extreme deformities in the ammonite shells indicate the plasticity and resilience of the ammonite shell. The ammonites were able to adapt and recover from a vast variety of problems, including bites and settlements of growing epizoa attached to their shell. As with all known species of ammonites, *Quenstedtoceras* was able to survive many different forms of trauma, such as bites. This resilience is consistent with living cephalopods, as extant species are able to survive a wide array of communal problems, along with friendly and predatory attacks.

It should be possible to calculate the growth rate of *Quenstedtoceras* (*L.*) *lamberti* based on the age and growth rate of the attached epizoa. But because *Placunopsis* were small bivalves throughout their life, the age of the bivalves and how fast these ammonites grew is still not known. It is still not known if the growth of one or two ammonite whorls would have taken several months to a year or more. Further research into *Placunopsis* could help determine more about their growth, which would then lead to a better understanding of the growth and lifespan of *Q*. (*L.*) *lamberti*. We may never know for sure why in the nine described genera of ammonites from the Dubki Quarry, only *Q*. (*L.*) *lamberti* was used by *Placunopsis* for settlement and why it was unable to remove them.

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