FIFTEEN

Basal Thyreophora

DAVID B. NORMAN

LAWRENCE M. WITMER

DAVID B. WEISHAMPEL

Dinosaurs that bear prominent and/or extensive dorsal armor on the body are known as thyreophorans. They are best represented by ankylosaurs and stegosaurs, but several more basal forms can also be included in this group. These include *Scelidosaurus* Owen, 1861a, from England, *Emausaurus* Haubold, 1990, from Germany, and *Scutellosaurus* Colbert, 1981, from the southwestern United States, all known from the Early Jurassic. *Scelidosaurus* also has the singular distinction of being the first reasonably complete, well-preserved dinosaur ever to be discovered and described (Norman 2000).

Thyreophora is the name applied to the stem clade representing all taxa more closely related to *Ankylosaurus* than to *Triceratops* (Sereno 1999a). Its sister clade is the stem clade first named Cerapoda (Sereno 1986) and subsequently renamed Neornithischia (Sereno 1997, 1999a). Unfortunately, nomenclatural confusion is generated as a by-product of recent systematic revisions. Neornithischia was originally coined by Cooper (1985) following his systematic revision of the clade as a rank of ornithischians that included Thyreophora *(sensu lato)* + heterodontosaurids + pachycephalosaurs + ceratopsians. In this respect retaining the name Cerapoda for the stem clade that includes Ornithopoda + Marginocephalia is preferable for reasons of consistency and stability. Together Thyreophora and Cerapoda are united as Genasauria (Sereno 1986).

Basal thyreophorans (table 15.1) are considered to fall outside the clade comprising Ankylosauria + Stegosauria. *Scelidosaurus, Scutellosaurus,* and *Emausaurus* may have had a regular arrangement of dermal armor on their backs and were either partial or obligate quadrupeds. All were herbivorous and ranged from one to four meters in total length; they arise in serial fashion along the stem lineage leading to Eurypoda (Ankylosauria + Stegosauria). Consequently, definitions and diagnoses for the major clades that successively include each of these forms within the basal nexus of Thyreophora are deferred to the "Systematics and Evolution" section.

Anatomy

Skull and Lower Jaw

The skull of *Scelidosaurus* is moderately well known (fig. 15.1A, B), having originally been described and illustrated by Owen

(1861a, 1863). *Emausaurus* (fig. 15.2) is known principally from a well-preserved skull (Haubold 1990), while the skull of *Scutellosaurus* (fig. 15.1C, D) is based on only a few parts of the skull (Colbert 1981).

Caudally the skull of both *Scelidosaurus* and *Emausaurus* is elevated but boxlike; the rostrum tapers, producing a wedgelike lateral profile (fig. 15.1A). In dorsal view the skull is widest across the orbitojugal region, from which it tapers gently rostrally (fig. 15.1B). The skull proportions of *Scutellosaurus* cannot be characterized.

The premaxilla of both *Emausaurus* (fig. 15.2B) and *Scelidosaurus* (Norman, in prep.) houses five simple, slightly recurved teeth. In *Scutellosaurus* the premaxilla contains six alveoli, in which only the tips of replacement crowns are preserved. These are simple, conical, and laterally compressed; no recurvature was reported by Colbert (1981). The caudolateral process of the premaxilla in *Emausaurus* (fig. 15.2B) is short and does not cover the contact between the nasal and the maxilla directly rostral to the lacrimal; the premaxilla is long and tapering in *Scelidosaurus* (Carpenter 2001a). A prominent foramen is shown at the base of the medial rostral process of the premaxilla just within the margin of the external naris in *Scutellosaurus* (Colbert 1981).

The maxilla of all three species is approximately triangular in lateral view; it may have been longer and lower in *Scutellosaurus,* but this bone is damaged, so its outlines are obscure (fig. 15.1C); the rostral two-thirds of the external surface is shallowly excavated to form the antorbital fossa. Fortunately, in both *Emausaurus* and *Scelidosaurus* the antorbital fossa is far better preserved; in both, it is roughly oval in outline and of modest size, though that of *Emausaurus* is considerably more extensive on the side of the snout than is that of *Scelidosaurus*. A small, internal antorbital fenestra is found caudally within the fossa in *Emausaurus*. An overhanging maxillary shelf projects lateral to the tooth row in *Scelidosaurus* and *Emausaurus* and to a lesser degree in *Scutellosaurus*. In *Scutellosaurus* the medial maxillary surface is well rounded. Dorsally the maxilla makes a long, butt-jointed contact with the nasal in *Emausaurus*. There are at least 10 maxillary tooth positions in *Scutellosaurus,* 21 in *Emausaurus,* and more than 19 in *Scelidosaurus*.

The nasal of *Scelidosaurus* and *Emausaurus* is a long, tapering plate (widest caudally) that arches across each dorsal quadrant of the snout. The nasal-maxillary suture in these taxa is

TABLE 15.1
Basal Thyreophora

	Occurrence	Age	Material
Thyreophora Nopcsa, 1915			
Scutellosaurus Colbert, 1981			
S. lawleri Colbert, 1981	Kayenta Formation (Arizona), United States	Hettangian or Sinemurian	Fragmentary skull and skeleton from at least 2 individuals
Emausaurus Haubold, 1991			
E. ernsti Haubold, 1991	Unnamed unit (Mecklenberg), Germany	early Toarcian	Nearly complete skull with associated postcrania
Scelidosaurus Owen, 1860			
S. harrisonii Owen, 1861a	Lower Lias (Dorset), England	late Sinemurian	Nearly complete skull with associated postcrania, articulated postcranial skeleton, partial skull and associated postcrania, juvenile and adult
?Thyreophora *incertae sedis*			
Tatisaurus Simmons, 1965			
T. oehleri Simmons, 1965 (= *Scelidosaurus oehleri* [Simmons, 1965])	Dark Red Beds of the Lower Lufeng Series (Yunnan), People's Republic of China	?Sinemurian or Hettangian–Pliensbachian	Isolated dentary
Bienosaurus Dong, 2001			
B. lufengensis Dong, 2001	Dark Red Beds of the Lower Lufeng Series (Yunnan), People'sRepublic of China	?Sinemurian or Hettangian–Pliensbachian	Dentary with teeth

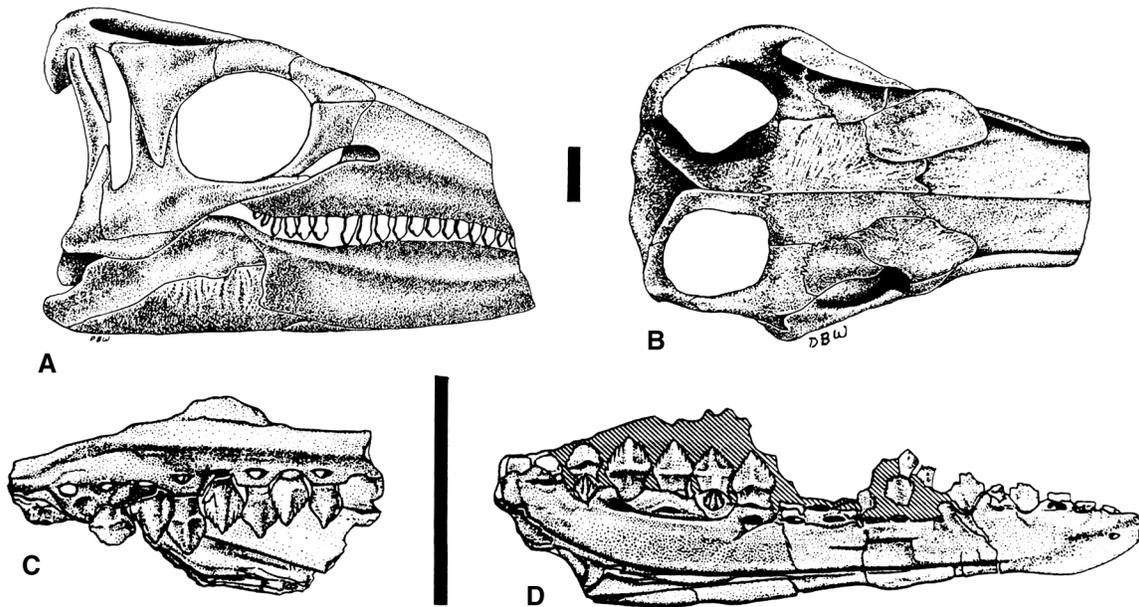| *Nomina dubia*	*Material*
Lusitanosaurus liasicus Lapparent et Zbyszewski, 1957	Skull fragment

FIGURE 15.1. A, B, *Scelidosaurus harrisonii,* skull in A, right lateral, and B, dorsal views. C, D, *Scutellosaurus lawleri:* C, medial view of right maxilla; D, medial view of left dentary. Scale = 2 cm. (C, D, from Colbert 1981.)
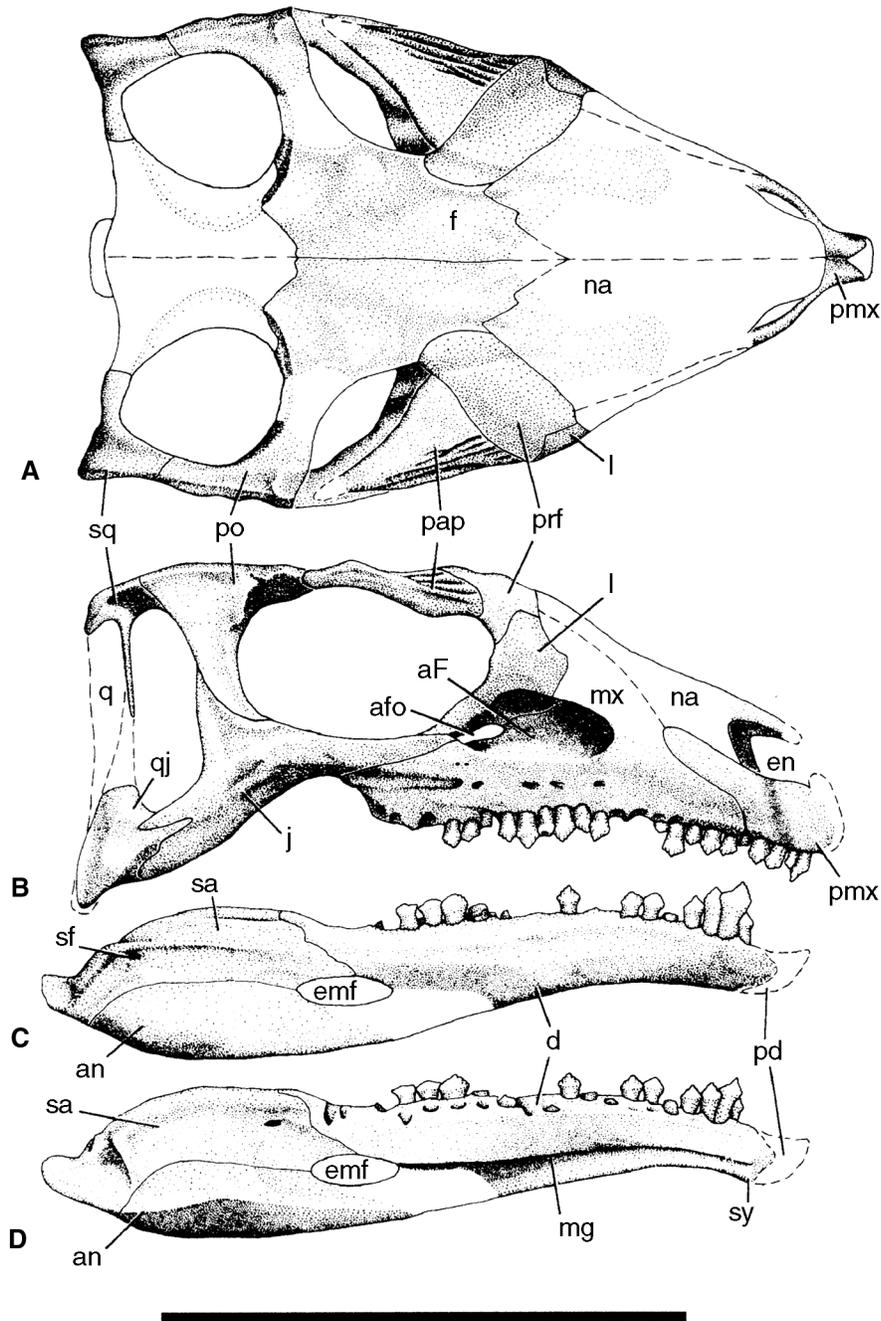
FIGURE 15.2. Skull and lower jaw of *Emausaurus ernsti:* A, B, skull in A, dorsal, and B, lateral views; C, D, lower jaw in C, lateral, and D, medial views. Scale = 10 cm. (After Haubold 1990**[JSA6]**.)

continuous with that between the prefrontal and the lacrimal. The lacrimal makes up the majority of the rostral margin of the orbit. The prefrontal contacts the frontal medially and the nasal rostrally, and the supraorbital is sutured firmly to the prefrontal along the orbital margin forming much of the dorsal orbital roof. In *Emausaurus* the supraorbital is large and occupies a chordlike position in the upper part of the orbit, partially enclosing a slit-shaped opening bounded by the frontal and the postorbital (fig. 15.2A).

The postorbital and the jugal form a transversely thickened caudal orbital bar between the orbit and the infratemporal fenestra. The jugal is long and tapers rostrally where it overlaps the maxilla and is in turn overstepped by the lower end of the

lacrimal. The remainder of the body of the jugal is essentially Y-shaped, with the upper part curving to meet the postorbital and developing a deep recess on its orbital surface for this tight scarf suture. In both *Emausaurus* and *Scelidosaurus* the lower part of the jugal extends to contact the quadratojugal using two fingerlike processes that overlap the external surface of the quadratojugal. The L-shaped quadratojugal partially overlaps the quadrate in lateral view in *Scelidosaurus,* and a similar arrangement is found in *Emausaurus.* The quadrate is pillarlike and slightly concave along its caudal edge. In *Scelidosaurus,* where this element is well preserved, the outer edge of the quadrate is expanded into a thickened but short jugal ramus that is directed toward the jugal arch. The leading edge of this ramus is strongly

etched for attachment along its entire length to the quadratojugal; just below the midheight of this ramus a discrete notch representing a quadrate (paraquadratic) foramen is enclosed rostrally by the quadratojugal. The medial (pterygoid) ramus is more extensive than the jugal ramus and medially concave; in addition, there is pronounced scarring along the upper and lower edges of its medial surface for attachment of the overlying ramus of the pterygoid. The quadrate head is capped by the squamosal, which is hollowed out ventrally to form a cotylus rostral to which there is a fingerlike process that locks against the upper part of the jugal ramus of the quadrate. The broad, well developed, slightly trochlear condyle for the lower jaw lies ventral to the level of the maxillary tooth row.

The frontoparietal suture is interdigitate throughout its length in *Scelidosaurus,* but this region is not well preserved in *Emausaurus* and is not known in *Scutellosaurus.* In *Scutellosaurus* the dorsal surface of the thin, triangular frontal is flat, while ventrally it is excavated to accommodate the cerebrum and the long olfactory tracts. The frontal-postorbital contact is a scarf joint. The frontal contributes to the dorsal margin of the orbit. The parietals of *Scelidosaurus* are fused into a single plate that is shaped like an hourglass in dorsal view, and there is a broad sagittal ridge between the supratemporal fenestrae. The squamosal forms the slender caudal and lateral boundaries of a nearly circular supratemporal fenestra. The occipital margin of the skull is notched to expose the occipital plate in dorsal view.

The floor of the braincase, which has been partially described in *Emausaurus* (Haubold 1990), comprises two hemicylindrical elements: the basioccipital and the basisphenoid. The former supports a broad, dorsoventrally convex occipital condyle, and the exoccipitals (not preserved, but represented by sutural surfaces) probably contributed to the dorsolateral corners of the condyle. Rostrally the sides of the basioccipital are uniformly concave and then expand to support the suture with the basisphenoid and the adjacent expansion for the basal tubera. The basisphenoid is an irregular block of bone that is generally recognizable as such but offers little detailed anatomy. It is pierced dorsally by the pituitary fossa and laterally by the carotid canal that runs diagonally through the external wall of the basisphenoid and enters the caudal wall of the pituitary fossa on either side of the midline.

The palate of *Scelidosaurus* has been illustrated only in cross section (Owen 1861a). The small, laterally compressed vomers partition the respiratory cavities in the midline**[JSA3]**. In fact the entire palate is well preserved in *Scelidosaurus* and has been exposed following extensive laboratory preparation (Norman, in prep.). The vomers form long triangular plates that are fused in the ventral midline and subdivide the nasal cavity. They extend backward to the level of the orbital cavity, where they meet and articulate with the thin rostral plates of the pterygoids. The latter form complex plates linking the quadrate with the forward part of the skull (palate, braincase, and upper jaw) via the palatines, the ectopterygoids, and the basipterygoid articulation.

In *Scutellosaurus* the lower jaw is straight and slender and tapers rostrally (fig. 15.1D). It has indications of a low coronoid eminence, and the ramus expands lateral to the tooth sockets to form a distinct recess; this morphology is similar to that of *Emausaurus* (fig. 15.2C, D) and to a lesser degree to that of *Scelidosaurus.* No predentary is known in any of the taxa under consideration, and there is certainly little space for such a bone in the distal end of the dentary of *Scelidosaurus.* The dentary symphysis has rugose articular surfaces that are inclined rostrally (Haubold 1990). The dorsal and ventral margins of the dentary of *Scelidosaurus* (fig. 15.1A) converge rostrally over the course of
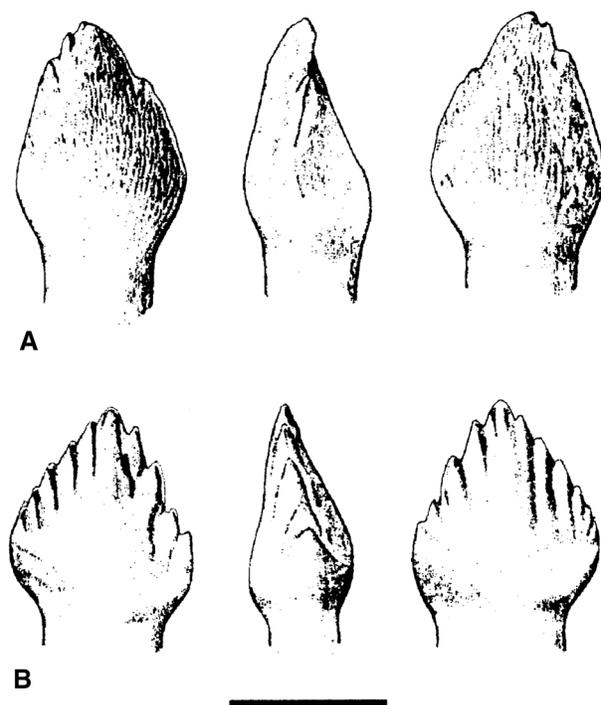

FIGURE 15.3. Teeth of *Emausaurus ernsti:* A, premaxillary tooth in lingual, distal, and buccal views; B, maxillary tooth in lingual, distal, and buccal views. Scale = 2 mm. (From Haubold 1990.)

the first six or so tooth positions to create a slightly sinuous profile, a feature that is also discernible in *Emausaurus.* There are as many as 18 tooth positions in *Scutellosaurus,* 21 in *Emausaurus,* and more than 17 in *Scelidosaurus. Scelidosaurus* lacks an external fenestra on the lower jaw (but this area is obscured by a discrete dermal ossification), while *Emausaurus* has a large fenestra in this region; the lower jaw of *Scutellosaurus* is not sufficiently well preserved for determination. The surangular is large, forming the majority of the coronoid eminence, and projects caudally to support the retroarticular process. In both *Emausaurus* and *Scelidosaurus* the surangular is marked by a horizontal ledge that extends forward horizontally from the rostral border of the glenoid, and in this area there is a well-marked surangular foramen. The wedge-shaped angular forms the ventral part of the caudal half of the lower jaw. The splenial is a narrow splinter of bone on the ventral margin of the lower jaw. A full complement of postdentary bones is preserved in newly prepared material of *Scelidosaurus* (Norman, in prep.).

Premaxillary tooth morphology is simple, with simple, laterally compressed, conical crowns in *Scutellosaurus.* In *Emausaurus* these teeth are small, slightly spatulate, and symmetrical (fig. 15.3A), while in *Scelidosaurus* they have cylindrical roots that taper slightly as they merge with the crowns, which have swollen bases tapering to a recurved, laterally compressed tip. The mesial and distal edges of the more distal crowns are ornamented by small denticles, and the overall tooth form converges on that seen in maxillary teeth. The maxillary and dentary tooth crowns in all taxa have cylindrical roots that taper to meet the swollen, mesiodistally expanded crown base (fig. 15.3B); the region of the tooth crudely approximates to a cingulum. Above the crown base the crown is laterally compressed and tapers to the apex, while the mesial and distal edges also converge and bear distinct but simple denticles. The apex of the tooth stands

above a thickened eminence that divides the lingual and labial faces of the smooth crown into roughly equal mesial and distal regions. The crown edges each bear four to six denticles in *Scutellosaurus* and *Emausaurus* (fig. 15.3B) and six to nine in *Scelidosaurus;* these decrease in prominence toward the apex of the crown. The lowermost denticles on each edge of the crown coalesce at the midline to form the cingulum. In all taxa the enamel is distributed equally on the labial and lingual faces of the crown. Adjacent teeth in the undisturbed jaw touch each other and in some instances *(Scelidosaurus)* exhibit a degree of notching caused by abrasion between teeth during growth and feeding movements. Roots are long, essentially cylindrical, and aligned with the crown.

Postcranial Skeleton

AXIAL SKELETON

The vertebral count of *Scelidosaurus* as preserved is 6 cervicals, 17 dorsals, 4 sacrals, and 35 caudals (fig. 15.4A). Owen (1863) suspected that one or two cervicals were missing. The vertebral column of *Scutellosaurus* consists of 24 presacral, 5 sacral, and about 60 caudal vertebrae (fig. 15.4B). Of the presacrals there are 6 or 7 cervicals (including the atlas and axis), 17 or 18 dorsals, and 5 sacrals. The neurocentral sutures are open in the presacral series but closed in the tail. All the vertebrae are amphiplatyan. Although the specimens are disarticulated, Colbert (1981) arranged the vertebrae in sequence, presumably based on size and the regional differentiation observed in other species. The vertebral column, as well as the remainder of the postcranial skeleton, is poorly known in *Emausaurus.*

In *Scutellosaurus* the cervical centra exhibit deep lateral excavations and a medial ventral keel that becomes smaller as the dorsal series is approached, and the articular faces of each centrum narrow ventrally. The cervical neural arches are poorly known. The length of the cervical centra is as great or greater than their diameter. The transverse processes are dorsoventrally compressed and project laterally to slightly caudally in the cervicals and the cranial dorsals. Parapophyses are not apparent on the cervical centra.

In *Scutellosaurus* and *Scelidosaurus* the dorsal centra are less constricted and more spool-shaped, lack ventral keels, and bear longitudinal striations. Their articular surfaces are round. In *Scutellosaurus* the neural spines are poorly known but expand dorsally to form a short but axially expanded blade. The transverse processes are less robust on the cranial dorsals but become broader and/or stouter toward the sacrum. This broadening reflects the migration of the parapophysis from the base of the transverse process in the cranial dorsals to a position on the transverse process near the diapophysis further back along the series. The diapophysis becomes progressively smaller as the parapophysis approaches it, until in the last dorsals all that remains is a single conjoined facet. In *Scelidosaurus* the transverse processes of the cranial dorsals bear a diapophysis distally, while the parapophyses are on the flanks of the neural arch pedicles. The parapophyses gradually shift dorsally to the underside of the transverse processes along the dorsal series. The last three dorsals have only the conjoined rib facet at the tips of their transverse processes; the last dorsal does not bear a rib. The neural spines are broad, compressed plates (in lateral aspect), short, and squared off.

In *Scutellosaurus* the sacral centra are broader than long with crescentic articular faces and smooth ventral surfaces. The trans-

verse processes are broad. The postzygapophyses are small, almost vertical, and close together. In *Scelidosaurus* the neural spines of the sacral series are in direct contact but do not exhibit any tendency to fuse with one another.

In *Scutellosaurus* the tail is about 2.5 times the presacral length as a consequence of the large number of elongate vertebrae. Individual vertebrae of the proximal two-thirds of the caudal series are longer than the presacral vertebrae. The proximal caudal centra are broad, and the distal caudals become narrower. Chevron facets are found in the proximal three-fifths of the series. The neural arches are fused to the centra throughout the tail. The thin, distally inclined neural spines, found in the proximal three-quarters of the series, become progressively smaller distally. The transverse processes are large in the most proximal caudals but become smaller distally and are absent in the distal two-thirds of the tail. The zygapophyses are small and close together. In *Scelidosaurus* the caudal series is short. The transverse processes are inclined 15°–20° in the caudal dorsals, and the distal caudals are comparatively long and slender.

In *Scutellosaurus* and *Scelidosaurus* the presacral ribs reflect the serial changes noted above for the vertebrae: the capitulum and the tuberculum are widely separated in the cranial dorsals and become closer together in the caudal dorsals. As noted, in the last few dorsal vertebrae the diapophysis and parapophysis are fused; consequently several ribs are single-headed. In *Scelidosaurus* the four sacral ribs are stout, long, and expanded at either end. They are sutured to their transverse processes and to the lateral surfaces of intercentral region, and they are progressively shorter from cranial to caudal; each projects horizontally and expands distally, but adjacent sacral ribs do not contact or suture with each other to form a sacral yoke.

The bladelike, laterally compressed chevrons are intervertebral at least to caudal 28 in *Scelidosaurus* and to caudal 30 in *Scutellosaurus.*

Colbert (1981) identified a few fragments of *Scutellosaurus* as possible ossified tendons. Substantial numbers of ossified tendons are preserved across the dorsal, sacral, and proximal caudal series in both juvenile and adult *Scelidosaurus.*

APPENDICULAR SKELETON

In *Scutellosaurus* the scapular shaft is broad in lateral aspect and bowed to reflect the curvature of the dorsal rib cage. The expanded proximal end supports a portion of the glenoid; its articular surface is reniform and oriented approximately perpendicularly to the long axis of the scapular blade. In addition, there is a truncated acromial ridge and, between these two areas, a broad, lateral depression. The articulation between scapula and coracoid is sinuous. The coracoid, which is roughly dishshaped in lateral view, is pierced by a coracoid foramen near the scapular suture. The glenoid portion of the coracoid is round. In *Scelidosaurus,* by contrast, the scapular blade is narrower with a pronounced expansion proximally and a mild expansion of the blade distally. The coracoid is a subcircular disc in lateral view.

In *Scelidosaurus* the humerus is slightly bowed and moderately thick and has a large deltopectoral crest extending almost to its midlength. In contrast, the humerus of *Scutellosaurus* is slender and slightly bowed laterally, and the triangular deltopectoral crest is proximally situated. In addition, the proximal end is expanded transversely and rounded. A small head lies just lateral to a medial tuberosity. The distal end is in approximately the same plane as the proximal. The radial and ulnar condyles are similar in size, and the olecranon fossa is slightly deeper than the cubital fossa.
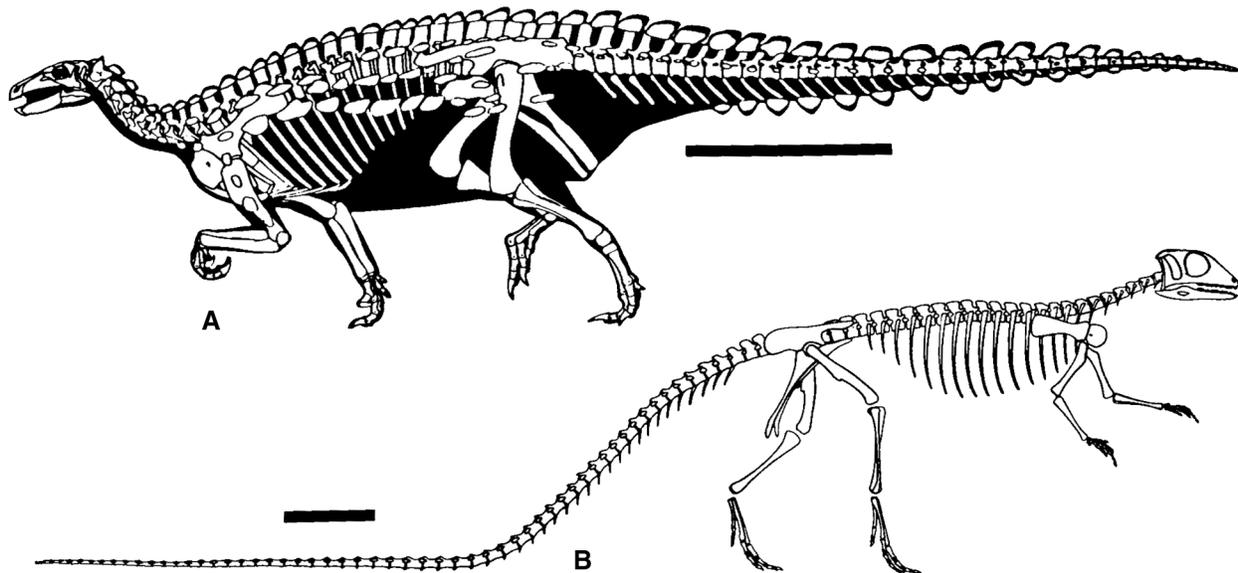
FIGURE 15.4. Skeletal reconstructions of A, *Scelidosaurus harrisonii* with dermal armor, and B, *Scutellosaurus lawleri*. Scale = 50 cm. (A from Paul 1987b; B from Colbert 1981.)

The radius and ulna are incompletely known in *Scutellosaurus,* and the length of the antebrachium cannot be estimated. Both bones are straight and cylindrical. The ulna lacks a well-developed olecranon. The distal ends of the bones, simple rounded articulations, are about the same size. Proximal fragments of the radius and ulna are preserved, but the carpus and manus are unknown in *Scelidosaurus.* In *Scutellosaurus* the carpus is similarly unknown, and just a few metacarpal fragments and several phalanges represent the manus. The unguals are small, pointed claws. Although incomplete, the hand has been described as being moderately large (Colbert 1981).

The pelvic girdle and femur of *Scelidosaurus* are well known (but incorrectly illustrated) from a partial skeleton identified as a juvenile (fig. 15.5B; Rixon 1968; Charig 1972). The post-acetabular process of the restored ilium of *Scutellosaurus* (Colbert 1981) is shown as laterally compressed, long, and near-vertical, and there is indication of a narrow brevis shelf ventrally. The preacetabular process is dorsoventrally compressed, resembling the condition in *Scelidosaurus,* in which the entire ilium (Charig 1972) has a deep, slightly inclined postacetabular process, no indication of a brevis shelf, and a long, markedly dorsoventrally compressed preacetabular process that swings laterally toward its distal end. In *Scutellosaurus* the dorsal margin of the ilium is thickened along its length and slightly overhangs the preacetabular process (fig. 15.5A). The pubic peduncle is prominent, triangular in cross section, and inclined cranially. The ischial peduncle in *Scelidosaurus* is smaller and forms a convex pad immediately behind the acetabulum. Colbert (1981) described but did not illustrate a supracetabular flange in *Scutellosaurus,* and a similar prominent flange is also found in *Scelidosaurus.*

In both *Scelidosaurus* and *Scutellosaurus* the rodlike ischium extends caudoventrally below the ilium and is bifurcated proximally into subequal iliac and pubic peduncles. These two forms have neither an ischial flange partially occluding the acetabulum (found in eurypodans) nor an obturator process on the ischium. The distal ends of the ischia expand into stout, blade-like structures.

The pubis is an elongate slender rod that extends the entire length of the ischium in *Scelidosaurus,* and it has been similarly
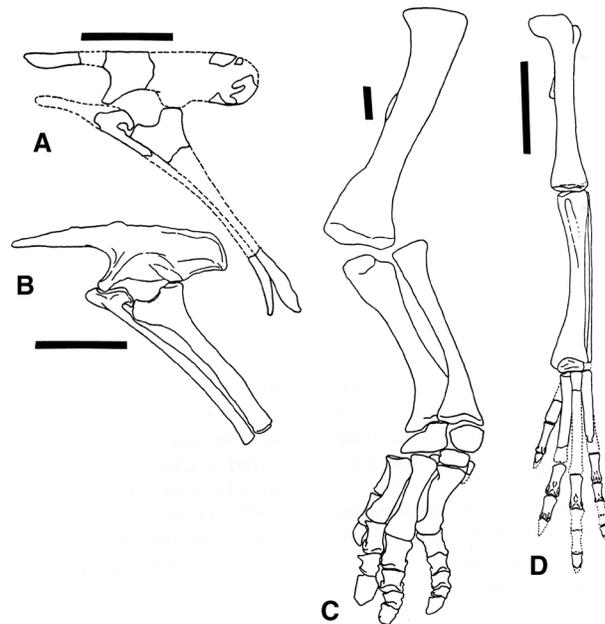

FIGURE 15.5. A, B, pelvic girdles of A, *Scutellosaurus lawleri,* and B, *Scelidosaurus harrisonii.* C, D, hindlimbs of C, *Scelidosaurus harrisonii,* and D, *Scutellosaurus lawleri.* Scale = 10 cm (A), 5 cm (B), 20 cm (C, D). (A after Colbert 1981; B after Charig 1972; C after Owen 1863; D from Colbert 1981.)

reconstructed in *Scutellosaurus*. The distal end of the pubic shaft curves away from the ischium in *Scutellosaurus*. In *Scelidosaurus* the prepubic process is short, blunt, and laterally twisted. The obturator foramen is a notch that is closed caudally by the articulation of the ischium.

The femur is slightly bowed in both *Scelidosaurus* and *Scutellosaurus* (fig. 15.5C, D). The medially displaced head is set off from the shaft by a slight neck in *Scutellosaurus* but not in *Scelidosaurus*. The greater trochanter is at the same level as the head and continuous with it. The cranial trochanter is prominent and

well separated from the greater trochanter by a deep notch. The large, pendant fourth trochanter arises from the proximal half of the shaft; its distal tip is positioned at about femoral midlength in both *Scutellosaurus* and *Scelidosaurus* (Charig 1972; Colbert 1981). The distal condyles are well developed and lie at about the same horizontal level. The medial femoral condyle is slightly larger and stouter than the lateral even though the lateral condyle bears a fibular ridge on its external edge. There is a distinct medial supracondylar ridge. The cranial intercondylar groove is absent, but caudally there is a deep, broad recess between the flexural buttresses for the knee joint.

The tibia of *Scutellosaurus* is slightly longer than the femur, the reverse of the proportions in *Scelidosaurus.* The expansion of the proximal end results from the considerable development of the cnemial crest. Despite this direction of expansion, the proximal end is also transversely broad. The lateral tibial condyle is much smaller than the medial condyle and bears part of the fibular articulation. The medial border of the shaft is sharp distally. The distal end of the tibia is twisted about 70° from the proximal end. The medial margin of the distal tibia is larger than the lateral and projects farther distally. The fibula is a long, slender bone that expands proximally.

Scelidosaurus has a large astragalus and a smaller calcaneum, which cap the distal ends of the tibia and fibula, respectively, and two distal tarsals. Except for the astragalus, the tarsus of *Scutellosaurus* is poorly known. The astragalus bears a low but well-developed ascending process; its apex is situated close to the medial border.

In *Scutellosaurus* the metatarsals are moderately long. Proximally they are closely appressed, metatarsals II–IV forming a curved row. Distally the metatarsals apparently diverged slightly. A deep median pit near the heads of the proximal phalanges receives a process from the second phalanges and suggests considerable extension at this joint. The unguals are clawlike and pointed, with deep lateral claw grooves. The phalangeal formula of *Scutellosaurus* is unknown. *Scelidosaurus* has four robust metatarsals and a vestigial metatarsal V; the phalanges are also short and have pulleylike articular surfaces. The unguals are blunt rather than pointed, medially twisted along their length, and bear only discrete claw grooves on their medial edges. The pedal digital formula of *Scelidosaurus* is 2-3-4-5-0.

ARMOR

The dermal armor of *Scelidosaurus* includes numerous roughly oval plates that have an outer median longitudinal ridge or keel. In front of its apex the ridge is long, upwardly convex, and obliquely slanted, whereas behind the apex it is shorter, straighter, and more vertically oriented. Larger plates are excavated on their internal surfaces. There are also numerous smaller plates, some with keels and some merely small nubbins. *In situ* plates indicate a pair of unique three-pointed plates just caudal to the skull on either side of the midline; ligaments attach these to the postzygapophyses of the axis vertebra. Immediately behind each triradiate element is a longitudinal row of plates running adjacent to the midline and extending to the sacral region; at least two additional longitudinal rows of plates lie over the flanks of the animal. Four longitudinal rows of plates—median dorsal, median ventral, and lateral rows—have been identified running down the tail (fig. 15.4A; Owen 1863). Padian (1989) identified *Scelidosaurus* sp. on the basis of a few cap-shaped dermal ossicles in the Kayenta Formation of northern Arizona; he claimed that these were "flatter and differently sculptured" than those of *Scutellosaurus,* an approximately coeval form (Padian

1989:440). Given the range and variability of the scutes of *Scutellosaurus* described by Colbert (1981), this feature is an insufficient basis for assignment to *Scelidosaurus* and these scutes simply merit the more general assignment Thyreophora indet., although we agree with Padian that these specimens are not like the scutes of aetosaurian archosaurs.

Scutellosaurus was covered in dermal armor comprising hundreds of scutes, although their exact number and pattern of placement are unknown. Colbert (1981) divided the scutes into six groups that presumably relate to regional differentiation, but only two or three of these groups are markedly different. All scutes are rugose with a high degree of pitting, and they almost always have a longitudinal keel on the dorsal surface. They are excavated such that they are generally of uniform thickness. Nearly all scutes are asymmetrical; some are low and flat or elongate and sharply keeled, while others are tall and triangular in profile. The scutes were probably positioned in rows on the back and flanks of the animal, with the larger scutes perhaps occupying a more dorsal position. Their asymmetry suggests that none were median structures. The remaining, symmetrical scutes are long and narrow; Colbert (1981) suggested that these belonged to a median series along the tail. Drawing comparison with Owen's (1863) observation in the articulated *Scelidosaurus* tail, there may well have been median dorsal, ventral, and bilateral rows of such scutes in *Scutellosaurus.* Finally, there are transitional scutes with double keels and symmetrical bases, whose position in life remains unclear.

Emausaurus also exhibits dermal scutes that range from simple conical elements with slightly caudally offset apices to tall, spinelike elements (Haubold 1990:fig. 15) reminiscent of those seen in eurypodans.

Systematics and Evolution

Thyreophora, originally proposed by Nopcsa (1915, 1917, 1923b, 1928c), has been redefined as a stem-based taxon, all genasaurs more closely related to *Ankylosaurus* than to *Triceratops* (Sereno 1999a; see also Coombs 1978b; Norman 1984a; Sereno 1984, 1986; Cooper 1985; Gauthier 1986; and Weishampel 1990c).

Basal tree topology has been the subject of some debate in recent years. Sereno (1984) recognized Thyreophora as a clade including Stegosauridae + Ankylosauria + Pachycephalosauria and Ceratopsia. In contrast, Norman (1984a) restricted Thyreophora to Stegosauridae + Ankylosauria with *Scelidosaurus* as the sister taxon to Ankylosauria. Cooper (1985) supported the latter pattern of armored taxa but proposed *Scelidosaurus* as a taxon basal to Stegosauria and Ankylosauria. Sereno (1986, 1997, 1999a) accepted Norman's restriction of Thyreophora to the armored ornithischians and followed Cooper (1985) in placing *Scelidosaurus* as a taxon basal to Eurypoda (Ankylosauria + Stegosauria) but added *Scutellosaurus* and subsequently *Emausaurus* (following Haubold 1990) to the basal grouping. Carpenter (2001a) reverts to the view of Norman (1984a) in placing *Scelidosaurus* as the sister taxon to Ankylosauria but retains basal thyreophoran status (basal to Eurypoda) for *Scutellosaurus* and *Emausaurus.*

In order to evaluate the basal tree topology of Thyreophora, the monophyletic status of the clade, and the positions of *Scutellosaurus lawleri, Emausaurus ernsti,* and *Scelidosaurus harrisonii* with respect to Eurypoda, a numerical cladistic analysis was carried out on these taxa using PAUP*4.02b (Swofford 1999). Based on 21 characters, outgroup comparisons were made with Cerapoda and *Lesothosaurus diagnosticus* successively. This analysis yielded a single most parsimonious tree, presented in
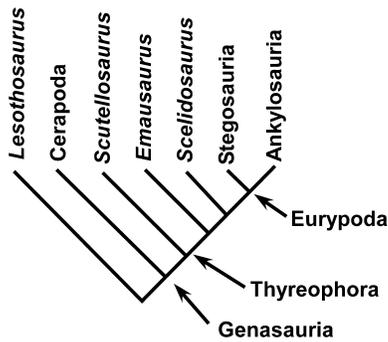
FIGURE 15.6. Cladogram of Thyreophora, emphasizing relationships of *Scutellosaurus lawleri, Emausaurus ernsti, Scelidosaurus harrisonii,* and higher taxa. Tree length = 25, CI = 0.92, RI = 0.94, RCI = 0.87.

figure 15.6. The tree length is 25 steps, CI = 0.92, RI = 0.94, and RCI = 0.87.

This clade can be diagnosed based on the following characters: a transversely broad postorbital process of the jugal; a single supraorbital with a large base (uncertain in *S. lawleri*); a median palatal keel (uncertain in *S. lawleri*); a vertically tall pterygoid and vomer (uncertain in *S. lawleri*); an elongate trunk region compared with the hindlimb length; an elongate ilium relative to the femur length; a pair of parasagittal rows of low, conical scutes on the dorsum of the body (uncertain in *Emausaurus*); one or more rows of low-keeled scutes positioned on the flanks of the body (probable but still unconfirmed in *Emausaurus*); differentiation of high- and low-keeled scutes, and ventrally excavated scutes.

Scutellosaurus, Emausaurus, and *Scelidosaurus* represent successive taxa on the stem lineage leading to Eurypoda, confirming the conclusions of Haubold (1990). *Scutellosaurus lawleri* is the sister taxon to the clade comprising *Emausaurus + Scelidosaurus* + Eurypoda. The latter, more exclusive grouping is supported by several characters: ventral deflection of the mesial dentary dentition; a high root-crown ratio; a horizontal ledge on the external surface of the surangular; a tightly sutured postorbital-jugal; and the shape of the jugal-quadratojugal suture.

Scelidosaurus harrisonii is the sister taxon to Eurypoda (comprising Thyreophoroidea *sensu* Sereno 1986). The latter clade is diagnosed by reduction of the antorbital fossa, narrowing of the infratemporal fenestra, and complete suturing of the supraorbital to the dorsal orbital margin.

Several other taxa have been allied with these basal thyreophorans. For example, Coombs, Weishampel, and Witmer (1990) referred the poorly known *Tatisaurus oehleri* to Thyreophora, although Simmons (1965) had originally referred it to Hypsilophodontidae. The sole feature in *T. oehleri* relevant here is the ventral deflection of the mesial end of the dentary tooth row, which is a synapomorphy of all thyreophorans above the level of *Scutellosaurus*. Beyond this, *Tatisaurus* is too incompletely preserved to determine its more inclusive position within Thyreophora.

Another form, *Echinodon becklesii,* was originally included by Galton (1978) in his Fabrosauridae, but later it was considered to have a close relationship with *Scutellosaurus* (Galton 1986a). At the same time, Galton also assigned the dermal scutes from the same locality to *Echinodon,* a referral that was followed by Coombs, Weishampel, and Witmer (1990). Based on more detailed analysis of the cranial and dental features of *Echinodon,* Norman and Barrett (2003) now regard this Early Cretaceous ornithischian as a possible heterodontosaurid. The dermal ossifi-

cations (granicones [Owen 1861b]) have nondinosaurian affinities (Barrett et al. 2002a).

Paleobiogeography and Paleoecology

The fossil record of *Scelidosaurus harrisonii, Emausaurus ernsti,* and *Scutellosaurus lawleri* is limited to the Early Jurassic of Laurasia (England, Germany, the United States, and the People's Republic of China). Given these data, it is impossible to assess the probable source area for Thyreophora.

The depositional environment in which the disarticulated remains of *Scutellosaurus* have been found (Kayenta Formation, southwestern United States) has been interpreted as broad floodplain habitats drained by moderate, sediment-rich streams (Clark and Fastovsky 1986). Water may have been abundant, although soil formation is known at several horizons. The fauna of the Kayenta is rich in terrestrial vertebrates, including a variety of basal archosaurs, crocodilians, theropod dinosaurs, and tritylodontids. The Kayenta Formation also has a freshwater bivalve fauna, indicating well-watered conditions. Unfortunately, floral evidence is lacking from the Kayenta. The Kayenta environment was probably stable, water-rich, warm, and humid.

Skeletal remains of both *Emausaurus* and *Scelidosaurus* are known to occur in nearshore marine deposits of Germany and England. *Scelidosaurus* was interpreted by Owen (1863) as terrestrial or perhaps amphibious in habit, living near the margins of watercourses, so that carcasses were occasionally washed out to sea. It is likely that this interpretation also applies to *Emausaurus.*

Early thyreophorans were active foragers on shrubby vegetation within a meter above the ground. It is likely that all forms under consideration relied solely on simple adduction of the lower jaws to produce a vertical or near-vertical tooth-tooth shearing motion between the maxillary and dentary teeth, similar to *Lesothosaurus* (Thulborn 1971a; Weishampel 1984a; Norman and Weishampel 1991; Barrett 2001).

Scutellosaurus may have been a bipedal herbivore (Colbert 1981), but the hindlimbs are shorter relative to the length of the preacetabular process than in species regarded as obligate bipeds (Colbert 1981). The notably elongate tail, slender hindlimb, and compact pes with slender metatarsals all suggest cursorial habits; however, the lengths of the femur and metatarsal III relative to the tibia are less reflective of cursorial habits than in other bipedal ornithischians (Colbert 1981). The disproportionately long trunk, the broad and stout scapular blade, the long forelimbs, a moderately large manus, a wide pelvis, and most important, extensive dermal armor are at least suggestive of quadrupedality. *Scutellosaurus* may have been derived from bipedal, cursorial ancestors but had adopted occasional quadrupedality, perhaps for foraging. As suggested by Colbert (1981), the species may be a harbinger of full quadrupedality in more derived thyreophorans.

Scelidosaurus and *Emausaurus* were in all probability "high-grade mediportal" quadrupeds (Coombs 1978b); this is certainly the case for *Scelidosaurus* given the nature of its limb proportions and foot construction (fig. 15.4A; unknown in *Emausaurus*). The skeleton of *Scelidosaurus* retains features indicative of a recent cursorial or subcursorial ancestry (Thulborn 1977; Colbert 1981); most notable is the pendant fourth trochanter of the femur. Although theoretically *S. harrisonii* may have been capable of assuming a bipedal or tripodal stance, as advocated for sauropods and stegosaurs (Coombs 1975; Bakker 1971a, 1978, 1986), whether such postures were biologically significant is dubious.