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## LESOTHO SAURUS, “FABROSAURIDS,” AND THE EARLY EVOLUTION OF ORNITHISCHIA

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**ABSTRACT**—New materials of *Lesothosaurus diagnosticus* permit a detailed understanding of one of the earliest and most primitive ornithischians. Skull proportions and sutural relations can be discerned from several articulated and disarticulated skulls. The snout is proportionately long with a vascularized, horn-covered tip. The premaxillary palate is broad and vomers are long and fused anteriorly. Unlike many later ornithischians, the postpalatine vacuities are broadly open. The basal tubera are short and gently depressed, and the epiotic contributes to the sidewall of the braincase. The mandibular symphysis is spout-shaped, and the dentition is marked by oblique wear facets, in contrast to earlier reports. The tooth-to-tooth wear facets and form of the predentary-dentary articulation suggest long-axis rotation of the mandibular rami during mastication.

The forelimb is proportionately very short, with a partially opposable pollex. The ischium lacks an obturator process. The reduced hallux is held well above the substrate during locomotion.

*L. diagnosticus* is diagnosed below on the basis of apomorphic features. Other “fabrosaurids” constitute a heterogeneous assemblage of poorly known ornithischians and hatchling prosauropods that do not share any apomorphic features with *L. diagnosticus*. *Fabrosaurus australis* is a nomen dubium, and, as a consequence, the family Fabrosauridae is invalid. *Echinodon becklesii* may represent a primitive heterodontosaur, and *Tawasaurus*, *Fulengia*, and portions of the holotype of *Technosaurus* represent hatchling prosauropods. *Pisanosaurus mertii* may be the most primitive ornithischian, as indicated by the form of the distal crus and astragalus, but a more precise phylogenetic assessment will require additional remains.

### INTRODUCTION

Ornithischian dinosaurs have been construed as a monophyletic, or “natural,” group as early as the middle of the nineteenth century, when known dinosaur remains were few and fragmentary (Cope, 1866). Conspicuous ornithischian synapomorphies, such as the horn-covered predentary bone that caps the anterior end of the lower jaw, were identified as soon as better material came to light (Baur, 1891; Marsh, 1895).

Despite longstanding consensus regarding ornithischian monophyly, there has been no historical scheme of relationships for the various distinctive subgroups of ornithischians, and until recently there were no fossil ornithischians that approached the hypothetical ancestor. In the late sixties, abundant remains of the basal ornithischian *Lesothosaurus diagnosticus* were discovered in the Lower Jurassic of southern Africa (Crompton, 1968; Thulborn, 1971a). Other early ornithischians have recently been reported from North America (Galton, 1978; Chatterjee, 1984; Hunt, 1989), Europe (Thulborn, 1973), and China (Young, 1982). These early ornithischians, collectively referred to as “fabrosaurids,” have been regarded as ornithischian ancestors (Thulborn, 1970, 1971a, 1972) or as ornithischian sister-groups (Galton, 1978; Norman, 1984; Milner and Norman, 1984; Cooper, 1985; Hunt, 1989).

The purpose of this paper is to augment our current

understanding of the basal ornithischian *Lesothosaurus* and to review the materials of other supposed primitive ornithischians.

### ABBREVIATIONS

**Institutional**—AMNH, American Museum of Natural History, New York; BGM, Beijing Geological Museum, Beijing; BMNH, British Museum (Natural History), London; CUP, Catholic University of Peking (housed in the Field Museum of Natural History, Chicago); IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; MNA, Museum of Northern Arizona, Flagstaff; MNHN, Muséum National d'Histoire Naturelle, Paris; PVL, Instituto Miguel Lillo, Tucumán; SAM, South African Museum, Cape Town; TTU, Texas Tech University.

### MATERIAL

The type dentary of *Fabrosaurus australis* was discovered in 1959 in the Red Beds of the Stormberg Series near Mapheteng in Lesotho, southern Africa (Fig. 1; MNHN LES9; Ginsburg, 1964). More complete material was discovered in 1963–1964 in Lesotho by an expedition from University College (London) and was referred to *Lesothosaurus diagnosticus* (BMNH RUB17,

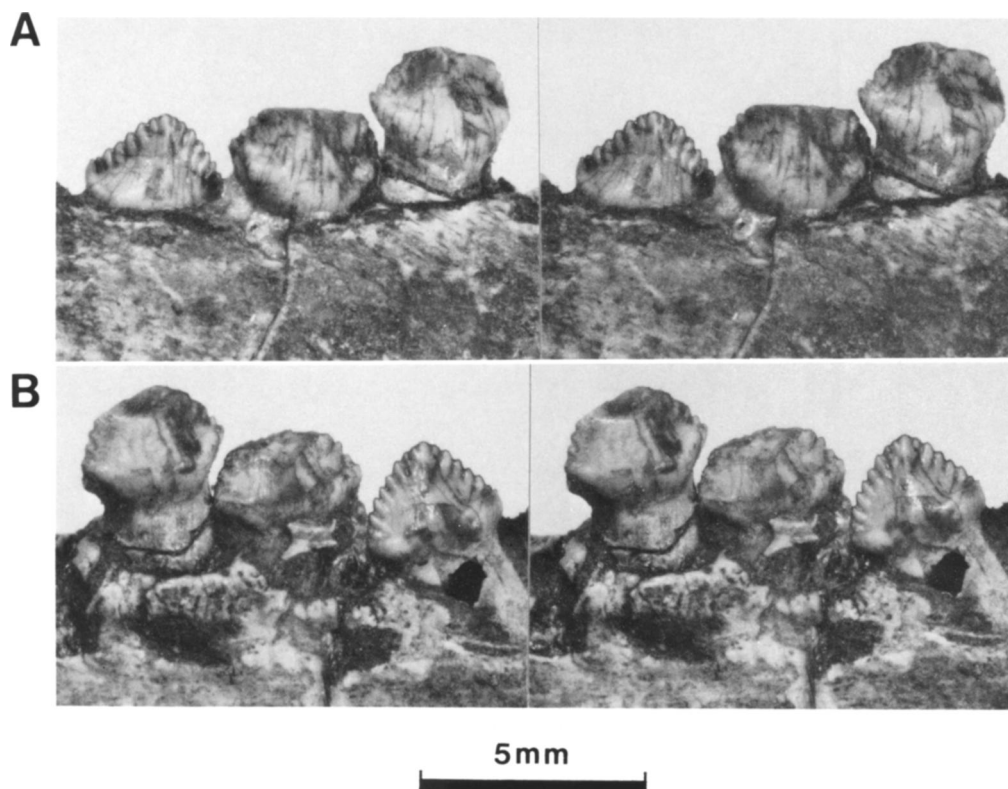


FIGURE 1. Stereopairs of posterior dentary teeth of the holotype of *Fabrosaurus australis* (MNHN LES9) in lateral (A) and medial (B) views.

RUB23; Galton, 1972). Current concepts of the cranial and postcranial morphology of primitive ornithischians has been based almost exclusively on this material (Thulborn, 1970, 1972).

Further well-preserved cranial and postcranial remains of *L. diagnosticus* were collected in 1967–1968 in Lesotho by a joint expedition from the British Museum (Natural History), London University, Yale University and the South African Museum (Crompton, 1968). Santa Luca (1984) described some of the postcrania in this collection; the well preserved cranial material (Crompton and Attridge, 1986; Weishampel, 1984) is considered below (Figs. 2–5; BMNH R8501, R11004).

#### SYSTEMATIC PALEONTOLOGY

##### Systematic hierarchy:

Dinosauria Owen, 1842

Ornithischia Seeley, 1888

Genus *LESOTHOSAURUS* Galton, 1978

**Type Species**—*Lesothosaurus diagnosticus* Galton, 1978.

**Diagnosis**—As for *Lesothosaurus diagnosticus*, diagnosed below.

##### *LESOTHOSAURUS DIAGNOSTICUS* Galton, 1978 (Figs. 2–13)

**Syntypes**—BMNH RUB17 (Figs. 6, 7, 8B–F, 9A, B, E, F); (Thulborn, 1970:figs. 2–7; Thulborn, 1971b:figs. 1–3, 8; Thulborn, 1972:figs. 2–12; Galton, 1978:fig. 2), mostly disarticulated remains of at least two individuals, one larger than the other, including most of one articulated skull with stapes, ceratohyals, and the anterior cervical vertebrae; BMNH RUB23 (Thulborn, 1970:fig. 1; Thulborn, 1971b:fig. 7); BMNH R11956, partial skull.

**Locality and Horizon**—Likhoele, near Mapheteng, Lesotho, southern Africa; “Red Beds,” upper Elliot Formation.

**Revised Diagnosis**—Small-bodied basal ornithischian with cranium distinguished by anterior premaxillary foramen and maxilla-lacrimal articulation with lacrimal inserting into a slot in the apex of the maxilla. Postcranium distinguished by proportionately short forelimbs (less than 40 percent hind-limb length), brevis surface on postacetabular process of ilium broadly exposed in lateral view, groove on the dorsal margin of the proximal ischial shaft, and reduced pedal digit I with the proximal end of metatarsal 1 splint-shaped and the distal end of the claw extending just beyond the second metatarsal.

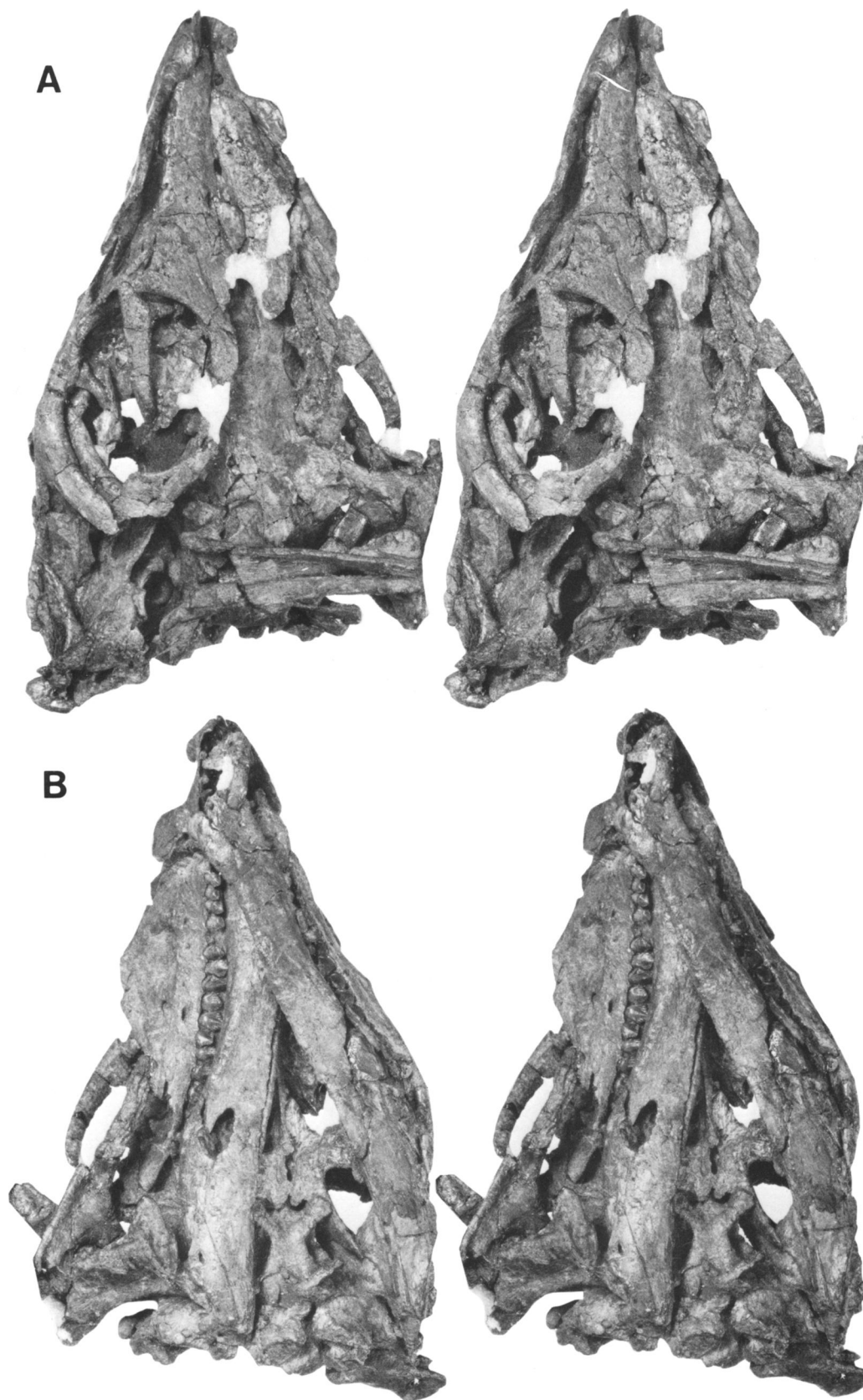
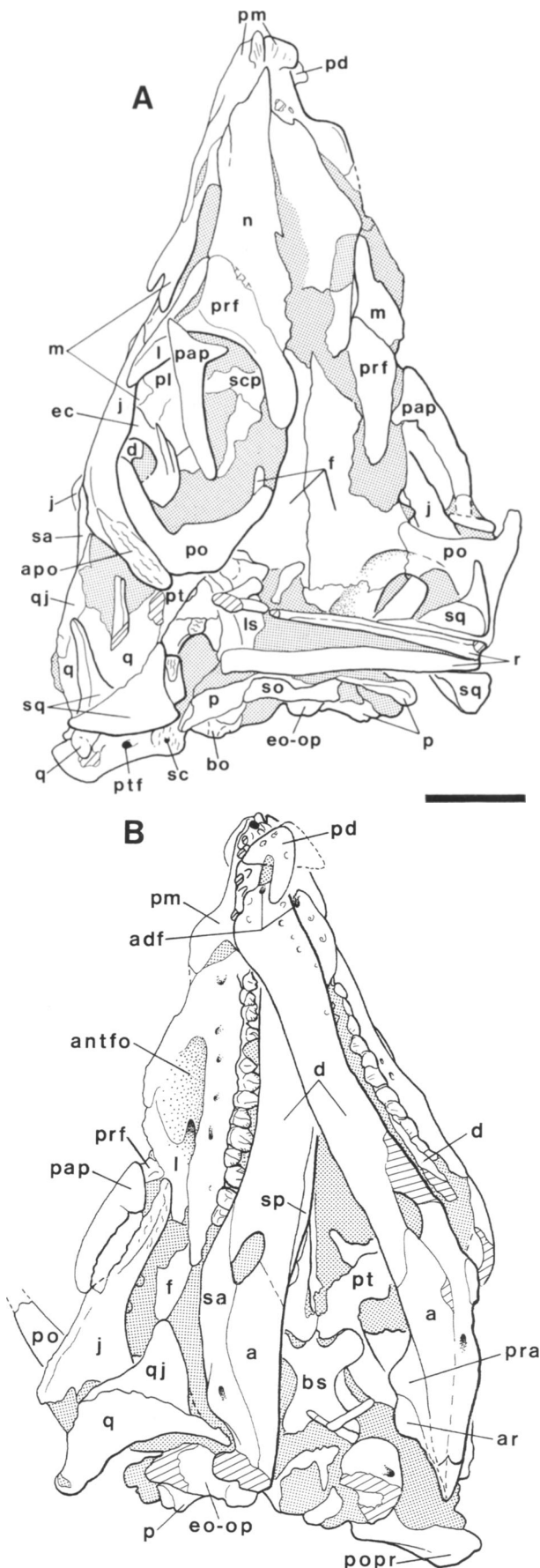


FIGURE 2. Stereopair of skull of *Lesothosaurus diagnosticus* (BMNH R8501) in dorsal (A) and ventral (B) views. See Fig. 3 for scale.



Compared to other ornithischians, *L. diagnosticus* appears to be plesiomorphic in all other respects. *L. diagnosticus* differs from *Pisanosaurus* by its advanced transversely expanded distal tibia and shallow ascending process. Unlike *Scutellosaurus*, dorsal body armor is absent. In contrast to *Echinodon*, maxillary cheek emargination, maxillary-premaxillary diastema, and dentary caniniform tooth are absent.

**Referred Specimens**—BMNH R8501 (Figs. 2, 3; Crompton, 1968:fig. 18; Weishampel, 1984:fig. 2), nearly complete, disarticulated skull; BMNH R11002 (Fig. 9C, D), right ilium; BMNH R11003, left ilium; BMNH R11004 (Fig. 8A), partially disarticulated posterior skull and anterior neck, including the braincase, parietals, right squamosal, right quadrate, right posterior lower jaw, axis, and third cervical; SAM unnumbered (Figs. 4, 5; Crompton and Attridge, 1986:fig. 17.9), right maxilla with complete tooth row; MNHN unnumbered, articulated cranium; SAM K400 (Santa Luca, 1984:figs. 10, 11), left ilium; SAM K401 (Santa Luca, 1984:figs. 12, 13, 18, 20, 24, 25, 27–32), partial postcranium; SAM K1106 (Santa Luca, 1984:figs. 1–9, 19, 21–23, 26), partial postcranium.

**Discussion**—A larger undescribed basal ornithischian from the same horizon as *Lesothosaurus* (Sereno, 1986:247; Crompton and Attridge, 1986:228) also has short forelimbs and a reduced pedal digit I, and these apomorphic characters may eventually emerge as synapomorphies for these taxa. Recently Weishampel and Witmer (1990) confused my remarks about the distinction of these undescribed specimens with Santa Luca's (1984) observation of minor individual variation in other material that, in my opinion, is referred correctly to *Lesothosaurus diagnosticus*. Compared to the syntype skeletons of *L. diagnosticus*, the only difference that Santa Luca considered taxonomically significant in his South African Museum material was the differing position of the attachment scars on the ilium. But the scars in the syntype to which he was comparing were figured inaccurately (Thulborn, 1972:fig. 8C; see below).

Previous diagnoses for *L. diagnosticus* (Steel, 1969; Thulborn, 1972; Galton, 1978) do not differentiate between autapomorphies and symplesiomorphies that apply to all ornithischians or more inclusive groups.

FIGURE 3. Skull of *Lesothosaurus diagnosticus* (BMNH R8501) in dorsal (A) and ventral (B) views. Abbreviations: a, angular; adf, anterior dentary foramen; antfo, antorbital fossa; apo, articular surface for postorbital; ar, articular; bo, basioccipital; bs, basisphenoid; d, dentary; ec, ectopterygoid; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; ls, laterosphenoid; m, maxilla; n, nasal; op, opisthotic; p, parietal; pap, palpebral; pd, predentary; pl, palatine; pm, premaxilla; po, postorbital; popr, paroccipital process; pra, prearticular; prf, prefrontal; pt, pterygoid; ptf, posttemporal foramen; q, quadrate; qj, quadratojugal; r, rib; sa, surangular; sc, semicircular canal; scp, sclerotic plate; so, supraoccipital; sp, splenial; sq, squamosal. Scale bar equals 1 cm.

TABLE 1. Maximum length (in mm) of the metacarpals and phalanges of right manus in *Lesothosaurus diagnosticus* (BMNH RUB17).

Metacarpals		Phalanges	
1	9.0	digit I, phalanx 1	5.3
2	12.1	ungual	5.0
3	12.6	digit II, phalanx 1	6.3
4	9.0	phalanx 2	5.3
5	4.8	digit III, phalanx 1	5.4
		digit IV, phalanx 1	3.9
		digit V, phalanx 1	1.8

Without this distinction the diagnosis functions principally as a non-phylogenetic identification key (Ax, 1987; Sereno, 1990). Thulborn's (1972:51) diagnosis, for example, lists about 70 characters that constitute an abbreviated description of the entire skeleton. Two of Thulborn's (1972:51) characters—a proportionately short forelimb and reduced pedal digit I—are apomorphic with respect to the condition among most other dinosaurs. As mentioned above, these characters are currently autapomorphic for *L. diagnosticus*, although eventually they may also characterize an undescribed larger ornithischian from the same formation.

Galton's (1978:156–157) revised diagnoses of *L. diagnosticus* includes 40 characters, the majority of which are plesiomorphic for Ornithischia rather than apomorphic for *L. diagnosticus*. As discussed below, several of the remaining characters are inaccurate (e.g., “anteriorly jugal deep [sic],” “parietals separate,” “slender descending process of the squamosal,” “about 14 teeth in maxilla,” and “no special foramina”).

The revised diagnosis presented above is based on the following autapomorphies that are present in the syntype specimens:

- 1) Slot in maxilla for lacrimal (Figs. 11A, 12A). At the apex of the antorbital fossa, a thin, tongue-shaped process extends posteriorly from the maxilla (BMNH RUB17, RUB23). The lacrimal inserts into a narrow slot behind the maxillary process, a configuration unknown elsewhere among ornithischians.
- 2) Anterior premaxillary foramen (Figs. 6C, 11A, B, 12A, B). An additional foramen, here termed the anterior premaxillary foramen (see description below), pierces the premaxilla near the alveolar margin (BMNH RUB17) and opens on the premaxillary palate immediately anterior to the first premaxillary tooth (Figs. 11C, 12C; BMNH R8501).
- 3) Short forelimb. The forelimb is very short (less than 40 percent of hind limb length), with limb length estimated by summation of propodials, epipodials and third metapodials in the forelimb and hind limb (Table 1; Thulborn, 1972).
- 4) Lateral exposure of the brevis surface on the post-

acetabular process (Fig. 10). The medial wall of the brevis fossa extends ventrally below the lateral wall and is visible along the length of the postacetabular process in lateral view. *Scelidosaurus* (BMNH R6704) appears to be the only other dinosaur that exhibits a similar condition, which I consider to have appeared independently.

- 5) Dorsal groove on the ischial shaft (Figs. 9A, B, 10). The narrow dorsal margin of the proximal shaft of the ischium is marked by a distinct groove that passes onto the medial side of the blade. A similar grooved margin on the ischium does not occur elsewhere within Ornithischia (BMNH RUB17).
- 6) Pedal digit I reduced (Fig. 8F). Pedal digit I is very slender and short, with the ungual extending just beyond the end of the second metatarsal, and would not have contacted the substrate. The straplike shaft of the first metatarsal, which is very thin in anterior view and very narrow in lateral view, is pressed to the side of the second metatarsal and does not contribute significantly to the proximal articular surface of the metatarsus. Although similar reduction or absence of the digit occurs elsewhere within Ornithischia (Stegosauria, Heterodontosauria, Ankylopollexia; Sereno, 1986), a longer and more robust first digit appears to be plesiomorphic for Ornithischia.

#### Ornithischia Incertae Sedis and Indeterminate

***Alocodon* and *Trimucrodon***—Thulborn (1973) described isolated crowns from the Middle and Upper Jurassic of Portugal as *Alocodon kuehnei* and *Trimucrodon cuneatus*. He stated that “*Alocodon kuehnei* . . . has a dentition which resembles that of *Fabrosaurus* in many respects (even though the cheek teeth of the two animals are not immediately reconcilable in structure)” and that “pronounced resemblances in tooth structure point to a close relationship between *Trimucrodon cuneatus* . . . and *Echinodon becklesii*” (Thulborn, 1973:129–130). No specific characters or outgroups were mentioned to support this claim. The assertion that “*Alocodon kuehnei* and *Trimucrodon cuneatus* appear to be relatives of *Fabrosaurus australis* and *Echinodon becklesii* (respectively) and might best be referred to the Family Fabrosauridae” (Thulborn, 1973:133) appears to lack support. Although Thulborn's (1973) reconstruction of the tooth rows is conjectural and based entirely on isolated teeth, these two poorly established tooth forms appear to be distinct from *L. diagnosticus*. As noted by Thulborn, in *Alocodon* the apical denticle is quite broad and in *Trimucrodon* the anteriormost and posteriormost denticles are very prominent. Recently Weishampel and Witmer (1990) regarded these tooth forms as nomina dubia but did so without comparison. The holotype teeth of *Alocodon* and *Trimucrodon* are referred here to Ornithischia incertae sedis on the basis of the following ornithischian synapomorphies: low, subtrian-

gular crowns that are separated from their roots by a basal constriction and the absence of recurvature in the maxillary and dentary crowns (Serenó, 1986).

**Fabrosaurus**—*Fabrosaurus australis* is based on a partial dentary with three teeth from the Lower Jurassic “Red Beds” of southern Africa (Fig. 1; MNHN LES9; Ginsburg, 1964). It is unfortunate that such fragmentary material was selected as the holotype; more complete material had already been discovered from the same horizon (Gow, 1981). As a result, comparison with the holotype is extremely limited.

Ginsburg (1964:2367) presented the following diagnosis for *F. australis*: “Dinosaure de petit taille, à dents uniradiculées, possédant de longues racines verticales; couronnes petits, étroites, à profil sensiblement équilatéral, crénelées régulièrement sur les deux trachants.” Unfortunately, these characters are present in many ornithischians and appear to be primitive within Ornithischia. Without apomorphic (diagnostic) character evidence, further materials cannot reasonably be assigned to this taxon.

Thulborn nevertheless referred more complete material to *F. australis* (Thulborn, 1970, 1972; BMNH RUB17, RUB23). Galton (1978) argued for taxonomic distinction of Thulborn’s material, erecting a new genus and species, *Lesothosaurus diagnosticus*. His revised diagnosis of *F. australis* included three characters: “Dentary tooth crowns triangular to diamond shaped with width greater than height, dentary broader than in other fabrosaurids, special foramina medially for entrance [sic] of replacement teeth” (Galton, 1978: 156).

The supposed low crown proportions in *F. australis* differ from taller crown proportions listed in Galton’s diagnoses of *L. diagnosticus* and *Nanosaurus agilis*, but the polarity of crown proportions is not specified. Are the supposed low crown proportions apomorphic in *F. australis*? Gow (1981) has noted, in addition, that crown proportions vary along the tooth row. The presence of “special foramina” is acknowledged to be a “progressive” character of *F. australis* (Galton, 1978: 153), but it also occurs in all other ornithischians, including *L. diagnosticus* (Gow, 1981; Norman, 1984), and cannot be considered unique to *F. australis*. Weishampel and Witmer (1990) considered *F. australis* a nomen dubium but did so without discussion.

The holotype of *F. australis* was reexamined to determine whether there are any diagnostic (apomorphic) characters. It consists of the posterior portion of the right dentary with nine alveoli (Fig. 1; MNHN LES9). The dentary teeth near the coronoid rise are inset to the medial side of the ramus, as in BMNH RUB17 and BMNH R8501. The dentary process extending toward the coronoid rise is broken away. As in BMNH RUB17 and BMNH R8501, the posterior dentary ramus is approximately twice as deep as thick. The suggestion that the dentary ramus in MNHN LES9 is “broader” than in specimens referred to *L. diagnosticus* (Galton, 1978) is not supported.

Although replacement foramina are present, most are incomplete due to resorption of bone during replacement. Similar replacement foramina and alveolar resorption occurs in material referred to *L. diagnosticus* (Fig. 4B, C). The alveolar margin is not exposed in the syntypes of *L. diagnosticus* (BMNH RUB17, BMNH RUB23), except for a short section near the symphysis. These species, therefore, cannot be distinguished on the basis of replacement foramina, the presence of which is plesiomorphic for Ornithischia in any case.

Only three crowns are preserved with their adjacent edges overlapping in an imbricate arrangement (Fig. 1). One crown, the fifth from the posterior end of the tooth row, is complete and was undergoing the final stages of eruption at the time of death. The proportions of the crown differ from side to side, because the crown base is lower on the lateral side. Galton’s (1978:153) observation that the crown proportions are wider than tall may have been based on the medial side of the crown. In this view the height closely approximates the width of the crown, as also occurs in referred material. But crown proportions in the holotype of *F. australis* do not appear to be distinct.

The enamel is symmetrically distributed on each side of the crown, as seen in cross-section. The erupting crown has nine denticles on its anterior edge and seven denticles on its posterior edge, with the crown apex offset slightly posteriorly. The lateral crown base is slightly more bulbous than the medial and situated slightly lower on the tooth. A prominent overlap ridge (see dentition below) is present on the posteromedial side of the crown. The medial crown surface is gently convex anteroposteriorly and flat dorsoventrally; the lateral surface is also gently convex anteroposteriorly but is slightly concave dorsoventrally. A rounded linear eminence occurs near the midline on both crown surfaces and joins the crown base ventrally.

The morphology of the dentary crowns in MNHN LES9 corresponds in detail with that of the syntype of *L. diagnosticus* (BMNH RUB17) and in the referred specimen BMNH R8501. These dental characteristics, however, occur in many other ornithischians (such as *Scutellostaurus*, *Scelidosaurus*, *Hypsilophodon*, *Psittacosaurus* and *Stegoceras*) and are viewed here as plesiomorphic within Ornithischia. These include the imbricate arrangement of crowns in the tooth rows, the subtriangular crown shape, symmetrical enamel, posterior offset of the crown apex, approximately six to nine denticles along anterior and posterior margins, a lateral crown base that is more prominent and ventral in position than the medial, anteroposteriorly convex crown surfaces, a lateral crown surface that is also gently concave dorsoventrally, at least a weak median (or paramedian) eminence on the lateral maxillary and medial dentary crown surfaces, and an overlap ridge near the crown base that contacts the adjacent crown margin. I cannot identify any autapomorphic characters in the holotype dentary or dentary teeth of *F.*



*australis* or, for that matter, in the dentitions of material currently referred to *L. diagnosticus*. Consequently, *Fabrosaurus australis* is regarded here as a nomen dubium (see also Charig and Crompton, 1974), and the holotype is considered Ornithischia indet.

**Nanosaurus**—Galton (1978:153) asserted that the Upper Jurassic *Nanosaurus agilis* “is a slightly modified descendant of *Lesothosaurus*.” No specific characters were mentioned to support this contention aside from noting the general similarities in the dentition and fragmentary postcranium. There are no derived characters that unite *N. agilis* with *L. diagnosticus* and few, if any, valid autapomorphies that characterize the fragmentary holotype of *N. agilis* (Galton, 1978:156). *N. agilis* is here considered Ornithischia incertae sedis but may eventually prove to be a nomen dubium.

**Pisanosaurus**—*Pisanosaurus mertii* was discovered in the Upper Triassic Ischigualasto Formation and may represent the oldest known ornithischian (Casamiquela, 1967). Bonaparte (1976) and most later authors have classified *P. mertii* with heterodontosaurids. Others tentatively place *P. mertii* as the sister-group to all other ornithischians (Novas, 1989; Weishampel and Witmer, 1990).

The material of *P. mertii* is fragmentary and weathered (PVL 2577). The original association (Bonaparte, 1976:fig. 1) is no longer available. The skull fragments, partial impression of the pelvis, and the distal right hind limb may well belong to a single individual, but the fragmentary scapula and other assorted small postcrania are too small. Portions of the right maxilla and lower jaw are preserved and show the presence of a well developed cheek emargination, a more advanced condition than in *L. diagnosticus*. In *P. mertii* the maxillary cheek emargination extends along the entire preserved external alveolar margin. Above the cheek emargination, the maxilla is damaged and the ventral margin of the antorbital fossa is not preserved. Previously this region was illustrated as a flat surface (Bonaparte, 1976:fig. 2A). No replacement foramina are visible in the maxilla or dentary. The lower jaw exhibits a distinct cheek emargination along its length, although this has been exaggerated in the posterior half of the dentary by dorsoventral crushing. The dentary has a coronoid process that projects posteroventrally as in other ornithischians. The coronoid region of the surangular is clearly incomplete (contra Bonaparte, 1976:fig. 2D, E). The thickened dorsal margin to which the adductor musculature would attach has broken away, leaving a thin broken edge. The coronoid process, therefore, is not necessarily “low” as in *L. diagnosticus* (Weishampel and Witmer, 1990). The lateral surface of the surangular and angular is depressed, reminiscent of the condition in *Heterodontosaurus*. Although the lower jaw has been reported as lacking an external mandibular fenestra (Casamiquela, 1967; Bonaparte, 1976), the anterior and ventral margins of a small opening are apparent. The crowns of the dentary and maxillary teeth have strong lateral cingula and are set at an angle to the roots as occurs in many

ornithischians. Wear facets cut deeply into the crowns, truncating the distal crown tips. The wear facets vary slightly in angle, and adjacent crown margins are not squared for close apposition. The facets, therefore, do not form a continuous occlusal surface as occurs in *Heterodontosaurus* (contra Bonaparte, 1976:814).

The central portion of the pelvis and sacrum are preserved as an impression in the matrix (Fig. 14A). As far as can be ascertained, the pelvis does not exhibit any ornithischian modifications but rather is primitive in these regards. The pubis appears to project anteroventrally and has a dorsoventrally deep contact with the ischium unlike other ornithischians. There is no evidence for a posterior pubic process (contra Bonaparte, 1976:811). The flangelike ventral margin of the proximal ischium is better developed than in other ornithischians and clearly approaches its opposite in the midline; the ischial shafts converge from a separation of 39 mm at their contact with the ilium to only six mm along the ventral margin of the proximal end, suggesting that the ischial symphysis is not limited to the distal tips of the ischial shafts as in other ornithischians (Serenio, 1986). There is no evidence to support the suggestion that five sacral vertebrae are present (contra Bonaparte, 1976:810). Although the impressions of the ventral surfaces of five centra are preserved, the anterior three centra are slightly disarticulated without any sign of sacral ribs near their sides. These three probably represent posterior dorsal vertebrae. The posterior two centra are closely united and the first shows a low, lateral projection for attachment of a sacral rib. The impression of the rib is present on the right side near the ischial peduncle of the ilium. The number of sacral vertebrae cannot be determined.

The right crus, proximal tarsals, and partial pes are preserved. The distal end of the tibia is subquadrate (see Table 2). Unlike any other ornithischian, the anteroposterior depth of the distal end exceeds the maximum transverse width. In fact, measured just above the fibular flange, the distal end of the tibia is significantly deeper than broad. This proportion must be autapomorphic for *P. mertii*, since the depth of the distal end never exceeds the width in the herrerasaurids *Herrerasaurus* and *Staurikosaurus*. A fibular flange is present on the lateral side of the distal end (Fig. 14B) and is transversely narrower than in other ornithischians. As seen in anterior view, the flange extends laterally beyond the shaft margin and, in this respect, is better developed than in herrerasaurids and *Lagosuchus*.

The very thick ascending process of the astragalus is plesiomorphic compared to all other ornithischians and saurischians; its thickness is more than half the depth of the astragalus (Fig. 14B). In contrast to the condition in herrerasaurids and sauropodomorphs, the ascending process does not form a wedge-shaped insert into the distal end of the tibia, but rather butts proximally against a horizontal shelf. A small vertical fibular facet is exposed in lateral view of the astragalus (Fig. 14B). The disc-shaped calcaneum is autapomorphous.



morphic; it is very reduced in transverse width and as a result forms less of the distal articular surface of the proximal tarsals than in other ornithischians and saurischians. The calcaneum is closely applied to the astragalus and possibly fused anteriorly. In my opinion there is no evidence to suggest that movement occurred between the astragalus and calcaneum as suggested by Bonaparte (1976:fig. 6C). The proximal articular surface on the calcaneum for the fibula has been described as convex by Bonaparte (1976:812) and Weishampel and Witmer (1990) but scored as concave in the analysis of the dinosaurian tarsus by Novas (1989:table 1). Since the calcaneum and fibula are tightly articulated, the transversely narrow proximal surface is not exposed. In lateral view (Bonaparte, 1976:fig. 5D), the fibulocalcaneal suture is sinuous, with a convex anterior margin on the calcaneum as described by Bonaparte (1976). In medial view, however, the fibulocalcaneal suture is distally convex (Fig. 14C), suggesting that the fibular surface on the calcaneum is cupped as in *Lagerpeton* (Arcucci, 1986) and other dinosaurs. The form of the fibular articular surface in *P. mertii*, therefore, may be more complex than previously realized. Bonaparte (1976:812–813) reported the presence of a calcaneal tuber, but I cannot locate such a process in the holotype calcaneum. Recently Novas (1989:fig. 6.3) refigured Bonaparte's (1976:fig. 5F) distal view of the proximal tarsals and crus and labelled a calcaneal tuber; the labelled structure, however, is actually the overhanging posterodistal corner of the fibula. Weishampel and Witmer (1990) noted the presence of a "small distal tarsal" in *P. mertii*, but no distal tarsals are preserved and none were described.

Only metatarsals 3 and 4 are preserved. The shaft of metatarsal 3 is flattened on its medial and lateral sides for close contact with metatarsals 2 and 4, respectively. The central three metatarsal shafts, therefore, were closely appressed proximally (contra Bonaparte, 1976:fig. 7) as is almost always the case among ornithomirans. The proximal end of metatarsal 3 is unnaturally flattened and twisted, and thus its overlapping relation with metatarsal 4 cannot be reliably interpreted (contra Weishampel and Witmer, 1990).

In summary, *P. mertii* is a valid species and, based on the cranial remains, clearly pertains to Ornithischia. The maxilla and dentary appear more advanced than *L. diagnosticus* with respect to the presence of a well developed cheek emargination. The distal tibia and astragalus, on the other hand, retain a more primitive structure than other ornithischians, as recognized by Weishampel and Witmer (1990). The distal end of the tibia is subquadrate, the fibular flange is poorly developed and does not extend behind the calcaneum, and the ascending process of the astragalus is very deep. There is no evidence to suggest that *P. mertii* and *L. diagnosticus* are more closely related than either are to other ornithischians. If the crania and postcrania of the holotype are correctly associated, *P. mertii* may be the sister-taxon to other ornithischians.

***Revueltosaurus***—*Revueltosaurus callenderi* is based

TABLE 2. Maximum length (in mm) of postcranial elements in *Pisanosaurus mertii* (PVL 2577). Measurements are from the right side.

Tibia						
Maximum length						159
Distal end						
Maximum dorsoventral depth						16
Maximum transverse width across fibular flange						15
Maximum width proximal to fibular flange						13
Fibula						
Maximum length						161
Maximum depth of proximal end						22
Maximum depth of distal end						14
Pes	Metacarpals	Phalanges	1	2	3	4
digit III	96		25	19	16	—
digit IV	83		17	12	11	8
						13

on isolated teeth from the Upper Triassic Bull Canyon Formation of New Mexico (Hunt, 1989). Three tooth forms were attributed to *R. callenderi* but no evidence was presented for their association. Given the absence of clear association or positional information, the differentiating characters listed in the diagnosis cannot be substantiated (e.g., "premaxillary teeth twice as tall as maxillary/dentary teeth" and "all teeth have denticulated margins"; Hunt, 1989:355). The holotype tooth is spoon-shaped, but so are the premaxillary teeth in many ornithischians such as *L. diagnosticus* (see below). *R. callenderi* has more denticles than in the largest crowns in *L. diagnosticus* and it lacks prominent basal anterior and posterior denticles and associated ridges. But these features vary among and, to some extent, within dentitions of basal ornithischians. The reference of additional fragmentary crowns to this tooth form (Padian, 1990) and the proposed sister-group position of *R. callenderi* relative to other ornithischians (Hunt, 1989) are difficult to maintain. *Revueltosaurus callenderi* is here regarded as a nomen dubium, and the type and referred material are considered Ornithischia indet.

***Xiaosaurus***—*Xiaosaurus dashanpensis* is based on a maxillary fragment and disarticulated postcrania from the Middle Jurassic Xiashaximiao Formation of China (Dong and Tang, 1983:figs. 1–4; IVPP V6730A). The denticulate subtriangular tooth crown and femur with vertically prominent anterior (lesser) trochanter and pendant fourth trochanter clearly places *X. dashanpensis* within Ornithischia. In anterior view of the femur, the proximal articular surface of the head angles ventromedially as in *L. diagnosticus*. However, unlike *L. diagnosticus* the fourth trochanter is positioned near mid shaft rather than more proximally, and the tibia is only slightly longer than the femur. The long symmetrical metatarsal 5 (Dong and Tang, 1983:fig. 5) does not resemble that in other dinosaurs and may be misidentified. Because no diagnostic characters are apparent and none have been described, *Xiaosaurus da-*

*shanpensis* is here considered a nomen dubium and the material is referred to *Ornithischia* indet.

#### Other "Fabrosaurids"

***Echinodon***—Galton (Galton, 1978:154) considered the Lower Cretaceous *Echinodon becklesii* "the most progressive fabrosaurid" and assigns *E. becklesii* to the Fabrosauridae on the basis of a "slender dentary," a "flat maxilla," and cheek teeth that "lack wear facets." The dentary, however, does not appear to be "slender" by comparison to that in other ornithischians, nor is there evidence that such a character (were it actually to apply to all "fabrosaurids") would be apomorphic. The maxilla in *E. becklesii* is not "flat" but rather has a gentle emargination along the entire length of the tooth row (BMNH R48211). Likewise the dentition is not devoid of tooth-to-tooth wear facets (e.g., BMNH R48210); wear facets are not only present in *E. becklesii* but also in *L. diagnosticus* (see below) and would not constitute an apomorphic resemblance in any case. There is no phylogenetic basis for referral of *E. becklesii* to the Fabrosauridae, but it does share apomorphic characters with heterodontosaurids (Seren, in prep.).

***Scutelosaurus***—Colbert (1981:46) referred *Scutelosaurus lawleri*, a primitive armored ornithischian from the Lower Jurassic Kayenta Formation, to the Fabrosauridae, but the characters listed in support of this assignment are plesiomorphic within Ornithischia. Colbert (1981:50), for example, lists "marginally placed maxillary and dentary teeth." Marginal tooth rows (i.e., absence of a cheek emargination) are plesiomorphic within Ornithischia and, in any case, do not accurately describe the condition in these taxa. In the dentary tooth row, all but the anteriormost teeth are inset in both *L. diagnosticus* and *S. lawleri* (MNA P1.175; MCZ 8797). In the maxillary tooth row, the anterior maxillary teeth are marginal in *L. diagnosticus* but are clearly inset in *S. lawleri*. *S. lawleri* thus has been referred to Thyreophora on the basis of other evidence (Gauthier, 1986; Sereno, 1986).

***Tawasaurus* and *Fulengia***—*Tawasaurus minor* was collected by Hu Chenji (Beijing Geological Museum) in 1957 from the Lower Jurassic of the Lower Lufeng Formation and described as a small fabrosaur by Young (1982). The holotype consists of a very small partial skull (Fig. 15; IVPP V15; skull length 23 mm) and, as with many of the taxa discussed above, has been referred to Fabrosauridae on the basis of characters that are plesiomorphic within Ornithischia. In the case of *T. minor*, however, several ornithischian synapomorphies are clearly absent: the first premaxillary tooth is positioned near the midline (rather than inset from the tip of the premaxilla); tooth size increases anteriorly in the maxilla (rather than toward the posterior center of the tooth row); the antorbital fenestra is large (rather than reduced to a foramen); the predentary is absent; and the surangular forms the apex of the coronoid rise (rather than the dentary).

Several characters in the skull indicate that *T. minor*

is a prosauropod, probably a hatchling judging from its small size. Derived characters of prosauropods and segnosaurs visible in the holotype and paratype skulls (IVPP V15, V11) include an L-shaped premaxilla-maxilla articulation and a posterior premaxillary process that twists into a horizontal plane (Fig. 15; Sereno, 1989). The broad anteroventral process of the nasal (IVPP V15) characterizes prosauropods. Because there are no discernable autapomorphies, *T. minor* is considered a nomen dubium, and the holotype and paratype skulls are referred to Prosauropoda indet.

Another small prosauropod skull was discovered in the Lower Lufeng Formation (Simmons, 1965) but subsequently was described as a new and very primitive lizard, *Fulengia youngi* (Carroll and Galton, 1977). Evans and Milner (1989) recently reconsidered this specimen (CUP 2037) and associated material (CUP 2038). They correctly dispel the supposed lepidosaur characters and reidentify the material as prosauropod, but they list only one synapomorphy that supports this reassignment—denticulate blade-shaped crowns (Evans and Milner, 1989:227). Other prosauropod synapomorphies visible in the type skull of *F. youngi* include the broad anteroventral process on the nasal and the downturned anterior end of the dentaries. The denticulate crown margins in *F. youngi* do not support synonymy with *Lufengosaurus huenei* as proposed by Evans and Milner (1989:228) because denticulate crowns are plesiomorphic within Prosauropoda. *F. youngi* is here considered a nomen dubium, and CUP 2037 and CUP 2038 are referred to Prosauropoda indet.

***Technosaurus***—*Technosaurus smalli*, from the Upper Triassic Dockum Group of Texas, is represented by fragmentary cranial and postcranial material (Fig. 16; Chatterjee, 1984:fig. 1). *T. smalli* was classified in Fabrosauridae as "the most primitive and oldest member of the family" (Chatterjee, 1984:631) and has recently been considered "one of the most primitive ornithischians yet known" (Weishampel and Witmer, 1990). Although listed under a single specimen number (TTU P 9021), it is clear that the size differential of the various cranial elements would preclude their pertaining to a single individual. As discussed below, the morphology of the cranial elements suggests that the holotype comprises at least two taxa, neither of which show any apomorphic resemblance to *L. diagnosticus*.

The holotypic right dentary appears to belong to an ornithischian, based on the form of the teeth (subtriangular crowns, well developed neck separating crown and root, imbrication of crown margins in the tooth row, and increase in tooth size toward the posterior center of the tooth row; Sereno, 1986). The posterior dentary teeth are not marginal (contra Chatterjee, 1984:630), but rather are inset from the lateral surface, as in *L. diagnosticus* and other ornithischians. Because the enamel thickness is equal on each side of the dentary crowns, the holotype dentary probably belongs to a relatively primitive ornithischian. Few additional details can be discerned in the worn and weathered den-

tion, and the holotype dentary is here considered Ornithischia incertae sedis.

The remaining parts of the holotype include a left premaxilla with five tooth positions (Fig. 16A–C), a posterior lower jaw fragment (Fig. 16D), an unusual vertebra, and a supposed astragalus (Chatterjee, 1984: fig. 1). The premaxilla and posterior lower jaw pertain to an individual that is significantly smaller than that represented by the dentary. The premaxilla lacks several ornithischian features, such as a low angle premaxillary secondary palate, rugose anterior premaxillary margin, premaxillary foramen in the anterior margin of the naris, recurved anterior premaxillary crowns, and inset of the first premaxillary crown from the anterior margin of the premaxilla. On the other hand, the premaxilla exhibits several sauropodomorph and prosauropod-segnosaur synapomorphies, such as the straight lanceolate crowns and L-shaped premaxilla-maxilla suture (as indicated by the vertical margin of the premaxilla posterior to the last premaxillary alveolus). In medial view (Fig. 16A) the steep, posteriorly positioned premaxillary palate and broad sutural surface for the opposing premaxilla are very similar to the condition in *Plateosaurus* (Galton, 1985) and other prosauropods. The premaxilla is here tentatively referred to Prosauropoda indet. and may constitute the first prosauropod remains reported from the Dockum Group.

The posterior lower jaw is also consistent with Prosauropoda, but exhibits no clear prosauropod synapomorphies (Fig. 16D). The external mandibular fenestra is large, and a strong lateral ridge on the surangular is absent. The dentary does not show the apomorphic ornithischian coronoid process but rather is overlapped by the surangular. The neural spine of the dorsal vertebra is broken near its base and is preserved projecting horizontally to one side. The broken neural spine has been misinterpreted as a “long and compressed” transverse process and an opposing process of similar dimensions has been reconstructed on the opposite side (Chatterjee, 1984:fig. 1g). The actual diapophysis can be seen in the same figure near the parapophysis, suggesting that it is a posterior dorsal vertebra. The remaining bone fragment was identified as an astragalus by Chatterjee (1984:fig. 1h, i) and regarded as primitive in structure by Weishampel and Witmer (1990). After examination of the specimen, I cannot verify that this fragment pertains to the tarsus.

## DESCRIPTION

A detailed description of *L. diagnosticus* will provide important comparative information for a deeper understanding of basal ornithischian phylogeny. The following review supplements and emends previous studies (Galton, 1978; Norman, 1984; Thulborn, 1970, 1971b, 1972; Weishampel, 1984) and incorporates new information from the type material and additional specimens (BMNH R8501, R11002, R11004, R11956; MNHN unnumbered).

## Cranium

**Dermal Skull Roof** (Figs. 11, 12)—The surface texture of the **premaxilla** in *L. diagnosticus* suggests that a horny beak covered the anterior end of the bone (Fig. 6C; Crompton and Attridge, 1986; BMNH RUB17, R8501). Judging by the rugose, pitted texture, the beak would have extended ventrally to a bill margin that would overlap laterally the first premaxillary crown.

Two foramina pierce the external surface of the premaxilla (Figs. 6C, 11B, 12B; BMNH R8501, RUB17). One foramen is located at the anteroventral corner of the external naris and will be referred to as the **premaxillary foramen**. This foramen occurs in nearly all ornithischians. In BMNH RUB17 a dorsally projecting flange obscures the opening of this foramen in lateral view (Fig. 6C). A groove passes anteroventrally from the premaxillary foramen to a second larger foramen, here termed the **anterior premaxillary foramen**. This foramen opens into a canal that passes through the ventral edge of the premaxilla, opening onto the premaxillary palate just anterior to the first premaxillary tooth. The premaxillary foramen also appears to pass in a canal through the premaxilla and open by the same foramen on the palate, here termed the **anterior palatal foramen** (Figs. 11D, 12D). Both of the major external premaxillary foramina pass to the palate via narrow canals that do not expand into a cavity within the premaxilla, as occurs in some individuals in *Hypsilophodon* (Galton, 1974:fig. 4B). A second smaller palatal foramen is located medial to the second and third alveoli (Figs. 11D, 12D; BMNH R8501).

The incised canal and large anterior premaxillary foramen appear to be unique to *F. australis*. The thin bar of bone that completes the external margin of the anterior premaxillary foramen is frequently broken away, leaving only the vessel channel, which has been illustrated previously as a short slit (Thulborn, 1970: fig. 6A) or fracture (Thulborn, 1971b:fig. 1).

Although the internarial bar is not in natural articulation in any available specimen, the slender processes of the premaxillae and nasals in BMNH R8501 (Figs. 2A, 3A) suggest that the internarial bar was complete, with the premaxillae extending in the midline between the tips of the nasals (Figs. 11B, 12B; Crompton and Attridge, 1986:fig. 17.7). Contrary to some previous illustrations, there is no evidence that the premaxillae meet the nasals along a transverse suture (Thulborn, 1970:fig. 8E) or that the internarial bar is incomplete (Weishampel, 1984:33, fig. 2b).

As occurs in most ornithischians, the premaxillary palate in *L. diagnosticus* is broad and flat and extends posteriorly beyond the last premaxillary tooth (Figs. 11B, 12B; BMNH R8501). In previous reconstructions, the premaxillary palate has been omitted (Thulborn, 1970:fig. 8E; Norman, 1984:fig. 1D), and the supposed absence of the premaxillary palate has been used to distinguish *L. diagnosticus* from *Echinodon* (Galton, 1978:140, 154; note that “maxilla” has been inadvertently substituted for premaxilla on p. 140).

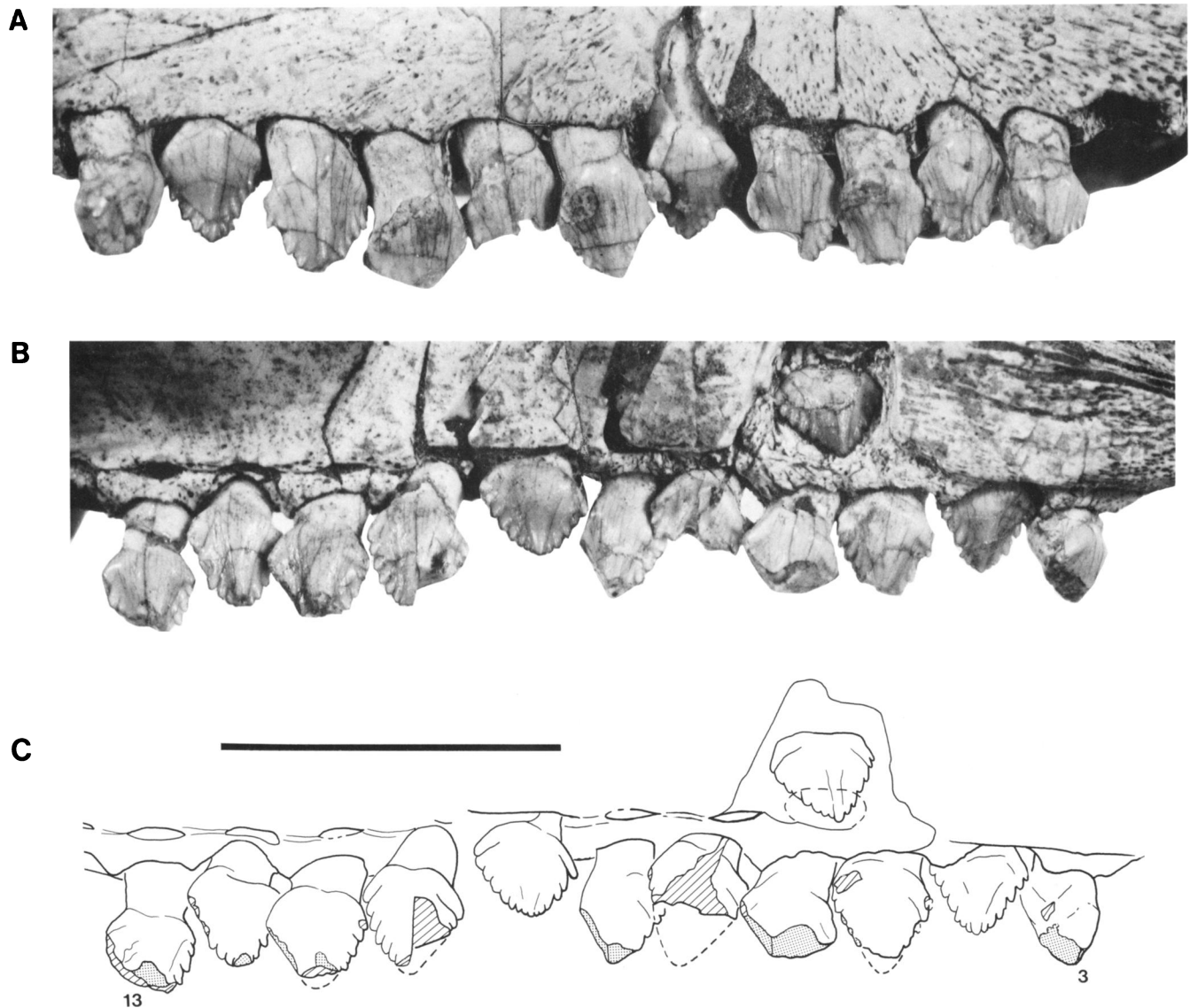


FIGURE 4. Right maxillary dentition of *Lesothosaurus diagnosticus* (SAM unnumbered) in lateral (A) and medial (B, C) views. Maxillary tooth positions 3 and 13 indicated. Wear surfaces indicated by even stipple. Scale bar equals 1 cm.

In *L. diagnosticus* the external alveolar margin of the maxilla is flat with a vertical orientation (Figs. 5, 11D, 12D; BMNH R8501, R11956; BMNH RUB17, RUB23; Thulborn, 1970, 1971b; Galton, 1973). A subtle linear prominence is present above the row of external maxillary foramina (Thulborn, 1971b:fig. 2), and the surface of the maxilla is gently everted near the maxilla-jugal suture (Fig. 5C, D), as in many archosaurs. This eversion of the posteriormost portion of the lateral wall of the maxilla, however, does not resemble the more marked medial offset of the entire maxillary tooth row that characterizes the maxilla in *Pisanosaurus* and other ornithischians (contra Weishampel and Witmer, 1990).

The maxilla forms the anterodorsal and ventral margins of the antorbital fossa and fenestra. The ventral

portion of the fossa is deeply incised into the maxilla whereas the anterodorsal portion rounds smoothly onto the lateral surface of the snout. The small, oval antorbital fenestra is situated posterior to the center of the fossa; it was originally reconstructed in the postero-ventral corner of the fossa because in BMNH RUB17 the maxilla has slid out of articulation toward the lacrimal (Thulborn, 1970; see Fig. 16A). The lacrimal inserts into a narrow slot above the apex of the antorbital fossa, an autapomorphy of *L. diagnosticus* (Figs. 11A, 12A; BMNH R8501; BMNH RUB23).

The internal alveolar margin is somewhat thickened, as seen in ventral view of the palate in BMNH R8501 and in cross section in BMNH RUB17 and RUB23 (Figs. 11D, 12D). The ventral surface of the thickened internal margin is flat, with a dorsomedial inclination

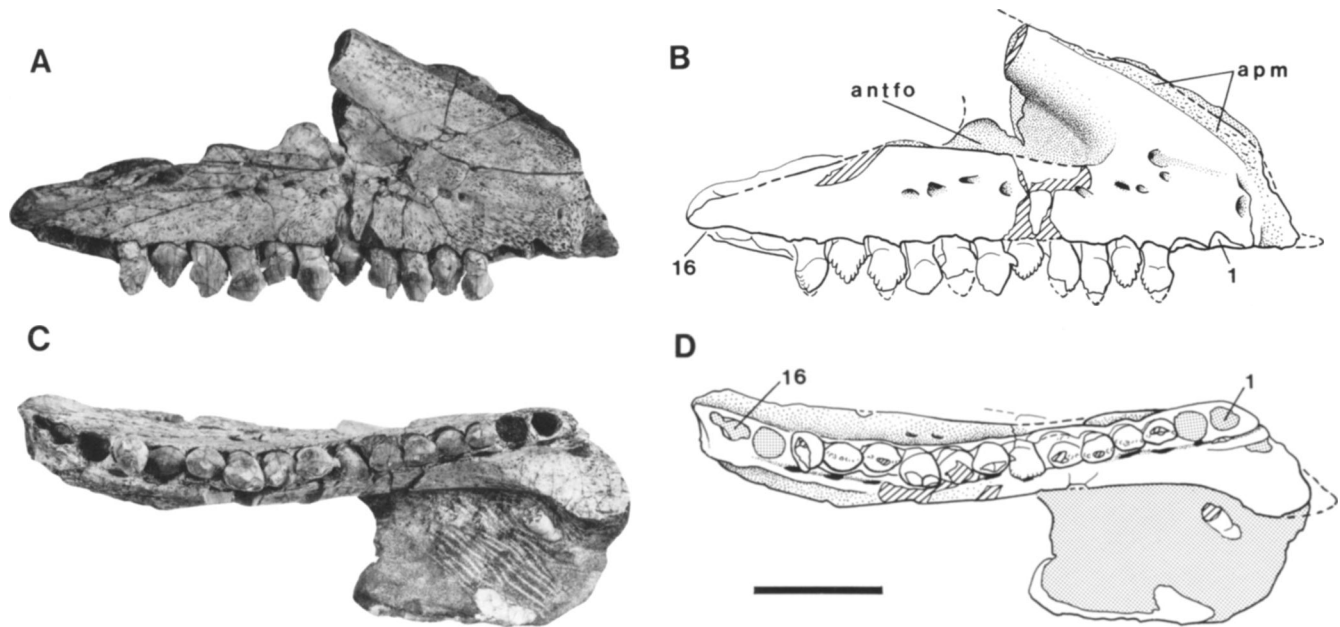


FIGURE 5. Right maxilla of *Lesothosaurus diagnosticus* (SAM unnumbered) in lateral (A, B) and ventral (C, D) views. Maxillary tooth positions 1 and 16 indicated. Abbreviations: **antfo**, antorbital fossa; **apm**, articular surface for premaxilla. Scale bar equals 1 cm.

of approximately 30 to 40 degrees. The sutural contacts of the maxilla on the anterior palate remain uncertain. In BMNH R8501 the anteromedial processes of the maxillae project above the premaxillary palate, and it is likely that the anterior end of the vomer inserted between them. Whether or not the maxillae excluded the premaxillae from the border of the internal nares cannot be determined from available specimens.

The **frontal** forms the interorbital skull roof, which is gently arched anteroposteriorly. An interfrontal suture clearly separates paired frontals in both BMNH R8501 and BMNH RUB23, contrary to a previous suggestion that they may be fused in the former (Norman, 1984:523). The concave external margin of the frontal broadly exposes the orbit in dorsal view of the skull. The frontal is deeply notched to receive the postorbital, such that the dorsal surface of the skull roof is flush across the suture. The anterior boundary of the supratemporal fossa forms an arcuate depression on the frontal, a primitive feature retained in only a few ornithischians.

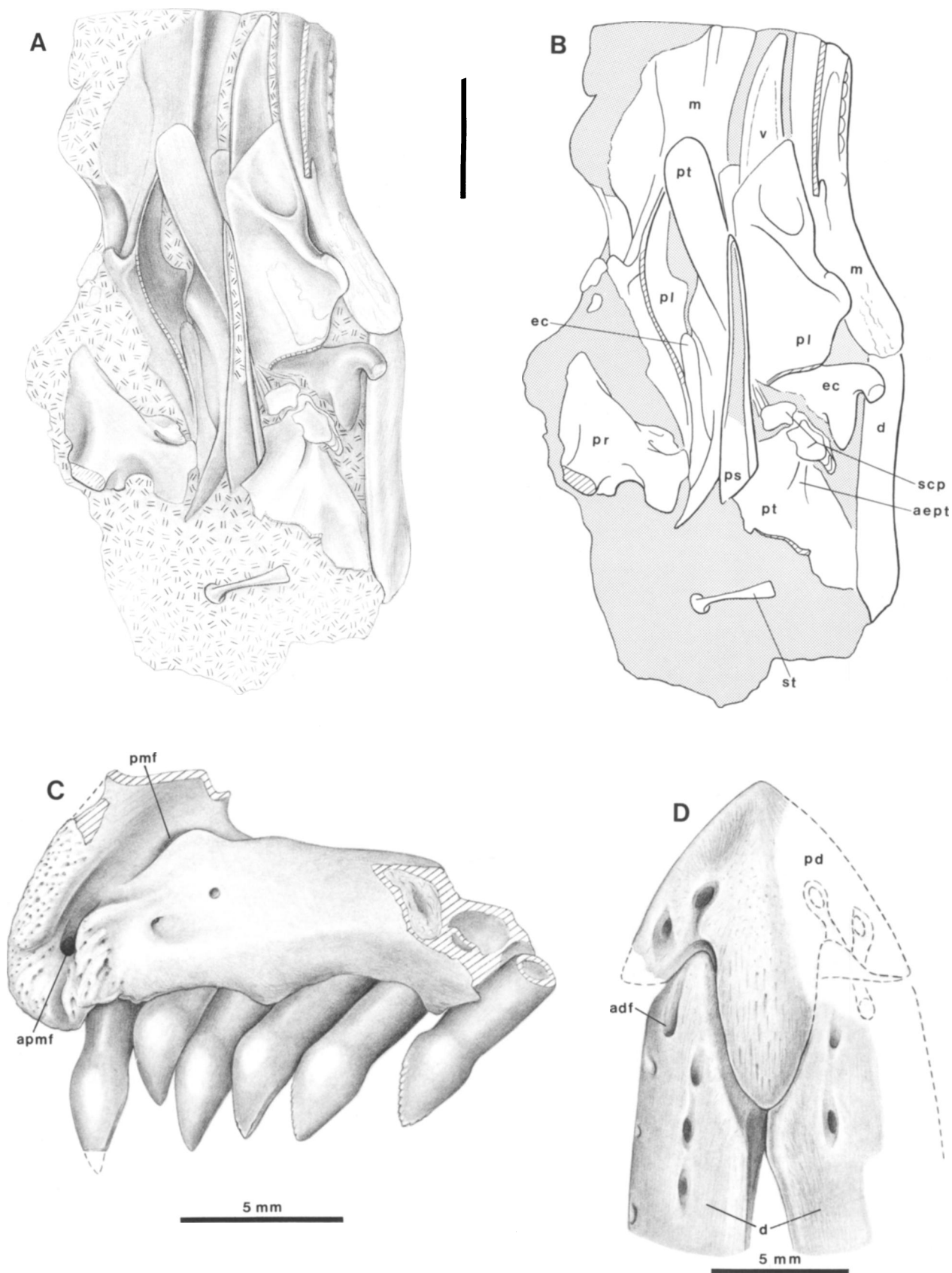
The **parietal** was described as a paired element in *L. diagnosticus*, a very unusual condition within Ornithischia (Thulborn, 1970:417–418). Norman (1984:523) reported the absence of an interparietal suture in BMNH R8501, although at least the anterior portion appears divided in the midline. A third disarticulated parietal also shows separation in the midline (BMNH R11004). The platelike median portion of the parietal is very thin (BMNH R11004), and in all three specimens the parietal is fractured. Misidentification of cracks as sutures remains a distinct possibility. BMNH RUB17

provides the best evidence to determine whether the parietal is paired or merely cracked in the midline. The supposed interparietal suture in this specimen is asymmetrical, passing to the right side of a low median sagittal crest and then diverging strongly from the midline near the posterior margin (Thulborn, 1971b:fig. 7). The sagittal crest is entirely on one side, strongly suggesting that the supposed suture is actually a crack and that the parietal in *L. diagnosticus* is a fused median element in the adult, as in *Protoceratops* (contra Thulborn, 1970:427) and other ornithischians.

The posterior margin of the parietal is pointed in the midline (BMNH R8501, RUB17), as occurs in other ornithischians such as *Hypsilophodon* (Galton, 1974). On the anterior wall of the supratemporal fossa, a narrow strut of the parietal extends anterolaterally to contact the postorbital, effectively separating the frontal from the laterosphenoid.

The **lacrimal** forms the posterodorsal margin of the antorbital fossa and fenestra. In BMNH R8501 a shallow channel passes posteroventrally from the antorbital fenestra. Dorsally, the tip of the lacrimal inserts into a narrow slot in the maxilla, and, posteriorly, the lacrimal tapers to a slender tip along the ventral margin of the orbit, overlapping the jugal laterally (BMNH R8501, RUB17, RUB23); it does not terminate posteriorly as a blunt, strut-shaped process (contra Thulborn, 1970; Weishampel, 1984:41:fig. 2b; Weishampel and Witmer, 1990).

Previous reconstructions of the skull of *L. diagnosticus* do not show appreciable nasal-lacrimal contact, with one exception (Norman, 1984; see Fig. 18B).





Weishampel (1984:32) stated that such contact does not occur in *L. diagnosticus*. But in BMNH R8501, RUB23, and R11956 the lacrimal extends past the posterior tongue-shaped maxillary process to establish a short suture with the nasal.

Four processes project from the central body of the squamosal in *L. diagnosticus*: anterior, ventral, medial, and posterior (Fig. 7). The anterior process of the squamosal, which expands toward its anterior end, is deeply slotted for the posterior process of the postorbital. The postorbital-squamosal suture is V-shaped in lateral view (Figs. 11A, 12A) rather than linear as shown previously (Weishampel, 1984; Norman, 1984; Crompton and Attridge, 1986; see Fig. 18). A prominent lateral rim overhangs the ventral process and quadrate. The strap-shaped ventral process caps the anterior edge of the quadrate shaft and wraps around onto its medial side (Fig. 7A; BMNH R8501, RUB17). In lateral view of the articulated skull, only the slender anterior portion of this process is visible. The tip of the ventral process overlaps the dorsal process of the quadratojugal, contrary to some previous accounts (Weishampel, 1984: 24). This articulation is preserved on the left side in BMNH RUB23, and a depression for the quadratojugal contact is visible on ventral tip of the process in BMNH R8501 (Figs. 2A, 3A). The short medial process overlaps the parietal on the posterior wall of the supratemporal fossa. Its squared distal end terminates before reaching the sidewall of the braincase. The posterior process extends over the quadrate head, passing between the quadrate and paroccipital process. In contrast to the crescent-shaped posterior process in *Hypsilophodon* (Galton, 1974:fig. 8) and other ornithomorphs, the posterior process is subrectangular in *L. diagnosticus* (Fig. 7B). The lateral margin of the posterior process follows the paroccipital process, extending laterally just beyond the quadrate head (BMNH R8501, RUB23).

The jugal forms the posteroventral corner of the antorbital fossa but is excluded by the lacrimal and maxilla from bordering the antorbital fenestra. The anterior process of the jugal is overlapped laterally by both the lacrimal and maxilla (Figs. 2B, 3B), leaving only a narrow lateral surface exposed as it approaches the antorbital fossa (Figs. 11A, 12A; BMNH R8501, RUB17, RUB23). The anterior process reaches the antorbital fossa but is not invaginated by a posterior extension of the fossa as in *Hypsilophodon*. The dorsal process of the jugal is slotted for the tapering ventral process of the postorbital, as previously described (Thulborn, 1970; BMNH R8501, RUB17.C.5, RUB23). The ventral process of the postorbital, in

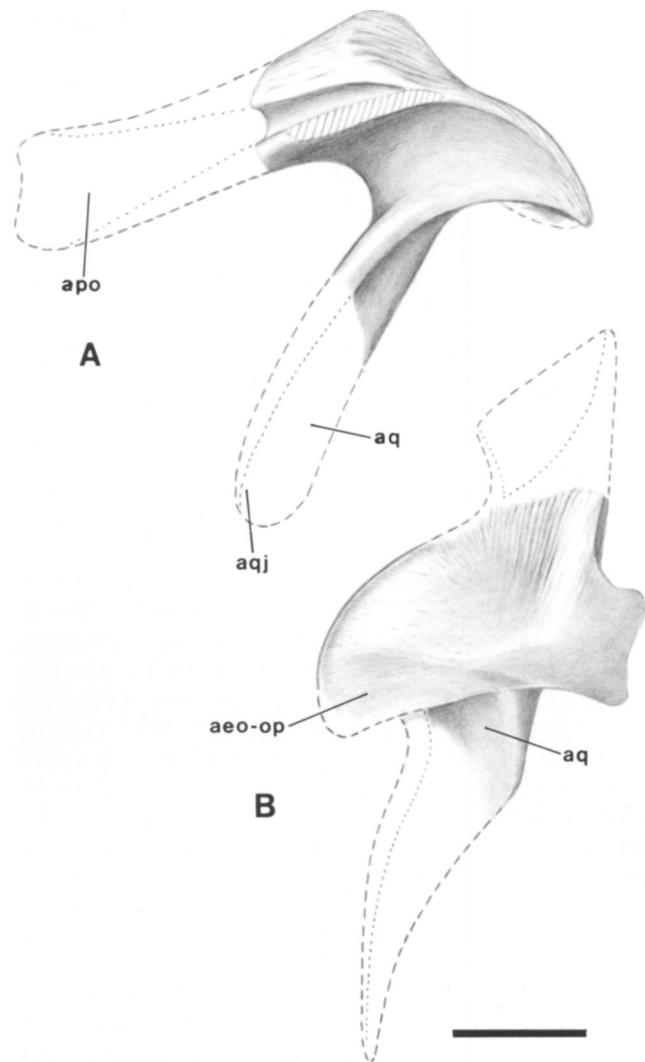


FIGURE 7. Left squamosal of *Lesothosaurus diagnosticus* in lateral (A) and posterior (B) views. Abbreviations: **ap**, articular surface for parietal; **apo**, articular surface for postorbital; **aq**, articular surface for quadrate; **aqj**, articular surface for quadratojugal. Scale bar equals 5 mm.

turn, is slotted medially to receive the tapered end of the dorsal process of the jugal (BMNH RUB17.C.7). Midway along the postorbital bar, the joint between these bones is planar but transforms into a tight tongue-and-groove articulation at either end. The articulation is not a short, planar scarf joint (contra Weishampel, 1984:43–44). In lateral view, the jugal-postorbital suture is V-shaped.

FIGURE 6. Skull of *Lesothosaurus diagnosticus*. Disarticulated palate (BMNH RUB17) in dorsal view (A, B); scale bar equals 1 cm. Left premaxilla (BMNH RUB17) in lateral view with tooth positions indicated (C). Predentary and anterior ends of the dentaries (BMNH RUB17) in ventral view (D). Abbreviations: **adf**, anterior dentary foramen; **aept**, articular surface for epipterygoid; **apmf**, anterior premaxillary foramen; **d**, dentary; **ec**, ectopterygoid; **m**, maxilla; **pd**, predentary; **pl**, palatine; **pmf**, premaxillary foramen; **pr**, prootic; **ps**, parasphenoid; **pt**, pterygoid; **scp**, sclerotic plate; **st**, stapes; **v**, vomer.



The **quadratojugal** has been described and figured as triangular (Thulborn, 1970; Norman, 1984; Weishampel and Witmer, 1990), based for the most part on the poorly preserved quadratojugal in BMNH RUB23. A tall, L-shaped quadratojugal is preserved in BMNH R8501 and is overlapped laterally by the jugal. The slender dorsal process of the quadratojugal articulates against the convex anterior edge of the quadrate shaft with its dorsal tip overlapped by the squamosal.

**Palate** (Figs. 6A, B, 11D, 12D)—The **pterygoid** is composed of three principal rami: palatal, mandibular, and quadrate (BMNH R8501, RUB17). The palatal ramus is the longest and projects anteriorly from the basiptyergoid articulation. It is composed of two planar sheets, one vertical and the other horizontal (Figs. 11D, 12D). As is typical among archosaurs, the vertical sheet expands anteriorly and inserts between the posterior ends of the vomers, as preserved on the right side in BMNH RUB17. The observation that the pterygoid does not contact the vomer in *L. diagnosticus*, therefore, is incorrect (Weishampel, 1984:44–45). Only a narrow interptyergoid vacuity separates opposing vertical sheets in the midline (BMNH R8501). The subtriangular horizontal sheet projects laterally at the base of the palatal ramus and is deflected ventrally to form the mandibular ramus. The horizontal sheet is overlapped dorsally by the palatine and ectopterygoid (BMNH R8501, RUB17). The subquadrate mandibular ramus projects toward the mandibular fossa of the lower jaw (Figs. 11A, 12A; BMNH R8501, RUB17). A short tab-shaped process extends to the midline where it meets its opposite. In BMNH R8501, the only specimen preserving the medial tab, a fracture has displaced the base of the left pterygoid into the interptyergoid vacuity (Figs. 2B, 3B). The small medial process occurs in many archosaurs. It articulates against its opposite in the midline and presumably stabilized interptyergoid movement, maintaining the interptyergoid vacuity. The fan-shaped quadrate ramus expands posteriorly from a narrow base near the basiptyergoid articulation and broadly overlaps the posterior aspect of pterygoid ramus of the quadrate. A depression for articulation with the epiptyergoid is clearly marked near the base of the quadrate ramus (Fig. 6A, B).

The structure and relationships of the palatal elements are now clarified with additional preparation of BMNH RUB17 (Fig. 6A, B). The palate in BMNH RUB17 is partially disarticulated and several of the elements were previously misidentified (Thulborn, 1970:fig. 4, 419–420). The palatal ramus of the pterygoid was identified as the vomer, the parasphenoid rostrum was identified as the palatal process of the pterygoid, and several disarticulated sclerotic plates were attributed to the ectopterygoid.

The broad trapezoidal **palatine** is exposed in dorsal view in BMNH RUB17 (Fig. 6A, B). Roofing the midsection of the palate, the palatine is inclined toward the midline and, based on BMNH RUB17, would have contacted the vomer anteriorly. A sharp diagonal crest crosses the dorsal aspect of the palatine, separating

anterior and posterior fossae. The crest extends to the lateral wall of the skull where it is thickened for contact with the jugal. Anterior to the jugal buttress, the palatine establishes a long contact with the maxilla. Posteriorly, the palatine overlaps the dorsal side of the ectopterygoid (contra Weishampel and Witmer, 1990). A subtriangular postpalatine fenestra is present between the palatine, ectopterygoid and maxilla, contrary to Thulborn's (1970:420) assertion that no such fenestra is present (note, however, that Thulborn includes a postpalatine fenestra in his reconstruction of the palate; Fig. 16D).

The barlike lateral portion of the U-shaped **ectopterygoid** butts against the maxilla and jugal on the side wall of the snout (Figs. 2A, 3A, 6A, B, 11D, 12D; BMNH R8501, RUB17). Anteriorly, the ectopterygoid is overlapped dorsally by the palatine, and, posteriorly, the ectopterygoid overlaps the dorsal surface of the mandibular ramus of the pterygoid. The lateral margin of the ectopterygoid is thickened by a dorsally projecting crest. The ectopterygoid does not contact the quadrate ramus of the pterygoid in *L. diagnosticus* or, to my knowledge, in any other ornithischian (contra Thulborn, 1970:420, fig. 4; Weishampel, 1984:38; Weishampel and Witmer, 1990).

The elongate, anteriorly tapering **vomera** form a sheetlike septum in the midline of the palate that extends from the premaxillary palate, anteriorly, to the palatal processes of the pterygoid, posteriorly. The vomera extend posteriorly as far as the antorbital fenestra. Paired along most of their length and joined along their ventral edges, the vomera taper anteriorly and fuse ventrally to form a narrow rod (BMNH R8501, RUB17). The broad posterior third of each vomer overlaps laterally the vertical portion of the palatal ramus of the respective pterygoid. Vomer-ptyergoid contact, as described here, is plesiomorphic within Archosauria and present in all ornithischians (contra Weishampel, 1984:44–45).

The **quadrate** has a well-developed lateral ramus, or shaft. The posterior margin of the quadrate is arched, with a distinct hamular process beneath the head and a quadrate foramen between the quadrate and quadratojugal. The mandibular condyle is broad transversely and set approximately six to seven mm below the level of the occlusal plane of the maxillary and dentary tooth rows (BMNH R8501, BMNH RUB23; Thulborn, 1970:419). The suture with the quadratojugal extends ventrally very near the jaw articulation.

Available descriptions of the quadrate are inaccurate in these respects. The mandibular condyle has been shown at about half its actual width (Thulborn, 1970; see Fig. 17B, F); the broad proportions of the ventral shaft and condyle are well exposed in BMNH RUB23. The supposedly narrow proportions of the condyle, therefore, cannot be used to distinguish *L. diagnosticus* and *Echinodon*, as previously proposed (Galton, 1978: 140, 154; the quadrate of *Echinodon* used in this comparison, in any case, is actually a left ectopterygoid, preserved very near its natural articulation with the

side wall of the skull). The jaw articulation in *L. diagnosticus* is not aligned with the tooth rows (Thulborn, 1974:171; Galton, 1978:155; Cooper, 1985:285) but, rather, is slightly offset ventrally as in basal thyreophorans, pachycephalosaurs, and ceratopsians. Finally, there is no separation of the quadratojugal and mandibular condyle (contra Weishampel, 1984; Norman, 1984; Crompton and Attridge, 1986; see Fig. 18) as occurs in Iguanodontia.

**Braincase** (Figs. 2B, 3B, 6A, B, 13A, B)—The **parasphenoid** is best exposed in the partially disarticulated skull BMNH RUB17 (Fig. 6A, B; Thulborn, 1970: fig. 4, labelled as palatal ramus of the pterygoid). The elongate parasphenoid is fused completely with the basisphenoid and projects anteriorly and slightly dorsally in the midline. In transverse section, the parasphenoid is V-shaped. It tapers to a slender tip anteriorly, which would have inserted between the palatal rami of the pterygoids.

The **basioccipital** is slightly shorter in length than the basisphenoid (Figs. 11D, 12D; BMNH R8501, R11004), a plesiomorphic condition within Ornithischia. The basioccipital forms the anterior half of the low basal tubera, which extend ventrally approximately to the level of the occipital condyle (BMNH R11004). In posterior view, the basioccipital forms the ventral border of the foramen magnum.

The **supraoccipital** is subtriangular in posterior view with a low median nuchal crest that diminishes in strength toward the foramen magnum. The supraoccipital is bounded dorsally and laterally by the parietal and ventrally by the fused exoccipital-opisthotic and forms the dorsal margin of the foramen magnum (Figs. 11C, 12C). The supraoccipital extends anteriorly under the posterolateral wings of the parietal to form part of the sidewall of the braincase as in *Hypsilophodon* (BMNH R2477). This portion of the supraoccipital, bounded by the prootic ventrally, the parietal dorsally, and a small section of the laterosphenoid anteriorly, may represent a coossified epiotic bone (Fig. 13A, B; exposed internally in BMNH R8501 and externally in RUB23). The epiotic is visible as a separate element in this position in juveniles of several ornithischians (e.g., *Bactrosaurus*, AMNH 6751).

The fused **exoccipital-opisthotic** forms the lateral margin of the foramen magnum and dorsolateral corner of the occipital condyle and extends posterolaterally as the paroccipital process, which forms the posterior margin of a distinct otic notch. In lateral view three foramina pierce the pedicel of the exoccipital-opisthotic and pass medially via canals into the braincase (Fig. 13A, B; BMNH R8501, R11004). The posterior foramen is largest and opens into a horizontal canal. The middle foramen is positioned below the others and leads to an anteroventrally inclined canal that opens internally just above the suture with the basioccipital (BMNH R11004). The posterior and middle foramina presumably conducted branches of the hypoglossal nerve (XII). The most anterior of the three foramina, located just posterior to the crista tub-

eralis, passes anteromedially into the braincase just internal to the jugular foramen. This foramen, present in all ornithischians, should not be confused with the fenestra pseudorotundum (DeBeer, 1937:431) and presumably provided passage for the vagus nerve (X). Anterior to the crista tuberalis, a notch arches over two larger openings that are divided by a slender septum (BMNH R11004). The anterior opening is the fenestra pseudorotundum (DeBeer, 1937:431), and foramen, and the slender septum is the crista interfenestralis.

In posterior view of the exoccipital-opisthotic, a small posttemporal foramen passes through the paroccipital process near its dorsal margin. A small planar facet on either side of the foramen magnum forms the articular surface for the proatlas. Just inside the foramen magnum, a small endolymphatic foramen passes into the paroccipital process, where it presumably communicates with the semicircular ducts (Oelrich, 1956). The superior semicircular canal opens dorsally on the sutural surface for the fused supraoccipital-epiotic (BMNH R8501).

The **prootic** forms the ventral margin of the fenestra ovalis and jugular foramen and the ventral half of the intervening crista interfenestralis. The posterior aliform process of the prootic extends along the anterior aspect of the base of the paroccipital process. Centrally, a small slitlike foramen provides passage for the facial nerve (VII), and the anterior margin is notched for the trigeminal nerve (V; Figs. 6A, B, 13A, B; BMNH R8501, RUB17).

In lateral view, a prominent ridge angles across the **basisphenoid** above the basipterygoid processes and overhangs the foramen for the internal carotid artery. In ventral view the central body of the basisphenoid is gently concave from side to side. Posteriorly, the basisphenoid forms the more prominent lateral portion of the basal tubera. The stout basipterygoid processes are preserved in natural orientation in a well preserved, disarticulated basisphenoid (BMNH RUB17). The bases of the processes are not positioned close to the midline as in the ornithopods *Heterodontosaurus* and *Hypsilophodon*. In lateral view, they project ventrally at 55 degrees from the horizontal (Fig. 13A, B). Previous reports of "slight" ventral deflection of these processes (Weishampel, 1984:14; Weishampel and Witmer, 1990) were based on BMNH R8501, the skull of which has been flattened postmortem (Figs. 2, 3). In posterior view they project laterally at 20 degrees from the sagittal plane, and in ventral view they project anterolaterally at 60 degrees from the sagittal plane (Figs. 11D, 12D). The oval distal articular surface faces anteriorly, laterally, and ventrally.

Forming the anterodorsal wall of the braincase, the **laterosphenoid** arches laterally from its posterior contact with the epiotic (or coossified epiotic-supraoccipital) and prootic to the junction of the frontal and postorbital near the orbit margin (Fig. 13A, B; BMNH R8501, RUB23). The lateral end forms a rounded articular head that butts against a socket on the ventral

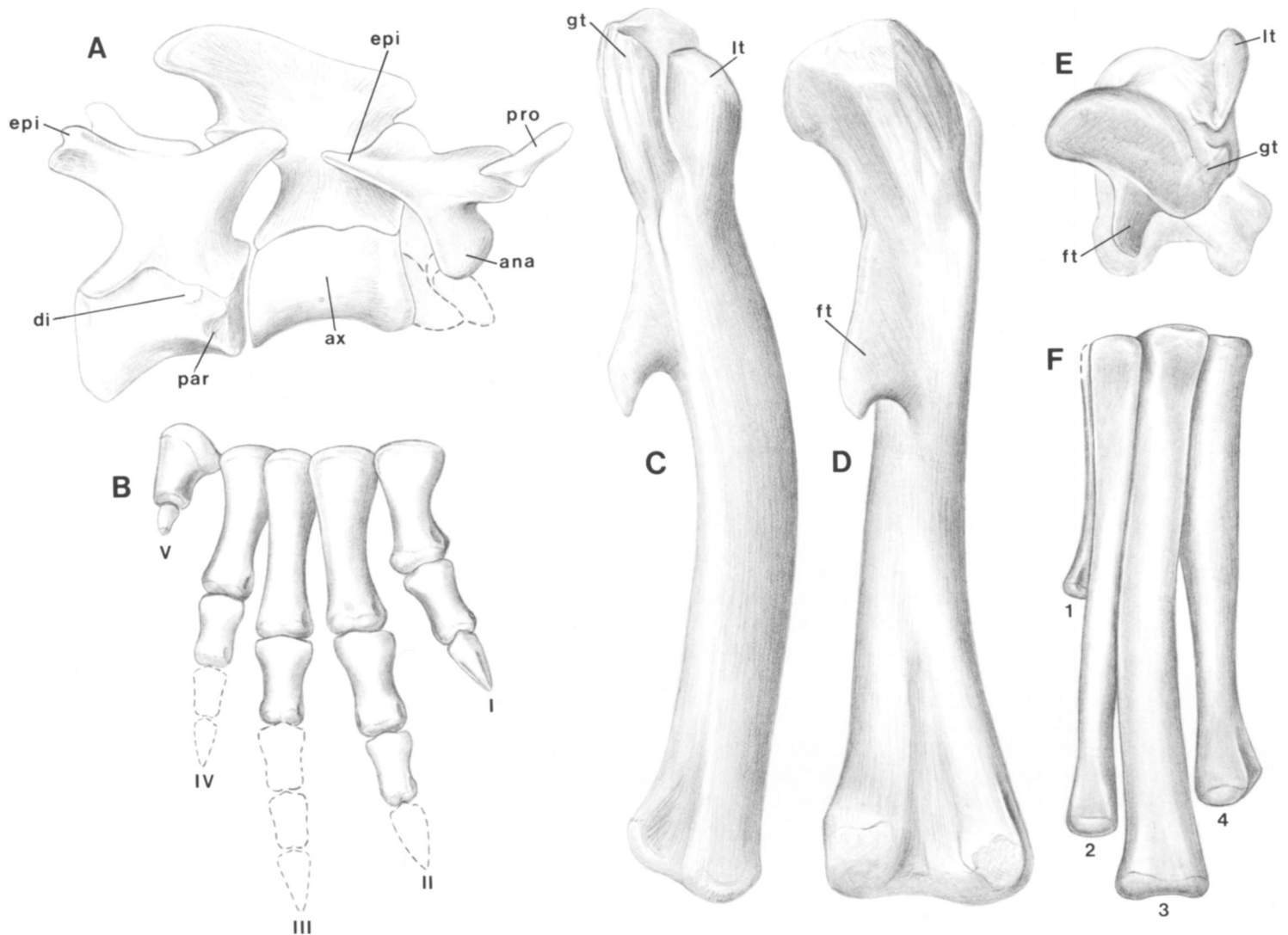


FIGURE 8. Reconstructions of postcrania of *Lesothosaurus diagnosticus*. Proatlas and first three cervical vertebrae (BMNH R11004) in right lateral view (A). Right manus (BMNH RUB17) in dorsal view with digit number indicated (B). Right femur (BMNH RUB17) in lateral (C), posterior (D), and proximal (E) views. Left metatarsus (BMNH RUB17) in dorsal view with metatarsal number indicated (F). Abbreviations: **ana**, atlantal neural arch; **ax**, axis; **di**, diapophysis; **epi**, epipophysis; **ft**, fourth trochanter; **gt**, greater trochanter; **lt**, lesser trochanter; **par**, parapophysis; **pro**, proatlas.

surface of the frontal and postorbital (BMNH R8501). The posterior margin is notched by the trigeminal foramen, with a horizontal groove passing anteriorly for the ophthalmic branch. A small foramen situated anterodorsally presumably accommodated the oculomotor nerve (III; BMNH R8501).

**Accessory Dermal Elements** (Figs. 2, 3, 11A, B, 12A, B)—The **palpebral** articulates against the prefrontal at the anterodorsal corner of the orbit (BMNH R8501, BMNH RUB23). Palpebral-lacrimal contact, if present at all, is minimal (contra Weishampel and Witmer, 1990).

**Lower Jaw** (Figs. 2B, 3B, 6D, 13F–H)—The **pre-dentary** is designed to stabilize the symphysis and to provide bony support for a cropping bill (Figs. 2B, 3B,

6D, 13C–E). As a stable, median element at the symphysis, the pre-dentary allows controlled twisting of the dentary rami about their long axes during occlusion while maintaining a symmetrical horn-sheathed cropping edge to oppose the premaxillary bill (Crompton and Attridge, 1986). The presence of wear facets (see **Dentition**) and the form of the articular joint between the pre-dentary and anterior dentary in *L. diagnosticus* strongly support the suggestion that bilateral occlusion with long-axis rotation and the presence of a pre-dentary are functionally interrelated and appeared simultaneously at the base of Ornithischia (Crompton and Attridge, 1986). In *L. diagnosticus* a synovial joint may have been present between the pre-dentary and the anterior apex of the dentary, and the primary vascular

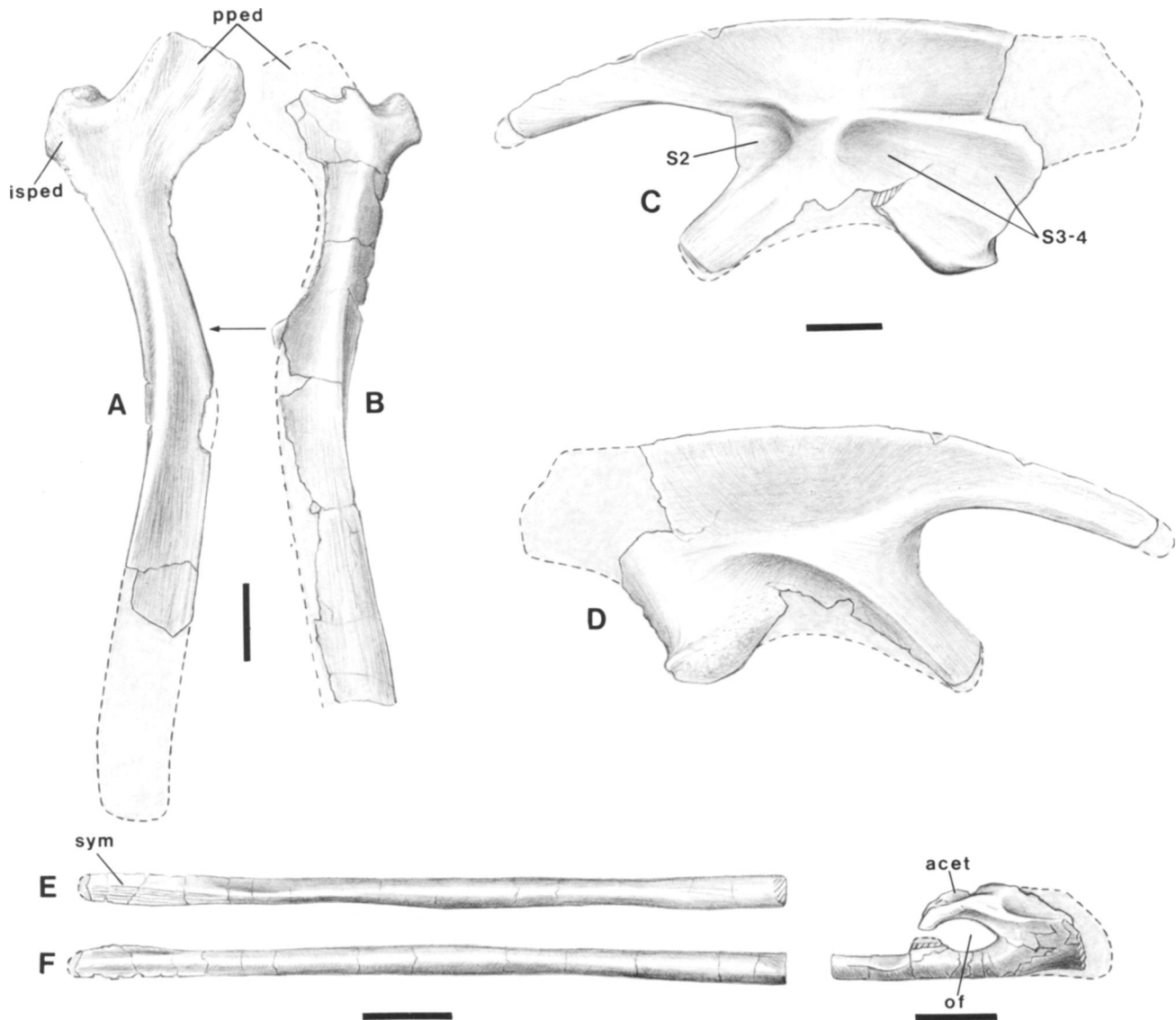


FIGURE 9. Postcrania of *Lesothosaurus diagnosticus*. Right (A) and left (B) ischia (BMNH RUB17) in lateral view. Right ilium (BMNH R11002) in medial (C) and lateral (D) views with sacral attachments indicated. Right pubis (BMNH RUB17) with posterior process in medial view (E) and entire pubis in lateral view (F). Abbreviations: **acet**, acetabular surface; **isped**, ischial peduncle; **of**, obturator foramen; **pped**, pubic peduncle; **s**, sacral; **sym**, symphyseal surface. Scale bars equal 1 cm.

supply to the predentary is positioned along the axis of rotation to avoid disruption. These characters occur in nearly all ornithischians.

The anterior end of the dentary in *L. diagnosticus* is V-shaped and twists into nearly a horizontal plane before contacting the predentary and opposing dentary (Fig. 6D). The lower limb of the V-shaped dentary end is longer and contacts its opposite in the midline to form a narrow, end-to-end dentary symphysis (Fig. 13G). The shorter upper limb of the V-shaped dentary end is grooved to receive the wedge-shaped lateral predentary process. The apex of the dentary end is rounded and fits into the notch between the ventral and lateral predentary processes. The axis of rotation of the

dentary passes through the apex, where the least amount of movement between predentary and dentary would occur. The main vascular supply of the predentary traverses this point of least relative movement; a large foramen, here termed the **anterior dentary foramen**, opens near the anterior end of the dentary and passes forward as a groove across the dentary-predentary junction (Fig. 6D). As it passes onto the predentary, the groove bifurcates, with the principal groove passing anteriorly to a large centrally-positioned foramen on the ventral aspect of the predentary.

In *L. diagnosticus* the predentary is shaped like an arrow in ventral view, with a long median ventral process and a short lateral process to each side (Figs. 6D,

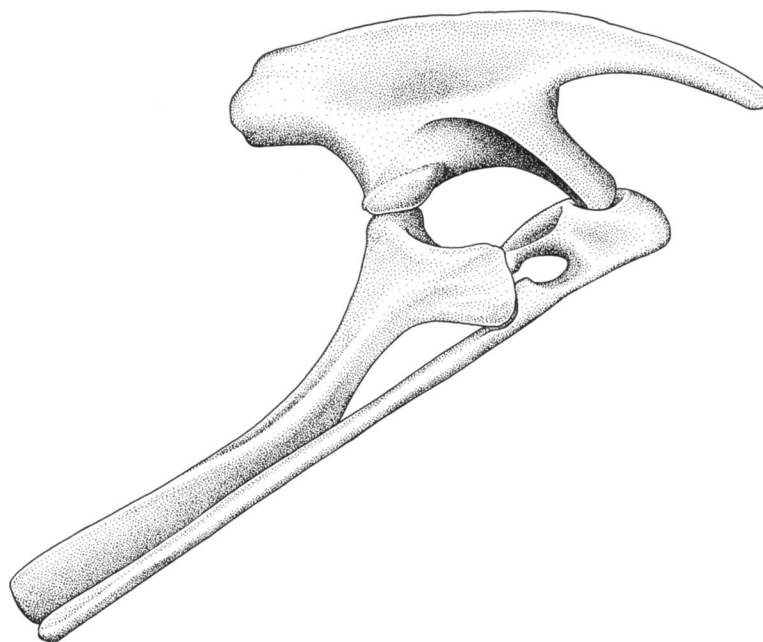


FIGURE 10. Reconstruction of the pelvic girdle of *Lesothosaurus diagnosticus* in lateral view.

13C-E; BMNH R8501, RUB17). The median ventral process laps the dentary symphysis, with shallow concave articular surfaces for each dentary end (BMNH R8501). A rudimentary median dorsal process projects posteriorly from the tip of the dentary symphysis, as seen in dorsal view (BMNH R8501).

The short lateral processes are wedge-shaped and do not extend along the side of the dentary as in ornithopods. The posterior margin is sharp due to beveling of the dorsal and, particularly, the ventral surfaces. The posterior end of the bill margin of each lateral process closely approaches the first dentary crown. In dorsal view, the body of the prementary is gently concave transversely with a sharp external rim. The ventral surface of the prementary is more sharply angled to each side of the midline.

The **dentary** is relatively straight along its length rather than broadly curved as shown by Thulborn (1970; see Figs. 13H, 16D). The anterior ends of the dentary, as mentioned above, twist medially to form a spout-shaped mandibular symphysis. Previously, the presence of a spout-shaped symphysis was used as a synapomorphy uniting all ornithischians except *L. diagnosticus*, because the dentary rami did not appear to twist near the symphysis in BMNH R8501 (Sereno, 1986). The dentary ends in this specimen, however, have been flattened postmortem, as can be seen by comparison with the partially articulated dentary symphysis in BMNH RUB17 (Fig. 6D). Indeed, the symphysis must be spout-shaped to bring the dentaries and prementary into articulation.

The dentary tooth row follows a gentle sigmoid curve in dorsal view (Fig. 13H). The posterior two-thirds of the dentary tooth row are inset from the lateral surface

of the dentary, contrary to several reports that the dentary in *L. diagnosticus* is "flat" with a "marginal" tooth row (Thulborn, 1972:50; 1973:127; 1974:171; Galton, 1972:465; 1978:155). Replacement foramina are clearly present on the medial alveolar margin (BMNH R8501), although most of these are covered in medial view by the slender coronoid (Fig. 13G; BMNH RUB17). Previous suggestions that replacement foramina are absent in *L. diagnosticus* (Thulborn, 1970, 1971b, 1974; Galton, 1972, 1973, 1978) are inaccurate, as pointed out by Gow (1981) and Norman (1984).

The sheetlike **splenial** covers most of the medial surface of the mandibular ramus, contacting the dentary, coronoid, prearticular and angular and forming the anterior margin of the internal mandibular fenestra (BMNH R8501, RUB17, RUB23). Contrary to Thulborn (1970:426; see Fig. 17C), the splenial in *L. diagnosticus* does not bound an internal mandibular fenestra larger than the external fenestra. The **surangular** forms all but the anterior margin of the low coronoid process and establishes sutural contact with the dentary, angular, articular, prearticular, and probably the coronoid (BMNH R8501, RUB17, RUB23). The dorsal margin of the surangular is medially inflected, increasing its apparent thickness in dorsal view (Fig. 13H). In lateral view the dorsal margin of the surangular is gently convex (Figs. 2B, 3B, 13F, G), not concave (Thulborn, 1970; see Fig. 17A). The surangular foramen is located a short distance anterior to the jaw articulation, the lateral third of which is formed by the surangular (BMNH R8501). The **angular** contacts the dentary, splenial, surangular, articular and prearticular and contributes to the ventral margin of the lower jaw. The **prearticular** forms a narrow bar under the adduc-

tor fossa but expands at each end, underlying the medial half of the retroarticular process posteriorly and bordering the adductor fossa and internal mandibular fenestra anteriorly. Sutural contacts of the prearticular include the splenial, surangular, angular, and articular. The proportions and contacts of the prearticular in *L. diagnosticus* are common among ornithischians. Previously the prearticular was reconstructed as an oval bone that occupied the area of the adductor fossa (Thulborn, 1970; Thulborn's internal mandibular fenestra was then labelled the adductor fossa by Norman (1984:fig. 1E); see Fig. 17E).

The **coronoid** has not been identified or figured previously but is partially preserved in situ on the left side in BMNH RUB17 (Fig. 13G). The dislodged left splenial obscures the central portion of the coronoid, and only an impression of the anterior portion is preserved. As in the ornithischians *Scelidosaurus* (BMNH R1111) and *Lycorhinus* (BMNH RUBA.100), the coronoid in *L. diagnosticus* is an extremely slender, strap-shaped element that curves anteroventrally from the coronoid region to the alveolar margin, extending along most of the length of the dentary. The coronoid overlaps the dental lamina and replacement foramina.

The **articular** is held in a cup formed by the surangular, angular, and prearticular (Fig. 13H). In adults the articular and surangular may coossify, but in BMNH R8501 they remain separate. The articular forms the medial two-thirds and the surangular the lateral third of the jaw articulation.

**Dentition** (Figs. 6C, 10)—There are always six premaxillary teeth, as described by Thulborn (1970), rather than five (Weishampel, 1984; Weishampel and Witmer, 1990; see Fig. 18A). The complete maxillary tooth rows in BMNH R8501 contain 15 teeth, and an additional complete maxilla contains 16 teeth (Fig. 5). Estimates of 15 or 16 teeth also obtain for several additional incomplete maxillaries (BMNH R11956, RUB17). The only complete dentary tooth row contains 18 teeth (BMNH R8501, left dentary). Previous dentary tooth counts of 14 (Thulborn, 1971b; Galton, 1978) appear to be too low, as pointed out by Gow (1981). Maxillary and dentary tooth counts, of course, will exhibit variation during growth as well as among adults.

Crown size gradually increases toward the posterior end of the maxillary and dentary tooth rows until the posteriormost two or three crowns, which decrease in size (BMNH R8501). Maximum tooth size, therefore, does not occur in the center of the maxillary and dentary tooth rows (Weishampel, 1984:52) but rather closer to the posterior end.

The recurved premaxillary crowns can be distinguished from maxillary and dentary crowns (Fig. 6C). All premaxillary crowns are recurved to some extent (less so in the fifth and sixth crowns) and thus all have concave, rather than convex, posterior margins in lateral view; the sixth premaxillary tooth has a concave posterior margin, but this has been obscured in lateral view of BMNH RUB17 by postmortem rotation of the

tooth in its socket (Fig. 6C). Previous figures of the sixth crown do not show this recurvature and give the false impression that posterior premaxillary teeth closely resemble anterior maxillary teeth (e.g., Thulborn, 1970:fig. 6B). Misidentification of posterior premaxillary teeth as maxillary teeth has reinforced this misimpression; an upper tooth row containing several maxillary teeth and the fifth and sixth premaxillary teeth has been attributed to the maxillary tooth row alone (Thulborn, 1971b:fig. 2). Subsequent authors have juxtaposed this composite premaxillary-maxillary tooth row with a complete set of six premaxillary teeth (Chargé and Crompton, 1974:fig. 1; Galton, 1978:fig. 2D).

The first premaxillary crown is the most slender, and the fifth and sixth crowns are shorter in height and broader near their bases as in *Hypsilophodon* (BMNH R197). The bases of the premaxillary crowns are oval in cross section. The first four crowns have smooth margins whereas the fifth and sixth premaxillary crowns are denticulate with a greater number of denticles on the anterior margin (BMNH R8501). The apices of the premaxillary crowns are offset posteriorly and medially relative to the crown base. The lateral crown surface is anteroposteriorly and dorsoventrally convex. The medial surface, in contrast, is convex in both directions near the crown base but becomes dorsoventrally concave toward the crown tip, as occurs more strongly in *Hypsilophodon* (BMNH R197). The premaxillary crowns, therefore, are gently spoon-shaped. The anterior and posterior crown margins are offset slightly toward the lateral side of the crown, the posterior margin more so than the anterior. A shallow furrow runs just inside the anterior margin (Thulborn, 1970:fig. 6D), which results in a thinner anterior than posterior margin (contra Thulborn, 1970:423–4).

In almost every regard, maxillary and dentary crowns are identical. Distinguishing between isolated maxillary and dentary teeth, thus, is extremely difficult. The apex of both maxillary and dentary crowns is slightly offset posteriorly, resulting in a slightly longer anterior margin with a somewhat higher denticle count (six to nine denticles anteriorly; five to seven denticles posteriorly). In both maxillary and dentary teeth, the crown base (i.e., the swelling that separates crown from root) is more bulbous and positioned slightly farther from the crown apex on the lateral side. The margin of the crown base on the medial side is often straighter or bowed toward the crown apex. A pair of marginal ridges near the base of the crown extend from the most anterior and posterior denticles on each side. The marginal ridge on the posteromedial side of the crown forms the dorsal margin of a flat facet that articulates against the anterior margin of the next posterior crown (e.g., BMNH R8501). This posteromedial ridge and facet indicate imbrication of adjacent crowns along the tooth row. In the largest crowns, one or two denticles may ornament the posteromedial marginal ridge, which is here termed the **overlap ridge** (interdental pressure facet; Weishampel, 1984:51). Medial and lateral crown surfaces in the maxillary and dentary teeth also show

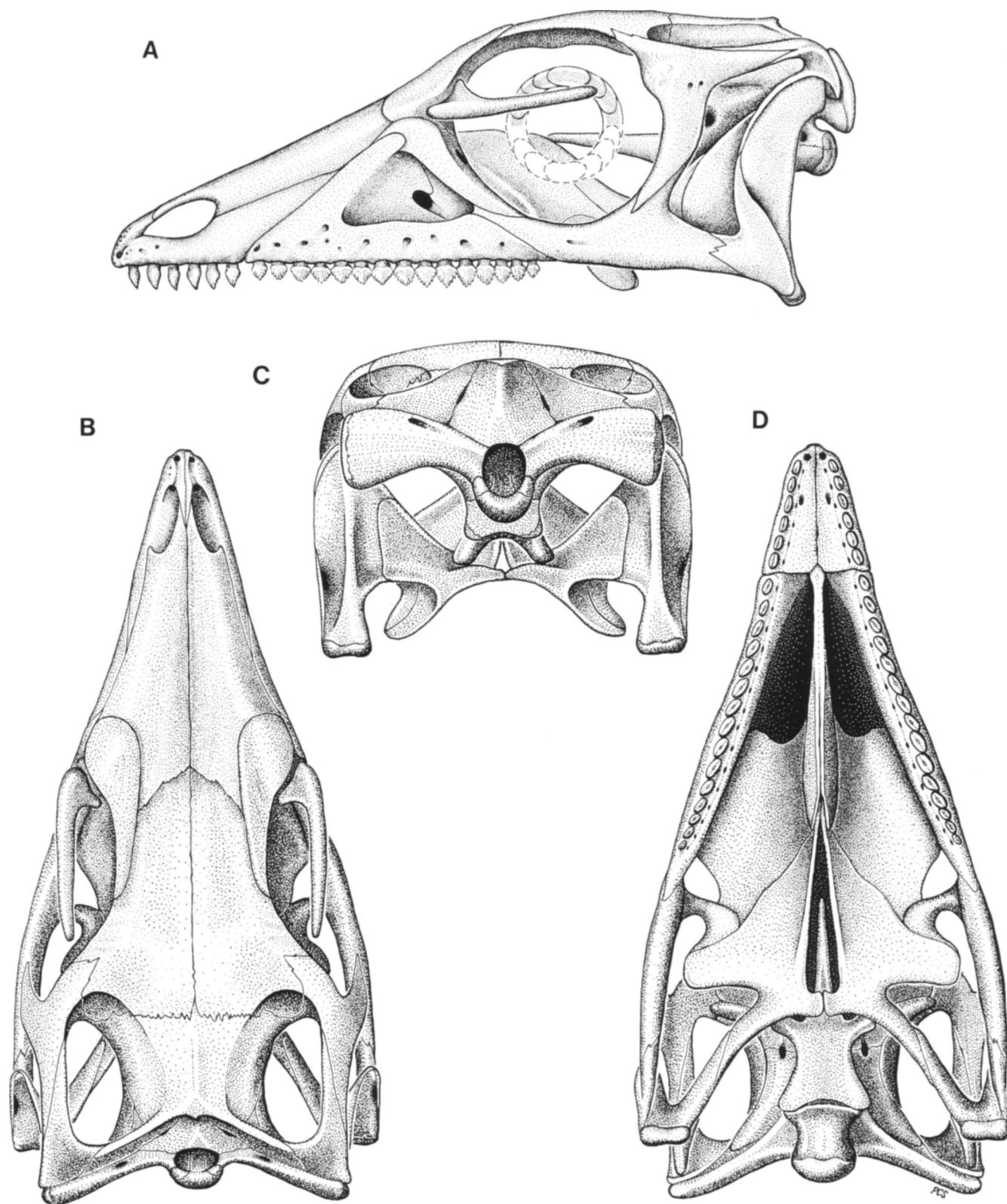


FIGURE 11. Cranial reconstruction of *Lesothosaurus diagnosticus* in lateral (A), dorsal (B), posterior (C), and ventral (D) views.



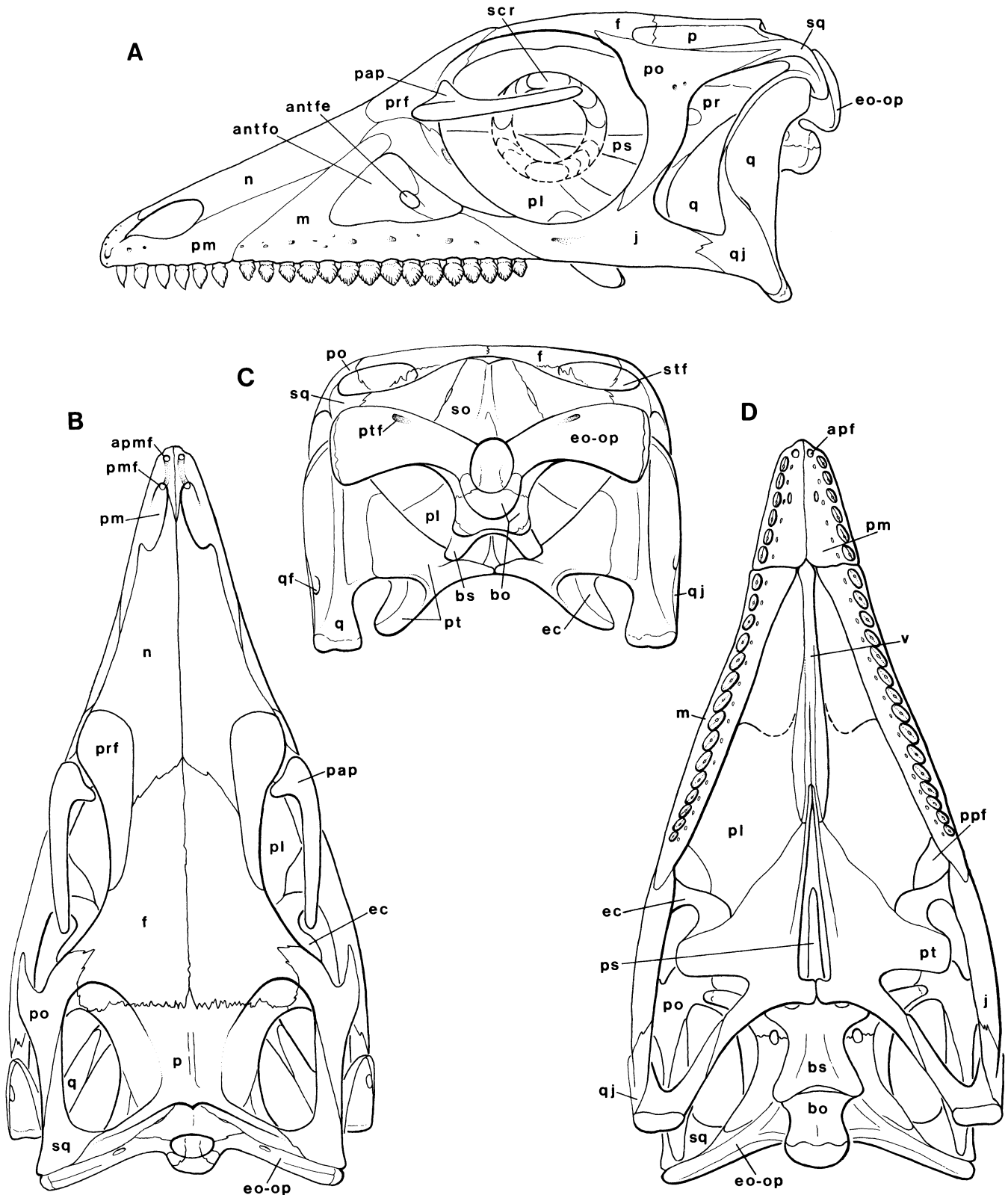


FIGURE 12. Cranial reconstruction of *Lesothosaurus diagnosticus* in lateral (A), dorsal (B), posterior (C), and ventral (D) views. Abbreviations: antfe, antorbital fenestra; antfo, antorbital fossa; apf, anterior palatal foramen; apmf, anterior premaxillary foramen; bo, basioccipital; bs, basisphenoid; ec, ectopterygoid; eo, exoccipital; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pap, palpebral; pl, palatine; pm, premaxilla; pmf, premaxillary foramen; po, postorbital; ppf, postpalatine fenestra; prf, prefrontal; ps, parasphenoid; pt, pterygoid; ptf, posttemporal foramen; q, quadrate; qf, quadrate foramen; qj, quadratojugal; scr, sclerotic ring; so, supraoccipital; sq, squamosal; stf, supratemporal fossa; v, vomer.

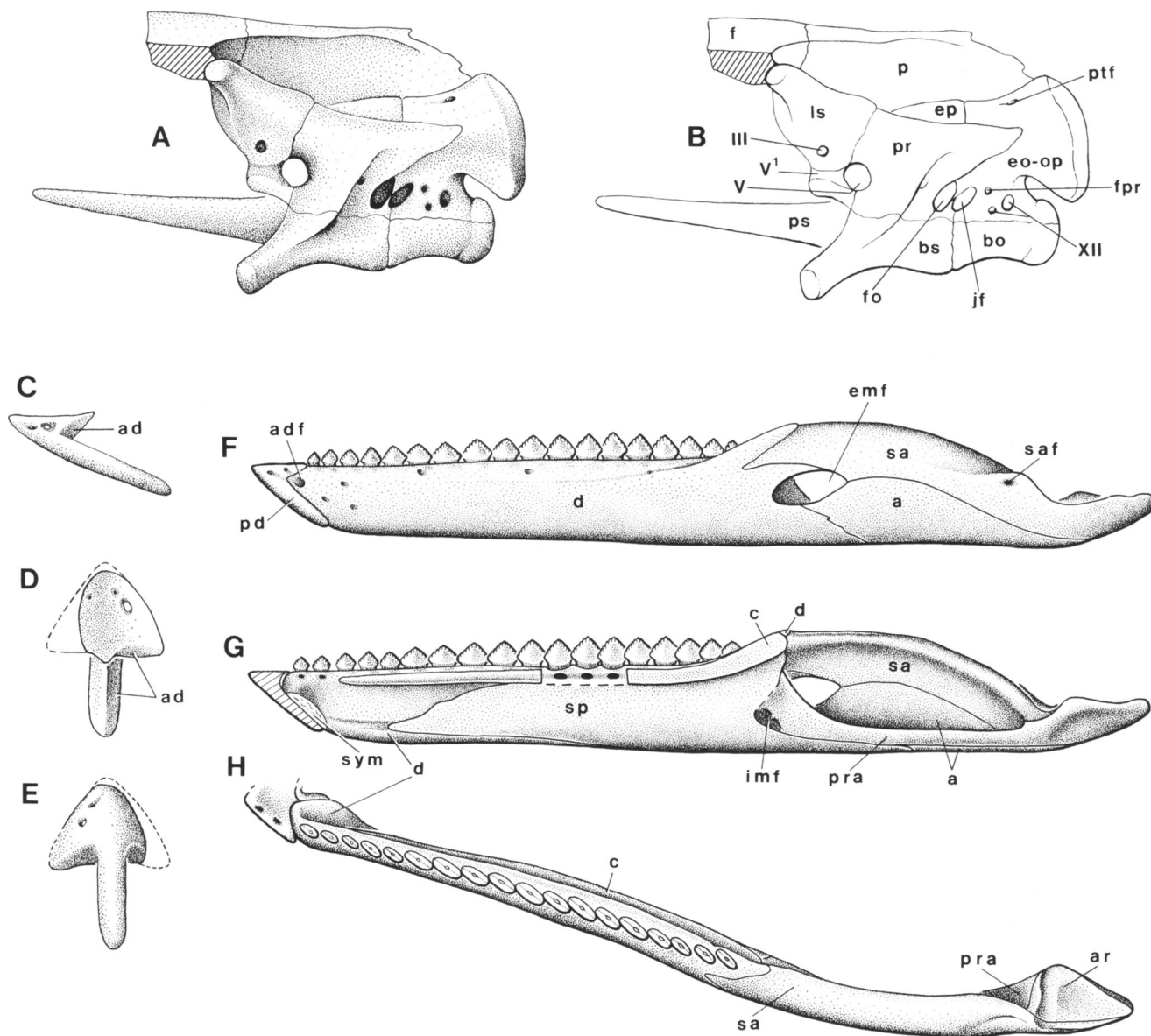


FIGURE 13. Reconstructions of the braincase and lower jaw of *Lesothosaurus diagnosticus*. Braincase in lateral view with foramina for cranial nerves III, V, VII and XII indicated (A, B). Predentary in lateral (C), dorsal (D), and ventral (E) views. Lower jaw in lateral (F), medial (G), and dorsal (H) views. Abbreviations: a, angular; ad, articular surface for dentary; adf, anterior dentary foramen; ar, articular; bo, basioccipital; bs, basisphenoid; c, coronoid; d, dentary; emf, external mandibular fenestra; eo, exoccipital; ep, epiotic; f, frontal; fo, fenestra ovalis; fpr, foramen for posterior exit of vagus nerve; imf, internal mandibular foramen; jf, jugular foramen; ls, laterosphenoid; op, opisthotic; p, parietal; pd, predentary; pr, prootic; pra, prearticular; ps, parasphenoid; ptf, posttemporal foramen; sa, surangular; saf, surangular foramen; so, supraoccipital; sp, splenial; sym, symphyseal surface.

subtle differences; the medial surface is convex anteroposteriorly and flat dorsoventrally, whereas the lateral surface is convex anteroposteriorly and slightly concave dorsoventrally. All of these crown asymmetries permit distinction of lateral from medial and anterior from posterior within a single crown, but it is very difficult to distinguish maxillary from dentary teeth and, as a result, left from right sides.

Available information on crown morphology in *L.*

*diagnosticus* is contradictory. Regarding the maxillary teeth, Thulborn (1970:425; 1971b:168) stated that the medial crown surface is flatter than the lateral surface and bears a faint median ridge. Weishampel (1984:51), on the other hand, reported that a noticeable median ridge occurs on the lateral side. But there is no prominent ornamentation on either the lateral or medial crown surfaces in *L. diagnosticus*; the well defined ridges that ornament the crowns in many ornithischians are

absent in *L. diagnosticus*. A low rounded eminence, however, is usually present on both sides of the maxillary and dentary crowns. It is offset slightly posteriorly, and is sometimes more strongly expressed on the lateral side of the maxillary crowns.

Premaxillary and maxillary tooth rows are separated by a small intervening diastema, equal to the width of the first small maxillary crown (BMNH R8501). The premaxillary tooth row is set back from the anterior end of the premaxilla by approximately the width of a single crown (Fig. 6C; Crompton and Attridge, 1986), contrary to previous assertions that the premaxillary crowns extend anteriorly to the midline (Thulborn, 1970:425, 427; 1971b:167; see Fig. 17F). In *L. diagnosticus* the anterior palatal foramen opens on the premaxillary palate along this toothless margin (Figs. 11D, 12D). Individual crowns in the maxillary and dentary tooth rows overlap in an imbricate arrangement in which the anterior edge of each crown is overlapped laterally by the posterior edge of the next anterior crown (BMNH R8501). Crown overlap is absent only in the anteriormost teeth. The maxillary tooth row is marginal except posteriorly, where there is slight eversion of the maxilla-jugal suture above the tooth row (Fig. 5). The dentary tooth row, on the other hand, is clearly inset medially along its posterior two-thirds (Fig. 13H).

The enamel is distributed symmetrically on premaxillary, maxillary, and dentary crowns as observed in cross-sections of many crowns at various levels (BMNH R8501, RUB17). Well developed wear facets appear to occur sporadically in dentitions of *L. diagnosticus*. There are several complete maxillary and dentary crowns in BMNH R8501 which do not exhibit wear facets. The fourteenth crown in the left dentary, however, preserves the ventral portion of a well developed wear facet on the lateral side of the crown. Other specimens exhibit several worn crowns. In a complete right maxillary tooth row (Fig. 4B, C), the third crown bears a single broad wear facet, and the eighth, tenth and thirteenth crowns show biplanar wear. Previous statements regarding the absence of tooth-to-tooth wear in *L. diagnosticus* (Galton, 1978:150) are inaccurate. These specimens, however, do not support the model of uniform "interlocking" occlusion proposed for *L. diagnosticus* (Thulborn, 1971b:fig. 6; Weishampel, 1984:52; Crompton and Attridge, 1986:228–229). The pattern of wear facets is irregular and the complete maxillary and dentary tooth rows in BMNH R8501 cannot be aligned to occlude with opposing crowns in alternation. Alternate occlusion and the development of biplanar wear facets on individual crowns appears to occur only locally within the dentition in *L. diagnosticus*.

### Postcranium

**Axial Skeleton** (Fig. 8A)—The right side of the proatlas has moved only a few mm from its natural articulation with the occiput and atlantal neural arch in BMNH RUB23 (Fig. 8A). The planar proatlantal

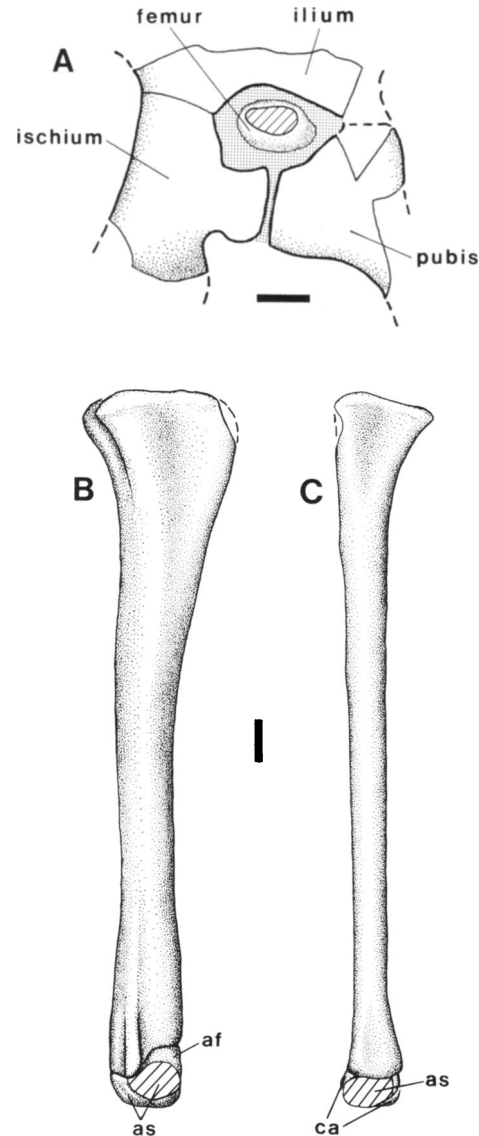


FIGURE 14. Postcrania of *Pisanosaurus mertii* (PVL 2577). Impression of central portion of right pelvis and femur head in medial view (A). Right tibia and astragalus in lateral view (B). Right fibula, calcaneum, and astragalar fragment in medial view (C). Abbreviations: af, articular surface for fibula; as, astragalus; ca, calcaneum. Scale bars equal 1 cm.

elements are crescentic in dorsal view and have a triangular lateral tab that is deflected ventrally. The lateral margin of each proatlantal element is convex and the medial margin concave. The proximal end is broader and articulates against a flat surface on the exoccipital-opisthotic near the foramen magnum. The narrower distal end articulates against the dorsal surface of the atlantal neural arch.

Only the neural arches of the atlas are exposed (8A; BMNH R11004, RUB17, RUB23). The atlantal arch is composed of a robust pedicel and neural arch that approaches, but does not contact, its opposite in the

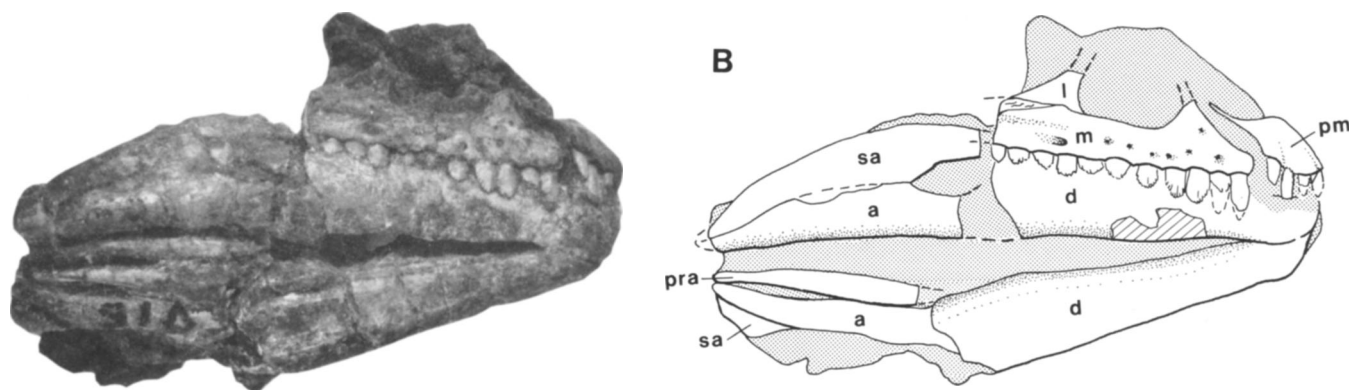


FIGURE 15. Skull of *Tawasaurus minor* (IVPP V15) in lateral view (A, B). Abbreviations: a, angular; d, dentary; l, lacrimal; m, maxilla; pm, premaxilla; pra, prearticular; sa, surangular. Scale bar equals 1 cm.

midline. A strong epipophysis extends posteriorly from the postzygapophysis. A small section of the rod-shaped atlantal rib is preserved in BMNH RUB23, but no part of the atlantal intercentrum or odontoid is exposed.

The **axis** is well preserved in BMNH R11004 (Fig. 8A). The absence of the axial intercentrum and odontoid attest to the immaturity of the specimen, which is somewhat smaller than BMNH R8501, RUB17, and RUB23. The spool-shaped centrum is weakly amphicoelous and lacks a ventral keel. The anterior rim is swollen for articulation with the parapophysis of the axial rib. The neural arch roofs a capacious neural canal and is surmounted by a strong neural spine that projects posterodorsally beyond the postzygapophyses. As is typical among diapsids, the atlantal and axial prezygapophyses face dorsolaterally, rather than dorso-medially as in other vertebrae.

The **third cervical** is preserved in articulation with the axis (Fig. 8A; BMNH R11004). The amphicoelous centrum has a trapezoidal profile with a low ventral keel. The parapophysis is located just beneath the neurocentral suture on the anterior rim of the centrum. As in all ornithischians, the cervical neural canal is relatively large, with a dorsoventral diameter approaching that of the centrum. The neural spine is low and offset to the posterior side of the neural arch. The articular surfaces of the pre- and postzygapophyses are inclined at a shallow angle, between 40 and 45 degrees. Delicate epipophyses extend posterodorsally from the postzygapophyses as in *Heterodontosaurus*.

**Forelimb** (Fig. 8B)—The forelimb is proportionately very short, measuring less than 40 percent hind limb length. The head of the **humerus** occupies the central portion of the proximal end, rather than the medial corner as previously described (BMNH RUB17; Thulborn, 1972:fig. 7A–C). As is common among ornithischians, a low eminence descends from the head on the posterior aspect of the proximal end. The **manus** is known from a single partially disarticulated speci-

men that preserves all five metacarpals and several of the phalanges. Thulborn (1972:fig. 7L) illustrated the manus as preserved (except for the position of the fourth metacarpal); additional preparation has exposed the phalanges of the first digit and the metacarpal and small terminal phalanx of the fifth digit. The first and fifth digits, therefore, are complete. The left third metacarpal is also present. New measurements of the elements of the manus are provided (Table 2) since they differ significantly from previous measurements (Thulborn, 1972:48). The complete phalangeal formula is probably 2-3-4-3-1, which differs only slightly from a previous estimate (2-3-4-3-0; Thulborn, 1972).

Metacarpal 1 is flattened dorsoventrally with a subrectangular proximal end and a length subequal to metacarpal 4. In dorsal view, the lateral margin of the shaft is straight whereas the medial is bowed (Fig. 8B). As in many other ornithischians (e.g., *Heterodontosaurus*, *Hypsilophodon*, *Psittacosaurus*), the distal end is asymmetrical, with the lateral condyle extending farther distally than the medial condyle. As a result the phalanges of digit I swing towards the center of the palm during flexion, which suggests rudimentary grasping capability. The proximal phalanx and ungual of digit I are subequal in length, the former lacking well developed distal condyles and the latter lacking a dorsal intercondylar process. The ungual is dorsoventrally flattened with grooves on each side for the claw.

The proximal ends of metacarpals 2 and 3 overlap the proximal ends of metacarpals 3 and 4, respectively. To accommodate this overlap, the ventral aspect of the proximal shafts of metacarpals 3 and 4 are bevelled. The proximal phalanx of digit II, which is better formed than the proximal phalanges of digits I and III, has clearly divided distal condyles, marked collateral ligament pits, and a shallow depression dorsally for the intercondylar process of the succeeding phalanx. The second phalanx of digit II is similar to, although larger than, the proximal phalanx of digit IV; the distal con-

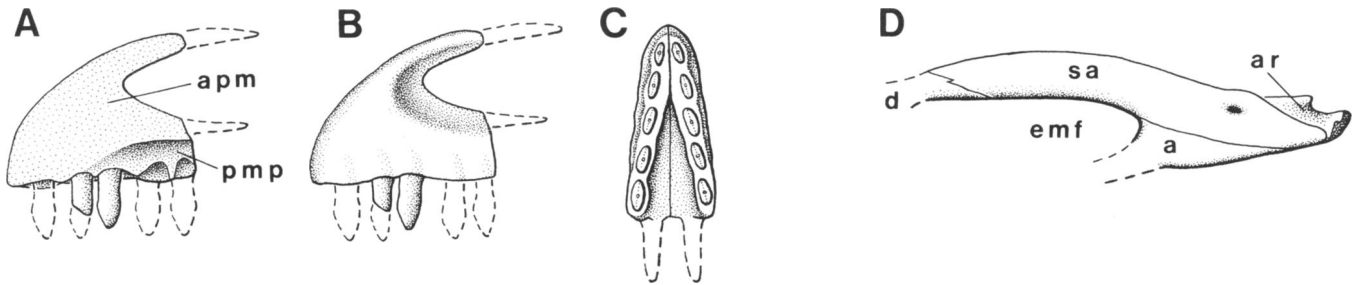


FIGURE 16. Skull elements attributed to *Technosaurus smalli* (TTU P 9021). Left premaxilla in (reversed) medial (A) and lateral views (B). Reconstruction of articulated premaxillae in ventral view (C). Posterior portion of left lower jaw in lateral view (D). Abbreviations: a, angular; apm, articular surface for premaxilla; ar, articular; d, dentary; emf, external mandibular fenestra; pmp, premaxillary palate; sa, surangular. Natural size.

dyles are weakly divided, with shallow collateral ligament pits on each side.

Metacarpal 5 is stout with a flared base as in other ornithischians such as *Hypsilophodon*, *Camptosaurus*, and *Leptoceratops*. The convex proximal end is bevelled on the medial side, and the medial shaft margin is bowed. The single distal condyle lacks collateral ligament pits and is turned slightly dorsomedially. A small, subconical proximal phalanx is preserved adjacent to the shaft of the fifth metacarpal. The fifth digit may have been directed posterolaterally as a stout prop to the remainder of the manus.

**Pelvic Girdle** (Figs. 9, 10)—The **ilium** retains the primitive ventral flange that backs the central portion of the acetabulum (Figs. 9C–D, 10). The iliac acetabulum extends as a broad sheet from the pubic peduncle to the ischial peduncle. In the region of the ischial peduncle, a subtriangular area of the acetabular surface is raised from the remainder of the acetabulum and distinguished by a finely porous texture (Figs. 9D, 10). This area constitutes the iliac contribution to the antitrochanter, the principal articular surface for the head of the femur (Sereno and Novas, 1990). The antitrochanter, present in all dinosaurs plesiomorphically, may have been capped by a cartilage pad.

The postacetabular process is subrectangular with a distinct angle between the dorsal and posterior blade margins (Figs. 9C–D, 10; Santa Luca, 1984:figs. 10–15). The postacetabular process is incomplete in BMNH RUB17, and reconstructions based on this specimen have shown a rounded end similar to that in *Hypsilophodon* (Thulborn, 1972:fig. 13; Galton, 1978:fig. 2B; Colbert, 1981:fig. 23C, mislabelled *Hypsilophodon*). In medial view of the ilium, the base of the preacetabular process in BMNH RUB23 is marked by a scar for the first sacral rib as in *Hypsilophodon*, *Psittacosaurus*, and several other ornithischians. Thulborn (1972:fig. 8C) figured, but did not discuss, this attachment scar. The attachment areas of the second, third, fourth and fifth sacral ribs are broad and occur on the ventral half of the ilium medial to the pubic and ischial peduncles, as is clearly marked in several specimens (Fig. 9C; Santa Luca, 1984:figs. 10–15). The small, elevated sa-

cral scars shown by Thulborn (1972:fig. 8C) are inaccurate.

The pubic peduncle of the **ischium** is very deep dorsoventrally (Figs. 9A, 10; Santa Luca, 1984:fig. 18). In a well-preserved right ischium (BMNH RUB17), the platelike pubic peduncle is nearly twice the width of the iliac peduncle. The pubic peduncle thickens only slightly toward its acetabular margin.

There is no obturator process in *L. diagnosticus* (Sereno, 1986:247). Thulborn (1972:fig. 9A–C) described and figured an obturator process in *L. diagnosticus* which has been widely cited in the literature. The supposed obturator process consists of little more than a prominent angle on the ventral margin of the

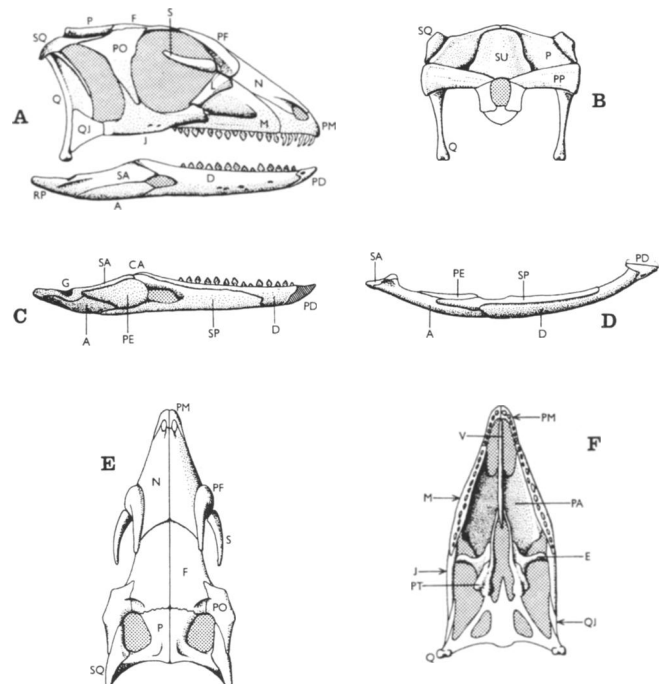


FIGURE 17. Skull reconstruction of *Lesothosaurus diagnosticus* (from Thulborn, 1970). Cranium in lateral (A), posterior (B), dorsal (E), and ventral (F) views. Lower jaw in lateral (A), medial (C), and ventral (D) views.

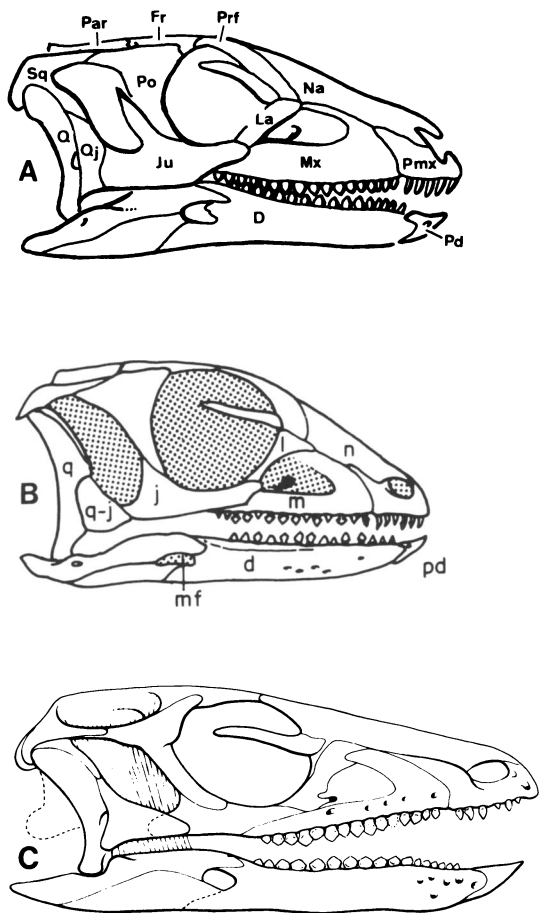


FIGURE 18. Skull reconstructions of *Lesothosaurus diagnosticus*. A, from Weishampel (1984); B, from Norman (1984); C, from Crompton and Attridge (1986).

ischial blade, quite unlike the tab-shaped process in ornithopods. But the left ischium, upon which description was based, is damaged along its entire ventral margin (Fig. 9B; BMNH RUB17). Two small fragments have been glued to this unfinished margin and form the pointed flange identified as the obturator process. The right ischium of the same individual was not figured but preserves the ventral margin of the ischium from the pubic peduncle to a point halfway along the ischial blade (Fig. 9A; BMNH RUB17). The ventral margin curves smoothly from the peduncle down the blade without any suggestion of an obturator process.

The **pubis** has a small central body that contributes to the acetabulum and joins ilium and ischium, a blunt tab-shaped anterior (prepubic) process, and a long rod-shaped posterior (postpubic) process. The central body and the base of the anterior process are preserved only on the left side. The delicate shaft of the left posterior process is crushed and fractured along its length in several places. The "sharp-edged flange" on the left posterior process (Thulborn, 1972:fig. 9E) is due to postmortem flattening of the shaft and is lacking in the uncrushed right posterior process.

The flat vertical surface of the pubic symphysis provides the key to proper orientation of the pubis. The symphyseal surface is well preserved on the distal end of the right posterior process and occupies the distal fifth or sixth of the shaft (Fig. 9E). With the symphyseal surface held in its natural vertical plane, the proximal third of the shaft of the right posterior process is flattened in a dorsolateral-ventromedial plane; the middle third of the shaft is subcylindrical; and the distal third of the shaft is flattened in a dorsomedial-ventrolateral plane. Thulborn (1970:fig. 9E–G) illustrated the posterior process of the left pubis, which has undergone postmortem torsion. His ventral view of the posterior process approximates lateral view of the right posterior process, and the acetabular surface is shown facing dorsally rather than dorsolaterally.

**Hind Limb** (Fig. 8C–F)—The proximal articular end of the **femur** is uncrushed on the left side and the shaft and distal end are free of distortion on the right side (Fig. 8C–E). The proximal end of the femur is strikingly primitive compared to other ornithischians. In posterior view the dorsal margin of the head is inclined ventromedially rather than horizontally (Fig. 8D). In proximal view the articular surface of the head angles anteromedially relative to the transverse axis of the distal condyles and is gently arched anteriorly (Fig. 8E). The broadest anteroposterior width of the articular head is located centrally rather than near the lateral margin. Unlike other ornithischians, the greater trochanter extends anteriorly as a short flange, paralleling the plane of the lesser trochanter. The lesser trochanter is blade-shaped, not "finger-like" (Thulborn, 1972:43), and exceeds the width of the greater trochanter (Fig. 8C). Relative to the length of the femur, the pendant fourth trochanter is large, attaching to more than one-quarter of the femoral shaft.

Two **distal tarsals** have been described and attributed to the left tarsus (Thulborn, 1972:46). The first bone resembles the disc-shaped distal tarsals in other ornithischians (Thulborn, 1972:fig. 12C, D). The second bone is not a tarsal but rather a fragment from the distal condyles of a long bone of the pes (probably a metatarsal judging from its size). The condylar surface is gently divided and rounded (Thulborn, 1972:fig. 12E), and the opposing side of the fragment exposes a broken surface of cancellous bone.

The left **metatarsus** is preserved with metatarsals 2 and 3 in natural articulation. Metatarsal 1 is dislodged from its natural position alongside the shaft of metatarsal 2 (contra Thulborn, 1972:46) and is inclined so that the broken tip of the shaft projects dorsally above that of metatarsal 2 with the distal condyles swung ventrally. The shaft of metatarsal 1 is very slender, no more than one mm in transverse width and just over 2 mm in dorsoventral depth (Fig. 8F). The splintlike shaft of metatarsal 1 appears to constitute an autapomorphy for *L. diagnosticus*, despite its occurrence elsewhere among ornithischians (e.g., *Othnielia*, *Iguanodon*) because metatarsal 1 primitively retains a significant proximal articular surface in Genasauria, Sauro-

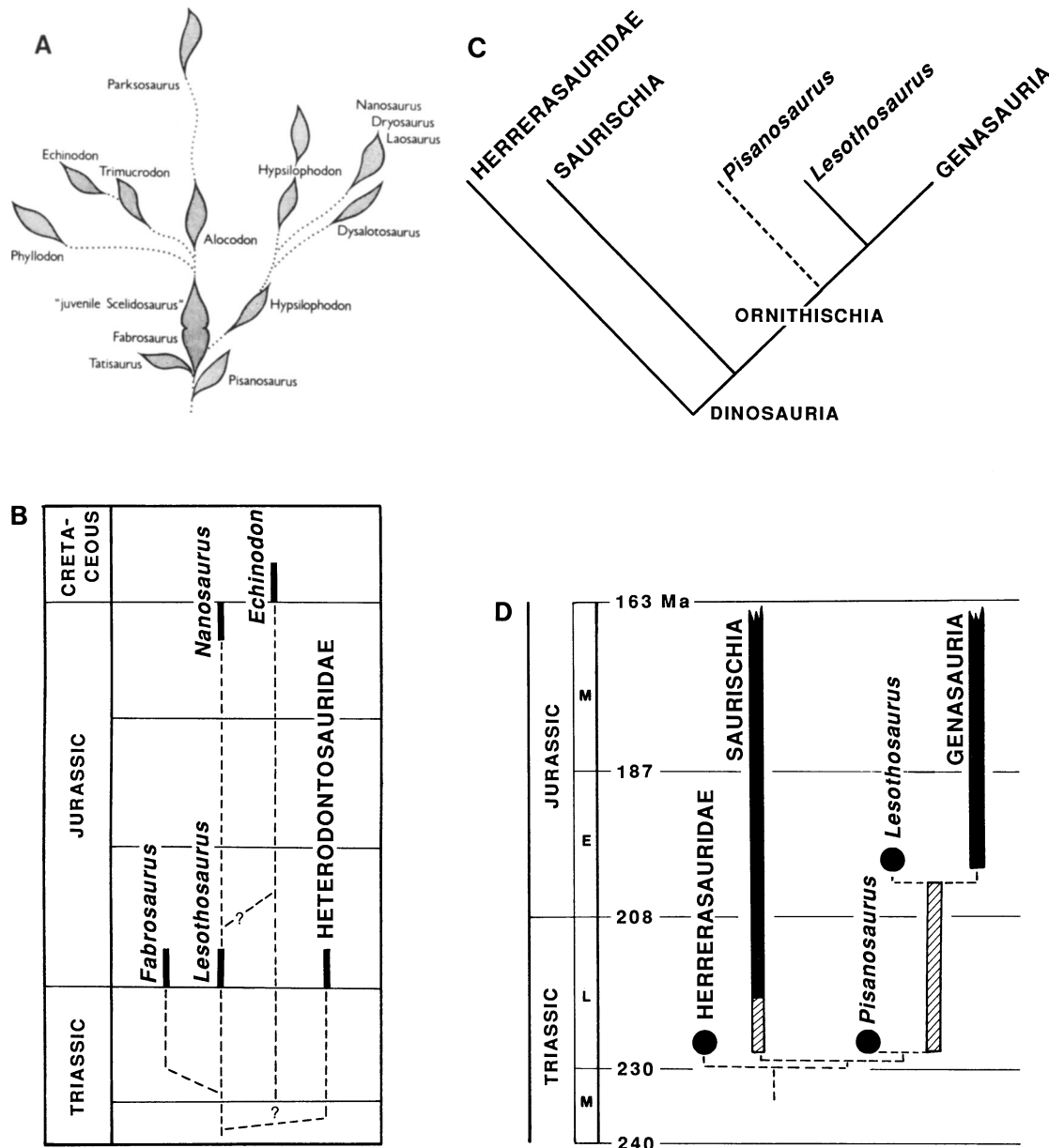


FIGURE 19. Phylogenetic interpretations of basal ornithischians. **A**, from Thulborn (1973); **B**, after Galton (1978); **C**, cladogram representing present analysis; **D**, minimum divergence times plotted from cladogenic and chronostratigraphic data (cross-hatching indicates missing lineage duration).

podomorpha, and Herrerasauridae. The distal condyles of metatarsal 1, which are divided ventrally but not dorsally, angle medially away from metatarsal 2.

Except for its distal third, the shaft of metatarsal 2 is closely pressed against metatarsal 3 (Fig. 8F). The proximal end is not as deep as the subrectangular end of metatarsal 3. The shaft of metatarsal 3 is gently sigmoid, curving laterally away from metatarsal 2 and then straightening along the axis of the metatarsus near the distal condyles. The shaft of metatarsal 4 is also sigmoid, despite previous description as "perfectly straight" (Thulborn, 1972:46). In posterior view the

shaft of metatarsal 4 is gently curved along its length, contacting metatarsal 3 in its proximal third and then swinging laterally. The distal condyles are canted back in line with the axis of the metatarsus, as in the third metatarsal, and the ventral rim of the collateral ligament pit flares laterally.

The proximal shafts of metatarsals 1 through 4 are closely appressed and must have been bound by ligaments. The dinosaurian sigmoid curvature in the shaft of metatarsals 4 (and to a lesser extent metatarsal 3) broadens the stance of the central three weight-supporting digits.



## DISCUSSION AND CONCLUSIONS

The "primitive stock" or "ancestral stem group" has been the focus in traditional scenarios that characterize the evolutionary history of higher taxa. From their debut in the literature, "fabrosaurs" have been recognized as the preeminent "primitive stock" for the Ornithischia—the first stage in the "main line" of ornithischians from which other subgroups were derived (Thulborn, 1971a, 1972; Galton, 1972; Romer, 1968). Thulborn, for example, writes that "This stock of hypsilophodontids [including fabrosaurs] ranges from the late Trias through the Cretaceous and is fundamental to the whole pattern of ornithischian history; it represents the ancestry, ultimately at least, of groups as diverse as the hadrosaurs, pachycephalosaurids and ceratopsians" (1973:123; see Fig. 19A).

The "primitive stock," by definition, is plesiomorphic with respect to other members of a monophyletic clade (e.g., "fabrosaurs" relative to other ornithischians). Plesiomorphy, as is now commonly acknowledged, is phylogenetically uninformative; the absence of synapomorphies that characterize other subclades does not clarify the relationships of the "primitive stock." In the years since its inception (Galton, 1972), Fabrosauridae has served primarily as a repository for indeterminate ornithischian material or basal ornithischians of uncertain relationship. "Fabrosaurids" thus constitute a grade that owes its recognition to the absence of obvious apomorphies that unite other ornithischian clades (Sereno, 1990). The incorporation of juvenile prosauropods (*Tawasaurus*, *Technosaurus* in part) is not surprising, with attention focussed on ornithischian symplesiomorphies.

Despite some recognition of Fabrosauridae as a grade (Thulborn, 1971a; Norman, 1984), it has been misinterpreted as a monophyletic clade with its attendant properties. Thus Fabrosauridae has appeared as a monophyletic clade in phylogenetic diagrams (Galton, 1972, 1978; Norman, 1984; Milner and Norman, 1984; Thulborn, 1974, 1977; see Fig. 19B). The group is believed to have originated in the Late Triassic, radiated during the Jurassic, and gone extinct in the Cretaceous, and the geographically widespread localities of included fossil material has suggested a Pangaeian distribution for "fabrosaurids" in the Lower Jurassic.

Recently Fabrosauridae has been criticized as constituting a paraphyletic assemblage (Sereno, 1986, 1990; Gauthier, 1986; Weishampel and Witmer, 1990). This review has lead to the following conclusions: (1) Fabrosauridae, as traditionally conceived, is an artificial assemblage of basal ornithischians and juvenile prosauropods. (2) *Echinodon* and *Scutelosaurus* are more closely related to other ornithischian subgroups than to *Lesothosaurus*. (3) Most "fabrosaurs" are ornithischians of unknown relation (*Alocodon*, *Trimucrodon*) or nomina dubia (*Fabrosaurus*, *Nanosaurus*, *Technosaurus* in part, *Xiaosaurus*). (4) The nomen Fabrosauridae should not be employed because *Fabrosaurus* is a nomen dubium and the holotype is referable only to

Ornithischia indet. (5) *Lesothosaurus* and the oldest members of its sister-taxon, Genasauria, must have diverged by the Early Jurassic (Sinemurian; Fig. 19C, D). (6) The Late Triassic ornithischian *Pisanosaurus* is potentially the sister-taxon to remaining ornithischians, which underscores the poor ornithischian fossil record during the Late Triassic.

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