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No. 1.—*Revisionary Notes on the Ant Genus Myrmecia of Australia*

By William L. Brown, Jr.

The ants of the subfamily Myrmeciinae have recently been revised by Mr. John Clark of Melbourne. In many respects, I find myself in disagreement with Mr. Clark's conclusions, and a recent study tour of Australia under the auspices of a Parker Travelling Fellowship from Harvard University, and later of a United States Educational Foundation (Fulbright) Fellowship in Australia has furnished evidence leading to the revisionary notes offered below. On returning to the United States from Australia, advantage was taken of a stay of a few days in London to restudy the *Myrmecia* types of species described by Fabricius and Frederick Smith. Most of Smith's types have already been redescribed by Crawley (1926), but nowhere in Clark's work do I find any mention of Crawley's important contribution. Data supporting certain conclusions I have reached may be found in Crawley's paper, although his paper does not in any way attempt a real taxonomic revision, but merely corrects and amplifies Smith's originally very faulty descriptions and supplies new figures.

I have returned to the original conception of *Myrmecia* as a single genus including the various "jumpers" and "bull-ants" of Australia and New Caledonia; my reasons for rejecting Clark's separation of *Promyrmecia* are fully stated elsewhere (Brown, 1953). Furthermore, I consider Clark's subfamily Nothomyrmeciinae as a tribe of subfamily Myrmeciinae; *Nothomyrmecia* Clark may be regarded as the type genus of tribe NOTHOMYRMECIINI (= Nothomyrmecii Clark, 1934). Subfamily rank for the Myrmeciinae is accepted, and will be discussed elsewhere.

Myrmecia Fabricius is a difficult genus taxonomically in the sense that many of its species are very variable in size, color and sculpture, while at the same time the specific differences are often based on characters that appear relatively trivial until their constancy is appreciated through the examination of large series from all parts of their ranges. This being the case, many of the species described by Mr. Clark must be considered as very doubtfully distinct. Since types of a majority of these forms were not available to me during my stay in Australia and have not become so since, no definite statements regarding many of Clark's species may be made at this time. A warning should be issued, however, that in many observed cases, Clark's descriptions and figures will not fit his type specimens that I have managed to see, and will not agree with the normally-collected individuals of species of older authors; since this author largely ignored variation beyond single nest series or single specimens, the inevitably confusing results of such procedure will have to be dealt with by some later resident Australian worker. The doubt surrounding Clark's species partly explains the difficulties in his keys to *Myrmecia* species, and at the same time makes revision of these keys impossible. In the revisionary matter to follow, I shall deal chiefly with some of the more obvious species, concerning which the mere statement of trailing synonymy will help to right the confusion; for fuller descriptive and synonymic data, the interested reader is referred with some reservations to Clark's monograph of the Myrmeciinae (1952). Most of the species I shall treat below are discussed, figured and characterized more fully, though with many inaccuracies, in Clark's volume, where they may be traced through the index beginning on page 228; I shall include in my own synonymies only the most essential of these references.

MYRMECIA MANDIBULARIS Fred. Smith

Myrmecia mandibularis Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 145, worker. Crawley, 1926, p. 385, fig. 10.

Myrmecia (*Promyrmecia*) *fulvipes coelatinoda* Wheeler, 1933, Colony-founding among ants, Harvard, p. 72, worker. NEW SYNONYMY.

Promyrmecia laevinodis Clark, 1943, Mem. Nat. Mus., Melbourne, **13**: 139, pl. 17, figs. 94–95, worker, female. NEW SYNONYMY.

The type of Wheeler's subspecies *coelatinoda* cannot now be found, but his description strongly suggests that it was merely an old, faded or originally teneral specimen of *mandibularis* that had suffered loss of much of its pubescence through age and handling.

M. laevinodis is supposed to differ from *mandibularis* in having an essentially non-rugose postpetiolar disc, but extensive series in the Museum of Comparative Zoology show complete intergradation in this respect. In series of this form from Margaret River and Pemberton, Western Australia, the discs vary from sharply longitudinally rugose to smoothly and very finely reticulate, without suggestion of rugation or large punctures; some of these series appear from the mounting to be uninidal, and are certainly sympatric. While certain populations I have observed personally appear to be purely smooth-postpetiolate (western Kangaroo Island), others from the Grampians Ranges were highly variable and contained a large proportion of undoubted intergrades. The gastric pubescence varies from red-orange to bright yellow-golden in series from South Australia and Victoria. Clark's types of *laevinodis* appear to be classifiable as intergrades toward the smooth-postpetiolate end of the range of variation, since he mentions large indistinct punctures that are not present in the extreme smooth forms.

On Kangaroo Island, this species was found nesting unobtrusively on the high sandplain heath, whereas on the South Australian mainland the nest sites were often in dry upland sclerophyll woodlands. It runs rapidly upon being disturbed, and is adept at hiding and dodging, but no amount of stimulation of the nest or its inhabitants (in hot, direct sunlight) induced the latter to jump, at least in the localities at which I have observed it. This is contrary to older observations, although such as are found in the literature are rather vague and uncertain. *M. mandibularis*, like most of its smaller relatives, is a diurnal forager, and the golden gastric pubescence is considered to function as warning coloration.

Localities for material examined: WESTERN AUSTRALIA: Pemberton; Margaret River; Bridgetown (W. M. Wheeler, P. J. Darlington *et al*). Swan River; Albany (J. Clark). Manjimup (W. S. Brooks). Kukerin (A. Douglas).

SOUTH AUSTRALIA: Cape Borda; south of Ravine des Casoars (W. L. Brown) (on Kangaroo Island). Mt. Remarkable, southern Flinders Ranges (W. L. Brown). Mt. Lofty; Ardrossan (J. G. O. Tepper). Mylor (G. F. Gross).

VICTORIA: Victoria Valley and Mt. Abrupt, Grampians Ranges (B. B. Given). Ballarat (H. W. Davey).

MYRMECIA RUGOSA Wheeler New status

Myrmecia michaelseni subsp. *rugosa* Wheeler, 1933, Colony-founding among ants, Harvard, pp. 60, 67, worker, "Clark (MS)."

Myrmecia mandibularis subsp. *rugosa* Wheeler, 1933, *Ibid.*, p. 72, *lapsus*.

Promyrmecia ruginodis Clark, 1943, Mem. Nat. Mus., Melbourne, **13**: 113, pl. 13, figs. 20–22, all castes, NEW SYNONYMY. (*Nec Myrmecia ruginoda* (Fred. Smith), as *Ponera ruginoda;* see below).

Clark (1952) disowns the name *rugosa* as a *nomen nudum*, but it is clear that Wheeler furnished sufficient descriptive material with the original proposal of the name. The name *rugosa* is written on a label in Clark's hand-printing affixed to specimens he had sent to Wheeler at some early date.

M. rugosa, unrelated but with a striking superficial similarity to the rugose-postpetiolate form of *M. mandibularis*, may copy that species in grading into a related smooth-discal form (*M. michaelseni*) apparently occurring over much the same range geographically. The present series, however, while showing some slight sculptural variation, do not suggest that the intergradation completely bridges the difference, and we must ask that more material be studied before judgement on this question can be made final. To date, I have seen only a few specimens referable to *M. rugosa:* WESTERN AUSTRALIA: Ludlow (two cotype workers in the Museum of Comparative Zoology, by present fixation) (J. Clark). Perth (Clark). Calgardup; Yallingup (Coll. Western Australian Museum).

MYRMECIA PILOSULA Fred. Smith

Ponera ruginoda Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 93, male. NEW SYNONYMY.

Myrmecia pilosula Fred. Smith, 1858, *Ibid.*, p. 146, worker, female, male. Crawley, 1926, pp. 383–385, fig. 9.

Ectatomma ruginodum Roger, 1861, Berl. Ent. Zeitschr. **5**: 168.

Rhytidoponera (*s. str.*) *ruginoda* Emery, 1911, Gen. Ins. **118**: 38.

Ponera ruginoda Clark, 1936, Mem. Nat. Mus., Melbourne, **8**: 14 (excluded from *Rhytidoponera*).

The type of *Ponera ruginoda*, a perennial puzzler, was examined in the British Museum. It proved to be a male of the common "black jumper" of southeastern and southwestern Australia; direct comparison with the male among the *M. pilosula* types certifies this identification.

M. pilosula, like other "jumpers," is normally a diurnal forager. It is an especially common ant in the southeastern part of Australia and Tasmania, where populations may become very dense in the higher mountains. Among a great many locality records for series examined, I may note as of more than usual interest the dense populations inhabiting the ravines at the western end of Kangaroo Island, South Australia, and a more dilute population sampled on the sandhills along the coast at Esperance, Western Australia (Brown). Like many another ant species in southern Australia, the range appears to be that of a relict clinging to widely separated favorable (relatively moist) areas with broad stretches of arid land intervening.

MYRMECIA FORCEPS Roger

Myrmecia forceps Roger, 1860, Berl. Ent. Zeitschr. **5**: 34, worker.
Myrmecia singularis Clark, 1952, Formic. Australia, Melbourne, **1**: 26–27, fig. 5, worker. NEW SYNONYMY.

The type of *M. singularis* is a worker with the structure of *M. forceps* and "colour almost entirely that of *M. rufinodis* Smith." Specimens taken by myself at Kingscote, Kangaroo Island, South Australia fit this description quite satisfactorily, and Kingscote is very probably the exact type locality for Clark's species. At Kingscote, *M. rufinodis* is the dominant *Myrmecia* along the coast, and its nests are very numerous and conspicuous there. I took the few *singularis* specimens in the midst of this area from a nest notable only for its inconspicuousness; the entrance consisted of a single hole without a mound or crater and was rather well concealed in the leaf litter. Considerable digging revealed only a very few ants, which contrasted in their timidity with the aggressive defenders of the populous neighboring *rufinodis* nests. I feel that the situation at this locality can be explained as a case of Müllerian mimicry. It should be noted that the Kingscote series copied most closely the coloration of the *rufinodis* workers of corresponding size, even to following exactly the same variations in pattern.

As interesting as this situation seems, I cannot support *singularis* as a species distinct from *forceps*. The series in the Museum of Comparative Zoology, while limited, show every degree of intergradation to the "typical" condition of *forceps* if one collects all specimens with *forceps*-type mandibles from all localities into one group for comparison. The "typical" coloration is ferruginous red, with gaster blackish, and mandibles and appendages much lighter and more yellowish; I have a series from Heathcote, New South Wales, answering to this color form (W. M. Wheeler *leg.*). A form with darker head, mentioned by Clark (1952, p. 24), is represented in my present series by examples taken at Sutherland, New South Wales (C. P. Haskins) and by myself on the high mallee heath of inland Kangaroo Island just east of Sandy River. In the latter locality, the nest was a low, flat mound about 2 feet in diameter, with a single entrance hole in the center surrounded by a radiating circle of short sections of twigs arranged with considerable symmetry on the surface of the mound. In both these and the Sutherland specimens, the alitrunk is unclouded ferruginous, while the head is largely or wholly brownish-black. Series from SOUTH AUSTRALIA: Port Lincoln (F. E. Wilson), Goolwa (Zeitz) and the Mt. Lofty Ranges (J. G. O. Tepper) vary so as to completely close the gap in color pattern between *forceps* and *singularis*, though variation in single nest series does not seem ever to express the full variability of the species. It is worthy of note that Port Lincoln and the Lofty Ranges also have large local *rufinodis* populations, and that *rufinodis-singularis* mixed collections with similar coloration, at least in part, were apparently separated by someone after the series had reached the Museum.

It appears to me probable that *forceps* is a species with highly variable color patterning lending itself to production, by natural selection, of local color forms which mimic effectively the dominant *Myrmecia* species of the respective areas.

MYRMECIA RUFINODIS Fred. Smith

Myrmecia rufinodis Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 145, worker, original description. Clark, 1952, *op. cit.*, pp. 37–40, figs. 15, 16, worker, female, male, with *M. gracilis* as distinct species.

Myrmecia gracilis Emery, 1898, Rend. Accad. Sci. Bologna **3**: 232, worker, NEW SYNONYMY.

Myrmecia (*s. str.*) *crudelis* var. *gracilis* Emery, 1911, Gen. Ins. **118**: 19.

As discussed above under *M. forceps*, I found this species to be abundant at Kingscote, the type locality for *M. gracilis*. In each nest, the individuals varied considerably in color, the extremes following the color details given by Clark for *rufinodis* and *gracilis*, while intermediates were even more common. It is difficult to believe that Clark's extensive series did not contain some of these intermediates, since I have found them consistently in the majority, not only in the Kingscote series, but also in those from Port Lincoln and other littoral localities widely separated in lower South Australia. At any rate, at least some specimens from each of the nests from Kingscote compare very well with the type and other specimens of *rufinodis* in the British Museum. Emery's *gracilis* is only a common variant found in every nest seen, and always accompanying the "typical" *rufinodis*. This species was found foraging in abundance late on a warm but windy and rainy morning at Kingscote. The nests are populous and are surmounted by a conspicuous mound up to 3 feet in diameter and about one foot high; the surface of the mound is frequently "decorated" with bits of gravel or short sections of twigs or straws. The inmates are very alert and aggressive — more so than most *Myrmecia* species —

in defending their nest. The coloration is considered to be of a warning type, as it renders the insects conspicuous in their natural surroundings. They appear to be chiefly diurnal foragers.

Among species from the same area, *rufinodis* is likely to be confused only with (1) *M. simillima* Fred. Smith, which is larger and more robust and does not include a form with reddish pronotum on blackish alitrunk such as is common in all *rufinodis* nests, and (2) *M. pulchra* Clark, a species of more robust stature and with quite different mandibles.

MYRMECIA PYRIFORMIS Fred. Smith

Myrmecia pyriformis Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 144, pl. 10, figs. 1–6, worker, female, male. Crawley, 1926, p. 377, fig. 4.

Myrmecia sanguinea Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 148, worker. Crawley, 1926, p. 378, fig. 5. NEW SYNONYMY.

Myrmecia simillima Clark (*nec* Fred. Smith), 1952, Formic. Australia, Melbourne, **1**: 89–91, figs. 68, 69, worker, female.

Myrmecia pyriformis Clark, 1952, *Ibid.*, pp. 99–101, figs. 78–80, worker, female, male.

Myrmecia forficata Clark, *partim* (*nec* Fabricius), 1952, *Idem*, p. 93.

M. pyriformis is a very common species in open sclerophyll woodland in southeastern Australia. It often builds conspicuous mounds, and is normally a night forager. In order to prevent any further confusion regarding this species, it is necessary to refer to some of the outstanding characters.

The stature is large, averaging larger than in *M. forficata*, the color is darker, with the head and alitrunk dark reddish-brown to blackish-brown, and the sculpture of head, alitrunk and nodes is more irregular and more opaque. The mandibles are essentially like those of *forficata*, but the angulate portion near the base (inner borders) is even broader and more strongly salient. The clypeus is densely pubescent, the whitish hairs usually hiding the surface here. Postpetiole and succeeding (basal gastric) tergite in unworn specimens normally bearing a very short but fairly dense reclinate pubescence of a light grayish or brownish color. The pronotal costulation (or striation) varies considerably in pattern, even in uninidal series; some specimens have longitudinal costulation in the middle, others have the lines converging anteriorly in a V, and still others are narrowly- to broadly-arched costulate in a more or less transverse direction.

The maladroit treatment accorded this species by Clark may be laid to his lack of consideration of Crawley's paper redescribing Smith's types, and also to his failure to study pronotal sculpture through sufficient series. My study of the types of *pyriformis* and *sanguinea* in the British Museum confirms the synonymy of these forms, also indicated (but not proposed) in Crawley's characterizations. The types and Crawley's paper also clearly contraindicate Clark's identification of *simillima*, the latter being a quite distinct species treated at length farther below. The two species *forficata* and *pyriformis* occur together throughout a wide area without a sign of intergradation, though small specimens, such as the *sanguinea* type, may resemble the *forficata* medias and minors in everything but pubescence.

MYRMECIA AURIVENTRIS Mayr

Myrmecia auriventris Mayr, 1870, Verh. Zool.-bot. Ges. Wien **20**: 968, worker. Clark, 1952, *op. cit.*, pp. 40–42, figs. 17, 18, worker, male.

Myrmecia auriventris var. *athertonensis* Forel, 1915, Ark. f. Zool. **9**: 8, worker, male. NEW SYNONYMY.

The type of the variety *athertonensis* is not available, but Forel's description applies to certain slight color variants that can be found in many nest series along with the "typical" form. *M. auriventris* ranges widely in the open forest country along the tropical coast of Queensland from the Maryborough region northward. The range is greatly extended by the following new records from Central Cape York: Lankelly Creek in the McIlwraith Range and the Rocky Scrub, near Coen (P. J. Darlington). I observed this species on the main Kuranda road east of Mareeba, northern Queensland, while I was in the company of Dr. J. G. Brooks of Cairns. At this locality, *M. auriventris* can be found foraging on eucalypt saplings in broad daylight. The coloration and bright golden gastric pubescence are of the warning type, in good correspondence with the diurnal foraging habits.

MYRMECIA ROWLANDI Forel

Myrmecia tarsata subsp. *rowlandi* Forel, 1910, Rev. Suisse Zool. **18**: 4, worker.

Myrmecia tarsata r. *malandensis* Forel, 1915, Ark. f. Zool. **9** (16): 9, worker, male. NEW SYNONYMY.

Myrmecia rowlandi Clark, 1952, Formic. Australia, Melbourne, **1**: 78–79, fig. 56, worker; see also *M. tarsata malandensis*, p. 32.

The characters cited by Forel for the separation of *M. rowlandi* and *M. tarsata malandensis* are either inconsequential, such as the depth of coloration and pubescence of the gastric apex, or are the distinctions to be expected between normally allometric *Myrmecia* workers of different sizes. It is perhaps significant that Clark assigned all material from the Cairns-Atherton Tableland area to *M. rowlandi*, and did not mention having seen specimens referable to *malandensis*. Specimens in the Museum of Comparative Zoology determined as *malandensis* by Wheeler either fit the characterization of *rowlandi* or are close to and intergradient with these.

I agree with Clark in separating this form from *M. tarsata* Fred. Smith. A live worker was seen at Kuranda in northern Queensland in deep rainforest, being borne along in an enfeebled condition by several workers of *Oecophylla virescens* Fabricius, the common green tree ant of coastal tropical Australia. The *Oecophylla* has apparently increased in the Kuranda area in recent years, according to local inhabitants, and this increase may well account for the present rarity of *Myrmecia* species in rain- and gallery-forest patches near the village.

MYRMECIA MJÖBERGI Forel

This very distinct, slender, long-headed species apparently also suffers from the invasion of *Oecophylla*, since it is found in its usual rainforest haunts only when these are free of the tree-ants. I found *M. mjöbergi* 12 to 20 miles north of Kuranda, along the Black Mountain timber track on the west side of the MacAlister Range in exceptionally fine rainforest. It nests high in the tops of trees in the "peat" gathered by epiphyte masses, including various ferns, orchids and the like; it is not restricted to any one plant group for this purpose. The colonies appear to be populous, and are greatly respected by the timber-cutters, who find them in most suitable epiphytic masses in the trees they cut down. As one might predict from the dull reddish-brown coloration of head and alitrunk, this species is a nocturnal-crepuscular forager (at least as observed at intact nests in recently-felled trees), but it will defend its nest quite aggressively if the mass is strongly disturbed in bright sunlight, occasionally taking short jumps toward the source of disturbance. For this reason, many of the bushmen know the ants as "jumpers", though the habit is certainly not very conspicuous or striking in this species. New northern records are from central Cape York: Lankelly Creek and the Rocky Scrub, Coen District (P. J. Darlington).

MYRMECIA SIMILLIMA Fred. Smith

Myrmecia simillima Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 144, *nec* Clark, 1952, p. 89. Crawley, 1926, p. 376, fig. 3.

Myrmecia crudelis Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 147. Crawley, 1926, p. 374, fig. 1. Clark, 1952, pp. 35–36, fig. 13, worker. NEW SYNONYMY.

Myrmecia tricolor Mayr, 1862, Verh. zool.-bot. Ges. Wien **12**: 724, worker. NEW SYNONYMY.

Myrmecia nigriventris Mayr, 1862, *Ibid.*, pp. 724, 727, worker. NEW SYNONYMY.

Myrmecia spadicea Mayr, 1862, *Idem*, pp. 724, 728, worker (*recte* ergatoid female).

Myrmecia paucidens Forel, 1910, Rev. Suisse Zool. **18**: 5, worker. NEW SYNONYMY.

Myrmecia tricolor var. *rogeri* Emery, 1914, Boll. Lab. Zool. Portici **8**: 181, worker. NEW SYNONYMY.

This species has mandibles with dentition similar to that of *M. forceps*, with four or five larger teeth and more or less reduced or vestigial teeth between these, but the external borders are approximately straight for most of their length. Looked at closely, this straightness of the external borders varies from very slightly convex to very slightly concave within uninidal series, and a further gross illusion of convexity or concavity is produced by various positions (degrees of closure) in which the dried specimens have the mandibles fixed. Forel's *paucidens*, types of which I have not seen, follows specimens of the red or "*nigriventris*" phase if one considers that Forel probably made his description with the use of a simple hand lens, as he frequently did with large specimens.

The numerous synonyms may be blamed partly on the wide range of color variation shown by the species, and to a lesser extent on the variation in the direction of the pronotal striation. Three color variants may be recognized on a strictly arbitrary basis; the present abundant material available (series from at least 32 nests from 29 localities, mostly numerous in individuals, and including the types of *M. crudelis* and *M. simillima* in the British Museum) shows that these phases are completely intergradient both inter- and intranidally. The intergradation has been recognized, in a rare discussion of color variation, by Clark (1952, p. 45), and also by Wheeler (1933, p. 44). The phases are, roughly: "black," with head, alitrunk and nodes black or brownish-black (*M. rogeri*, types of *M. simillima* and *M. crudelis*);

"tricolored," as in the black phase, but with propodeal apex and both nodes more or less reddish (*M. tricolor*); "red," with head, alitrunk and nodes varying shades of deep red, the nodes and propodeal apex often lighter than the remainder, and gaster blackish (*M. nigriventris, M. paucidens*). The full range of variation seems only rarely to occur within one nest series, or possibly never, if some of my series really represent collections from two or more nests at the same locality, but it is certain that intranidal variation is great and that the internidal overlaps are broad and without discontinuities throughout the range of differences, considering all safely uninidal series.

In general, the darker phases tend to occur in mountainous areas, and the redder phases in lowland areas with slightly drier, more open forest, but the intergradation in the Blue Mountains of New South Wales and other areas is so broad that apportionment of geographical races seems impossible, at least without further evaluation of the situation through close field work. I personally feel that the variation, like that of *Camponotus consobrinus* (Erichson) and other ants with a similar range and color variation featuring progressive melanization, may be due to ecological (non-genetic) influences, such as temperature, humidity and insolation, rather than to genetotypic differences of such magnitude and geographical consistency as to be worth racial recognition.

Material examined, exclusive of the types of *M. simillima* and *M. crudelis* in the British Museum, is now largely in the Museum of Comparative Zoology With the localities for these series, I have indicated the phases to which individuals from each of the localities may be arbitrarily assigned according to a choice based on the discussion above. A worker specimen now deposited in the Museum of Comparative Zoology: Mt. William, Grampians Range, Victoria, 8–12–51 (F. E. Wilson), has been closely compared with the *crudelis* type ("type" in B.M. chosen as lectotype) and is so similar as to be safely considered a reliable digm. The *simillima* type is also closely similar to this specimen, but has the external mandibular borders extremely slightly concave. The specimen indicated as the "type" in the British Museum under *M. simillima* should be considered as lectotype of that species.

Other material studied from: New South Wales: Uralla; Gosford; Parramatta; Salisbury Court (black); Hornsby (black, tricolor); Wentworth Falls; Mt. Wilson; Sutherland; Leura; Katoomba (tricolor, red) (W. M. Wheeler). Pymble (black) (J. McAreavey).

Megalong Valley (black, tricolor, red) (P. J. Darlington). Blue Mountains (tricolor) (H. J. Carter). Jenolan Caves (tricolor, red) (J. C. Wiburd). Leura; Katoomba (tricolor, red); Otford; La Perouse; Heathcote; Manly (red) (W. M. Mann). The Creel, Mt. Kosciusko, 3000 feet (red) (W. M. Wheeler).

VICTORIA: Arthur's Seat near McCrae, 900 feet; Dandenong Creek at Vermont; Burwood (red) (W. L. Brown). Eltham (red) (F. E. Wilson). Dee Creek, Warburton Range (red) (W. M. Wheeler). The specimens from western Victoria and southern South Australia include all color phases, black being predominant in the Grampians Range, at least in the higher parts, according to series examined in several Australian collections and in the British Museum, and to the records given by Emery and Clark (see Clark, 1952, pp. 36, 45).

My observations on this species, made on the red phase in the vicinity of Melbourne, indicate that it is predominantly a crepuscular-nocturnal forager but that it may forage in the early morning or late afternoon during cool weather. The close resemblance of the red phase to *M. forficata* may indicate that mimicry is operating; *M. simillima* is the less common where the two occur together. The nest is made in the earth, with or without a small mound. Near Melbourne, the nests are not very populous; I once found a half-dozen ergatoid females and two large workers with a small amount of brood in a two-chambered cavity reached by a hole beneath a rusted bit of tin lying on the ground (September, 1952, at Burwood, Victoria). The ergatoid females from this group foraged freely for several days before I finally traced one of them back to the entrance. I cannot satisfactorily explain this aggregation; it may have represented part of a disrupted nest remaining from the previous year. In various parts of New South Wales where *M. tarsata* is abundant, the black phase of *simillima* closely resembles it. *M. tarsata* is distinct, however, in possessing a bluish metallescence over the jet-black body and in having the gastric apex yellowish. The species described by Clark as *M. simillima* is actually *M. pyriformis*, following an old confusion of the two that could have been avoided through attention to Crawley's paper (*op. cit.*).

MYRMECIA VARIANS Mayr

Myrmecia varians Mayr, 1876, Jour. Mus. Godeffroy **12**: 94, worker.
Promyrmecia wilsoni Clark, 1943, Mem. Nat. Mus., Melbourne, **13**: 127, pl. 15, fig. 69, worker. NEW SYNONYMY.

Promyrmecia shepherdi Clark, 1943, *Ibid.*, p. 128, pl. 15, figs. 50–52, all castes. NEW SYNONYMY.

Promyrmecia goudiei Clark, 1943, *Idem*, p. 129, pl. 15, figs. 48–49, worker, female. NEW SYNONYMY.

Promyrmecia marmorata Clark, 1952, Formic. Australia **1**: 188, fig. 157, worker. NEW SYNONYMY.

M. varians and the four junior synonyms listed above constitute what Clark (1952, pp. 120–122, 181–189) called the "varians group" of *Promyrmecia*, characterized chiefly on the basis of the long, slender worker mandibles with externally concave borders and the larger teeth more or less recurved, or "hook-shaped," as Clark put it. Several other *Myrmecia* species outside this "group" have dentition which could be described as "hook-shaped," a fact that does not seem to have been properly taken into account in the 1952 or earlier works. More or less hook-shaped teeth occur widely in the group about *M. pilosula* ("pilosula group" of Clark), though not indicated in Clark's figures. A cotype of *M. elegans* (Clark) in the Museum of Comparative Zoology has mandibular teeth no less strongly recurved than those of *M. varians*.

When Mayr named this species, he did so most appropriately and wisely, and it is unfortunate that Clark has not seen fit to consider the extreme variation in the same sound and conservative way. In the series before me, including at least 11 nest-samples from three states, I find variation encompassing all of that mentioned in Clark's key and following descriptions. The key characters cut broadly in all directions across single nest series from my own collection. For instance, in single nests from Wilpena Pound, where this species is very common, I took specimens with solid black, solid red, and mottled red-and-black postpetiolar surfaces. Mandibles in my present series range from yellow to dark brown in color, and the alitrunks from entirely red to black with a hint of red on the propodeum. The carina between the frontal carinae may be distinct, or it may be so indistinct as to be virtually non-existent; the pubescence of the first gastric segment is likely to be rubbed off in old specimens or mishandled ones, a fact that could easily account for the condition described by Clark for *M. marmorata*. Comparison of types of *varians* and *shepherdi* before me reveals no significant difference in propodeal sculpture as described by Clark. I can only conclude from these series that the synonymous forms listed are slight individual variants of one species, *M. varians*, ranging widely through the dry savannah country of Queensland far south into the desert country of South Australia and the more arid portions of New South Wales and Victoria. In the true desert country of South Australia, such as at Leigh Creek, the nests appear to be pretty well confined to creek beds supporting red gum or coolabah trees.

The nests are entered by one or two small holes without mound or crater, and are usually situated near trees or shrubs upon which the ants do much of their foraging. Outside the entrance gorge at Wilpena Pound, in mixed red gum-*Callitris* woodland, *M. varians* is the dominant day-foraging *Myrmecia*. A similar-appearing form, "*scabra*" of the *M. harderi* complex, also occurs at the same locality, and there is no sign of intergradation between the two.

Localities for *M. varians* material studied in the Museum of Comparative Zoology: SOUTH AUSTRALIA: Lake Callabonna (A. Zeitz). Nuriootpa, one male (J. O. Tepper). Barren Falls, at the eastern edge of the Lofty Ranges near Mannum, in arid inlier; Leigh Creek, in shade of red gums in dry creek bed, foraging in thin leaf litter; Wilpena Pound (W. L. Brown). NEW SOUTH WALES: Broken Hill, type of *Promyrmecia shepherdi* Clark (F. W. Shepherd). QUEENSLAND: without further locality, type of *M. varians* from Coll. Mus. Godeffroy. Brisbane (H. Hacker).

MYRMECIA HARDERI Forel

Myrmecia harderi Forel, 1910, Rev. Suisse Zool. **18**: 8, worker.
Promyrmecia harderi Clark, 1952, Formic. Australia, Melbourne, **1**: 215–217, figs. 181, 182, worker, female.
? *Promyrmecia scabra* Clark, 1943, Mem. Nat. Mus., Melbourne, **13**: 118, pl. 14, figs. 40, 41, worker, female. NEW SYNONYMY WITH DOUBT.
? *Promyrmecia maloni* Clark, 1943, *Ibid.*, p. 121, pl. 14, fig. 43, worker. NEW SYNONYMY WITH DOUBT.

M. harderi and its close relatives listed above have longitudinally rugose postpetioles. Clark describes *M. harderi* itself as having a "yellowish red" alitrunk and the center of the petiole of the same color. A specimen before me from the type series, *ex* Gunnedah, New South Wales, has the center of the postpetiole black, with a lateral red patch on each side, and the center of the mesonotum bears a small but distinct blackish spot. Otherwise, I have a number of specimens taken from three nest series at Wilpena Pound, Flinders Ranges, South Australia, by myself, and these vary considerably in color. Some specimens have only the mesonotum blackened, while in others a broad black strip extends forward the length of the pronotum. The mandibles and antennae also vary somewhat in the depth of light brownish infuscation over their yellowish base color. Considering the total variation in color and, to a much lesser degree, in postpetiolar sculpture in the present material, I believe that the chief differences recognized by Clark between his species *scabra* and *maloni*, and between these two and *harderi*, can no longer be considered significant. No other differences cited by Clark appear to be particularly important, and in the absence of types of his species, I must consider the synonymy of all of these species highly probable. Types of Clark's species are in the National Museum at Melbourne, and Mr. E. F. Riek, who has kindly examined them at my request, states *in litt.* that he can find no differences between them save those discussed above, except possibly a very minor divergence in mandibular dentition. The variation in this species is so marked that it is not beyond possibility that *M. celaena* (Clark) is only an extreme melanic variant synonymous with *M. harderi;* the two have been found once at the same station, according to Clark: Narrabri, New South Wales.

At Wilpena Pound, the *scabra-maloni* color form of *M. harderi* nested in the dry leaf litter beneath the "native pines" (*Callitris*) in fine, reddish sandy loam, at this point covered with open *Callitris-Eucalyptus camaldulensis* woodland. The entrance to the nest was a slender, tapered turret fashioned from fine vegetable detritus and projecting upwards through the thin leaf litter to a height of about 2 centimeters, with the circular opening at the apex. No auxiliary entrance was seen in either of two nests dug up. *M. varians* was also common at this locality, but tended to nest more in the open; both species run very rapidly and jump when disturbed.

MYRMECIA FROGGATTI Forel

Myrmecia froggatti Forel, 1910, Rev. Suisse Zool. **18**: 9, worker.

Promyrmecia froggatti Clark, 1952, Formic. Australia, Melbourne, **1**: 128–129, figs. 96, 97, worker, female; see for further synonymy.

Myrmecia (*Promyrmecia*) *aberrans* subsp. *taylori* Wheeler, 1933, Colony-founding among Ants, Harvard, p. 53, worker. NEW SYNONYMY.

Myrmecia (*Promyrmecia*) *aberrans* subsp. *sericata* Wheeler, 1933, *Ibid.*, p. 53, worker. NEW SYNONYMY.

In the Museum of Comparative Zoology are a specimen from the type series of *M. froggatti*, *ex* Manilla, New South Wales (W. W. Froggatt) and the unique types of subsp. *taylori*, *ex* Roma District, Queensland (F. H. Taylor) and subsp. *sericata*, *ex* Wagga Wagga, New South Wales (W. W. Froggatt). The *M. froggatti* specimen has been badly rubbed, thereby lacking most of the gastric pubescence and appearing somewhat more shining than the two sub-species. Otherwise, the differences are rather trivial — scarcely more than what one would expect in the way of variation among members of single nest series in this complex. While even this slight variation might, allopatry considered, be indicative of valid geographical races, I feel that in this case the burden of proof must be shifted to anyone who wants to consider them as such. Certainly, the differences do not look half so impressive when the actual specimens are compared as they do in Wheeler's descriptions. Clark's species *Promyrmecia cupoecila*, *P. greavesi* and *P. excavata* appear to me, from Clark's characterizations, to be scarcely distinguishable from *M. froggatti*. Quite possibly they are synonyms.

MYRMECIA MAURA MAURA Wheeler New status

Myrmecia (*Promyrmecia*) *aberrans* subsp. *maura* Wheeler, 1933, Colony-founding among Ants, Harvard, p. 51.

Promyrmecia maura Clark, 1952, Formic. Australia, Melbourne, **1**: 132–134, figs. 100, 101, worker, female; see for further synonymy.

M. maura has always been considered rather distinct because it is the only known all-black member of its group. Close inspection of the type series in the Museum of Comparative Zoology, however, reveals that some of these specimens show a feeble hint of reddish discoloration on the sides of the head and on the pronotum. Since the types are from Bathurst, New South Wales, and since other *m. maura* records are cited by Clark from Western Slope and Southern Tableland localities in New South Wales, but not from the Northern Tablelands, it appears at present as though *m. maura* and the forms with much bright red on head and alitrunk may be allopatrically and subspecifically separated. The graded series of reddened forms described by Wheeler under the names *formosa* and *haematosticta* come from Uralla on the Northern Tableland. Possibly the main range of the red-and-black form extends into Queensland, with Uralla at one edge of the intergrade zone. If further collection bears this out, the name of the red-and-black form should be *M. maura formosa*, and the name *haematosticta* will sink as applying to the intergrades. On the other hand, it is entirely possible that the red-and-black forms are merely non-geographical variants appearing at intervals through the *maura* range, in which case the names *formosa* and *haematosticta* will both sink as synonyms. I prefer for the moment to consider the situation as a probable case of polytypy in the species *maura*.

Clark's specific separation, based on types of the three forms sent him in 1947, fails to take into account the great variation in color of the Uralla series. Since this variation bridges the *maura-formosa* differences almost perfectly, I cannot accept Clark's artificial three-way split. The synonymy of *M. maura formosa* follows.

MYRMECIA MAURA FORMOSA Wheeler New status

Myrmecia (*Promyrmecia*) *aberrans* subsp. *formosa* Wheeler, 1933, Colony-founding among Ants, Harvard, p. 52, fig. 19, worker.

Myrmecia (*Promyrmecia*) *aberrans* subsp. *haematosticta* Wheeler, 1933, *Ibid.*, p. 51, worker. Intergrade, *maura maura* × *maura formosa*, NEW SYNONYMY.

Promyrmecia haematosticta Clark, 1952, Formic. Australia, Melbourne, **1**: 130, fig. 98, worker.

Promyrmecia formosa Clark, 1952, *Ibid.*, p. 131, fig. 99, worker.

Wheeler's series from Uralla in the Museum of Comparative Zoology consist of a half-dozen *formosa* cotypes and (at present) a single cotype of *haematosticta;* all of these specimens are dated November 26. The *formosa* series includes variations leading up to *haematosticta*, which latter is only slightly more extreme than the darkest *formosa* worker.

MYRMECIA NOBILIS (Clark) New combination

Promyrmecia nobilis Clark, 1943, Mem. Nat. Mus., Melbourne, **13**: 97, pl. 12, figs. 2–4, all castes; see Clark, 1952, p. 124 for further synonymy.

While the present material seems to indicate that *M. froggatti*, *M. maura* and *M. nobilis* represent very closely related, but probably distinct species, I am by no means so sure of the distinctness of *M. nobilis* from *M. aberrans*. Without type material of *aberrans*, it is perhaps wise to accept tentatively Clark's judgement on these forms. I took *M. nobilis* at Lara, Victoria, on the savannah west of Melbourne, in a nest surmounted by a slender earthen spout about one cm. high.

MYRMECIA PILIVENTRIS Fred. Smith

Myrmecia piliventris Fred. Smith, 1858, Cat. Hym. Brit. Mus. **6**: 146, worker. Crawley, 1926, p. 385, fig. 11, worker.

Promyrmecia piliventris Clark, 1952, Formic. Australia, Melbourne, **1**: 156–158, all castes; see for further synonymy, figures.

Myrmecia piliventris var. *rectidens* Forel, 1910, Rev. Suisse Zool. **18**: 5, worker. NEW SYNONYMY.

Promyrmecia rectidens Clark, 1952, Formic. Australia, Melbourne, **1**: 159–161, figs. 126–128, worker, subapterous and ergatoid females; see for further synonymy.

M. piliventris shows great differences in size between different nest series, so that two nests located within 25 meters of one another may appear like two totally different species. Large series, however, if representing numerous nests, show all intermediate size stages. Sometimes one notices slight differences, apparently following allometric patterns, between size extremes, and it appears that Forel named the var. *reetidens* on the basis of smaller specimens. In attempting to strengthen the distinction between the two "species," Clark has on different occasions utilized different characters, such as presence or absence of postpetiolar pilosity and supposed constant mandibular differences. From the series present in the Museum of Comparative Zoology, I am satisfied that such distinctions will not hold with sufficient constancy, particularly when the probable internidal allometry is fully considered. Clark found the smaller variety to produce subapterous or ergatoid females, a phenomenon possibly correlated with the stature of the workers and one that might indicate a strong effect of environmental influences on body size and form in this species. A similar effect is also seen in the related *M. fulvipes* and to a lesser degree in other *Myrmecia* species.

This species is much more common in South Australia than published records indicate, and is especially abundant in the Flinders Chase area of western Kangaroo Island, where it nests under stones and logs or grass-tree stumps in the luxuriant sugar gum ravines as well as in the much drier *Casuarina* and mallee scrubs and occasionally on the heathland. Individuals from colonies taken on the heath are noticeably smaller than are those from the Ravine des Casoars. A colony taken along Weetangeera Road in the Black Mountain Forest near Canberra (*Eucalyptus macrorrhyncha-E. melliodora* woodland) contained the largest workers seen (T. Greaves and W. L. Brown).

MYRMECIA FULVIPES Roger

Myrmecia fulvipes Roger, 1861, Berl. ent. Zeitschr. **5**: 36, worker.
Promyrmecia fulvipes Clark, 1952, Formic. Australia, Melbourne, **1**: 165–167, figs. 133–135, all castes; see for further synonymy.
Myrmecia (*Pristomyrmecia*) *piliventris* var. *femorata* Santschi, 1928, Bull. Soc. Vaud. Sci. Nat. **56**: 466, worker. NEW SYNONYMY.
Myrmecia (*Promyrmecia*) *fulvipes* subsp. *barbata* Wheeler, 1933, Colony-founding among Ants, Harvard, p. 71. NEW SYNONYMY.
(Cf. Clark assignments and additional synonymy for these forms in his 1952 revision, pp. 158–159, 162–167.)

This species may be recognized by means of its greenish-golden gastric pubescence and the contrasting color of the legs against the black of the body; the femora and usually most of the rest of the legs are yellowish-red, with varying areas of infuscation. Clark's reasons for assigning var. *femorata* and subsp. *barbata* to *piliventris* instead of to *fulvipes* are enigmatic, especially since Wheeler had correctly stated their close relationship to *fulvipes* in 1933. I can think of no reason for Clark's action other than that he merely followed Santschi's original thoughtless assignment of *femorata* to *piliventris*. Obviously, Santschi never took *fulvipes* into account in describing his variety, or he would have realized that the latter was *fulvipes* to begin with. *M. piliventris* is, in my view, a completely distinct species, as proved by the absence of intergrades to *M. fulvipes* despite the slightly variable extent of infuscation of the tibiae in the latter. *M. fulvipes* is an eastern coastal species with a range extending into the higher mountain forests of the southeastern regions and Tasmania, west at least into the Grampians Ranges of western Victoria; it prefers a relatively moist, cool climate. *M. piliventris* prefers to nest in dry, open woodlands or even on open heath, and hence it is more common in the western and Tablelands regions of New South Wales and in northern and western Victoria and southern South Australia. The record of *M. fulvipes* cited by Clark from Murray Bridge, South Australia, is rather unusual and should be checked, although *M. fulvipes* may occur in the moister Lofty Ranges of South Australia.

Wheeler's subsp. *barbata*, the types of which have recently been found among the Wheeler miscellany, is a large, slightly more hairy form occurring with and intergrading to the average-sized form in the wet mountain forests of New South Wales; the present evidence does not indicate that nomenclatorial distinction for this local variant should be maintained. *Myrmecia fulviculis* Forel is a *fulvipes*-like form occurring along the North Coast of New South Wales from about Sydney northward, and around Brisbane in extreme southeastern Queensland. It differs from the typical *fulvipes* in the color of the gaster, which is brown shading into yellowish toward the apex; while certain entire nest series seem to show this color pattern more or less distinctly, the typical *fulvipes* pattern is also reported from just about exactly the same range of localities by Clark (1952, as *M. piliventris femorata*, p. 159), although without information concerning presence or absence of intergrades. Later investigation will establish whether *fulviculis* is a genetically independent species, a northern race of *fulvipes*, or an environmentally-induced variant, synonymous with *fulvipes*.

MYRMECIA BREVINODA Forel

Myrmecia forficata var. *brevinoda* Forel, 1910, Rev. Suisse Zool. **18**: 2, worker, female, *nec* Clark, 1952, pp. 96–97.

Myrmecia pyriformis race *gigas* Forel, 1913, Rev. Zool. Afr. **2**: 310, female. NEW SYNONYMY.

Myrmecia gigas Clark, 1952, pp. 104–109, fig. 83, all castes, including various sizes of workers and ergatoid female; see for further synonymy.

The Museum of Comparative Zoology possesses a cotype minor worker of var. *brevinoda* sent by Forel to Wheeler. Close comparison shows that this worker agrees very well with minors of the species assigned by Clark to *M. gigas*. The *brevinoda* type locality, Walcha, New South Wales (W. W. Froggatt), also agrees well with the range of *gigas*, and the latter name must therefore fall. The species Clark described and figured as *M. brevinoda* appears to me to be a slight and common variant of *M. forficata*.

MYRMECIA FERRUGINEA Mayr New status

M. nigriceps var. *ferruginea* Mayr, 1876, Journ. Mus. Godeffroy **12**: 95 (p. 40 of reprint), worker.

Myrmecia (*Myrmecia*) *vindex*, Emery (*partim*), 1911, Gen. Ins. **118**: 19, *nec* Fred. Smith.

Mayr described this species very briefly in passing, believing it to be a mere color variant of *nigriceps*, so we do not have a very clear idea of its true identity. Mayr mentions variation in color that could apply to two or more species, so I hereby restrict the name *ferruginea* to that part of his type material having a light-colored "forebody." It is quite possible that this form is the senior synonym of *brevinoda* and *gigas*, coming as it does from localities in central Queensland. It might also be the same as *M. dimidiata* Clark, since the first gastric segment is said by Mayr to be reddish in tone. Variation in *M. brevinoda* includes forms with persistent or deciduous anterior gastric pubescence and a range of forms of petiolar node; *M. ferruginea* will have to be considered as a name available for one species in this group. Besides *M. dimidiata*, Clark's inadequately distinguished species *M. decipians* and *M. hirsuta* may also be involved in this complex. The solution depends on a fuller characterization of the *M. ferruginea* types and a study of the variation in *M. brevinoda* and related forms. Curiously, Clark does not appear to have mentioned *M. ferruginea* in his revision, and it is not in the index.

MYRMECIA FLAMMICOLLIS New species

Diagnosis. A medium-sized, slender *Myrmecia* of the *apicalis* group, most closely resembling *M. petiolata* Emery, from which species it differs most conspicuously in color, the body being black, with the prothorax largely or entirely orange-red.

Holotype worker. Comparison is largely made with *M. nigrocincta* Fred. Smith, a closely related and common eastern Australian species.

General body color black; entire prothorax clear light orange-red. Mandibles, antennal scapes and legs deep reddish-brown; funiculi, extreme bases and apices of scapes, inner margins of mandibles, palpi and anterior tarsi shading into sordid yellow. Mandibular teeth infuscated.

Dimensions (in millimeters). Total length fully outstretched, not including mandibles, 13.0 ± 0.1; length of head, including clypeus, 2.37; width of head without eyes 2.34, with eyes 2.66; straightline exposed length of left mandible while in closed position 2.41; full length of scape 2.85; full exposed length of alitrunk in lateral view 4.64; of petiole 1.46, of postpetiole 1.17, and of gaster 3.4.

Sculpture as in *M. nigrocincta*, but slightly stronger and more opaque, especially on the cephalic dorsum. Pronotal sculpture as in *nigrocincta*, very finely reticulo-striate in front, with superimposed costulation or rugulation following the striation, largely transversely arched. Mesonotum similar, except that here the superimposed transverse costulation becomes much feebler posteriorly on the disc.

Petiole, postpetiole and gaster moderately shining, very finely and rather densely punctulate, the petiole more strongly shining than in *nigrocincta*.

Pilosity as in *nigrocincta*, except that the scapes bear sparsely distributed, very fine and short oblique erect hairs throughout, and not just at the apices. Pubescence appressed, whitish except on the center of the basal gastric tergite, where it has a feeble yellowish tinge; rather abundant and generally distributed over the body and appendages; most dense on gaster (but not hiding sculpture on basal tergite) and on clypeus.

Mandibles resembling those of *nigrocincta*, but a little broader just distad of their bases, their inner margins more definitely angulate in this region. Petiolar node distinctly longer than broad seen from above; anterior peduncle slightly shorter than node; a very short posterior narrowing or semi-peduncle behind node. Seen from the side, node evenly rounded above. Postpetiole very slightly longer than broad, the anterior sides approximately straight as seen from above, much as in Clark's figure of *petiolata* (1952, fig. 86). Legs and antennae with about the same inter-segmental proportions relatively as in *nigrocincta*, but all parts correspondingly a little longer and more slender, in keeping with the slightly larger and relatively more slender general body build.

Holotype worker taken in the region called locally "The Rocky Scrub," around the headwaters of the Rocky River, in the McIlwraith Range, northeast of Coen, Cape York Peninsula, Queensland (P. J. Darlington). Deposited in the Museum of Comparative Zoology.

Paratypes (Queensland Museum, Museum of Comparative Zoology). Three workers taken with the holotype and an additional three workers collected at Lankelly Creek, in the McIlwraith Range, a few miles east of Coen (P. J. Darlington). Dr. Darlington informs me that at both localities he collected most extensively in rainforest patches, although some collecting was also done in the surrounding open monsoon forest, which is very much drier. From its affinities, one would suspect that *M. flammicollis* is a rainforest species, but this is far from certain.

Variation in size in this small sample is very slight, less evident than in single nest-series of *M. nigrocincta*. The extreme lower portions of the prothorax are sometimes lightly infuscated, and mandibular dentition varies slightly in minor details. Specimens with gastric pilosity missing anteriorly are obviously rubbed. Chief variation is in sculptural detail, especially on the pronotum. One specimen has the costulation running in an asymmetrical oblique pattern across the posterior ¾ of the pronotum; in others, the transverse costulation of the mesonotum is denser and more distinct.

This species is apparently most closely related to *M. petiolata*, a blackish-brown species with yellow mandibles, funiculi and tarsi found in the Cairns-Bellenden Ker region of North Queensland, but differs from *petiolata* in being even more slender and in having the pronotum colored in bright contrast to the remainder of the body. The differences from *M. nigrocincta* have already been covered; the latter species has both the pronotum and the propodeum ferruginous yellow, and the postpetiole is decidedly broader and more rounded seen from above. In Clark's key to the "nigrocincta group," given in his 1952 work (p. 110), *M. flammicollis* disagrees with both alternatives in the first couplet on account of its color. Like *M. nigrocincta*, the new species may be able to make short leaps when threatened; the color pattern marks it as a diurnal forager like the common species.

Since the presence far up on Cape York Peninsula of at least three species of *Myrmecia* (*auriventris*, *mjöbergi* and *flammicollis*) has now been demonstrated, and since the occurrence of *M. apicalis* Emery on New Caledonia is well established (despite Clark's puzzling statement of 1952, p. 112, concerning Emery's earlier footnote) it seems not at all unlikely that one or more species of *Myrmecia* may yet be found in southern New Guinea. There are, however, no safe records of *Myrmecia* coming from the Darwin area, despite search by several interested entomologists, and my questioning of aboriginals in this region with alcoholic specimens at hand drew no signs of recognition of *Myrmecia*.

MYRMECIA DESERTORUM Wheeler

Myrmecia vindex var. *desertorum* Wheeler, 1915, Trans. R. Soc. S. Australia **39**: 805, worker.

Myrmecia lutea Crawley, 1922, Ann. Mag. Nat. Hist. (9) **9**: 429, worker. NEW SYNONYMY.

Myrmecia princeps Clark, 1952, Formic. Australia, Melbourne, **1**: 46–47, fig. 24, worker. NEW SYNONYMY.

Myrmecia fuscipes Clark, 1952, *Ibid.*, pp. 62–63, fig. 39, worker. NEW SYNONYMY.

This species has a blackish head and gaster; the alitrunk, nodes, clypeus, mandibles, antennae and most often the legs are ferruginous yellow. Variation in size and in allometric characters is considerable, both inter- and intranidal, and it is very largely these differences which Clark utilizes in separating *M. desertorum*, *M. lutea*, and *M. princeps*. However, material in the Museum of Comparative Zoology, including types of *M. desertorum* and *M. lutea*, shows no such striking differences as Clark claims for them, and it seems evident that he has exaggerated, particularly in characterizing the petiole. He also depends on the density and extent of the gastric pubescence, which may be dense on the first segment, or lacking, or partly so, even in uninidal series. As with other *Myrmecia* species, this gastric pubescence is frequently deciduous, and is often lost in old or roughly handled specimens. The pronotal sculpture is also unreliable, since single nest series show the complete range of patterns linking and including *desertorum* and *lutea*. Clark's figures 24, 36, 38 and 39 will serve to demonstrate the similarity of the mandibles of *M. princeps* to those of the other three species, although Clark brings *princeps* out to a separate group in his key (p. 23) on the basis of mandibular differences. Even with the comparatively moderate amount of material available to me at present, I find the limits between these forms impossible to set.

M. fuscipes is a slightly darker form of *M. desertorum* marked chiefly by having more or less deeply infuscated middle and posterior legs. Such specimens have been examined from Port Lincoln, South Australia (A. M. Lea), which is the type locality, but even in this series I find that the legs are sometimes completely yellowish. In series from Pioneer Siding in the Dundas (Norseman) region of Western Australia (W. L. Brown), and in a dealate female from Koonalda Siding, South Australia, on the Nullarbor Plain (N. F. Wallman), the legs are consistently fuscous, but series from the Flinders Ranges of South Australia: Mt. Patawerta (A. R. Riddle) and Wilpena Pound (W. L. Brown) include specimens with both light and fuscous legs. The dark-legged form, which is most typically found nesting at the roots of chenopodiaceous desert shrubs (*Kochia*, *Atriplex*, etc.), may possibly be a southern race, but the yellow-legged form penetrates so far into its range that this seems unlikely. Until it has been studied more thoroughly, it seems preferable to consider the dark-legged form a sporadic, possibly environmentally-impressed variant without further distinction by name. The darkest specimens may have even the postpetiole strongly mottled with deep brown (Port Lincoln).

In addition to the localities mentioned already, I have seen *M. desertorum* specimens from SOUTH AUSTRALIA: Todmorden, type locality (S. A. White); Renmark, in mallee (J. G. Myers). WESTERN AUSTRALIA: Jigalong (J. Hickmer); Geraldton; Yandil (W. M. Wheeler); Corrigan (collector?); Kukerin (A. Douglas). NORTHERN TERRITORY: Ellery's Creek in the MacDonnell Ranges (S. A. White). In the north, the nest is usually excavated, with or without a small mound, under or near eucalypts. Foraging, at least in the warmer months, is strictly nocturnal.

MYRMECIA PULCHRA Clark

Myrmecia pulchra Clark, 1929, Vict. Naturalist **46:** 119, figs., worker, female.

Myrmecia fallax Clark, 1952, Formic. Australia, Melbourne, **1:** 79–80, fig. 57, worker. NEW SYNONYMY.

Myrmecia murina Clark, 1952, *Ibid.*, pp. 80–82, figs. 58–60, worker, female, male. NEW SYNONYMY.

? *Myrmecia crassinoda* Clark, 1934, Mem. Nat. Mus., Melbourne, **8:** 50, pl. 4, fig. 2, worker, female. NEW SYNONYMY WITH DOUBT.

M. pulchra, with *M. esuriens* Fabricius and perhaps one or two other species, is intermediate between the larger and smaller branches of *Myrmecia*, and combines characters of both. In the Museum of Comparative Zoology are cotypes of *M. pulchra*, and also manuscript cotypes of *M. murina* and *M. fallax*, with Clark's type labels, the last two bearing different names than those now applied; these were sent years ago to Wheeler. These agree well, allowing for the usual discrepancies and contradictions, with Clark's descriptions. Other scanty series accumulated from various sources show all degrees of intergradation linking these three forms, with intranidal variation in some cases completely bridging the *pulchra-fallax* gap. The available type of *fallax* bears a small, diffuse brownish spot mesally along the posterior border of the pronotum, but this grades through to "typical" *murina* specimens with the pronotum entirely black. Except for the color differences, which are striking enough in the extreme forms, I can see nothing of any value that can be used to separate any forms from this continuously intergradient series in which the nest series overlap broadly. The black forms (*murina*) come mostly from eastern Victoria and the Alps, while the forms with some red on the alitrunk and nodes are more characteristic of western Victoria and the Lofty Ranges of South Australia. However, the possibility that distinct eastern and western races exist is made very unlikely by the occurrence of the extreme red form (*pulchra*) at its type locality, Cann River, which is on the southern fringe of the Alps in the south-eastern corner of Victoria. Since intergradation must have been present in the fairly extensive collections available to Clark, his failure to discuss color variation lends a spurious distinctness to the forms he has separated as species. This failure is evident in species after species throughout the 1952 work, which leads me to believe that many of the types of forms I have not been able to see are mere intergrade-linked color variants. Future Australian workers having access to the types will be able to correct this situation in the presence of adequate series showing the trends of variation. Clark's *M. crassinoda* seems, from the original description, to be merely one intermediate stage of variation in the *pulchra-murina* intergrade set, but this will have to be checked by type examination.

Material studied in addition to types, with alitrunk and nodes very nearly entirely or entirely black (*murina*): Blundell's Creek, 2600 feet, A. C. T.; Mt. Kosciusko, 4–5000 feet, New South Wales (P. J. Darlington); Mt. Buffalo, 4500 feet, Victoria (F. E. Wilson). Alitrunk with at least the posterior pronotum and entire mesonotum largely reddish, postpetiole red, black or mottled (*fallax* through *pulchra*): Grampians Ranges, Oct. 1928; Mt. William, Grampians Ranges, Victoria, Dec. 1951 (F. E. Wilson); Mt. Lofty (W. M. Wheeler), and Aldgate, South Australia (W. L. Brown). The workers have been found foraging in warm weather at midday.

MYRMECIA CARDIGASTER New name

pro Myrmecia cordata Clark, 1952, Formic. Australia, Melbourne, **1**: 116, fig. 90, worker.

nec Myrmecia cordata Fabricius, 1805, Systema Piezatorum, p. 425, worker. (Dacetini).

MYRMECIA FORFICATA (Fabricius)

Formica forficata Fabricius, 1787, Mant. Ins. **1**: 310, worker.

Myrmecia forficata Clark, 1952, Formic. Australia, Melbourne, **1**: 93, figs. 72–74, worker, female, male, part, synonymy given.

Myrmecia brevinoda Clark, 1952, *Ibid.*, p. 96, figs. 75, 76, worker, female; *nec* Forel (see farther above under *Myrmecia brevinoda* Forel).

Myrmecia forficata var. *rubra* Forel, 1910, Rev. Suisse Zool. **18**: 3, worker. NEW SYNONYMY.

Myrmecia rubra Clark, 1952, Formic. Australia, Melbourne, **1**: 98, worker; additional synonymy given.

This is the common bull-ant of the higher-rainfall areas of southeastern Australia; it is most abundant in the Australian Alps at elevations of 1000 feet or more (higher in New South Wales), but is found at sea level in medium-rainfall sclerophyll forest in the Melbourne area and over much of Tasmania. It is sporadically distributed in the Western District of Victoria, including the moister savannah of the Camperdown district (Brown), and is common in the Lofty Ranges of South Australia (Brown). *M. forficata* has been confused by all former authors with several other species, among them *M. pyriformis*, *M. simillima*, *M. brevinoda*, and perhaps others. There is still an open problem concerning its relationship to *M. regularis* Crawley and the enigmatic *M. lucida* Forel. *M. regularis* is a southwestern Australian species with ecological requirements much like those of *M. forficata;* that is, it prefers heavy forest of the wet sclerophyll type. *M. regularis* is (in southwestern Australia) a light-to-medium reddish-brown ant with dark gaster, perhaps *averaging* a little smaller than the usual series of *forficata* from the Melbourne area; the entire head, alitrunk, and especially the gaster show purplish metallic reflections that become feeble in dried cabinet material and may disappear altogether. The chief distinguishing feature of the worker is supposed to be the coloration of the gaster, in which the posterior segments are broadly banded at their apices with sordid yellowish or reddish; the apical segment is usually entirely yellow. This apical gastric pattern is also found in, and appears to be constant and specific for, some other *Myrmecia* species of different groups (*analis* Mayr, *tarsata* Fr. Smith, *tepperi* Emery, *nigriscapa* Roger) as far as investigation has gone. I am inclined to agree with former authors that it is often a constant and most useful character in the species mentioned, plus some others as well.

The difficulty with this character in the present instance, however, is that it appears in certain series from South Australia, Victoria and the Australian Alps in New South Wales which on other criteria, such as deeper color, would be placed as *forficata.* Forel's description of *lucida,* while ambiguous, may apply to such a form from Tasmania. I found this form to be the dominant night-foraging *Myrmecia* in the wooded ravines at the western end of Kangaroo Island in 1951, but did not attach any special significance to the light-tipped gaster as a character until I had begun this taxonomic study after my return to the United States. Since I assumed that the Kangaroo Island form was the ordinary *forficata*, I unfortunately failed to secure any females. I say unfortunately because the females may be the key to this problem. The females of *regularis* differ from those of *forficata* in having a much smaller thorax; Wheeler and Clark have assumed that they are "subapterous," i.e. lacking developed wings, but Haskins and Haskins (1951) found that the females may be eclosed with wings that reach to the gastric apex, but which are shed while the young queens are still virgin and callow. The colonies of *M. forficata* frequently, probably normally, produce fully winged females capable of flight (Clark, 1952, p. 19), but these same colonies may also, according to Clark, contain various kinds of queen-worker intermediates without well-developed wings. The status of females of the *forficata*-like form from the southeastern states with light gastric apex is not specifically mentioned by Clark, and must be presumed to be unknown. Clark (1952, p. 93) records *regularis* from Kangaroo Island and from Portland, southwestern Victoria, the records very probably being based on specimens of the *forficata*-like (dark) form like those I found to be so common on Kangaroo Island myself, but he does not record *regularis* from the Dandenong Ranges or elsewhere in the vicinity of Melbourne despite the fact that the form in question is not uncommon in these districts where he has long resided and collected. It therefore seems very probable that Clark has confused two forms, the typical *forficata* and the form with light gastric apex, in this area; consequently, his remarks concerning wingless females in the nests may apply to the latter. Only further collecting by someone aware of the problem beforehand will settle the status of the forms known as *forficata-lucida-regularis*.

The problem is made less easy by the fact that *M. forficata* (with concolorous blackish gaster) throws light reddish-colored variants in Victoria and elsewhere in the southeastern states; like the typical *forficata* (and *regularis*), these light variants frequently show violet, blue or green metallescence in fresh specimens, particularly on the gaster where the background color is darker. To these variants, the names *rubra*, *violacea* and *brevinoda* (*nec* Forel) have been applied, and slight differences in petiolar shape have been supposed also to distinguish them. The petiolar differences seem to have been overemphasized by Clark, and his figures of the petioles of the different forms are somewhat ambiguous and contradictory in different views.

In my own collecting in the region around Melbourne and various other localities from which Clark records these forms, I have found the light-colored variants, but I have been unable to establish any constant differences in petiolar form; the variation in petiolar shape is slight but distinct within each nest series, and appears to be at least partly an allometric feature, but each series seems to vary in just about the same way. The color difference is not so extreme when one takes into account the possibility that certain broods may not have attained full adult color in some cases; intranidal color variation is often considerable at midsummer and perhaps other periods of the year. I believe that these forms will have to be considered as straight *forficata* until proof is forthcoming that they are anything else.

As mentioned above, *forficata* (and also *regularis*) is primarily a nocturnal forager. Workers may leave the nest some time before dusk and remain out after sunrise, and occasionally one may see them out on dark, rainy or cool days, but all of my numerous observations indicate strongly that the greatest force of workers is outside the nest during the hours of total darkness when the weather is warm enough. On warm summer nights, I have found that the forests where they occur may be swarming with them, far more workers being visible under a hand electric torch than are ever seen abroad during daylight. I find that this fact is well known to people who have slept out often in the bush, but it has been little appreciated by previous writers on *Myrmecia*, who either, like Clark, maintain flatly that all *Myrmecia* are daylight foragers, or else state the facts in an ambiguous and perfunctory way.

I have noted wherever possible the foraging activities of *Myrmecia* with respect to diurnation, and I believe that I can state with confidence that many species are strictly diurnal foragers, some, like *M. desertorum*, normally completely nocturnal, and a large number either predominantly nocturnal or predominantly crepuscular. Furthermore, there seems to be a more or less definite correlation between the worker color pattern and diurnation: those species having (a) black coloration with prominent yellow mandibles, antennae and fore tarsi; (b) bold patterning of red and black; or (c) conspicuous golden or orange pubescence on the gaster, sometimes in combination with (a) or (b) patterns, are predominantly or entirely diurnal foragers, so far as I have seen. Examples in which I have been able to observe diurnal foraging at or near midday in bright, warm weather include: *auriventris*, *pilosula*, *piliventris*, *mandibularis*, *gulosa*, *nigriscapa*, *varians*, *?harderi*, *nigrocincta*, *pulchra*, *tarsata*, and others. The nocturnal-crepuscular species lack brilliant metallic pubescence (so far as I am aware) and are generally colored in dullish reds, browns or yellows; the color in *desertorum*, with its usually dark brownish head and gaster and often rather light yellow alitrunk, while appearing rather strikingly contrasted, is nevertheless not at all like any of the red-and-black arid-country day foragers, and the yellowish coloration of the alitrunk may reflect a degree of metabolic conservation affecting the pigment, for this species is certainly very markedly nocturnal as I have seen it at widely separated localities in South and Western Australia. Species figuring strongly as nocturnal foragers in my notes, in addition to the *forficata* complex, are: the "red phase" of *simillima* (perhaps more crepuscular), *brevinoda* (= *gigas*), *nigriceps*, *pyriformis*, *mjöbergi*, *rindex* or closely related species, Esperance district of Western Australia, and *analis* (crepuscular).

I believe that the bright colors of the day-foraging forms are of the warning type (as in diurnal Mutillidae); the (a) type of coloration may also function as an inter-individual recognition pattern, though this is purely speculative and has not been borne out by tests made on *pilosula* by Haskins (*in litt.*), wherein the color pattern of mandibles, antennae and fore tarsi were modified by adding pigments, etc. Such a recognition pattern might operate best in the case of foraging individuals among flowers and foliage where the prey is stalked. The warning coloration hypothesis, however, seems very likely to hold for the day-foraging species even though observations on predators that might be affected are scarcely begun.

In a recent comprehensive paper, Haskins and Haskins (1951) add a great deal of new material to the biological knowledge of several *Myrmecia* species, and their work should be consulted by anyone interested in formicid biology. Unfortunately, the "Background" section of this paper contains some misstatements of fact (often following earlier statements of Clark), particularly concerning the geographical and ecological distribution of the genus, and the authors appear to support Clark's "excellent general habit notes" in spite of the fact that Clark's notes are often strongly in error and are neither extensive nor very general, considering his excellent opportunities for making a detailed study. It has also been determined that some of the Haskins' observations suffer from taxonomic confusion of closely related species, particularly as regards the smaller-sized workers and their foraging activities. I have found that, in nature at least, the smallest workers of populous nests of several species rarely or never forage outside the nest. This fact, once appreciated, leads to a reopening of the whole question of possible trophallaxis in *Myrmecia;* the Haskins team has undertaken a new investigation of this question and has come up with results that will force a modification of their views of 1951. With publication of their results, it is hoped that a new review of myrmeciine biology, correcting previous errors and providing an accurate summary of knowledge of the tribe, will be forthcoming.

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INDEX[1]

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[1] The index includes only specific and infraspecific names here considered in he genus *Myrmecia*. Chief reference in bold face.

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TICKS (IXODOIDEA) OF THE MALAGASY FAUNAL REGION (EXCEPTING THE SEYCHELLES)

Their origins and host-relationships; with descriptions of five new *Haemaphysalis* species

By Harry Hoogstraal

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CONTENTS

I. INTRODUCTION

The bizarre endemic fauna of Madagascar and its nearby islands remains but poorly explored. It is hoped that the presentation of results of study of ticks collected on two brief trips for other phases of medical research, and of a few collections from stuffed mammal study-skins, will stimulate further study of vertebrate parasites in this unique area. Much remains to be learned about all the parasites already known to inhabit this archipelago. Not a few unknown species undoubtedly await discovery.

Specimens on which this report is chiefly based were collected by the writer in 1948, while studying blood parasites as a member of the Naval Medical Science Group-African Expedition; by Lt. V. J. Tipton of the Army Medical Service Graduate School in 1951 and 1952, while making disease control studies; and by Dr. J. Bequaert, from study-skins of mammal specimens in the Museum of Comparative Zoology at Harvard University. In addition, I have had the pleasurable opportunity of studying cotype specimens of pertinent species in the British Museum (Natural History).

As Lt. Tipton's and my own collections, and those of the Museum of Comparative Zoology, were obtained from the endemic vertebrate fauna, our tick collections are largely of species also endemic to the area. These add considerably to the meagre existing knowledge of endemic ticks of the Malagasy Faunal Region. The overall picture of this tick fauna, including the introduced species, is so inadequately treated in the literature that I have attempted to correlate with the new data a brief review of all tick species now known from the Madagascan Archipelago, exclusive of the Seychelles.

It should be stated in passing that the Seychelles are not known to harbor any of the endemic ticks herein reported, but that they have two unique species of *Amblyomma* of their own. Because we have no new data from the Seychelles, and since both this group and the other island groups of the Madagascan Archipelago must be more extensively explored before adequate conclusions of their interrelations can be made, it appears best to omit the Seychelles from the present review.

The names of avian hosts appearing in this report have been checked by Dr. A. L. Rand, Curator of Birds, Chicago Natural History Museum, and follow Sclater's "Systema Avium" (1924–1930). The scientific names of mammals are those in Allen's (1939) Checklist of African Mammals and Simpson's (1945) The Principles of Classification and the Classification of Mammals. Lt. Tipton's and my mammal-host specimens were identified by Dr. Henry W. Setzer, Associate Curator of Mammals, United States National Museum, and Dr. E. Schwartz.

The following abbreviations are used in listing the specimens: HH for Harry Hoogstraal, with the host number; R.P. for R. Paulian; RTB for Robert Traub, with the collection number; N. for Nuttall, with the collection number; MCZ for Museum of Comparative Zoology, with the host number.

II. THE GENUS HAEMAPHYSALIS

The *Haemaphysalis* tick fauna of Madagascar Island has thus far been known only by *H. elongata* Neumann, 1897, *H. simplex* Neumann, 1897, and *H. hoodi madagascariensis* Colas-Belcour and Millot, 1948. Except for the last-named species, these are represented in our collections by fairly sizeable lots from this island.

A fourth species, *H. obtusa* Dönitz, 1910, known previously from Reunion Island of the Madagascan Archipelago and from specimens from the zoological gardens near Tananarive, is present in our Madagascar Island collections in good numbers.

These collections furnish enough material to provide descriptions of certain females and immature stages not previously known, and to associate both sexes of certain species which have been confused by earlier workers because of superficial similarity.

In addition, five clearly distinct, previously unknown species of *Haemaphysalis* ticks are also represented and described.

These nine haemaphysalid ticks comprise all but one of the endemic tick species now known from the Malagasy Faunal Region (excepting the Seychelles) and are therefore treated as a separate unit in this report.

In sections III and IV (pages 95 to 106), a discussion of host-parasite relationships and origins of these species is presented.

Characters in the following *Haemaphysalis* key amount to a diagnosis of each newly described species of this genus in the Malagasy fauna.

Key to Malagasy HAEMAPHYSALIS *Species (Males and Females)*

(Characters mentioned are sufficient to serve as a diagnosis of new species described herein)

1. Palpi narrow, longer than greatest width, pedunculate, segment 1 distinctly visible, lateral salience hardly exceeding lateral margins of basis capituli. Basis capituli convex posteriorly in ♂, straight in ♀; lacking cornua. (Scutum with rather few, shallow punctations; lateral grooves short, indistinct, or obsolete. Coxae with moderate spurs. Insectivore parasite) . . . . *H. theilerae*, new species (Figures 32 to 39)

   Palpi wider than long, not pedunculate, segment 1 concealed, lateral salience greatly exceeding lateral margins of basis capituli. Basis capituli not convex posteriorly; cornua present (very small in *H. simplex* and small or absent in *H. lemuris*) 2

2\. Palpi with basal margin displaced at about a 65-degree angle forming postero-lateral margin of segment 2. (Cornua very small in ♂, lacking in ♀. Body broadly ovate; scutal punctations numerous, large in ♂, small in ♀; lateral grooves conspicuous. Coxal spurs very small, pointed or ridge-like. Lemur parasite) . . . . *H. lemuris*, new species (Figures 44 to 49)

Palpi with basal margin (except for spurs) horizontal, curved, or sloping medially (*not laterally*) at less than 20-degree angle (as is common in this genus) 3

3\. Coxae and trochanters with short, triangular or ridge-like spurs, or without spurs 4

Coxae and trochanters with long, needle-like spurs on at least one pair and large conspicuous spurs on most other pairs (*elongata* group. Insectivore parasites) 7

4\. Tarsi very stubby and distally abruptly narrowed. Palpal segments 2 and 3 about equally long[1]. Cornua very small or obsolete. (Palpal segment 3 with a small ventral retrograde spur. Scutum elongate, very convex, with numerous small punctations, lateral grooves faint or obsolete. Coxal spurs small, blunt. Trochanters lacking ventral spurs. Insectivore parasite) . . . . *H. simplex* (Figures 10 to 15)

Tarsi moderately elongate and tapered. Palpal segment 2 markedly longer than segment 3. Cornua well developed 5

5\. Palpi with tremendous dorsal and ventral posterolateral spurs, cornua similar to these spurs, palpal segment 3 with a very long ventral spur. (Scutum elongate, punctations few and shallow, lateral grooves lacking. Coxal spurs comparatively small, pointed. Carnivore parasite) . . . . *H. fossae*, new species (Figures 40 to 43)

Palpi without basal spur dorsally, with or without basal spur ventrally; cornua moderate; palpal segment 3 with small or moderate ventral spur 6

6\. Palpal widest salience at mid-length or sub-basally, a basal spur present ventrally. Scutum with few, fine punctations, lateral grooves lacking. (Carnivore parasite) . . . . *H. obtusa* (Figures 1 to 7)

Palpal widest salience basally, no basal spur. Scutum with numerous larger punctations, lateral grooves well marked. (Avian parasite) . . . . . *H. hoodi madagascariensis* (Figures 8 and 9)

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[1] In ♀♀, segment 3 may sometimes be only 3/5 length of segment 2.

7. Palpi basally with a stout ventral spur. (Palpal segment 3 with ventral spur short. Scutal surface markedly carinate and rugose with rather few, shallow punctations; long shallow lateral grooves. Coxa I with needle-like spur about two-thirds as long as coxa, succeeding coxae with conspicuous triangular spurs not half as long as on I. Trochanters I to III with long, subequal spurs, IV with shorter spur. ♂ integument stretched with engorgement to a broadly rounded posterior protrusion. Total ♂ length from 2.10 to 2.40 mm.) . . . . *H. tiptoni*, new species (Figures 20 to 23)

Palpi basally without ventral spur. Scutal surface mildly rugose or smooth. (Combination of coxal and trochantal spur characters considerably different) 8

8. Palpal lateral margin mildly curved; segment 3 with ventral spur no equalling its own length. Scutum with one or more weak carinae punctations from few to moderately many of medium to large size and fairly shallow. Coxae III and IV with longer spurs than I and II. Trochanter I with very small or no spur, II and III with long spur, IV with shorter spur. ♂ integument greatly stretched with engorgement to a narrowly rounded posterior protrusion. Total ♂ length from 2.10 to 3.45 mm. . . . . *H. elongata* (Figures 16 to 19)

Palpal lateral margin deeply concave, forming an almost perpendicular basal salience; segment 3 with ventral spur longer than its own length. Scutum smooth, with numerous small, deep, regular, cleanly cut punctations; lateral grooves shallow, long. Coxa I with long spur; II to IV shorter, subequal. ♂ integument only slightly stretched posteriorly but bulging ventrally with engorgement. Total ♂ length from 2.64 to 3.30 mm. . . . . *H. subelongata*, new species (Figures 24 to 31)

HAEMAPHYSALIS OBTUSA Dönitz, 1910.

(Figures 1 to 7, 50, 51, 64, 65)

Haemaphysalis obtusa Dönitz (1910), p. 492, Plate 17, figs. 11 and 12; described from many ♂♂ from Reunion Island (Madagascan Archipelago). Type material from Berlin Museum. Nuttall and Warburton (1915), p. 477, fig. 413, redrawn from Dönitz, cf. REMARKS below. Millot (1948), p. 153, mentioned species in review of Madagascan invertebrates. Zumpt (1950), pp. 171 and 173, recorded 9 ♂♂ from *Galidia galera* (Schreber, 1777) (= *elegans* I. Geoffroy, 1837), the Malagasy mongoose, in zoological gardens, Tsimbazaza Park, Tananarive, Madagascar Island.

MATERIAL EXAMINED: Two nymphs, 52 ♂♂, 42 ♀♀.

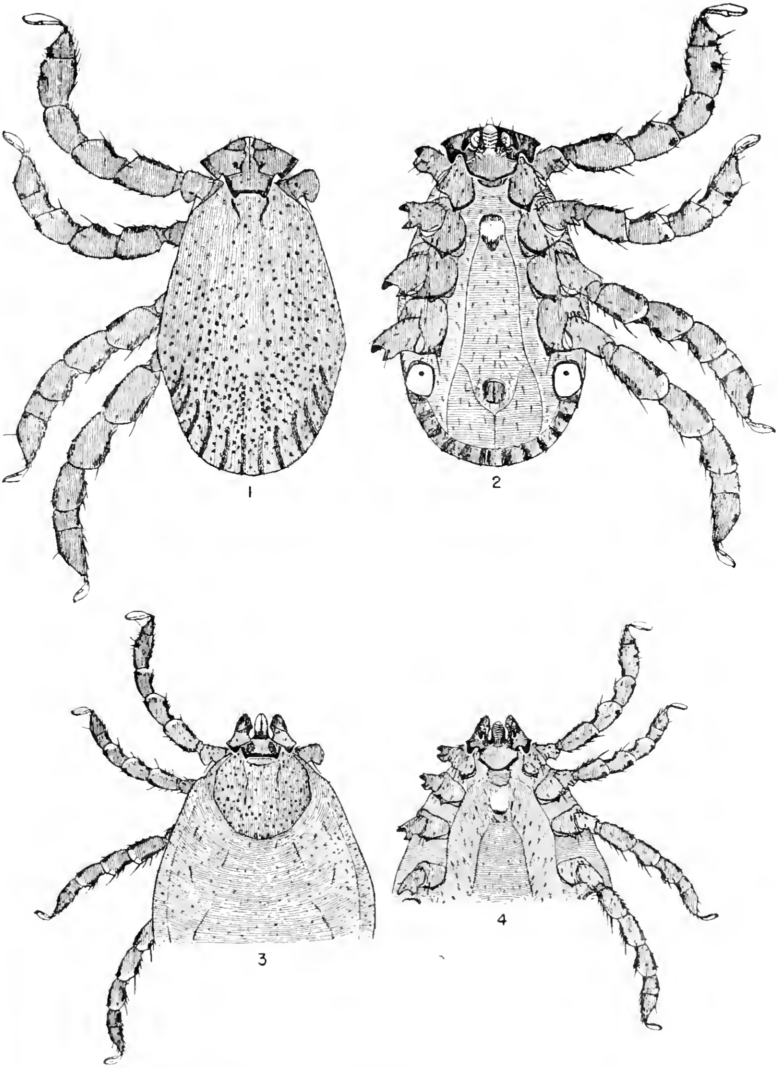
From four fanalokas or Malagasy civets, *Fossa fossa* (Schreber, 1777), Bemangidy, Poste Mananteina, Fort Dauphin, 23 November to 4 December 1948: 1 ♂ (HH4480), 12 ♂♂, 5 ♀♀ (HH4468), 4 ♂♂ (HH4510), 1 nymph, 7 ♂♂, 10 ♀♀ (HH4495). From four Malagasy mongooses, *Galidia galera* (Schreber, 1777) same locality as above, 29 November to 26 December 1948: 6 ♂♂, 5 ♀♀ (HH4522), 2 ♂♂ (HH4532), 5 ♂♂ (HH4509), 1 nymph, 7 ♂♂, 4 ♀♀ (HH4494). All H. Hoogstraal *legit*.

From Museum of Comparative Zoology, Harvard University: 8 ♂♂, 18 ♀♀ from a fossa, *Cryptoprocta ferox* Bennett, 1833, several miles west of Vangaindrano; collected by Archbold, Greenway, and Rand, 1929.

OTHER MATERIAL EXAMINED: 1 ♂ cotype (N2816) in British Museum (Natural History) from Reunion Island; in soft, pale, transparent condition but agrees perfectly with original description and with Madagascar Island specimens.

Redescription. MALE: *Length* from tip of palpi to posterior scutal margin 1.62 mm. to 1.86 mm., width 0.71 mm. to 0.91 mm. *Body* elongate oval, lateral margins almost parallel or slightly widening to level of coxa IV, converging to level of third festoon, bluntly rounded posteriorly. *Color* brownish yellow, rarely straw colored or brown, margins of palpi and basis capituli sometimes lined with black.

CAPITULUM: *Basis capituli* measures 0.15 mm. long, 0.25 mm. wide; lateral margins widely divergent anteriorly; posterior margin between cornua straight or very slightly concave; dorsal surface impunctate or with three or four very shallow, faint punctations; cornua short, rounded posteriorly, forming about an equilateral triangle. *Palpi* broadly salient from apex to mid-length or slightly posterior of mid-length; lateral margin straight or somewhat concave; salience never tilted anteriorly; basal margin at an acute angle and more or less sharply notched, recurved, or indented anterior of scapulae; between this point and inner margin basal margin is straight or sloping; inner margin concave basally, sinuous anteriorly; apex very broadly rounded; segment 3 about a third the length and half the width of segment 2. Laterally, basal margin straight or slightly convex. Ventrally, basal margin sharply recurved laterally and extended sublaterally to form a broad, tapered, bluntly pointed spur overlapping anterior half of coxa I; from spur to inner margin basal margin usually slightly concave; segment 3 with a retrograde spur arising between pit of segment



Figs. 1–4. *Haemaphysalis obtusa* Donitz, 1910: 1, male, dorsal; 2, male, ventral; 3, female, dorsal; 4, female, ventral.

4 and lateral margin of segment 3, this spur of variable length and shape, always tapered, always distinct, maximum length extending

almost to inner basal margin of segment 2. Bristles fairly conspicuous, situated as illustrated. *Hypostome* (Figure 50) stoutly elongate, apex broadly rounded, length about 0.12 mm., dentition 4/4, denticles stout, broad, closely spaced, exterior files with seven or eight denticles, inner files with five to seven denticles, apical and basal rows smaller than others; corona moderate. Corona-like denticles extend over anterior half of cheliceral sheath in close, regular rows and files.

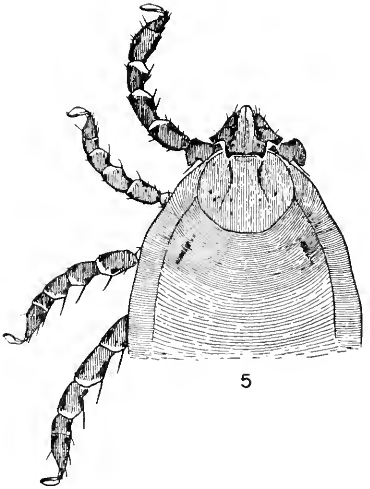
SCUTUM: *Lateral grooves* absent. Cervical grooves short, deep pits, followed by very short, usually shallow, converging grooves which are almost obsolete in some specimens. *Scutal surface* flat centrally, strongly curved laterally; shiny; punctations few, scattered, mostly well-separated, shallow, fine, some tending to form rows of three to five punctations; numerous minute punctations visible only under high magnification. *Festoons* clearly marked by deep grooves, three times as long as wide.

LEGS: *Coxae* each with a subequal short, pointed, posterior spur, coxa IV with spur at inner margin, other coxae with medial spur; coxae each with long bristles laterad of posterior spur. *Trochanters* unarmed except for a broadly rounded, plate-like spur (and a long, conspicuous hair just internally of spur) dorsally on I. Tarsus I dorsally with small basal knob and gradually tapered distally; tarsi II to IV with dorsal and ventral surfaces parallel basally, moderately tapered distally.

VENTRAL SURFACE: *Spiracular plate* as illustrated (Figure 64). *Genital aperture* between anterior half of coxae II, anterior margin convex, lateral margins almost parallel anteriorly, then angled to form angular or rounded posterior margin. *Genital grooves* slightly sinuous, gradually diverging, extending to posterior festoons. *Anal grooves* commencing at anterior level of anus, do or do not extend to genital grooves, more or less broadly arched posteriorly; ano-median groove usually short and obscure.

Description. FEMALE: Females, which have not previously been described, are readily associated with males. Their palpi are structurally similar but differ in proportions. Coxal armature is almost exactly alike in both sexes.

Length from tips of palpi to posterior body margin when unengorged about 1.79 mm.; width about 0.99 mm.; when engorged length reaching 3.50 mm.; width 2.60 mm.; body when engorged pod-shaped with almost parallel lateral margins and broadly rounded anterior and posterior margins.



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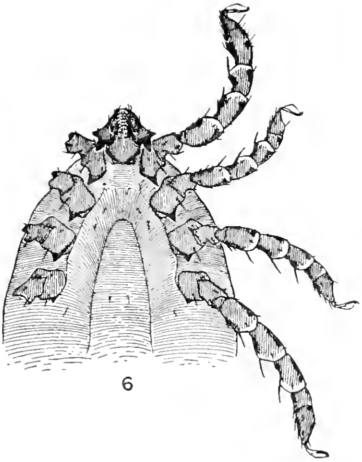

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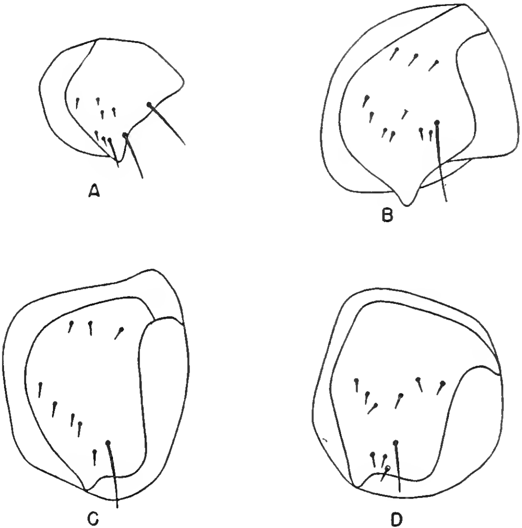

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Figs. 5–7. *Haemaphysalis obtusa* Dönitz, 1910: 5, nymph, dorsal; 6, nymph, ventral; 7, coxae of male from Reunion Island (cotype N2816, in British Museum (Natural History), drawn by Mr. E. Browning): A, coxa I; B, coxa II; C, coxa III; D, coxa IV.

CAPITULUM: *Basis capituli* average measuring 0.10 mm. long, 0.33 mm. wide; surface impunctate; lateral margins more or less divergent anteriorly; posterior margin between cornua slightly concave; cornua very short, widely triangular; porose areas deeply hollowed, elongate, narrow, oval, converging anteriorly, extending from posterior to anterior margin of basis capituli, widely separated; rounded carina bordering porose areas externally *Palpi* more elongate and less broadly salient than in male; lateral margin straight or slightly concave, with a slight uptilt at lateral salience; greatest width at posterior fourth of palpal length; basal margin ventrally with a long spur situated as in male, but wider than in male; segment 3 dorsally about five-sevenths as long as segment 2 and ventrally with spur more robust than in male. *Hypostome* (Figure 51) with same dental formula as in male but with two or three additional denticles in each file.

SCUTUM: *Length* averaging 0.75 mm., width 0.80 mm. *Outline* diverging from scapulae to mid-length, thence gradually and broadly rounded, (appearing more angular from dorsal view in engorged specimens). *Surface* with few, small, well separated, scattered punctations very slightly deeper than those of male; minute punctations visible only under highest magnification. *Cervical grooves* moderately deep, extending about two-thirds of scutal length, slightly converging for half their length, slightly diverging posteriorly.

LEGS: *Coxae* with small posterior ridge and very small, blunt or pointed posterior spurs laterally on II and III, small posterior median spur on I; minute posterior spur medially or none on IV.

Genital aperture between coxae II and III, in greatly engorged specimens forming a semicircle with posterior margin straight or slightly convex. Anal groove deeper than in male, extending to genital groove; ano-median groove reaching posterior body margin. Spiracular plate as illustrated (Figure 65).

Description. NYMPH: (This stage, which has not previously been described, is represented in our collection by only two specimens). *Length* (partially engorged) from tips of palpi to posterior body margin 1.75 mm.; width 1.10 mm.

CAPITULUM: *Basis capituli* like that of female except for size, slight surface punctations, and absence of porose areas and carina. *Palpi* like those of the female except for size, reduction of baso-lateral uptilt, narrower spurs, and slightly less disparity of proportional length between segment 2 and 3. *Hypostome* with 2/2 formula, outer file of five denticles, inner of six denticles.

SCUTUM: Size very slightly wider than long. *Outline* rather widely diverging from anterior to about three-fifths length, bluntly and regularly rounded posteriorly. *Surface* with numerous fine, shallow, adjacent or almost adjacent punctations. *Cervical grooves* shallow, extending for about three-fourths scutal length, slightly divergent posteriorly and anteriorly.

LEGS: *Coxa* I with pronounced, pointed, posterior spur at basal angle, coxa II and III each with shorter and blunter spur in middle of posterior margin, coxa IV with very small spur or without spur. *Trochanters* unarmed except for dorsal spur on I similar to that of female. *Tarsi* as in adults except that the hump of I is absent.

LARVA: Unknown.

Remarks: On the basis of the rather vague original description of *H. obtusa* and the subsequent interpretation of certain parts of it (*i.e.* by Nuttall and Warburton 1915), it would appear that Madagascan material differs from that of Reunion in enough details to warrant separate species or subspecies rank. Comparison of the cotype specimen (N2816) in British Museum (Natural History) reveals however, that these assumed differences do not exist.

In the original description, Dönitz stated that the hypostome has four rows of teeth; the accompanying figure shows somewhat more. Nuttall and Warburton interpreted this to mean 2/2. Actually the Reunion cotype specimen has 4/4 dentition as does all of our Madagascan material. Although the original description states that the coxae are not spurred, the cotype specimen actually does have small coxal spurs (cf. Figure 7) as do those of the Madagascar collection. Dönitz's figures do not accurately show the shape of the basis capituli.

The female and nymph of *H. obtusa* have not heretofore been described.

The listing of the host *Galidia elegans* under *G. galera* (page 42) was suggested by Dr. E. Schwartz, and differs from the name applied by most other authors, including Allen (1939).

Related Species: H. obtusa has a general resemblance to *H. leachii* (Audouin, 1827) and its several subspecies (*cf.* Theiler 1943) but may readily be distinguished by the former's lack of lateral grooves, sparse and fine punctation, characteristic palpal shape and proportions which differ from those of any known *leachii* subspecies, long and narrow porose areas, short cervical grooves, long and narrow festoons, etc. Nuttall and Warburton (1915) considered *H. obtusa* as a doubtful species, but since their admirable generic review, enough additional data on variation and species concepts in the genus *Haemaphysalis* have appeared to allow us to regard this as a species of considerable distinction which probably evolved from the same stock as *H. leachii* of Africa and Southern Asia (see page 102).

Hosts: The hosts of this species have not previously been known except for Zumpt's (1950) report from *Galidia galera* (= *elegans*). All specimens in the present collection are from the unique, endemic carnivores of this insular group, the fanaloka or Malagasy civet, *Fossa fossa*, the galidia or Malagasy mongoose, *Galidia galera*, and the fossa, *Cryptoprocta ferox*, (*cf.* pages 102 to 103). The only other tick known to parasitize any of these carnivores is *H. fossae*, new species, which I took from the same hosts parasitized by *H. obtusa*.

HAEMAPHYSALIS HOODI MADAGASCARIENSIS
Colas-Belcour and Millot, 1948.

(Figures 8 and 9)

Haemaphysalis hoodi madagascariensis Colas-Belcour and Millot (1948), pp. 384–387, figs. 1–2, of ♂ and ♀, described from a single ♂ (mounted in gum chloral) and 3 ♀ ♀ from the head of a coucal, "*Centropus madagascariensis*", at Moramanga, Madagascar; depository of type material not stated. The correct name of the host bird is *Centropus toulou toulou* (Müller, 1776). Bück (1948A), p. 3, and Zumpt (1950), p. 173, mention original report of this species.

MATERIAL EXAMINED: None.

Original Description (Freely translated from original French): *Male* of oval shape, narrower anteriorly than type subspecies (i.e. *H. hoodi hoodi*) or the subspecies *H. hoodi orientalis*, measuring 2 mm. long (including the capitulum) and 1.2 mm. wide. Examined in daylight the scutal color is blackish brown and appears to be divided into a pseudoscutum corresponding to the female scutum, and a conscutum. Cervical grooves extend the anterior two-thirds of the pseudoscutum and do not reach the posterior border of the regularly rounded margin. The well-marked lateral grooves continue anteriorly to the lateral border of the pseudoscutum and so reach the anterior third of the total scutal length; posteriorly their terminal bifurcation delimits the last marginal festoon. The strongly chitinized scutal surface is shiny; besides two foveae at the limits of the pseudoscutum and scutum there are numerous punctations of perceptibly equal size and uniform distribution, except in the area of the last lateral festoons where some are larger.

The short *capitulum* (0.27 mm.) has a rectangular base and is terminated posteriorly by rounded cornua, differing from type subspecies in which they are pointed, and from the variety *orientalis* in which they do not exist.

Palps: The second palpal segment very salient laterally; terminated posteriorly by a border perpendicular to the long axis of the body; the lateral angles are not turned towards the front and are narrower than in the figure given by Warburton and Nuttall for type subspecies; the second palpal segment is larger than the third. The last possesses a ventral more or less curving spur pointed inwardly as is characteristic of the *hoodi* group. The hypostome has a 4/4 formula consisting of longitudinal rows of seven large teeth (and not six as in the variety) preceded by three smaller teeth and a sizeable corona of denticles.

Each *coxa* is provided with a more or less rounded spine (*cf.* Fig. 8) the size of which decreases slightly from the first to the fourth; coxa IV in this specimen possesses a spine which, although of smaller size, is still more clearly extended and also differs from that of the same coxa of the type in which it is practically non-existent. The coxae of the Madagascan specimen are equally distinguished from those of the variety *orientalis,* which, except for the first, are unarmed. The more slender end of the cuneiform spiracular plate is directed dorsally.

Female: The three specimens are more or less engorged; their length is about 7.5 mm. and their width from 6.0 to 6.5 mm.; their shape generally oval, more or less elongated according to state of repletion. The integument is reddish brown; the scutum set apart from the rest of the dorsal surface by brighter coloration. Measuring 1.4 mm. by 0.8 mm., the scutum is oval, longer than in type subspecies; its posterior border is regularly rounded and not angled as in the variety *orientalis.* The well-marked cervical grooves are almost parallel and are more than two-thirds the length of the scutum, they diverge slightly anteriorly and posteriorly where they terminate by a series of wrinkles especially marked exteriorly. The scutal surface is uniformly covered by fairly large punctations. The *capitulum* recalls the general form of the male. The rectangular base has rounded cornua which are more extended than in type subspecies, in which they are hardly apparent. The porose areas are of an irregular oval form, their long axis diverges posteriorly; they are separated anteriorly by an interval of about the length of each. *Palpi:* The second palpal article is, as in the male, very salient laterally; the length of the palpi is clearly greater than in the male. The hypostome formula is 4/4.

The coxae are provided with rounded, more exactly formed spines, the first three pairs with a strongly chitinized and salient posterior border, the fourth with a rounded spine more clearly separated than the preceding ones; coxae of the type subspecies are neither figured nor described by Nuttall and Warburton who mention, on the other hand, that the variety *orientalis* is practically unarmed. The spiracular plate has its wide axis perpendicular to the axis of the body; it is rounded inwardly and drawn out on the dorsal face of the body; the macula is eccentric and internal, the screen area clearer, distinctly separated from the surrounding integument. In engorged females, the postanal groove is V-shaped with a posteriorly rounded angle, broadly evading the level of the anus.

Related Species: H. hoodi madagascariensis is only slightly different from *H. hoodi hoodi* Warburton and Nuttall, 1909, an avian parasite of tropical Africa, and from *H. hoodi orientalis* Nuttall and Warburton, 1915 an East African hyrax parasite, but its differentiating characteristics appear to be valid. All these subspecies are closely related to *H. doenitzi* Warburton and Nuttall, 1909, an avian parasite from Singapore and Selangor. It is difficult to say whether the Madagascan tick is more closely related to the African subspecies or to *H. doenitzi* which, in turn, has at least two other closely related avian-parasitizing species, *H. centropi* Kohls, 1949, of Upper Burma, Malaya, and Palawan (Philippines), and *H. minuta* Kohls, 1950, of Ceylon.

Host: A bird, the Madagascan coucal, *Centropus toulou toulou* (Müller, 1776), usually referred to in French literature as *Centropus madagascariensis*.

Lt. Tipton examined several birds on Madagascar without finding this tick. I examined over a hundred ground birds (which more commonly harbor ticks than most other birds) in Madagascar but found only a single specimen of *H. simplex* on one bird. The coucals which I examined yielded no ticks.

HAEMAPHYSALIS SIMPLEX Neumann, 1897.

(Figures 10 to 15, 52 to 54, 66, 67)

Haemaphysalis simplex Neumann (1897), pp. 345–346, figs. 10–12 of ♂, described from 13 ♂♂ and 1 nymph from "*Erinaceus* sp.", Madagascar, Sikora *legit* with ♀♀ *H. elongata*; types said to be in Toulouse. Dönitz (1907), p. 70, quoted Neumann. Blanchard (1909), p. 157, mentioned species. Neumann (1911), p. 111, figs. 55–56 from Neumann (1897).

Nuttall and Warburton (1915), pp. 458–460, figs. 394–397, redescription of ♂, illustrated (though not very exactly in palpal characters) from specimen from *Setifer* (= *Ericulus*) *setosus* in British Museum (Natural History) and from Neumann, nymphal description from Neumann. Bück (1948A), p. 3, states that specimens have been found on commensal rats at Tananarive. Zumpt (1950), p. 173, mentions species and states that it had been collected on *Hemicentetes semispinosus*, a statement which I have been unable to verify. Millot (1948), p. 153, mentions species in review of Madagascan invertebrates.

MATERIAL EXAMINED: Total 23 nymphs, 110 ♂♂, 17 ♀♀

From five Madagascan "hedgehog" tenrecs, *Setifer setosus* (Schreber 1777), at Bemangidy and Tanosy, Fort Dauphin, 13 to 24 November 1948: 7 ♂♂, 1 ♀ (HH4478), 21 nymphs, 9 ♂♂, 4 ♀♀ (HH4454 to 4456), 8 ♂♂, 2 ♀♀ (HH4462). A single ♂ from a bird, crested wood-ibis, *Lophotibis cristata cristata* (Boddaert), at Tanosy, Fort Dauphin, 20 November 1948. All H. Hoogstraal *legit*.

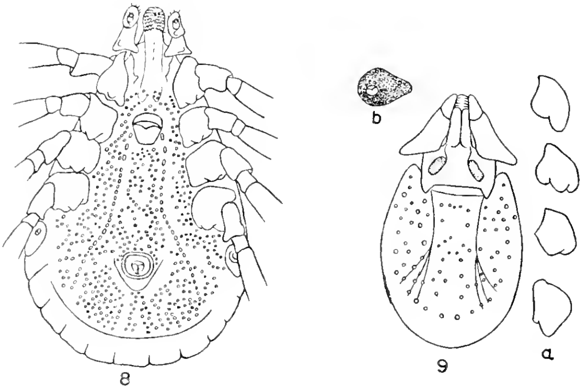
From skins of *Tenrec ecaudatus* (Schreber, 1777) or unidentified tenrecs in Museum of Comparative Zoology, Harvard University: a single nymph and 19 ♂♂ without precise locality data from skins of tenrecs, *Tenrec ecaudatus* (Schreber, 1777) (MCZ45538 to 45540 and 45564); 2 ♀♀, Ambovombe (MCZ45351, 45415); 3 ♀♀, near Fort Dauphin (MCZ45765).

From 44 specimens of *Setifer setosus*, January and February 1952, Lt. V. J. Tipton *legit:* 6 ♂♂ (RTB9659) and 1 ♂ (RTB9660) Morazano near Fianarantsoa; 1 nymph, 20 ♂♂ (RTB9664) Tulear; 1 nymph, 1 ♂ (RTB9817) 30 kilometers south of Fianarantsoa; 38 ♂♂, 5 ♀♀ (RTB9650, from 40 host specimens) 25 kilometers south of Fianarantsoa.

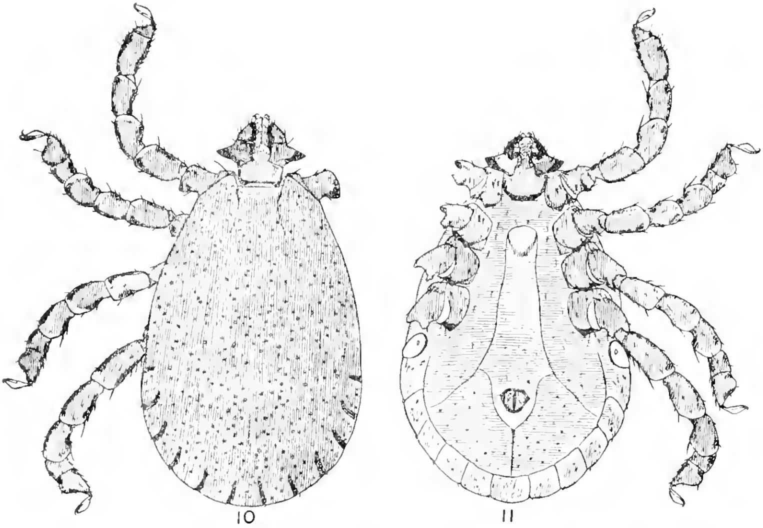
OTHER MATERIAL EXAMINED: Cotype ♂ (N2891) in British Museum (Natural History), which agrees with original and redescription in all respects.

Redescription. MALE: *Length* from tips of palpi to posterior scutal margin 1.98 mm. to 2.64 mm., width 1.10 mm. to 1.50 mm. *Body* globose, elongate oval, widest just posterior of coxa IV, lateral margins diverging from scapulae to level between coxae III and IV, thence parallel for a short distance to broadly rounded posterior margin. *Color* unengorged straw color, engorged reddish brown.

CAPITULUM: *Basis capituli* average measures 0.11 mm. long, 0.25 mm. wide; lateral margins parallel or slightly divergent anteriorly; posterior margin between cornua straight or slightly concave; cornua



Figs. 8–9. *Haemaphysalis hoodi madagascariensis* Colas-Belcour and Millot, 1948: 8, male, ventral; 9, female, dorsal; *a*, coxae of female; *b*, spiracular plate of female. (After Colas-Belcour and Millot, 1948.)



Figs. 10–11. *Haemaphysalis simplex* Neumann, 1897: 10, male, dorsal; 11, male, ventral.

very short, broad, rounded or pointed; dorsal surface downcurved laterally and posteriorly, usually impunctate, sometimes with a few small, scattered punctations. *Palpi* quite variable though within narrow limits; broadly salient basally, characterized by wide salience of lateral margin commencing at or just posterior of juncture of segments 2 and 3, narrow baso-lateral angle, length of segment 3 which is almost as great as that of segment 2, straight or slightly convex basal margins, widely inflated baso-lateral area with convex margin, presence of conspicuous bristles and of a very small ventral retrograde spur on segment 3, and generally by comparatively long distance between basal palpal margin and anterior surface of leg I and scapulae. Lateral margin of segment 3 at about a 65 degree angle (range 60 degrees to 80 degrees), lateral margin of segment 2 at about a 40 degree angle (range 30 degrees to 45 degrees) forming a wide, narrowly-angled basal salience. Basal margin straight or slightly convex, extending from lateral margin slightly anteriorly or horizontally to inner margin. Inner margin with a slight basal concavity, thence straight to apex. Laterally, basal margin more or less convex. Ventrally, basal margin usually straight and extends at an angle from lateral juncture posteriorly to inner margin; lateral margin frequently appearing to be more right-angled centrally than from dorsal view; segment 3 with a stout, very short, bluntly tipped, inwardly directed, ventral retrograde spur. Bristles long, pale, fairly conspicuous; from dorsal view consisting of three or four pairs apically, two laterals at base of segment 3, one near the inner apical corner of segment 2 and about four near the basal margin; ventrally bristles arise about the same as dorsally and several horizontal pairs arise from the inner margins. *Hypostome* (Figure 52) elongate, broadly rounded apically, about 0.17 mm. long, dentition 4/4, denticles subequal, overlapping, narrow and sharply pointed, elongate, in files of seven or eight denticles; corona very small. Corona-like denticles of narrow elongate shape continue over distal half of cheliceral sheaths in rows of about 20 and files of about 30.

SCUTUM: *Lateral grooves* absent, rarely very faintly indicated by a short, shallow groove. *Cervical grooves* consist usually only of short, linear, converging pits, otherwise with short, shallow, almost parallel or very slightly diverging, shallow extensions extending as far as coxa III. *Surface* strongly downcurved laterally and posteriorly, smooth and shiny. Punctations few to moderately numerous, small and medium-size mixed, shallow, rare on central anterior dorsum. *Festoons* deeply separated, length equalling width of median festoons, anterior festoons wider.

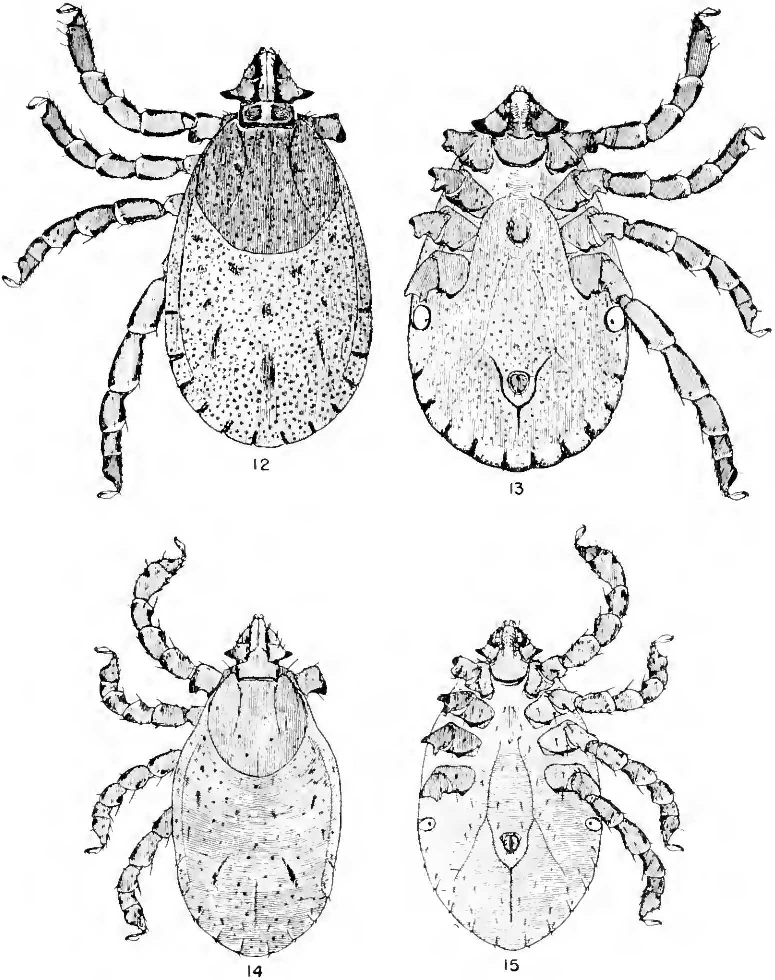
LEGS: *Coxae* each with a short, broadly rounded posterior spur formed as a continuation of the coxal surface, salient over the sloping posterior area; in some specimens tending to obsolescence on II and III. Coxa I subtriangular with spur breaking basal margin centrally, other coxae elongate rectangles with posterior spurs on lateral half. *Trochanters* unarmed ventrally, dorsally trochanter I with a fairly large, triangular, plate-like spur; anterior surface of trochanter I (facing palpi) with a row of several long, pale, laterally pointed bristles. Legs short but robust with angular margins. *Tarsi* especially stubby and robust, basally with parallel margins, subapically with a very small hump, apically abruptly tapered at almost right angles. Pads and claws small, no longer than dorsal-ventral length of tarsi.

Spiracular plate as illustrated (Figure 66). *Genital aperture* large, surface slightly rugose and convex, situated between coxae II, anterior margin straight or convex, lateral margins converging posteriorly, posterior margin broadly rounded or truncate, apron armed with a row of numerous, closely adjacent, needle-like projections of varying length. *Genital grooves* uncurved and very slightly diverging from genital apron to level ranging from posterior margin of coxa IV to level of anus, thence sinuous and broadly diverging to festoons. *Anal grooves* broadly rounded or arched posteriorly, anterior arms commencing at genital grooves and meeting posterior arms at a more or less acute angle at anterior level of anus; ano-median groove well marked. *Festoons* especially heavily marked and punctate ventrally.

Description. FEMALE: The female *which has not heretofore been described,* is much like the male in details of color, capitulum, scutal punctation, legs, coxal armature, tarsal shape, etc.

Length from tips of palpi to posterior body margin when unengorged, 2.3 mm. to 2.6 mm., width 1.4 mm. to 1.5 mm.; when engorged length reaching 5.40 mm., width 3.60 mm., and depth 3.20 mm. Body pod-shaped with rounded margins when engorged.

CAPITULUM: *Basis capituli* average measuring 0.15 mm. long, 0.38 mm. wide; much wider than that of male, lateral margins slightly converging anteriorly, cornua merely slightly extended, rounded latero-basal corners, posterior margin concave; porose areas deeply hollowed, almost circular, extending from anterior margin almost to posterior margin, separated by a distinct, wide-angled triangle with from two to four punctations, laterally usually bounded by a low carina.



Figs. 12–15. *Haemaphysalis simplex* Neumann, 1897: 12, female, dorsal; 13, female, ventral; 14, nymph, dorsal; 15, nymph, ventral.

Palpi more elongate and less widely salient than in male, lateral margin salient at almost right angles near basal margin; segment 3 three-fifths to as long dorsally as segment 2; otherwise similar to male palpi. *Hypostome* (Figure 53) with 5/5 dentition in files of seven to ten denticles.

SCUTUM: Average length 0.92 mm., width the same. *Outline* slightly diverging or almost parallel laterally, at three-fifths scutal length commencing to gradually and regularly narrow to form broadly rounded posterior margin. *Cervical grooves* extending almost to posterior scutal margin, forming slight arc; moderately deep anteriorly, becoming gradually more shallow posteriorly. Surface crazed and minutely punctate with few widely scattered medium and small punctations which are as shallow or slightly deeper than in male; central surface may have several shallow, horizontal wrinkles.

BODY INTEGUMENT: Rather coarse, heavily punctate dorsally and ventrally; deep lateral grooves dorsally from scutum to anterior margin of third festoon; festoons heavily marked dorsally and ventrally. *Genital aperture* situated between coxae II and III, forming a rectangle slightly longer than wide, distal margin may be slightly convex. *Genital grooves* more widely divergent anteriorly than in male, almost or completely joined at anterior level of coxae II by a horizontal arm. *Anal groove* closer to anus and more arched posteriorly than in male; ano-median groove distinct, almost reaching central festoon. *Spiracular plate* as illustrated (Figure 67).

LEGS: Essentially similar to those of male except that coxal spurs may be somewhat more apparent because of slightly greater width and deeper pigmentation.

Redescription. NYMPH: All nymphal specimens at hand are more or less engorged. The largest is as long as the male, the smallest about 1.0 mm. long when partially engorged. Nymphs are readily associated with adults by palpal characters, which are like those of the female, distance between the palpal base and scutal shoulders, robust legs, tarsal features, etc.

Capitulum like that of the female, except for smaller size and greater concavity of the posterior margin of the basis capituli; external palpal margin is variable in degree of concavity. *Hypostome* (Figure 54) with 3/3 dentition in files of five to seven denticles. *Scutum* with numerous fine, shallow, adjacent punctations arranged in wavering rows; the cervical grooves are rather shallow but quite distinct and extend from half to full length of the scutum as slightly concave arcs; the scutal outline is like that of the female, very slightly (one-tenth) wider than long, but becomes more elongate as the integument is stretched during feeding.

The *coxae* have small suggestions of posterior spurs as in adults. The *tarsi* are similar to those of adults except that they are less blunt distally.

LARVA: Unknown.

Remarks: In the above descriptions of this species a number of slight variations are noted, as might be expected from fair-sized collections from several localities and hosts. From these specimens it can be determined that the queries by Nuttall and Warburton (1915) about differences between their few specimens and remarks and illustrations in Neumann's original description (*i.e.* placement of ventral spur on palpal segment 3 and coxal spur variations) refer to actual slight variations from specimen to specimen, though these differences are easily within allowable limits for a species in this genus.

Related Species: It is difficult to associate this with any group of species or single species in this genus. In a general way *H. simplex* has the facies of *H. hoodi* though with globose body and unusually robust and stubby legs and with reduced scutal margins and punctations.

Hosts: Two insectivores, the Madagascan "hedgehog" tenrec, *Setifer setosus*, and the tenrec, *Tenrec ecaudatus*. A commensal, introduced rodent, the house rat, *Rattus rattus*. A bird, the crested woodibis, *Lophotibis c. cristata*.

This tick appears to have few highly specialized adaptations for life on spiniferous mammals. It has been found on but few of the insectivores examined, and has also been taken on non-insectivores and on birds in Madagascar. It is, therefore, suggested that host predilections of *H. simplex* may eventually prove to be much less specific than those of species in the *elongata* group. In interesting contrast to species of the *elongata* group, most specimens of which are found among the body hairs and spines, most specimens of *H. simplex* are found on the host's ears.

Other tick species found on the same host individuals with *H. simplex* are *H. elongata* and *H. theilerae*, new species.

HAEMAPHYSALIS ELONGATA Neumann, 1897.
(Figures 16 to 19, 55, 56, 68, 69)

Haemaphysalis elongata Neumann (1897), pp. 354–356, fig. 19 of ♂, described from 4 ♂♂ and 1 ♀ from a tenrec, *Tenrec ecaudatus* (Schreber, 1777) (= *Centetes madagascariensis*) at Zura, 2 ♂♂ from *Tenrec* (= *Centetes*) *ecaudatus*, and 2 ♀♀ from "*Erinaceus* sp.", Sikora *legit*, Madagascar; types said to be in Toulouse. Dönitz (1907), p. 73 quoted Neumann.

Blanchard (1909), p. 150, figs. 186, 187, copied from Neumann. Neumann (1911), p. 113, fig. 61 (abstract from 1897 paper with same illustration). Nuttall and Warburton (1915), pp. 498–500, figs. 438–439, redescription and illustration of ♂ and ♀ from different material; however, the ♀ description and illustration is actually of *H. tiptoni,* new species, and the ♂ description and figure include coxal and other characters of *H. tiptoni,* new species. Schulze (1942), p. 358 briefly mentioned the extension ot the ♂ integument after feeding. Millot (1948), p. 153 mentioned species in review of Madagascan invertebrates. Zumpt (1950), p. 172 mentions species and states that it had been recorded from *Hemicentetes semispinosus,* a statement which I have been unable to confirm.

MATERIAL EXAMINED: Total 37 ♂♂, 21 ♀♀.

A single ♂ from a Madagascan "hedgehog" tenrec, *Setifer setosus* (Schreber, 1777), (HH4462), at Tanosy, Fort Dauphin, 20 November 1948, H. Hoogstraal *legit.* From three tenrecs, *Tenrec ecaudatus* (Schreber, 1777), 1 ♀ (HH4469), 1 ♂ 1 ♀ (HH4486), 1 ♂ (HH4507), at Bemangidy, Poste Mananteina, Fort Dauphin, 23 November to 2 December 1948, H. Hoogstraal *legit.*

From *Tenrec ecaudatus* skins in Museum of Comparative Zoology at Harvard University: 1 ♀ from Ambovombe (Grandidier collection), 1 ♀ from Moramanga.

From "hedgehog" tenrecs, *Setifer setosus,* December 1951 to March 1952: 2 ♂♂ (RTB9657) Vohiposa near Fianarantsoa; 2 ♀♀, 1 ♂ (RTB9624) Tsaramandroso; 3 ♂♂ (RTB9830) kilometer 68 on Tamatave road; 8 ♀♀, 11 ♂♂ (RTB9650, forty host specimens) 25 kilometers, south of Fianarantsoa; 1 ♂ (RTB9809) Ambohimahasoa; Lt. V. J. Tipton *legit.* From tenrecs, *Tenrec ecaudatus,* 6 February 1952, 7 ♀♀, 5 ♂♂ (RTB9811) Ambohimahasoa, Lt. V. J. Tipton *legit.* From streaked tenrecs, *Hemicentetes semispinosus* (G. Cuvier, 1798), January and February 1952: 1 ♂ (RTB9803) Ambatofinandrahana; 7 ♂♂ (RTB9665) Tsimbazaza-Tananarive; 3 ♂♂ (RTB9639) Andrambovata; Lt. V. J. Tipton *legit.*

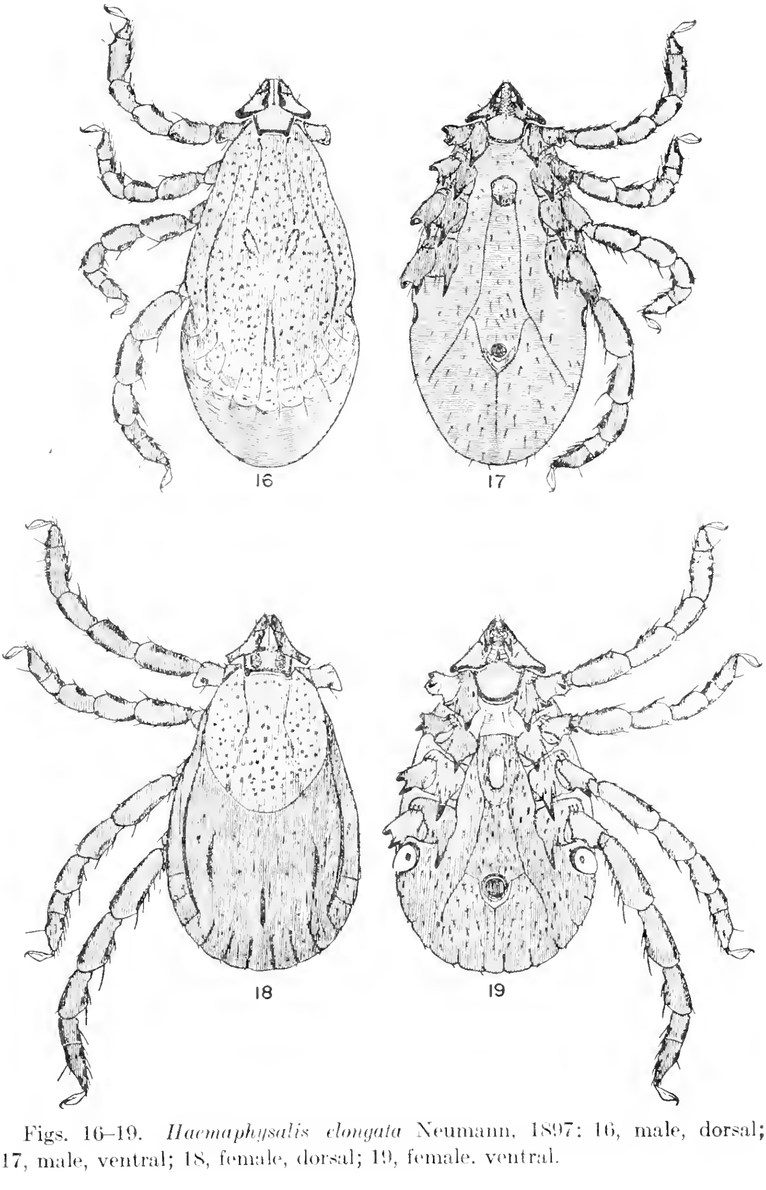
From "a bat in Namoroku grotto, Ambovomombe, September 1952; R. P. *legit*". This ♂ specimen, sent to me by Lt. Colonel R. Traub, is probably from an adventitious host. It is accompanied by a nymph, of the same genus, which I cannot identify.

OTHER MATERIAL EXAMINED: *H. elongata* "type series" in British Museum (Natural History). This consists of a single ♂ "Cotype" marked "from Neumann, Tura (par Sikora) 1894, *Centetes madagascariensis*", which agrees fully with the description of *H.*

elongata as given in the original description and below. Also seven specimens (5 ♂♂, 2 ♀♀) in a vial with a blue label marked "TYPE" and a white label marked "670. Coll. G. H. F. Nuttall F. R. S. *Haemaphysalis elongata* off *Centetes ecaudatus*, R. 172". This is the lot mentioned by Nuttall and Warburton (1915). In this lot is 1 ♂ *H. elongata* with all legs on right side broken, leg IV on left side broken; the others are *H. tiptoni*, new species. This lot is listed as "no particulars" in Nuttall's catalogue, and Mr. Browning believes its "type" designation to be erroneous.

Redescription. MALE: *Length* from tips of palpi to posterior body margin 2.10 mm. to 3.45 mm. (the posterior integument may stretch as much as 0.75 mm. beyond the scutum when engorged), width 1.00 mm. to 1.40 mm. *Body* narrow, elongate oval, widest between legs III and IV; posterior integument considerably stretched to a narrowly rounded protrusion when engorged and lateral margin indented around spiracular plate. *Color* reddish brown when unengorged; ranging to almost black when engorged; legs golden brown; peripheries of palpi and basis capituli frequently outlined by black lines.

CAPITULUM: *Basis capituli* average measuring 0.15 mm. long, 0.28 mm. wide, a moderately broad rectangle with lateral margins markedly divergent anteriorly and posterior margin between cornua straight or rarely slightly concave; cornua pointed or rounded apically, forming about equilateral triangles; surface crazed, impunctate or with a few scattered, shallow, moderate punctations. *Palpi* triangular, usually about twice as wide as long, rarely as little as 1.6 times as wide as long; gradually salient from apex to base; lateral margin a mild, gradual arc varying slightly in degree of concavity but rarely deeply concave; baso-lateral angle narrow, never tilted anteriorly; basal margin in a continuous arc with laterobasal margin, recurved above scapulae and extending anteriorly to inner margin; inner margin slightly convex, meeting basal margin above anterolateral corner of basis capituli; apex of palpi narrowly rounded; segment 2 from two to almost three times as long as segment 3. Laterally, palpi widely inflated over leg I and with slightly concave basal margin. Ventrally, baso-lateral angle narrowly pointed, basal margin usually extending to inner margin in straight or concave line at about 10-degree angle, rarely as a convexly angled line; segment 3 with a straight, parallel-sided, bluntly tipped, ventral retrograde spur arising anywhere from its center to adjacent to the external margin and slightly overlapping the juncture of segments 2 and 3. Bristles comparatively small and inconspicuous; con-



Figs. 16–19. *Haemaphysalis elongata* Neumann, 1897: 16, male, dorsal; 17, male, ventral; 18, female, dorsal; 19, female, ventral.

sisting at least of two apical and two medial on segment 3, two ventrals and two sublaterals on segment 2, and about 5 horizontal pairs on the inner ventral margins. *Hypostome* (Figure 55) stoutly elongate, broadly rounded apically, about 0.17 mm. long; dentition 3/3 consisting of fairly large, broad, closely-spaced, subequal denticles in an outer file of 7 to 9 denticles, a median file of 7 or 8 denticles, and an inner file of 6 or 7 denticles; corona very small.

SCUTUM: *Lateral grooves* shallow but distinct because of rounded external carina, extending from level of leg III (rarely II) to anterior margin of first festoon, in a few specimens continuing though more shallow to second festoon. *Cervical grooves* more or less converging, short pits followed by shallow, slightly diverging grooves extending as far as leg III. *Scutal surface* with one or more weak carinae of variable extent and degree; always well marked postero-medially, often sublaterally in central area and bordering cervical grooves. Punctations ranging between rather few to moderate numbers on various specimens, scattered, medium-size with a very few large on some specimens, tending to confluent lines of two to four punctations especially centrally, shallow but usually appearing slightly deeper anteriorly than posteriorly; fine reticulation (crazing) or minute punctations visible under medium magnification. *Festoons* clearly marked, fairly widely delimited, ventral half extending posteriorly in the same plane as scutum in engorged specimens.

LEGS: All coxae and trochanters II and III with long spurs. *Coxae* I and II each with a bluntly or sharply pointed spur about two-fifths as long as coxal length; coxae III and IV each with longer, narrower, needle-like spur equalling half or more of coxal length. *Trochanter* I with a more or less pointed ventral knob which in some specimens is spur-like but never more than barely overlaps posterior trochantal margin; trochanters II and III each with a narrow, tapered spur from a third to three-fifths as long as corresponding coxal spur; trochanter IV with a very small rounded spur, always less than half as long as trochantal width; trochanter I dorsally with a broadly rounded spur of only moderate length. Leg segments with three or four pairs of fairly conspicuous ventral bristles; an additional row of four on inner surface facing spiracle. *Tarsus* I half again as long as wide, dorsal surface forming a small basal knob, thence narrowing in a deeply concave arc; other tarsi elongate, basal half with parallel dorsal and ventral surface basally, distal half with dorsal surface gradually tapering.

Spiracular plate as illustrated (Figure 68). *Genital aperture* situated between coxae II, almost circular in outline though posterior margin is more narrowly rounded than anterior margin, apron with long, needle-like projections of varying length. *Genital grooves* slightly sinuous and sub-parallel between genital apron and level midway between coxa IV and anus, posteriorly widely divergent to level of juncture of anal grooves with ano-median groove. *Anal grooves* forming a pointed arch closely bounding anus, joining genital groove in unengorged specimens, but juncture not apparent when integument of engorged specimens is tightly stretched; ano-median groove well marked and extending to posterior body margin even in greatly engorged specimens.

FEMALE: In palpal characters, coxal and trochantal spur characters, and stretching of integument from engorgement, females so closely resemble males that the two sexes are readily associated. *Length* from tips of palpi to posterior body margin when unengorged 2.64 mm., width 1.16 mm., when engorged length reaches 7.50 mm., width 4.6 mm., and depth 2.6 mm. The body shape is very narrowly elongate in most engorged specimens and appears to be more widely stretched only near the end of feeding.

CAPITULUM: *Palpi* like those of males except that they are slightly more elongate than those of all but extremely elongate males, not quite so inflated latero-basally as in males, basal margin dorsally and ventrally usually at a more acute angle from lateral to inner margins than in males. *Basis capituli* about three times as wide as long, otherwise similar to that of male; porose areas rather shallow and ambiguously defined, elongate, oval, tilted. *Hypostome* (Figure 56) with 3/3 dentition in files of eight or nine denticles.

SCUTUM: Average *measures* 1.04 mm. long, 0.96 mm. wide; *outline* longer than wide, parallel or very slightly divergent from scapulae to mid-length, thence gradually and regularly narrowing posteriorly. *Surface* usually uneven and crinkled posteriorly; punctations shallow, few, scattered, moderate-size; minute punctations mixed with crazing visible under medium magnification. *Cervical grooves* moderately deep and slightly converging on anterior third of scutum, either slightly diverging, wider, and more shallow to posterior scutal margin or obsolete posteriorly; short, sublateral grooves sometimes present about mid-length of scutum.

LEGS: As in male; the dorsal spur of trochanter I may be even smaller than that of males.

BODY INTEGUMENT usually black when engorged, retaining traces of festoons and lateral grooves but with integumental features obscure. *Genital aperture* between anterior half of coxae III; in unmated specimens anterior and posterior margins parallel, anterior margin slightly longer than posterior; lateral margins elongate, diverging from posterior to anterior margins; in engorged, mated specimens with stretched intercoxal area, genital aperture, which is broadly V-shaped with a narrowly truncate base, is situated at a level between coxae II and III. Posterior half of venter with from two to three times as many hairs as on male, these hairs also somewhat shorter than on males. *Spiracular plate* (Figure 69) as illustrated.

NYMPH and LARVA: Unknown.

Related Species and *Remarks: H. elongata, H. tiptoni*, new species, and *H. subelongata*, new species, have so many peculiar characters in common that they may be considered as a closely related trio which, for convenience of reference, we shall call the "*elongata* group". Each has a characteristic arrangement of exceptionally highly developed coxal and trochantal spurs, a unique extension of the ♂ posterior integument (to a long, broadly rounded protrusion, a long, narrowly rounded protrusion, or a small postero-lateral protrusion), and each has a characteristic degree of scutal rugosity or surface depressions. The general facies of these three, especially in palpal characters and elongate body shape, is that of a closely-related group, but the differentiating characters within the group are constant in all specimens I have seen. There appears to be no problem of intermediate variations. The fairly large number of specimens examined the wide geographical range on the island, and the numbers of specimens from certain single hosts and from a number and variety of hosts suggest that intermediate varieties do not exist.

The similar development of extreme coxal spurs in males and females of each species in the *elongata* group is in exception to Nuttall and Warburton's (1915, p. 351) statement that "wherever the coxal spines (in *Haemaphysalis*) are strongly developed in the male their peculiarities are only very faintly echoed in the female."

The spiniferous legs, elongate body shape, and bulging body posteriorly are undoubtedly adapted to life among spiny hairs of the *elongata* group's insectivore hosts (*cf.* page 104).

I consider the *elongata* group as a divergent unit with a *leachii* prototype. Although *Haemaphysalis leachii* is best known from its wide distribution in Africa, I have come to regard it as a tick which probably originated in southern Asia. Its presence in southern Asia and the large number of species in that area which resemble it but tend either to extreme spur development on one hand, or, at the other extreme, to obsolescence of outstanding characteristics, suggest that this is a dominant group of southern Asia, with some forms extending to Madagascar (*elongata* group and *H. obtusa*), southern Europe and Russia, and North Africa as far as Algeria (*H. leachii leachii* [Audouin, 1827], *H. l. indica* Warburton, 1910, *H. l. humerosoides* Theiler, 1943, *H. numidiana* Neumann, 1905, etc.). I am at present engaged in a more complete survey of the interesting *leachii* "supergroup" which I hope to present shortly.

Hosts: The three species in the *elongata* group are insectivore parasites as is *H. simplex*, which appears to be a more generalized member of the *leachii* "supergroup", and *H. theilerae*, new species, which is one of the most primitive of known haemaphysalid ticks.

H. elongata has been found on the tenrec, *Tenrec ecaudatus*, on the streaked tenrec, *Hemicentetes semispinosus*, and on the Madagascan "hedgehog" tenrec, *Setifer setosus*. *H. elongata* was removed from the same host individuals parasitized by *H. tiptoni*, new species, *H. subelongata*, new species, *H. theilerae*, new species, and *H. simplex*.

HAEMAPHYSALIS TIPTONI, new species

(Figures 20 to 23, 57, 58, 70, 71)

Haemaphysalis elongata Neumann, 1897, was included with our *H. tiptoni* by Nuttall and Warburton (1915); on page 498 male characters of both species were mentioned, on page 499 the male coxae of both species were confused in a generalized sketch (figure 438), on page 500, the female description and sketch (figure 440) are entirely those of *H. tiptoni*. No such confusion exists in Neumann's original description and illustration of *H. elongata*. Also, both species are mixed under *H. elongata* in Nuttall's collection, which I have examined in British Museum (Natural History).

Holotype: Male from a tenrec, *Tenrec ecaudatus* (Schreber, 1777), Tanandavy (Ambohimahasoa), Madagascar, 30 January 1952, Lt. V. J. Tipton *legit* (RTB9807). Deposited in United States National Museum, Number 2124.

Allotype: Female, same data as holotype.

Paratypes: Total 59 ♂♂, 21 ♀♀, all collected by Lt. V. J. Tipton from various genera and species of tenrecs.

From streaked tenrecs, *Hemicentetes semispinosus* (G. Cuvier, 1798):

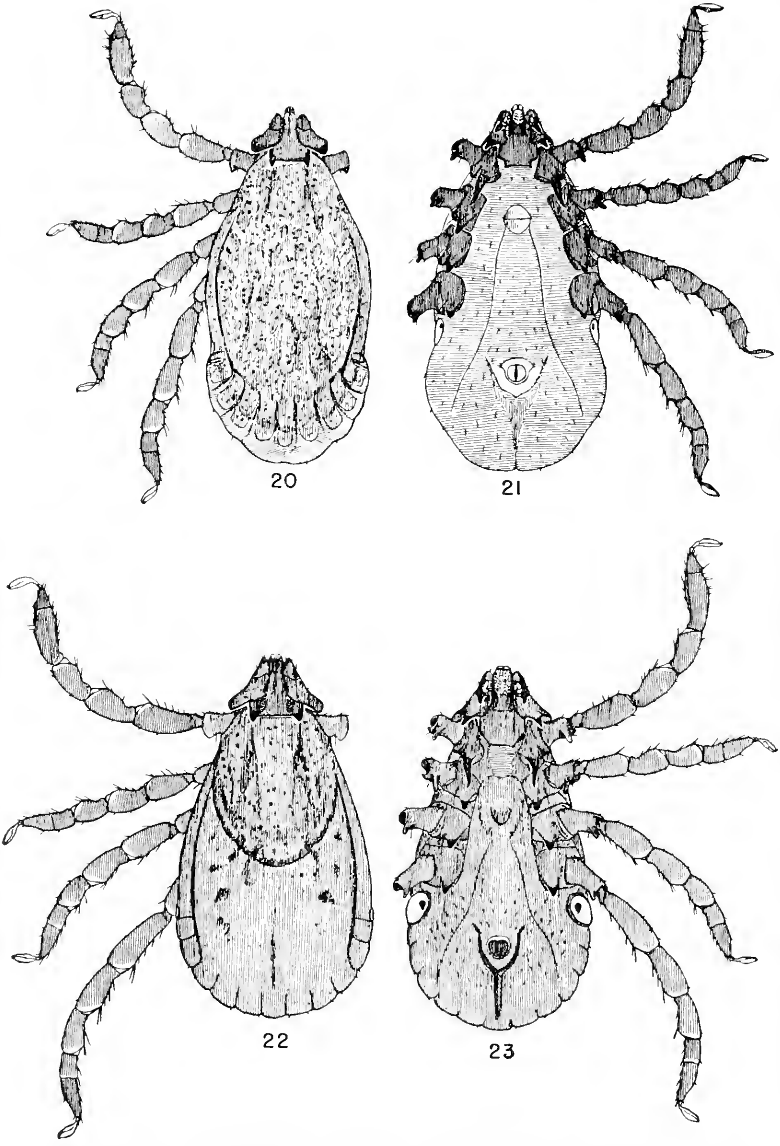
1 ♂ (RTB9825), kilometer 59 on Tamatave Road, 29 February 1952, 1 ♂ (RTB9803), Ambatofinandrahana, 28 January 1952 (RTB9803). From *Hemicentetes nigriceps* Günther, 1875: 2 ♂♂ (RTB9661), Vohiposa near Fianarantsoa, January 1952. From *Tenrec ecaudatus:* 33 ♂♂, 10 ♀♀ (RTB9811), Ambohimahasoa, 6 February 1952; 1 ♂, 2 ♀♀ (RTB9812), Mandalahy, 28 January 1952; 22 ♂♂, 10 ♀♀ (RTB9807), same collecting data as holotype.

Paratype specimens deposited in the United States National Museum; Museum of Comparative Zoology, Harvard University; Rocky Mountain Laboratory, Hamilton, Montana; British Museum (Natural History); Division of Veterinary Services, Onderstepoort; Institut Scientifique de Madagascar, Tsimbazaza-Tananarive; Chicago Natural History Museum; Museum National d'Histoire Naturelle de Paris; and the writer's collection.

This species is named for Lt. V. J. Tipton, who, as an investigator for the Army Medical Service Graduate School of Washington, D. C., made the excellent collection reported on in this paper.

Description. MALE: *Length* from tips of palpi to posterior scutal margin 2.10 mm. to 2.40 mm., width 1.11 mm. to 1.16 mm. *Body* narrow, elongate, slightly converging anteriorly from about level of coxae III, laterally almost parallel, posteriorly broadly rounded. Posterior integument considerably extended upon engorgement to form a usually broadly rounded posterior protrusion. *Color* yellow to brownish yellow.

CAPITULUM: *Basis capituli* average measures 0.10 mm. long including cornua, 0.22 mm. wide; lateral margins straight or very slightly diverging anteriorly; posterior margin between cornua straight or almost straight; surface flat or slightly depressed between cornua, impunctate or slightly punctate as on scutum; cornua usually somewhat longer than wide, sometimes no longer than wide, pointed or narrowly rounded distally. *Palpi* laterally normally forming a slight arc broadly expanded and recurved basally and joining basal margin over scapulae at a more or less obtuse angle; depth of lateral arc, length of basal salience, and degree of basal curvatures subject to variation but the basic pattern is not altered; the slightly convex or straight inner margin is about as long as lateral palpal length, and basal margin extends to it as a concave, straight, or curved line. Segment 3 dorsally about two-thirds as long as segment 2 and half as wide as segment 2. Laterally, basal margin widely expanded over leg I from dorsal aspect but ventrally rather deeply concave and cari-



Figs. 20–23. *Haemaphysalis tiptoni*, new species: 20, male, dorsal; 21, male, ventral; 22, female, dorsal; 23, female, ventral.

nate over trochanter I. Ventrally, basal margin forms a stout, bluntly or sharply tipped external spur (as an extension of the inner margin of the ventro-lateral concavity); basal margin extending from spur to inner margin in a more or less curved line. Segment 3 ventrally with a small straight, narrow, slightly laterally-pointing, retrograde spur which is not so long as segment 3. *Hypostome* (Figure 57) robust, length about 0.14 mm., widely rounded distally; dentition 3/3 in files of seven broad, subequal, closely and regularly spaced denticles; corona moderately large.

SCUTUM: *Lateral grooves* shallow but marked by a distinct, narrow, external carina extending from apex or base of anterior festoon to level of coxa II; in engorged specimens the shallow groove (but not the carina) may be continuous posteriorly around anterior end of festoons. *Cervical grooves* greatly varying in depth from specimen to specimen, converging to level of anterior margin of trochanter II; shallow, diverging extensions may be present posteriorly, or obsolete. *Scutal surface* marked by several mild rugosities or low carinae of variable length and width, a narrow postero-median carina always present. Punctations few, of mixed sizes and variable from specimen to specimen but always mostly shallow and mostly well separated, a few close together and in lines of several punctations, these lines often slightly depressed; minute interstitial punctation visible under high magnification on some specimens, especially just internally from lateral grooves. *Festoons* no longer than broad, widely though shallowly separated; their ventral extensions in a plane with dorsal surface (so festoons appear long and narrow) when body integument is stretched posteriorly with engorgement, at which time the delimiting grooves also appear deeper.

LEGS: All trochanters and coxae with a prominent spur. *Coxa* I with a needle-like spur about two-thirds as long as coxa; other coxae each with a shorter, broader, slightly tapering or curving, more or less bluntly rounded spur with flat or slightly-curved surface arising from posterior half of coxal surface and extending slightly beyond posterior coxal margin (distal portion of spur especially distinct because coxal surface slopes beneath it and spur tip is often more or less darkly pigmented). *Trochanters* ventrally each with a spur which is straight or slightly curved, not tapering, bluntly rounded distally, arising from posterior half of trochanter; spur on trochanter I from one-half to three-fifths trochantal length, spur on II usually slightly shorter but sometimes equalling I, on III about equalling or very slightly larger than I, on IV about half the size of that on III; dorsally trochanter I with a broad, triangular, plate-like spur. *Legs* moderately long and wide. *Tarsus* I as wide as long, dorsal surface basally with a narrow, slight bump, distally gradually tapered; tarsi II, III, and IV with dorsal half basally paralleling ventral margin, distally gradually tapered.

VENTRAL SURFACE: *Genital aperture* situated at level of coxae II, with anterior margin convex, posteriorly broadly triangular (quite variable in shape laterally and posteriorly), apron with closely-spaced needle-like projections of varying length, surface usually convex. *Genital grooves* slightly sinuous and diverging to about level half way between coxa IV and anus, thence diverging towards lateral margin. *Anal groove* broadly arched posteriorly, lateral arms to genital groove either shallow or obsolete, if present may be almost horizontal, slightly curved; ano-median groove from well defined to obsolete. *Spiracular plate* (Figure 70) as illustrated.

FEMALE: The female is readily associated with the male by similarity of palpal outlines and other palpal characters, rugose scutal surface, development of coxal and trochantal spurs, etc.

Length from tips of palpi to posterior body margin when unengorged 2.3 mm. to 2.7 mm., width 1.1 mm. to 1.3 mm., when engorged length reaching 4.7 mm., width 3.4 mm. *Body* shape when engorged flat dorsally and ventrally, lateral margins beyond scutum about parallel, posterior margin bluntly rounded.

CAPITULUM: *Basis capituli* average measuring 0.13 mm. long including cornua, 0.35 mm. wide; wider than that of male but otherwise with similar outline and cornua; with a carinate extension of cornua reaching anterior margin of basis and bordering porose areas externally; porose areas short, wide oval to circular, pits varying from shallow to deep. *Palpi* like those of the male except that they are very slightly more elongate, the baso-lateral concavity is slightly less emarginate than usual in males, and the baso-ventral spur is slightly stubbier. *Hypostome* (Figure 58) with 3/3 dentition in files of eight or nine denticles.

SCUTUM: *Size* averaging 0.92 mm. long, 0.79 mm. wide. *Outline* longer than wide, diverging from shoulders to level of anterior fourth, laterally parallel or very slightly converging, posteriorly regularly rounded. *Cervical grooves* deep, narrow, slightly converging, reaching distal level of anterior fourth of scutum, thence wider but shallower, slightly bowed or diverging, and extending to posterior scutal margin.

Surface uneven, usually with several wide ridges and depressions paralleling cervical grooves, posterior margin frequently crinkled. A few small, shallow, widely-spaced punctations scattered over surface; minute punctations visible under high magnification especially in grooves.

Body integument with uneven surface when unengorged, impunctate; deep lateral grooves extending from scutum to anterior margin of second festoon; festoons deeply marked dorsally and ventrally. *Legs* like those of male. *Genital aperture* between coxae II and III, somewhat depressed, forming an elongate rectangle, sometimes with rounded corners or slightly convex sides or ends. *Genital grooves* commencing at about mid-level of coxae III, joined by a shallow horizontal groove, slightly diverging to anterior level of anus, thence widely diverging to third festoon. *Anal groove* joined to genital grooves by curved or almost horizontal arms, widely arched posteriorly; ano-median groove deep, reaching central festoon. *Spiracular plate* (Figure 71) as illustrated.

Related Species: H. tiptoni is a member of the *elongata* group (page 104) which parasitizes Malagasy insectivores. Both sexes are easily differentiated from *H. elongata* and other species by characters which appear in the key (couplets 7 and 8).

Hosts: The tenrec, *Tenrec ecaudatus,* and the streaked tenrecs, *Hemicentetes semispinosus* and *H. nigriceps*. See page 104 for further details.

Remarks: It is of interest that we did not obtain this species from *Tenrec ecaudatus* in southern Madagascar, but that Lt. Tipton collected a sizeable lot in other parts of the island. We obtained no specimens of *Hemicentetes* in southern Madagascar. Other species of ticks which were found on the same host specimens as *H. tiptoni* are *H. elongata* (rarely), *H. subelongata*, new species, and *H. theilerae*, new species. The other Madagascan insectivore parasite, *H. simplex*, was not found on the same host individuals with *H. tiptoni*.

HAEMAPHYSALIS SUBELONGATA, new species

(Figures 24 to 31, 59, 60, 72 to 74)

Holotype: Male, from a tenrec, *Tenrec ecaudatus* (Schreber, 1777), (HH4469), Bemangidy, Poste Mananteina, Fort Dauphin, Madagascar, 23 November 1948, H. Hoogstraal *legit*. Deposited in United States National Museum, Number 2 23.

Allotype: Female, same data as holotype.

Paratypes: Total 43 larvae, 526 nymphs, 143 ♂♂ and 17 ♀♀, all from the tenrec, *Tenrec ecaudatus.*

From Bemangidy, Poste Mananteina, Fort Dauphin, 23 November to 2 December 1948: H. Hoogstraal *legit:* 42 larvae, 202 nymphs, 98 ♂♂, 11 ♀♀ (HH4469); 7 nymphs, 6 ♂♂, 1 ♀ (HH4487); 1 larva, 7 nymphs, 8 ♂♂ (HH4486); 5 ♂♂ (HH4507); 6 ♂♂ (HH4498).

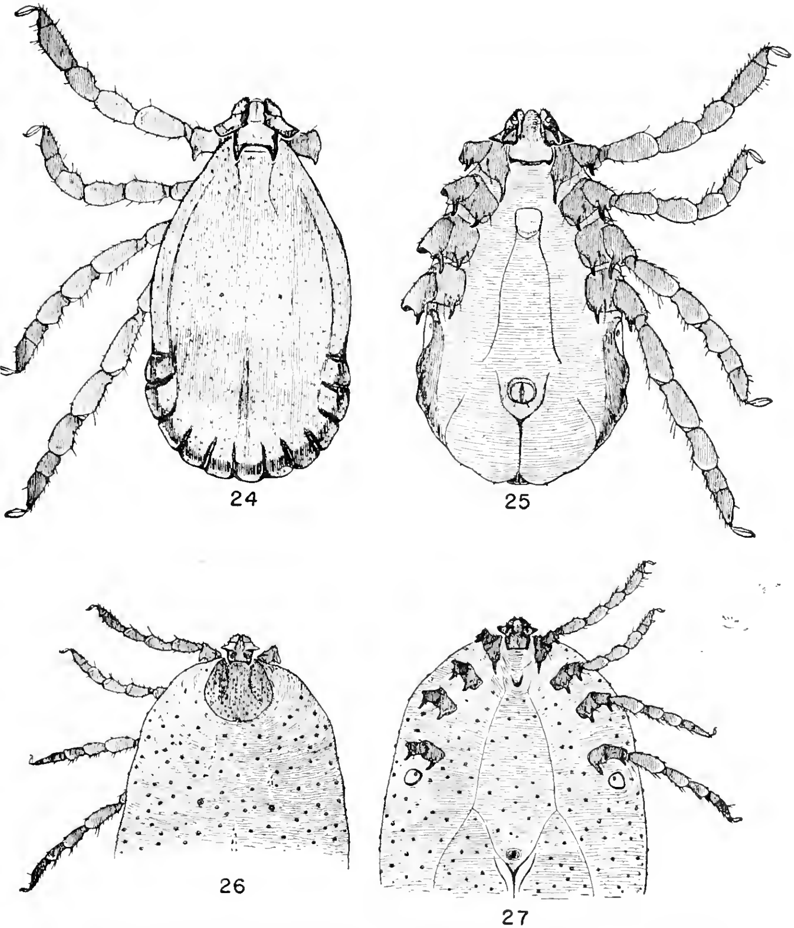
From skins in Museum of Comparative Zoology, Harvard University: 4 ♂♂, 3 ♀♀ from Ambovombe; 310 nymphs, 9 ♂♂, 1 ♀ from forest south of Moramanga, east-central Madagascar.

Lt. V. J. Tipton *legit:* 4 ♂♂ (RTB9811), Ambohimahasoa, 6 February 1952; 1 ♀ (RTB9660), Morazano near Fianarantsoa, 25 January 1952; 3 ♂♂ (RTB9812), Mandalahy, 28 January 1952.

Paratype specimens deposited in collections of United States National Museum; Museum of Comparative Zoology, Harvard University; Rocky Mountain Laboratory, Hamilton, Montana; Institut Scientifique de Madagascar, Tsimbazaza-Tananarive; British Museum (Natural History); Division of Veterinary Services, Onderstepoort; Chicago Natural History Museum; Museum National d Histoire Naturelle de Paris; and that of the writer.

Description. MALE: *Length* from tips of palpi to posterior scutal margin 2.64 mm. to 3.30 mm.; width 1.45 mm. to 1.65 mm. *Body* fairly narrow, elongate, diverging from scapulae to level of coxa IV, thence about parallel to juncture of second and third festoon; bluntly rounded posteriorly; posterior integument slightly stretched but following scutal contours with engorgement, ventral posterior integument including festoons bulging. *Color* shiny reddish brown; when engorged more deeply brown with reddish brown legs.

CAPITULUM: *Basis capituli* average measuring 0.15 mm. long including cornua, width the same; lateral margins parallel or slightly diverging anteriorly; posterior margin between cornua straight or slightly concave; cornua stout, from one-half to three-fourths as long as basis capituli, tapering, pointed distally; dorsal surface either flat or depressed posteriorly between cornua, with four to twelve small punctations. *Palpi* with several combinations of different peripheral patterns from specimen to specimen or from side to side on the same specimen; these differences, however, within narrow limits. The lateral margin is always deeply concave, the basal salience always great and always horizontal or down-tilted and always narrow; peripheral spurs never present; from a lateral aspect the basal salienee always great and always horizontal or downtilted and always narrow; from a lateral



Figs. 24–27. *Haemaphysalis subelongata*, new species: 24, male, dorsal; 25, male, ventral; 26, female, dorsal; 27, female, ventral.

aspect the basal salience always forming a narrow rectangle with distal margin (*i.e.* closest to the viewer) straight or slightly convex. Segment 3 may be triangular (*i.e.* narrowly pointed apically), almost rectangular (*i.e.* truncate apically), or intermediate between these two forms; its length varies from usually two-thirds to almost fully as long as that of segment 2; its external margin may almost be vertical or at an acute angle. The lateral margin of segment 2 becomes acutely salient at a greater or lesser distance posterior of its juncture with segment 3 but the length of the salience is usually greater but always at least equal to the length of the anterior lateral margin. The curvature of the baso-lateral margin to the baso-dorsal margin forms a variably pointed tip which is, however, always more or less narrow and never uptilted. The basal margin extends from its lateral juncture either as a straight, anteriorly directed line to the inner margin or as a more or less sharply convex recurved line to the inner margin. Laterally, the elongate, rectangular basal salience always has a straight or slightly convex apical margin; this salience may be either widely inflated over leg I (in which case the dorsal and ventral basal margins are usually straight) or it may be distally not so (in which case the basal margins dorsally and ventrally are more or less recurved). Ventrally the basal margin which is almost always a straight line or rarely almost so, is either horizontal or tilted at almost any angle; the lateral margins appear to be more acutely angled than they do from a dorsal view; segment 3 has a stout, tapered, more or less sharply pointed ventral retrograde spur arising between the pit of segment 4 and the lateral margin of segment 3 and overlapping at least the apical half of segment 2 and often much of the basal half as well. Several conspicuous pairs of pale bristles are present especially apically, on the ventro-lateral, ventro-basal, and dorso-basal surface and horizontally from the inner ventral margins. *Hypostome* (Figure 59) stoutly elongate, broadly rounded apically, about 0.21 mm. long; dentition 4/4, denticles large, subequal, sharply tapered, closely spaced and overlapping, consisting of eight denticles in outer files and six denticles in inner files, apical row of denticles appearing somewhat smaller than others; corona small. Corona-like denticles on apical half of cheliceral sheaths in regular, close rows and files.

SCUTUM: *Lateral grooves* as such quite narrow and shallow, however very distinctly emphasized by downcurving of scutal surface and sharp juncture of external carina; groove (or depressed area) and external carina extending from level between legs I and II or between II and III to anterior festoon or to anterior margin of third festoon; in engorged specimens groove may be entirely continuous posteriorly. *Cervical grooves* converging and usually fairly deep to level of anterior margin of trochanter II, thence shallower and diverging for distance varying between very slight to twice length of deep end. *Scutal surface* bright and shiny, usually smooth, variably depressed laterally; foveae exceptionally distinct. Punctations numerous but small, cleanly cut and fairly deep and regular; those of anterior half of some specimens indistinctly slightly larger than on posterior half; mostly well scattered, a few adjacent but not contiguous to each other, rather evenly distributed over entire surface; no minute punctations visible under high magnification. *Festoons* about as long as wide, distinctly marked by narrow, deep, darkened grooves; ventral extensions of festoons raised when tick is engorged but curving ventrally rather than in same plane as scutum as in other species of *elongata* group.

LEGS: All coxae and trochanters with a prominent long, narrow, usually slightly curved, pointed, spine-like spur, coxae with a pair of long, fine, pale bristles about as long as each spur arising just outside and inside of the origin of each spur. *Coxa* I with spur more than half length of coxa arising in basal angle; succeeding coxal spurs slightly over half length of I, subequal, arising between middle and inner edge of posterior margin. *Trochanter* I ventrally with spur varying from half to fully as long as trochantal width; trochanters II and III each with spur equalling that of I or (especially frequently on III) slightly longer; trochanter IV with spur slightly shorter than that of I; trochanter I dorsally with triangular, comparatively narrow, sharply pointed spur. *Legs* moderately long and wide dorso-ventrally; lateral margins somewhat appressed; each segment with two to four ventral pairs of fine, pale, conspicuous hairs and about an equal number of shorter hairs dorsally. *Tarsus* I dorsally with slight basal hump and deeply concave distally, other tarsi with dorsal surface paralleling ventral surface basally and gradually tapered distally. Claws long, pads almost equally long.

Spiracular plate as illustrated (Figure 72). *Genital aperture* situated between mid-level of coxae II, surface convex, posterior margin of apron with closely spaced needle-like projections of varying length. *Genital grooves* slightly sinuous and diverging till about anterior level of anus thence gradually more widely divergent to level of juncture of second and third festoons. *Anal groove* usually wide, deep, and sharply arched, anteriorly shallower and usually fading before juncture with genital grooves; ano-median groove deep, reaching central festoon. *Ventral integument* with scattered, minute punctations among the fine, horizontal surface striations. *Festoon* divisions ventrally varying from well to poorly marked.

FEMALE: Females of this species are easily associated with males by close similarity in form of palpi, coxal and trochantal spur development, scutal punctation, color, presence of pale hairs, etc. All specimens at hand are somewhat engorged, most greatly engorged.

Length from tips of palpi to posterior body margin, when fully engorged, up to 5.0 mm., width 2.8 mm. The characteristic *body shape* with engorgement is comparatively narrow with parallel, rounded sides, broadly rounded posterior margin, and acutely narrowing margins bordering scutum, the rather short scutum occupying the anterior seventh of the body.

CAPITULUM: *Basis capituli* average measures 0.24 mm. long, 0.57 mm. wide, margins and cornua as in male except that the cornua are slightly wider and shorter; porose areas fairly deep, widely spindle-shaped, tilted, not quite reaching anterior or posterior margin; surface impunctate, slightly raised laterally and centrally. *Palpi* almost a third larger than those of male, lateral salience usually more basal and not quite so elongate in proportion to anterior length as in male; basal margin dorsally always straight or almost straight (in specimens at hand), and segment 3 triangular (not variable as in male); ventral spur of segment 3 equally long as that of male but with straight sides and broadly rounded posteriorly; other features as in male. *Hypostome* (Figure 60) with one to three more denticles in each file than in male.

SCUTUM: *Shape* almost circular (appearing slightly more angular on sloping surface of greatly engorged individuals), 4 mm. long, 4.4 mm. wide in large (stretched), engorged specimens. *Cervical grooves* moderately deep anteriorly, bowed at mid-length of scutum, extending almost to posterior scutal margin. Punctations like those of male in depth, number and spacing, but size medium rather than small, edges cleanly cut as in male.

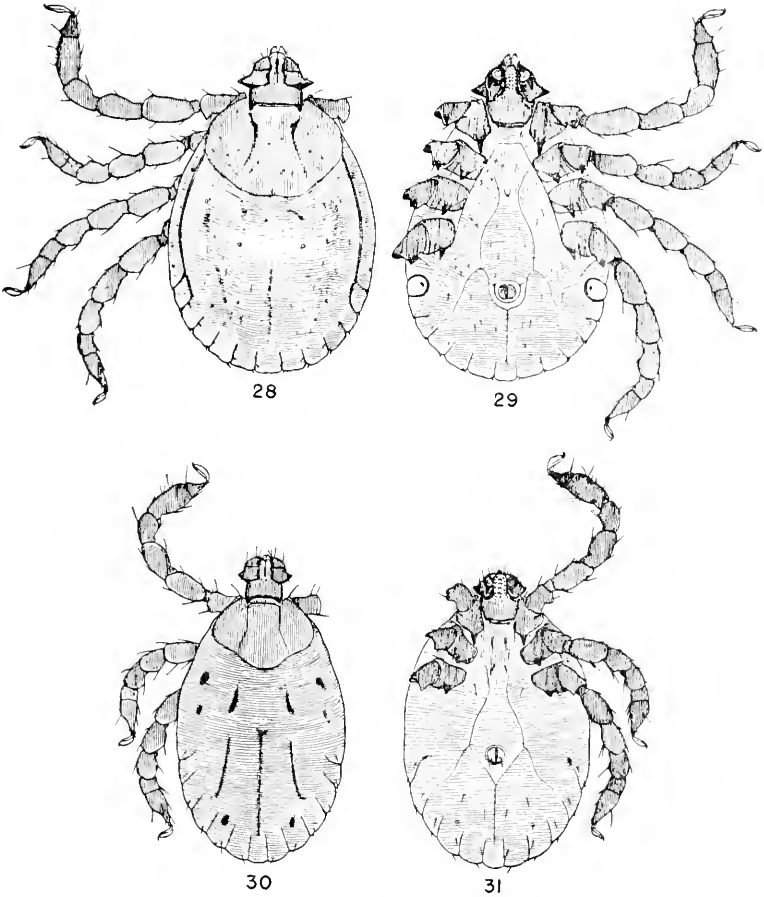
LEGS: Coxal and trochantal spurs like those of male except that the dorsal spur of trochanter I may be somewhat narrower and longer.

SPIRACULAR PLATE (Figure 73) as illustrated.

Other characters modified by engorgement in specimens at hand.

NYMPH: Nymphs are miniature facsimiles of females and differ in only minor details from them. The palpal outline is like that of females in which the basal salience is not so great as in males, the degree of lateral concavity in palpal outline is very variable, and the ventral retrograde spur of palpal segment 3 reaches the mid-length of segment 2. The hypostome has 2/2 dentition.

The scutum is only about two-thirds as long as wide; has a broadly rounded posterior margin; few, small punctations; and long, deeply bowed cervical grooves.



Figs. 28–31. *Haemaphysalis subelongata*, new species: 28, nymph, dorsal; 29, nymph, ventral; 30, larva, dorsal; 31, larva, ventral.

The location and proportions of the coxal and trochantal spurs are almost exactly like those of adults but, except for coxa I, most of these spurs are broader than on adults. Tarsal shape is similar in nymphs and adults.

In unengorged specimens, lateral grooves are deep and enclose the first festoon. Spiracular plate as illustrated (Figure 74).

LARVA: In larvae the general palpal shape of females is present and though the basal salience is much reduced, the ventral retrograde spur of segment 3 is strong and, comparatively, equally as long as in males.

The impunctate scutum has the same proportions as in nymphs, i.e. about two-thirds as long as wide, and with long cervical grooves which are either deeply bowed or basally parallel and distally diverging, but the posterior border is bilaterally concave.

Coxal spurs recall those of nymphs, coxa I has a longer spur and II and III each have a shorter spur. Trochanter I has wide, short dorsal and ventral spurs, but the others have none or only suggestions of spurs.

Related Species: H. subelongata is a member of the Madagascan *elongata* group (page 104) and distinctly differs from others in this group by several characters as listed in key couplets 7 and 8 (page 41).

Host: An insectivore, the tenrec, *Tenrec ecaudatus.*

Remarks: The huge number of ticks (42 larvae, 202 nymphs, 98 ♂♂ and 11 ♀♀) found on one host specimen (HH4469) formed a dense mass over the animal's hindquarters, both among the more spiny hairs and the soft hairs. As may be expected from this crowding, many of the tick specimens in this lot are more or less misshapen.

Other tick species found on the same host individuals as *H. subelongata* were *H. simplex* (rarely), *H. elongata*, *H. tiptoni*, new species, and *H. theilerae*, new species.

HAEMAPHYSALIS THEILERAE, new species

(Figures 32 to 39, 61, 75 to 77)

Holotype: Male from a tenrec, *Tenrec ecaudatus* (Schreber, 1777), (HH4469). Bemangidy, Poste Mananteina, Fort Dauphin, Madagascar, 23 November 1948, H. Hoogstraal *legit.* Deposited in United States National Museum, Number 2122.

Allotype: Female from *Tenrec ecaudatus* (RTB9812), Mandalahy, Madagascar, 28 January 1952, Lt. V. J. Tipton *legit.* Deposited in United States National Museum.

Paratypes: Total 4 larvae, 12 nymphs, 10 ♂♂.

Four larvae, 10 nymphs, 6 ♂♂ with same collecting data as holotype. Two ♂♂ with same collecting data as allotype. A single ♂ from a Madagascan "hedgehog" tenrec, *Setifer setosus* (Schreber, 1777), 25 kilometers south of Fianarantsoa, 12 January 1952 (RTB9650);

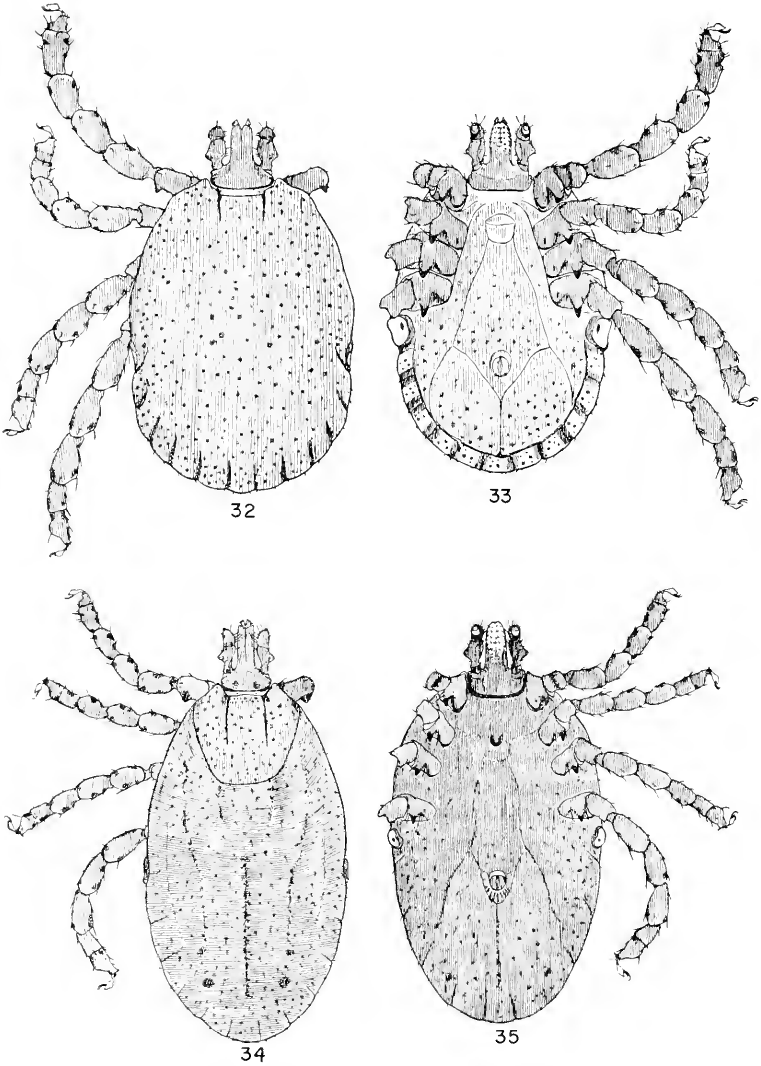
two nymphs, 1 ♂ from *Tenrec ecaudatus*, Tanandavy (Ambohimahasoa), 30 January 1952 (RTB9807); Lt. V. J. Tipton *legit*.

Paratype specimens deposited in United States National Museum; Museum of Comparative Zoology, Harvard University; Rocky Mountain Laboratory, Hamilton, Montana; British Museum (Natural History); Division of Veterinary Services, Onderstepoort; Chicago Natural History Museum; and the writer's collection. The four larval specimens are in collections of U. S. National Museum, Rocky Mountain Laboratory, Onderstepoort, and that of the writer.

This remarkable species is named for Dr. Gertrud Theiler of Onderstepoort, not only in recognition of her considerable contributions to knowledge of African ticks but also in appreciation for her generous and selfless assistance to all colleagues.

Description. MALE: *Length* from tips of palpi to posterior scutal margin 2.0 mm. to 2.3 mm., width 1.1 mm. to 1.3 mm. *Body* elongate oval, widest at level of coxa IV; lateral margins gradually converge anteriorly, almost parallel posterior of coxa IV; posterior margin broadly rounded. *Color* straw-color, yellowish brown, or brown.

CAPITULUM: *Basis capituli* measures 0.10 mm. long, 0.33 mm. wide; lateral margins parallel; posterior margin slightly convex, joining lateral margins at rounded corners, cornua absent; dorsal surface downcurved laterally, posterior half is or is not slightly depressed centrally and is either impunctate or has a few scattered punctations like those on scutum. *Palpi* narrow, elongate, pedunculate. somewhat clavate, strongly appressed laterally. Segment 1 distinctly visible, forming a narrow peduncle. Segment 2 basally forms an extension of the pedunculate segment 1; the juncture of segments 1 and 2 may be impossible to discern in dark specimens. Segments 2 and 3 strongly appressed laterally, their combined inner margin (from dorsal aspect) slightly convex; lateral margin concave centrally and with sub-basal salience extending very slightly beyond lateral margins of basis capituli. Segment 3 about half as long as segment 2, slightly wider than palpal width at juncture of segments 2 and 3; distally broadly rounded; ventrally with a small retrograde spur (best observed from lateral aspect) arising from basal margin of pit of segment 4. Segment 4 arising from pit situated apically on ventral surface of segment 3 and extending very slightly beyond apex of segment 3. About four long and four shorter pale bristles on inner dorsal margins of segments 2 and 3. Inner surface of segments 2 and 3 slightly concave. *Hypostome* (Figure 61) elongate, broadly rounded apically; dentition 3/3, in files



Figs. 32–35. *Haemaphysalis theilerae*, new species: 32, male, dorsal; 33, male, ventral; 34, female, dorsal; 35, female, ventral.

of six or seven large denticles and a few small basal denticles in the outer files; external file large and jagged, middle file slightly smaller, inner file very small; corona moderately large; length about 0.25 mm.

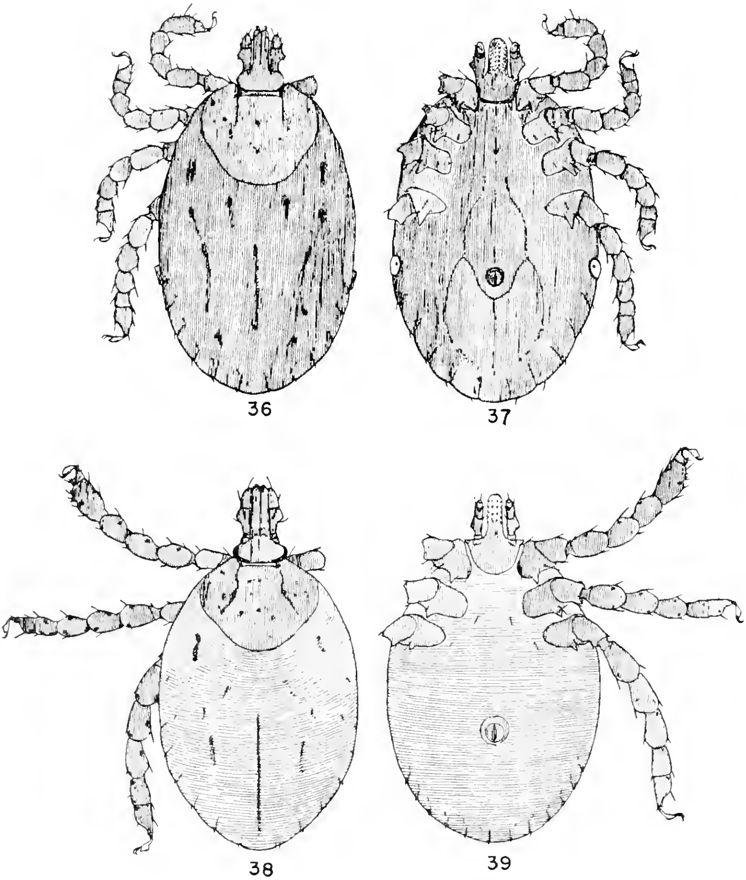
SCUTUM: *Lateral grooves* either totally indiscernible or very shallow and indistinct and extending only to mid-length of scutum. *Cervical grooves* parallel, fairly deep, V-shaped, extending to level of trochanter II. *Scutal surface* slightly arched, smooth, pseudoscutum of some specimens well marked. Punctations moderately numerous, shallow, mostly small, some medium-size anteriorly, all well spaced, scattered over entire surface. *Festoons* slightly wider than long, separated by deep grooves.

LEGS: *Coxae* each with prominent, subequal, lateral posterior spur; coxa I also with a prominent, broadly triangular, inner posterior spur separated from lateral posterior spur by deep groove; coxa II usually without inner posterior spur, in some specimens this spur slightly developed; coxae III and IV without inner posterior spur; conspicuous groove just mesad of lateral spur becoming successively more shallow and wider from coxa I to IV. *Trochanters* without ventral spurs; trochanter I dorsally with a short, knob-like, pointed spur, ventrally with external half of surface abruptly raised from internal half. *Tarsi* humped, each with a small terminal ventral spur.

Ventral integument with longitudinal roughly parallel rows of punctations, each with a short, fine, pale bristle. *Spiracular plate* as illustrated (Figure 75). *Genital aperture* between coxae II, lateral margins slightly convergent posteriorly, posterior margin straight or slightly convex, anterior margin broadly angular; apron without needle-like projections. *Genital* and *anal grooves* as illustrated.

FEMALE (described from partially engorged allotype specimen only): Critical morphological characters, i.e. general shape of palpi and basis capituli, similar in both sexes. *Length* of this specimen from tip of palpi to posterior margin of scutum 1.32 mm., from tip of palpi to posterior margin of body 3.86 mm., greatest body width 1.98 mm. *Body shape* narrow, elongate, with rounded, parallel lateral margins and rather narrowly converging anterior and posterior margins.

CAPITULUM: *Basis capituli* measures 0.45 mm. wide, 0.13 mm. long, and is shaped as in the male except that the posterior border is straight and the lateral margins slightly divergent anteriorly; the reticulate surface causes the fairly shallow, apparently circular porose areas to be of somewhat ambiguous outline; the surface is somewhat raised towards the postero-lateral corners. *Palpi* as in the male except that



Figs. 36–39. *Haemaphysalis theilerae*, new species: 36, nymph, dorsal; 37, nymph, ventral; 38, larva, dorsal; 39, larva, ventral.

they are slightly narrower, segment 3 is not wider than segment 2 and dorsally proportionately slightly longer in respect to segment 2; the ventral spur of segment 3 is reduced to a slight ridge in the female. *Hypostome* slightly notched apically, otherwise apparently as in male (not dissected).

SCUTUM: *Length* from tip of scapulae to posterior margin 1.02 mm., width almost the same. *Shape* widest at anterior fifth, lateral margins slightly converging from widest point to posterior margin which forms a slight arc; lateral margins anteriorly more acutely convergent. *Surface* lightly reticulate, with only a very few shallow, widely scattered, medium-size punctations. *Cervical grooves* moderately deep, parallel, extending to mid-length of scutum.

LEGS: Coxae, trochanters, tarsi, and other segments similar to those in male except that tarsi are slightly less humped, and the anterior margin of coxa I slopes towards the lateral rather than to the median area.

SPIRACULAR PLATE (Figure 76) as illustrated.

NYMPH: Available specimens are all more or less engorged. They resemble females so closely that only the few points of difference require elucidation. *Size* of slightly engorged specimens averages 1.32 mm. from tip of palpi to posterior body margin, 0.76 mm. from tip of palpi to posterior scutal margin, and 0.77 mm. at greatest body width; the most engorged specimen is 1.98 mm. long and 0.99 mm. at greatest width. The elongate, tapering body shape is like that of the female and the lateral margins of the scutum are slightly more convergent posteriorly in nymphs. Palpi and basis capituli are similar except for porose areas lacking in nymphs. Trochanter I lacks the dorsal spur but the coxal spurs are slightly larger in proportion to the size of the coxa as compared with the female. Hypostome dentition is 2/2. Spiracular plate as illustrated (Figure 77).

LARVA: Available specimens are pale and engorged. The body shape is like that of the female and nymph or a little more tapering posteriorly, and measures 1.32 mm. from tip of palpi to posterior body margin, 0.46 mm. from tip of palpi to posterior scutal margin, and 0.66 mm. at greatest body width. The capitulum is like that of the nymph except that palpal segment 3 is almost as long as segment 2. The scutum, which averages 0.26 mm. long and 0.30 mm. wide, is shorter in proportion to width than in nymphs, and the cervical grooves are divergent posteriorly. Coxae and tarsi are similar to those of nymphs and adults, except that the larval stage is the only one in which the posterior spur of coxa I is not lateral but rather in the middle of the length of the posterior margin.

Related Species: The shape of the basis capituli of *H. theilerae*, which in both sexes is postero-laterally rounded, and in the male lacking cornua and posteriorly convex, differs from that of all other species in this large genus throughout the world. A similar shape may be present in immature stages of a few species, but is lost in adults. Females of a few species may show a tendency to the male shape of the present species, though in no case equal it, but the associated male always differs widely in this character.

A few species of India, Indochina and the Moluccas may approach *H. theilerae* in palpal structure, but (in addition to palpal differences) are also dissimilar in position of coxal spurs and a combination of other body characters. These species are *H. obesa* Larrousse, 1925, *H. lagrangei* Larrousse, 1925, *H. kinneari* Warburton, 1913, *H. roubaudi* Toumanoff, 1940, *H. mesnardi* Toumanoff, 1940, *H. toxopei* Warburton, 1927, and a few others of southern Asia. In none of these are the palpi so markedly pedunculate, the external palpal margin concave, the pit of palpal segment 4 so distally located, or the ventral retrograde spur of palpal segment 3 so small as in *H. theilerae*. In all these species, the basis capituli differs widely from that of both sexes of the new species in that cornua are present.

Possibly *H. inermis inermis* Birula, 1895, of Caucasia, Transcaucasia, Bulgaria, France, Iran and Japan, and *H. inermis aponommoides* Warburton, 1913 (the male of which I believe is still unknown) of India and Japan are most closely related to *H. theilerae* because of somewhat similar characteristics of *both* palpi and basis capituli. The basis capituli of these forms lacks cornua and is postero-laterally rounded, but is not posteriorly convex in the male. The palpi are narrow, somewhat similarly pedunculate, and have the pit of segment 4 in about the same position as in the new species, but differ in general contour and structure and numerous other body characters.

The *Aponomma*-like features of the two subspecies of *H. inermis* were remarked upon by Nuttall and Warburton (1915), who considered *H. warburtoni* Nuttall, 1912, as a link between these aberrant forms and the rest of the genus *Haemaphysalis*. It is now apparent that *H. theilerae* shows even closer similarity to the primitive *H. inermis* than does *H. warburtoni*. Nevertheless, *H. theilerae* more closely approaches the rest of the genus in one striking character — the common basal (in this case sub-basal) palpal salience, which is absent in *H. warburtoni*. Though not considerable, this salience is present in *H. theilerae* and absent in *H. inermis* subspp. The Madagascan species can hardly be considered as a link between *H. inermis* and the rest of the genus because of its tangential geographic position, but it probably did evolve from the same stock as *H. inermis* and must be considered as an exceedingly primitive member of the genus.

Schulze (1918) considered *H. inermis* distinctive enough to erect a new genus, *Alloceraea*, for it. *H. theilerae*, however, shows so nicely the development from a primitive "*inermis* type" to a "normal *Haemaphysalis* type" that any excuse for a separate genus is entirely obviated.

Hosts: Insectivores, the tenrec, *Tenrec ecaudatus*, and the Madagascan "hedgehog" tenrec, *Setifer setosus*. See page 104 for further details.

Remarks: Other tick species collected from the same host with *H. theilerae* were: *H. simplex*, *H. elongata*, *H. tiptoni*, new species, and *H. subelongata*, new species. It appears that *H. theilerae* is quite rare, for less than 30 specimens were found on over 150 tenrecs examined by Lt. Tipton and myself, and these specimens were all taken on four hosts.

HAEMAPHYSALIS FOSSAE, new species
(Figures 40 to 43, 62, 78, 79)

Holotype: Male from a fanaloka or Malagasy civet, *Fossa fossa* (Schreber, 1777), (HH4468), Bemangidy, Poste Manantenina, Fort Dauphin, Madagascar, 23 November 1948, H. Hoogstraal *legit*. Deposited in United States National Museum, Number 2120.

Allotype: Female, same data as holotype.

Paratypes: Total 17 ♂♂ from four fanalokas, *F. fossa*, all from Bemangidy, Poste Manantenina, Fort Dauphin, Madagascar, 23 November to 4 December 1948, H. Hoogstraal *legit:* 1 ♂ (HH4480), 7 ♂♂ (HH4468), 1 ♂ (HH4510), 8 ♂♂ (HH4495).

Paratype specimens deposited in collections of United States National Museum; Museum of Comparative Zoology, Harvard University; Rocky Mountain Laboratory, Hamilton, Montana; British Museum (Natural History); Division of Veterinary Services, Onderstepoort; Institut Scientifique de Madagascar, Tsimbazaza-Tananarive; Chicago Natural History Museum; Museum National d'Histoire Naturelle de Paris; and that of the writer.

Description. MALE: *Length* from tips of palpi to posterior scutal margin 1.8 mm. to 2.1 mm.; width 0.8 mm. to 0.9 mm. *Body* narrow, elongate, converging only slightly from level of coxae II to scapulae, laterally parallel or almost so, posteriorly broadly rounded. *Color* yellowish brown.

CAPITULUM: *Basis capituli* average measuring 0.18 mm. long including cornua, 0.10 mm. long excluding cornua; 0.30 mm. wide; lateral margins carinate, slightly diverging anteriorly, posterior margin between cornua straight or very slightly convex; surface depressed between lateral carina and central area, impunctate; cornua remarkable for length which varies from half to fully as long as basis capituli and for width which is from a third to a half their length; inner margins straight, lateral margins gradually converging and more acutely curved to a point apically. *Palpi* four and a half times as wide as long (excluding posterior spur), about one and a half times as wide as long when posterior spur is included; segment 2 dorsally twice as long (excluding posterior spur) as segment 3 and at least two and a half times as wide as segment 3; apex broadly rounded. Lateral margin somewhat variable in degree of divergence bordering segment 3 and in degree of angle at which segment 2 meets segment 3 — this varies from obtuse angle illustrated to an acute angle. Segment 2 with postero-lateral margin extended to form a huge spur at least as long as cornua but wider basally and more acutely tapered to a sharp point apically; basal margin from spur to inner margin an almost straight and horizontal line; inner margin sinuous; juncture of segments 2 and 3 a straight horizontal line. Laterally, basal margin deeply concave over leg I and forming a triangular hollow between dorsal and ventral external spurs. Ventrally, basal margin with long baso-lateral spur opposite its dorsal counterpart and exactly like it or slightly narrower; basal margin from spur to inner margin slightly concave; segment 3 ventrally with a conspicuous, pointed retrograde spur arising between pit of segment 4 and lateral margin of segment 3 and overlapping anterior half of segment 2; at least two fine, pale, horizontal bristles arise from internal margin of segment 2, three or four short, fine bristles on ventral and ventro-lateral surface of segments 2 and 3. *Hypostome* (Figure 62) stoutly elongate, length about 0.16 mm., broadly rounded apically, dentition 4/4, in files of six to eight regularly and closely spaced denticles, those in the outer file slightly larger than others; corona moderate.

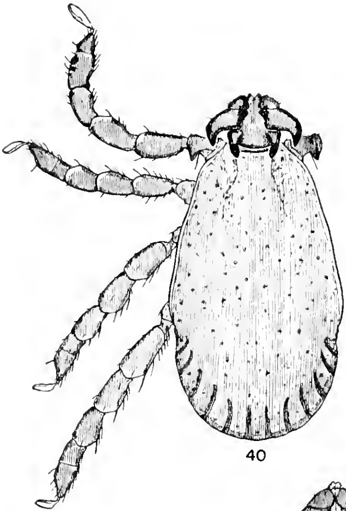
SCUTUM: *Lateral grooves* obsolete. *Cervical grooves* extending as moderately deep pits only slightly beyond apex of overlapping cornua; posteriorly of variable length and becoming gradually more shallow, slightly converging and thence widely divergent. *Scutal surface* very slightly convex centrally, sharply downcurved laterally, somewhat less downcurved posteriorly, smooth except for a few shallow depressions of variable shape and extent. Punctations rare, shallow, small or medium-sized, distantly spaced, usually entirely absent on central dorsum; a few minute punctations visible under high magnification on ome specimens, absent on others. *Festoons* about twice as long as vide, demarcating grooves fairly deep.

LEGS: *Trochanters* unarmed except for a broad, triangular spur lorsally on leg I. *Coxae* each with a comparatively small posterior pur, that on I forming a narrow triangle which may or may not reach o or slightly overlap anterior margin of II, that of II not quite so ong as I and forming a broad triangle, that of III about half as long s II, that of IV only about half as long as III; posterior spurs on I nd IV arising near inner coxal margin, those of II and III at about niddle of margin; coxae each with two pairs of fine, pale bristles. *Femora* with five pairs of conspicuous ventral bristles increasing in size listally, those of posterior legs especially strong; femur IV also with our robust pairs of bristles on anterior internal surface (opposite spiracle), those of other femora less conspicuously developed. Distal segments of legs also with three to five pairs of conspicuous, ventral oristles. *Tarsi* with dorsal margin paralleling ventral margin basally and gradually tapering as a more or less concave arc distally.

Ventral integument soft, pale, with a number of long, pale hairs especially postero-medially. *Spiracular plate* as illustrated (Figure 78). *Genital aperture* situated between coxae II, anterior margin straight, sides converging posteriorly, posterior margin narrow or pointed, surface convex; apron without needle-like projections. *Genital grooves* slightly sinuous and gradually diverging from genital aperture to posterior festoons. *Anal groove* fairly long and pointed posteriorly but not extending to genital grooves; ano-median groove fairly deep, extending to central festoon. *Festoons* more or less well marked ventrally.

FEMALE (described only from allotype specimen which was collected dead and unengorged and with legs broken): This sex is readily associated with males by similarity of palpal spurs, cornua, elongate body shape, light scutal punctation, and coxal spurs. *Length* from tip of palpi to posterior body margin 2.31 mm., from tip of palpi to posterior scutal margin 1.16 mm.; greatest body width 1.16 mm. *Body shape* flat, slightly diverging from scapulae to mid-length of scutum, laterally parallel, posteriorly broadly rounded. *Color* pale yellow.

CAPITULUM: Differing from that of male in that the palpi are only almost twice as wide as long (excluding posterior spur), the lateral margin is a straight line at a 50-degree angle, the posterior spur is somewhat inflated and segment 2 (at level of basal margin) is less than twice as wide as segment 3 and only slightly longer than segment 3; ventrally the spurs of segments 2 and 3 comparable with those of the



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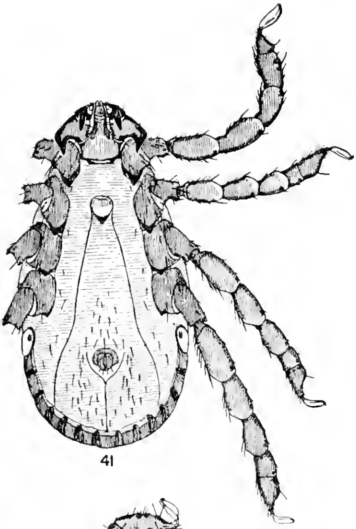

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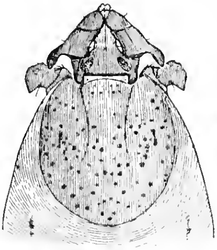

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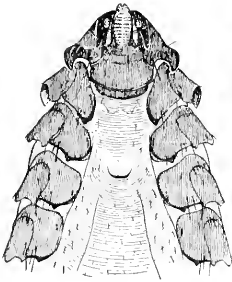

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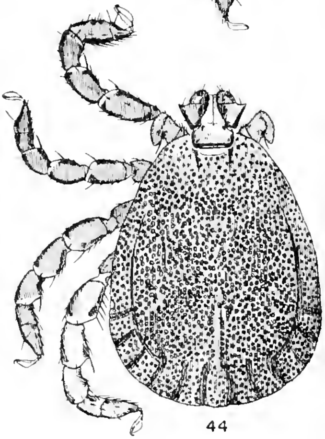

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Figs. 40–43. *Haemaphysalis fossae*, new species: 40, male, dorsal; 41, male, ventral; 42, female, dorsal; 43, female, ventral.

Fig. 44. *Haemaphysalis lemuris*, new species, male, dorsal.

male. The *basis capituli* is 0.38 mm. wide and 0.15 mm. long (including cornua), lateral margins slightly carinate and divergent anteriorly, posterior margin between cornua straight; cornua slightly over half as long as basis capituli about three-fifths as wide as long, with inner margin straight, outer margin parallel anteriorly and sharply curved to form a blunt tip distally; porose areas deep, narrow, spindle-shaped, tilted. *Hypostome* not dissected.

SCUTUM: *Measures* 0.88 mm. long, 0.75 mm. wide; *outline* converging at anterior fifth, about parallel laterally, broadly rounded posteriorly; punctations rare, scattered, shallow, large or medium size, inconspicuous; *cervical grooves* moderately deep and converging on anterior third of scutum, thence gradually more shallow and distally diverging to about three-fifths length of scutum.

LEGS: *Trochanter* I with dorsal spur. Coxae much wider than those of males but with similar spurs except that the spur of coxa IV is medial rather than near the inner margin. Other segments mostly broken.

SPIRACULAR PLATE as illustrated (Figure 79).

NYMPH and LARVA: Unknown.

Related Species: The only species in which the extreme palpal spur and cornual spur development of *Haemaphysalis fossae* is approached is *H. dentipalpis* Warburton and Nuttall, 1909, a parasite of the wild cat in Malaya and also of the tiger, tiger cat, and wild fowl in Annam (Toumanoff 1944). The palpal margins differ in that *H. dentipalpis* has two dorsal posterior spurs in place of one in *H. fossae*, and these spurs and the cornua are not nearly so elongate as in *H. fossae*. In the Asiatic species, the ventral spur of palpal segment 2 is internal rather than external as in the Madagascan species, the scutum is more heavily punctate, and the dorsal spur of trochanter I is smaller.

This species and *H. dentipalpis* might be considered as members of the *leachii* group with extremely developed capitular spurs.

Host: A carnivore, the fanaloka or Malagasy civet, *Fossa fossa*. For further details, see page 102.

Remarks: Haemaphysalis obtusa was taken from the same host individuals parasitized by *H. fossae*.

HAEMAPHYSALIS LEMURIS, new species
(Figures 44 to 49, 63, 80, 81)

Holotype: Male from a ring-tailed lemur, *Lemur catta* Linnaeus, 1758, (HH4429), Ambohimahavelona, Tulear, Madagascar, 27 October 1948, H. Hoogstraal *legit*. Deposited in United States National Museum, Number 2121.

Allotype: Female, same data as holotype, except that it is from a different host specimen (HH4433).

Paratypes: Total 3 nymphs, 4 ♂♂, 3 ♀♀.

From three specimens of *Lemur catta*, Tulear District, Madagascar, October 1948, H. Hoogstraal *legit:* 1 nymph, 1 ♀, 4 ♂♂ with same collecting data as holotype; 1 ♀ from a local captive specimen at Tulear. A single ♀ from a sikafa lemur, *Propithecus verreauxi verreauxi* A. Grandidier, 1867, (HH4432), Ambohimahavelona, Tulear. Madagascar, 27 October 1948, H. Hoogstraal *legit.*

From two skins in Museum of Comparative Zoology, Harvard University: one damaged ♀ from "*Lemur vari.*, S. Madagascar, 75.1.29.10" (this host is the ruffed lemur, *Lemur variegatus* Kerr, 1792); two damaged nymphs from "*Lepilemur leucopus*, MCZ44945, Bekily, S. E. Madagascar" (this host name is synonymized under *Lepilemur ruficaudatus* A. Grandidier, 1867, the black-tailed lemur).

The Museum of Comparative Zoology paratype specimens are deposited in their collections. The other specimens are deposited in the collections of Rocky Mountain Laboratory, Hamilton, Montana, and the writer. One paratype male is in the collection of the Museum of Comparative Zoology and another in the Division of Veterinary Services, Onderstepoort.

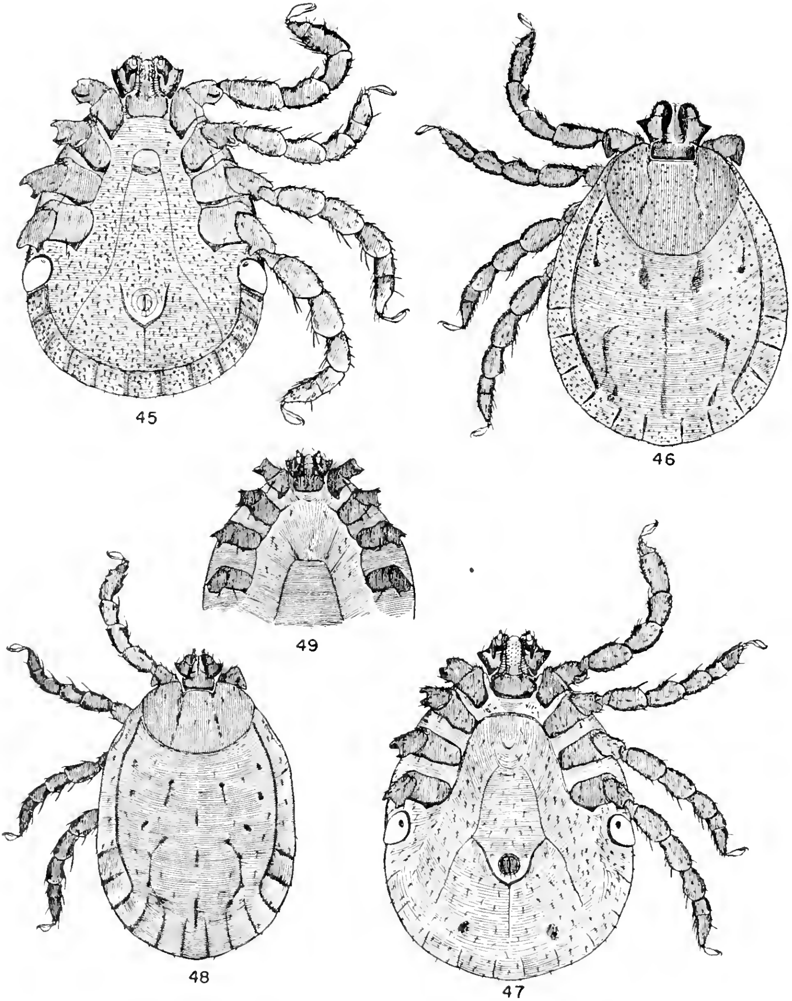
Description. MALE: *Length* from tips of palpi to posterior scutal margin 1.84 mm. to 2.05 mm.; width 1.32 mm. to 1.40 mm. *Body* broadly oval, widest at level of spiracle or first festoon, margins gradually converging anterior of spiracles, broadly rounded posteriorly from juncture of first and second festoon. *Color* brownish yellow to yellowish brown.

CAPITULUM: *Basis capituli* average measures 0.13 mm. long, 0.29 mm. wide; lateral margins parallel or minutely divergent anteriorly; posterior margin straight centrally, slightly expanded laterally to form very small, almost obsolete cornua; surface flat, lightly reticulated, impunctate. *Palpi* with reticulate surface; remarkable for the 65-degree upthrust of basal margin to a postero-lateral position and reduction of lateral surface of segment 2 to a horizontal or slightly concave margin at almost the same plane as the level of juncture of segments 2 and 3. Segment 2 forming an almost equilateral triangle with postero-lateral margin slightly flanged, and with antero-lateral margin almost straight or slightly concave. Segment 3 dorsally five-eighths as long as segment 2, meeting segment 2 in a straight line and broadly rounded apically. Ventrally, palpal outline similar except that margins are slightly more sinuous than dorsally; segment 3 with a ventral spur arising beside and posterior of pit of segment 4 and tapering to a narrow point ending about mid-length of segment 2. Bristles conspicuous, consisting of one on anterior surface near salience of segment 2, three or four on apex of segment 3, and a row of about 8 horizontal bristles arising from inner ventral margin of segment 2. *Hypostome* (Figure 63) stout, broadly rounded apically, measuring about 0.17 mm. long; dentition 3/3, consisting of jagged, adjacent, overlapping denticles in files of five or six large ones and an apical row of smaller ones; corona small. Corona-like denticles continue over anterior half of dorsal surface of cheliceral sheaths.

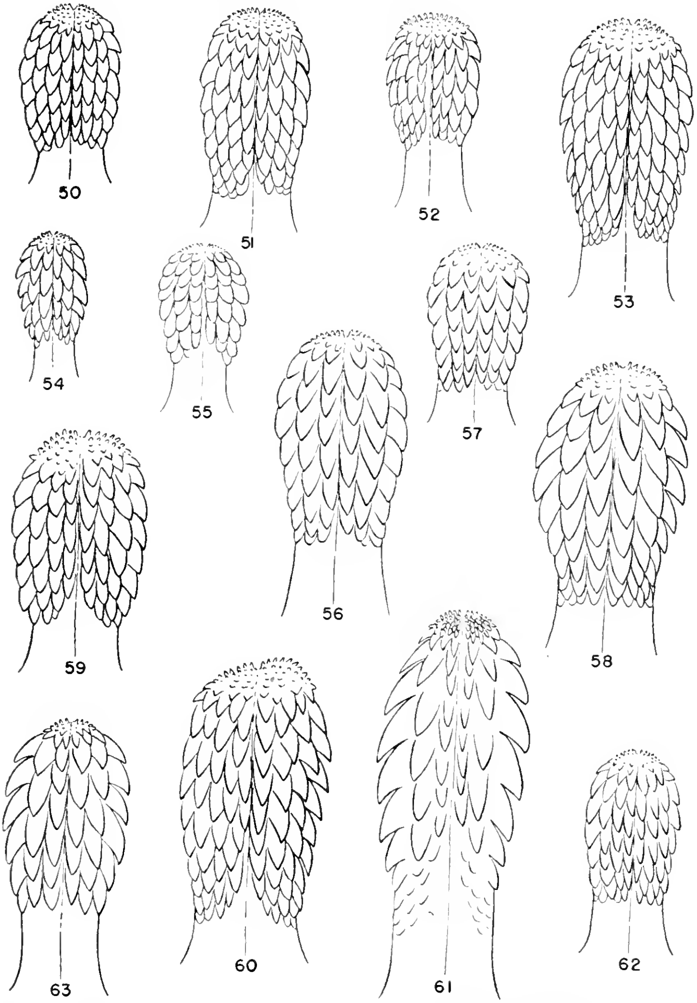
SCUTUM: *Lateral grooves* wide and deep, extending from level of coxae III to juncture of third and fourth festoons. *Cervical grooves* shallow, faint or obsolete, converging, short. *Scutal surface* flat centrally, slightly sloping around periphery; finely reticulate. Punctations numerous, subequally large, shallow, mostly evenly spaced; punctations (in some specimens) absent in a narrow posterior median line extending to level of spiracle. *Festoons* deeply and widely demarcated; anterior three pairs forming squares enclosed by lateral grooves; posterior pairs open, more elongate.

LEGS: *Coxae* each mildly spurred; coxa I pointed posteriorly and with a short, rounded or obtusely angled spur slightly overlapping posterior angle; coxae II and III rectangular, each with a broadly rounded, ridge-like spur slightly salient over posterior margin; coxa IV very large, rectangular, with a slightly more pointed and elongate posterior spur near inner margin; each coxa with a conspicuous long, pale bristle at external end of posterior spur. *Trochanters* I to III ventrally each with small, stubby, almost obsolete spur, trochanter IV ventrally with a stout blunt spur about two-fifths as long as width of trochanter; trochanter I dorsally with a long, broad, pointed, shield-like spur with reticulate surface and with a conspicuous, long, pale bristle arising just beneath internal margin of spur. *Femur* IV with a conspicuous row of about five long, pale bristles ventrally adjacent to spiracles. *Tarsus* I with concave dorsal margin, tarsi II, III, and IV with dorsal margin basally parallel to ventral margin and distally narrowing in a slightly concave arc.

VENTRAL SURFACE: *Integument* soft, pale; finely horizontally striated; with numerous large, shallow punctations most of which bear a short pale bristle. *Spiracular plate* as illustrated (Figure 80). *Genital aperture* situated between coxae II, lateral margins slightly converging anteriorly, anterior margin straight, posterior margin forming a very obtuse angle; margin of apron with needle-like projections. *Genital*



Figs. 45–49. *Haemaphysalis lemuris*, new species: 45, male, ventral; 46, female, dorsal; 47, female, ventral; 48, nymph, dorsal; 49, nymph, ventral.



Figs. 50–63. Hypostomes of species of *Haemaphysalis:* 50, *H. obtusa* Dönitz, 1910, male; 51, *H. obtusa* Dönitz, 1910, female; 52, *H. simplex* Neumann, 1897, male; 53, *H. simplex* Neumann, 1897, female; 54, *H. simplex* Neumann, 1897, nymph; 55, *H. elongata* Neumann, 1897, male; 56, *H. elongata* Neumann, 1897, female; 57, *H. tiptoni*, new species, male; 58, *H. tiptoni*, new species, female; 59, *H. subelongata*, new species, male; 60, *H. subelongata*, new species, female; 61, *H. theilerae*, new species, male; 62, *H. fossae*, new species, male; 63, *H. lemuris*, new species, male.

and *anal grooves* as illustrated. *Festoons* conspicuous.

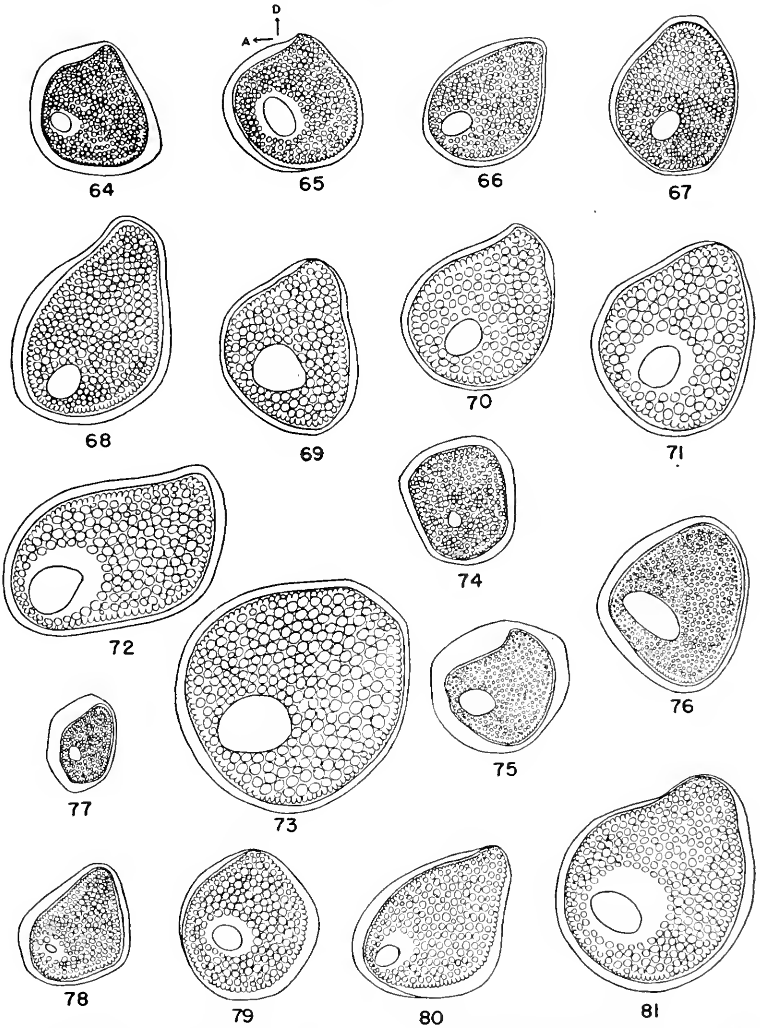
FEMALE (Described from engorged specimens only): The female is essentially similar to the male in critical diagnostic criteria of palpal structure, coxal armature, conspicuous reticulation, shape of basis capituli, and general body shape. *Length* from tips of palpi to posterior body margin from 2.86 mm. to 4.00 mm.; from tips of palpi to posterior margin of scutum from 1.20 mm. to 1.45 mm.; greatest body width from 1.90 mm. to 3.00 mm. *Body shape* broadly ovate, more narrow anteriorly than posteriorly, periphery elevated dorsally. *Color* brownish amber or brown.

CAPITULUM: *Palpi* as in male except that postero-lateral margin of segment 2 is usually concave and at a 45- to 65-degree angle, the antero-lateral margin of segment 2 may be as in male or more concave, and the slight uptilt of the lateral salience is absent. *Basis capituli* measures 0.15 mm. long, 0.38 mm. wide; surface heavily reticulate; posterior margin straight, cornua absent; porose areas very shallow and shape difficult to discern because of heavily reticulate surface. *Hypostome* apparently as in male (not dissected).

SCUTUM: Slightly wider than long, measures 0.86 mm. long from tips of scapulae to posterior margin; 1.00 mm. wide. *Shape* broadest at anterior two-fifths, gradually curved anterior of greatest width, sharply convergent posterior of greatest width; posterior border straight, half as long as greatest width of scutum. *Surface* markedly reticulate, with moderately numerous small, shallow, inconspicuous punctations. *Cervical grooves* superficial, forming concave arcs extending somewhat beyond mid-length of the scutum.

Body dorsally with broad, deep lateral grooves extending from widest point of scutum to juncture of third and fourth festoon; festoons conspicuous; median and paramedian posterior grooves present. Integument horizontally striated with numerous small, shallow punctations. Body ventrally with similar integumental striations but punctations less numerous and each with a short bristle. Genital aperture of indefinite shape situated at basal level of coxae II. Genital and anal grooves as illustrated. Spiracular plate as illustrated (Figure 81).

LEGS: *Coxae* proportionally narrower than in male, spurs on I, II and III all but obsolete, spur on IV about as in male but situated in middle of posterior border. *Trochanters* ventrally with only a suggestion of a spur formed by a subapical groove delimiting a faintly ridged apical surface; trochanter I dorsally as in male.



Figs. 64–81. Spiracular plates of species of *Haemaphysalis:* 64, *H. obtusa* Dönitz, 1910, male; 65, *H. obtusa* Dönitz, 1910, female; 66, *H. simplex* Neumann, 1897, male; 67, *H. simplex* Neumann, 1897, female; 68, *H. elongata* Neumann, 1897, male; 69, *H. elongata* Neumann, 1897, female; 70, *H. tiptoni,* new species, male; 71, *H. tiptoni,* new species, female; 72, *H. subelongata,* new species, male; 73, *H. subelongata,* new species, female; 74, *H. subelongata,* new species, nymph; 75, *H. theilerae,* new species, male; 76, *H. theilerae,* new species, female; 77, *H. theilerae,* new species, nymph; 78, *H. fossae,* new species, male; 79, *H. fossae,* new species, female; 80, *H. lemuris,* new species, male; 81, *H. lemuris,* new species, female. *A,* anterior; *D,* dorsal.

NYMPH (described from a single very small engorged specimen from lot HH4429): Salient characters as in female with some modifications. *Length* from tips of palpi to posterior body margin 1.45 mm., from tips of palpi to posterior scutal margin 0.36 mm.; greatest body width 1.02 mm. *Body* shape as in female except that lateral margins are not so expanded and diverge only slightly.

CAPITULUM: *Basis capituli* measures 0.07 mm. long, 0.17 mm. wide; surface markedly reticulate; lateral margins slightly divergent anteriorly, posterior margin straight; cornua very small. *Palpi* as in female except that postero-lateral margin of segment 2 is slightly convex; surface markedly reticulate.

SCUTUM: Shape ovate, three-fifths as long as wide; measuring 0.33 mm. long; 0.53 mm. wide; widest at anterior third and forming a wide arc posteriorly and a flatter arc anteriorly. *Surface* highly reticulate, impunctate. *Cervical grooves* somewhat deeper than in female, traces extending to posterior margin.

LEGS: *Coxae* each with a small, pointed, posterior spur, on I at posterior point, on II and III at about middle of margin, on IV near inner margin; at least one conspicuous bristle arising just externally from beside each spur. *Trochanters* without spurs except dorsally on I.

LARVA: Unknown.

Related Species: Because of extreme displacement of the basal palpal margin to a lateral position and reduction of the lateral surface of segment 2 to a short, horizontal or slightly concave margin, it appears that *Haemaphysalis lemuris* has stemmed from *H. vidua* Warburton and Nuttall, 1909, which was collected from a palm civet, *Paradoxurus*, sp., in the Federated Malay States. *H. vidua* is, however, a narrow, elongate species with cornua, without lateral margins, and with a long spur at least on coxa IV.

In addition to the new Madagascan species, another primate-infesting species appears to have evolved from *Haemaphysalis vidua*. This is *H. hylobatis*, described by Schulze (1933) from *Hylobates syndactylus*, a gibbon of south Sumatra. *Haemaphysalis hylobatis* is remarkably similar to *H. lemuris*. It differs, however, in that the displacement of the posterior palpal margin in both sexes is not so extreme as in *H. lemuris*; very pronounced cornua are present in both sexes (obsolete or almost obsolete in *H. lemuris*); dentition is 4/4 rather than 3/3 as in *H. lemuris*; coxal spurs are stronger and coxal shape is slightly different than in *H. lemuris*, etc.

Hosts: Several species of lemurs (Primates), *Lemur catta*, *L. varia-*

gatus, *Lepilemur ruficaudatus*, and *Propithecus v. verreauxi*. See page 100 for further details.

Remarks: No other species of ticks were taken from numerous other lemurs which we collected or examined in Madagascar.

III. OTHER GENERA OF TICKS IN THE MALAGASY FAUNAL REGION

Endemic Species

Argasidae: No endemic species of the family Argasidae have been reported from any of the islands of the Madagascan archipelago. Lt. Tipton found several engorged larval argasid ticks on unstated species of bats near Fianarantsoa and Andranobaka on the Tananarive-Majunga road. These larvae are somewhat similar to those of *Ornithodoros salahi* Hoogstraal, 1953, and, I presume, belong to an undescribed, endemic species.

Ixodidae: It is not likely that *Boophilus fallax* Minning, 1934, is an endemic Madagascan tick although it has been sometimes considered or at least inferred to be in this category.

Ixodes lunatus Neumann, 1907, is the only definitely known endemic Madagascan tick species, aside from the haemaphysalid ticks already discussed. Lt. Tipton obtained specimens from *Rattus rattus* at the following localities: kilometer 69 on the Tamatave road, Tanandavy (Ambohimahasoa), Morazano and Andrambovata near Fianarantsoa, and Ambatofinandrahana. He took three nymphs, two males, and ten females from seven rats. Dr. G. Theiler informs me in correspondence that she has identified this species from collections made from *Rattus alexandrinus* in Madagascar. Lt. Tipton also took two larvae from a long-tailed, shrew-like tenrec, *Nesogale dobsoni* (Thomas, 1884), at kilometer 69 on the Tamatave road, a female from a Madagascan "hedgehog" tenrec, *Setifer setosus* (Schrēber), at Ambohimahasoa, and a female from the same host species on the Tamatave road.

The only host previously reported for *I. lunatus* has been *Nesomys* (= *Hallomys*) *audeberti* Jentinck, 1877, a monotypic endemic genus of murid rodent. Lt. Tipton's and Dr. Theiler's records for both domestic rats and two kinds of endemic insectivores are, therefore, of some interest. The close relationship between *I. lunatus* and *I. schillingsi* Neumann, 1901, has been discussed by Colas-Belcour and Grenier (1942), who believe that the two may be entitled to only subspecific rank of one species. *I. schillingsi* is known only from certain monkeys in Mozambique (Neumann, 1901), Kenya, and the Anglo-Egyptian Sudan (Hoogstraal, personal collecting).

As noted on page 39, except for the nine *Haemaphysalis* species and *Ixodes lunatus* discussed above, we are certain of no other endemic ticks in the Madagascan archipelago (excluding the Seychelles). The unidentified argasid parasite mentioned above will probably prove to be an addition to this small representation.

Introduced Species

Argasidae: The eyeless tampan, *Ornithodoros moubata* (Murray, 1877), an important vector of human relapsing fever in many areas of Africa, is present in the central-western part of Madagascar, principally in the Morandava-Majunga area, where it has frequently been associated with relapsing fever (Lamoureux, 1913A, B; Suldey, 1916; Poisson, 1927; Poisson and Decary, 1930; Bück, 1935, 1948A, C; Le Gall, 1943; Millot, 1948; Neel, Payet and Gonnet, 1949; Decary, 1950; and Colas-Belcour, Neel and Vervent, 1952). The tick is very common between the Betsiboka and Manambola rivers, and is most numerous in Soalala District. It is said that Vazimba tribesmen used to keep tampans in their houses to scare their Sakalava neighbors from entering. (Lamoureux, 1913A; Decary, 1950).

Although *O. moubata* has not been reported from the Comoros group, Neel, Payet, and Gonnet (1949) state that relapsing fever of the apparent type borne by this tick exists at Dzaoudzi.

Argas persicus (Oken, 1818), the fowl tick, has not been reported from Madagascar according to Millot (1948); but Bück (1935, 1948A, C) states that it is present in coastal areas of that island, although the fowl diseases frequently transmitted by this tick have not been recognized there.

The fowl tick has been long known from Mauritius Island (Guérin-Méneville, 1837) as *Argas mauritianus*; cited by De Charmoy, 1915. According to Moutia and Mamet (1947) it occurs only sporadically and seems to be held in check by unknown factors. De Charmoy (1925) advised strict quarantine of imported fowls in order to prevent new introductions of *A. persicus*. In Reunion, this tick is particularly abundant in coastal areas (Gillard, 1949).

Otobius megnini (Dugès, 1883), the spinose ear tick of cattle, which sometimes causes severe discomfort when it lodges in ears of human beings, has been reported from Madagascar only recently (Bück, 1948A, B; Courdurier, Bück and Quesnel, 1952). It is found in Tananarive area, and Bück believes that it may have been introduced via air travellers. This is a well-known species in southern Africa whither it has been introduced from the Americas.

O. megnini is readily overlooked during usual searching for ticks and it is probable that it was introduced on African cattle and is more widely spread in Madagascar than present knowledge indicates. If specimens had entered Madagascar in ears of air travellers, they would have been quickly noticed and destroyed. Larvae secrete themselves in walls or under rocks or wood and it is unlikely that this stage could have been exported from Africa.

IXODIDAE: *Amblyomma variegatum* (Fabricius, 1794) is well known from Madagascar where it occurs practically everywhere, but chiefly in the western lowlands and in the south. It is uncommon on the plateau. Aside from specimens on usual hosts, Lt. Tipton took a nymph from a bird, *Centropus toulou toulou* (Müller), the Madagascar coucal, at Marovoay. Dr. G. Theiler informs me in correspondence that she has identified nymphs from domestic chickens and larvae from dogs from Madagascar. I took a nymph from a tenrec, *Tenrec ecaudatus* (Schreber), at Bemangidy, Poste Mananteina, Fort Dauphin. I have also seen a nymph in the British Museum (Natural History) collection from a chameleon, *Chamaeleo pardalis*, from Antongil Forest, Eastern Madagascar. An adult specimen of *A. variegatum*, in the Neumann collection, taken from a sailor at Nossi-Be, has been reported by Joyeux (1915). Zumpt (1950) recorded a male and two nymphs from cattle, and a nymph from a dog, at Lac Alaotra. Courdurier, Bück, and Quesnel (1952), in a Q fever study, mention this as a common tick on cattle.

A. variegatum also occurs in the Comoros Group (Millot, 1948) and in Mauritius (De Charmoy, 1915; Moutia and Mamet, 1947). In Reunion, it is found chiefly in the lowlands and is most abundant from December to March, during the rains (Gillard, 1949).

A. variegatum is an ubiquitous bovine parasite of tropical Africa and mountainous areas of Arabia, and has become an important pest in the West Indies, where it has been long established from early introductions.

In Madagascar, *A. variegatum* is an important vector of heartwater (*Rickettsia ruminantium*). Lesions from bites of this tick so frequently result in bacillary infections leading to ulcerous lymphangitis that horse raising is badly hampered (Bück, 1935, 1948A, C). This latter affliction is also common in the coastal areas of Reunion (Gillard, 1949). *A. variegatum* is also associated with *Babesia berbera* (Bück and Metzger, 1940) of cattle.

Amblyomma hebraeum Koch, 1844. the South African bont tick, arrives in Madagascar on imported cattle, but is destroyed before it can establish itself (Bück, 1948A).

Neumann's (1901) report of *Amblyomma rhinocerotis* (de Geer, 1778) (= *A. petersi* of authors), from Madagascar has been widely quoted by subsequent authors. This rhinoceros tick, which ranges from the Sudan to Zululand, and which rarely parasitizes other hosts, is obviously an unlikely inhabitant of Madagascar. Neumann's record, from the Hildebrandt collection, like that of *Aponomma exornatum*, is probably due to mixed locality labels.

Aponomma exornatum (Koch, 1844) was reported from Madagascar by Neumann (1901). Howard (1908), Poisson (1927), Bedford (1932), and Millot (1948) copied this record. *A. exornatum* is a widely-spread African parasite of *Varanus* lizards. Neumann's material from the Hildebrandt collection was possibly mislabeled. There is some question as to the presence of this tick in Madagascar.

Boophilus fallax Minning, 1934, is considered by some workers as a "native" Madagascan parasite. Colas-Belcour and Millot (1948) surmise that *B. fallax* is of Indian origin. Anastos (1950) believes that this species is actually *B. microplus* (Canestrini, 1888), a widely-spread tropical American and Oriental cattle parasite.

Dr. G. Theiler, who has studied African ticks and their movements probably more intensively than anyone else, informs me in correspondence that she now believes that Madagascan populations of *B. fallax* were introduced from Africa at about the same time as *Amblyomma variegatum*. Although *B. fallax* is not widely distributed in Africa, it is quite common in scattered localities in eastern and southern Africa.

Numerous early reports of *B. decoloratus* (Koch, 1844) of Africa in the Madagascar islands are all referred by Minning (1934) to *B. fallax*. The possibility that the common African *B. decoloratus* has been or will be introduced into this area should be considered, especially because of its small size and inconspicuousness.

B. fallax (or more probably *B. microplus*) occurs in Madagascar chiefly in the western and south-western coastal areas (Morandava, Tulear, Diego Suarez, Tamatave, Nossi-Be) and also on the plateau around Tananarive (Courdurier, Bück, and Quesnel 1952). Zumpt (1950) recorded four females from cattle at Lac Alaotra. Reports of

B. decoloratus from Mauritius (De Charmoy, 1915; Moutia and Mamet, 1947) and from Reunion (Gillard, 1949) probably actually refer to *B. fallax*. Minning (1934) and Millot (1948) report *B. fallax* from the Comoros group and Millot reports it from Mauritius also.

Diseases associated with *B. fallax* are redwater (*Babesia bigemina*) in Madagascar (Bück, 1935, 1948A, C) and in Reunion (Gillard, 1949); and bovine anaplasmosis or gallsickness (*Anaplasma marginale*), ovine babesiosis (*Babesia ovis*) (Bück, *loc. cit.*). equine biliary fever (*Nuttallia equi*) (Bück and Ramambazafy, 1950), and bovine babesiosis (*Babesia berbera*) (Bück and Metzger, 1940) in Madagascar.

Boophilus caudatus Neumann, 1897, has been provisionally identified from Maroantsetra, Madagascar, from a male and a nymph removed from a child (Colas-Belcour and Millot, 1948), and was reported from Reunion by Neumann (1897). Anastos (1950) considers *B. caudatus* to be actually *B. microplus* (Canestrini, 1888).

Hyalomma transiens Delpy, 1949, and *Hyalomma rufipes rufipes* Koch, 1844, have been identified by Dr. G. Theiler from Madagascan goats, according to correspondence from Dr. Theiler. These are both widely-ranging African parasites of domestic animals and of some wild animals.

The genera *Haemaphysalis* and *Ixodes* are represented in this area only by endemic species. It is surprising that the common dog-tick of Africa and southern Asia, *Haemaphysalis leachii* (Audouin, 1827), does not appear to have established itself here.

Rhipicephalus sanguineus sanguineus (Latreille, 1806), the cosmopolitan brown dog-tick, occurs, but is not common, in coastal areas of Madagascar. In 1943 it appeared for the first time in Tananarive dog kennels and was incriminated in the transmission of canine biliary fever (*Babesia canis*) (Bück and Lamberton, 1946; Bück, 1948A, C). Gillard (1949) reports this tick from Reunion. De Charmoy (1915) and Moutia and Mamet (1947) noted it from Mauritius.

R. evertsi evertsi Neumann, 1897, has been reported from Mauritius (De Charmoy, 1915; Moutia and Mamet, 1947), but whether it is established was not stated. Bück (1940, 1948A) noted that it is imported into Madagascar from Africa but is destroyed before it can become established.

Rhipicephalus simus simus Koch, 1844, was reported from Madagascar by Neumann (1911). This record has been repeated by Brumpt (1921), Tonelli-Rondelli (1938), and possibly others. Bück's (1948A) remarks (as "*Haemaphysalis simus*", apparently copied from Poisson's

[1927] vague remarks) would appear to indicate that this tick is not established in Madagascar.

Rhipicephalus capensis Koch, 1844, has been identified from collections from cattle arriving in Madagascar from the Union of South Africa, according to Dr. G. Theiler in correspondence. This species is apparently not established in Madagascar.

Margaropus winthemi Karsch, 1879. The same remarks as for *Rhipicephalus capensis* apply to this tick.

IV. HOST-PARASITE RELATIONSHIPS AMONG ENDEMIC MALAGASY TICKS

Long isolation has produced in the Madagascan archipelago a bizarre array of endemic vertebrates consisting largely of a wide variety of species in a few, tightly-restricted groups. The known endemic ticks are almost all narrowly host-specific on certain of these groups.

MAMMALS

A count of endemic Malagasy land-mammals, exclusive of bats, in Allen's (1939) checklist shows that there are 32 forms of insectivores, 12 of rodents, 10 of carnivores, and 41 of lemurs (primates) in this area. The combination of so few major groups in one great tropical or temperate land area is unequalled except in Australia. The composition of the Malagasy fauna — relatively many insectivores and primates and very few rodents and carnivores — is entirely unique. The origins of this mammalian fauna are difficult to ascertain but its tick parasites appear to be definitely easier to associate with other continental faunae, possibly because of slow and moderate speciation in the genera concerned, *Ixodes* and *Haemaphysalis*.

It is readily seen that the composition of the indigenous tick fauna — so far as now known — follows the same pattern as that of mammals. Endemic ticks consist of nine known *Haemaphysalis* species and one *Ixodes* species.

LEMURS

Haemaphysalis lemuris, new species, a parasite of lemurs, is one of the very few distinctive ectoparasites that has evolved on primates. Most ectoparasites now confined entirely or mostly to primates are either typically rodent or insectivore parasites or, even if now confined to primates, are only slightly modified from those of rodents or insectivores. This lemur parasite seems to have evolved from stock now represented in Asia by carnivore parasites. It is very closely related to another primate parasite, *H. hylobatis* of Sumatran gibbons.

The unique composition of the Malagasy mammal fauna immediately suggests a plausible reason for the evolution of a primate parasite. Here primates (lemurs) comprise 43 per cent of the local forms of land mammals. This percentage of primates is probably at least ten times that of any other area in the world.

Many of the Madagascan lemur species are still locally surprisingly common in spite of intense persecution from the indigenous and European human population, at least in the southern areas which I visited. There is considerable evidence to show that the fantastic deforestation of Madagascar has considerably reduced the number of lemur species and the range of remaining species. The current wanton slaughter of lemurs for food, which we saw in many places, is said to result from only a few generations of "civilized" appetites. The known abundance of primate species and the surmised large populations of many of these species in relatively recent times indicate why chances for evolution of a primate parasite here have been greater than probably anywhere else in the world.

In view of lemurs' highly developed dental and digital adaptations for meticulous combing, picking, rubbing, and grooming of skin and hair, the existence of tick parasites on their bodies would appear to be indeed precarious. The rarity of individuals found on any single host, and the very few hosts found infested out of the numbers which I examined, may attest to the success of lemurs' grooming efforts.

H. lemuris is characterized especially by extreme displacement of the posterior palpal margins and is undoubtedly derived from southern Asiatic carnivore-parasite stock. A closely related Sumatran gibbon parasite, *H. hylobatis*, has also evolved from this stock (*cf.* page 94). Although several morphological features of this species are unique in this genus, no readily explainable functional reasons for these characters present themselves.

We do not yet have sufficient data to draw valid conclusions concerning host-preferences of *H. lemuris* among the various groups of lemurs. Of the four species of hosts on which these ticks have been found, *Lemur catta*, *Lemur variegatus*, *Lepilemur ruficaudatus*, and *Propithecus v. verreauxi*, the first three belong to one of the three subfamilies of Madagascan Lemuridae (*i.e.* Lemurinae), and the last-named to the family Indriidae. We did not collect the aye-aye, the single species of Daubentoniidae. The following lemur species which I examined yielded no ticks: four *Cheirogaleus major major* E. Geoffroy, three *C. medius medius* E. Geoffroy, two *Microcebus murinus murinus* (J. F. Miller), three *M. murinus rufus* Wagner (all Lemuridae, Cheirogaleinae); six *Lemur macaco collaris* E. Geoffroy (Lemuridae, Lemurinae); and a single *Avahi laniger laniger* (Gmelin) (Indriidae). Whether the absence of ticks on all Cheirogaleinae, which are small lemurs, is significant or not remains to be seen.

CARNIVORES

Since many species of haemaphysalid ticks show strong predilection for carnivore hosts it is not surprising to find that although Malagasy carnivores comprise only about ten per cent of the local fauna they harbor two distinct species of the nine known haemaphysalid ticks of this area.

These two ticks, *H. obtusa* and *H. fossae*, new species, are of interest in that they both have obviously evolved from "*leachii* stock" of southern Asia (*cf.* page 48 and 87). One shows obsolescence of *leachii* characters while the other shows extreme development of typical characters. *H. obtusa* retains the general *leachii* facies (palpal shape and spur development, body and scutal shape, coxal and leg characters) but has many degenerate features. *H. fossae*, on the other hand, has become quite elongate, like certain others in the *leachii* group (*i.e. H. numidiana, H. dentipalpis, H. l. humerosoides*, etc.), and has developed massive spurs but retained other group features in normal fashion.

It is surprising that *H. leachii* itself has thus far not been found in the Malagasy Region, either as an introduced species on dogs from Africa or Asia, or as a native tick which has evolved little or not at all from the several African and Asiatic subspecies.

Unfortunately, we examined very few dogs or cats for ticks during our stay in Madagascar. Only a few *Rhipicephalus s. sanguineus* were found on dogs. Another introduced carnivore, the rasse, *Viverricula indica rasse* (Horsfield, 1821), (a native of Java which has been brought to Madagascar since the coming of man) yielded no ticks when examined.

Both *H. obtusa* and *H. fossae* were found on the fanaloka or Malagasy civet, *Fossa fossa* (Schreber, 1777) (Viverrinae), a monotypic genus between the true civets and the genets. *H. fossae* was found on no other carnivore examined. *H. obtusa* was also found on the fossa, *Cryptoprocta ferox* Bennett, 1833, a unique monotypic "cat" in a subfamily of its own (Cryptoproctinae), and on the endemic galidia or Malagasy mongoose, *Galidia galera* (Schreber, 1777) (Herpestinae). We examined none of the very few other Malagasy carnivores.

RODENTS

Lt. Tipton examined few endemic rodents in Madagascar, and the few we managed to secure were obtained under conditions not conducive to parasites remaining on them until removed from the traps. Except for the ubiquitous introduced house rats, the dozen kinds of Malagasy rodents are all endemic and most of them are rare and difficult to obtain.

Ixodes lunatus was originally described from one of these endemic rodents, *Nesomys* (= *Hallomys*) *audeberti* Jentinck, 1879, a monotypic endemic murid genus. As reported on page 95, Lt. Tipton also found specimens on an insectivore, the Madagascan "hedgehog" tenrec, *Setifer setosus* (Schreber), and on *Rattus rattus*. Dr. Theiler has identified specimens from *Rattus alexandrinus* from Madagascar. It would appear that *Ixodes lunatus* is typically a rodent parasite which also attacks certain insectivores, but the survey of rodent parasites in this area is so meagre that no valid conclusions can be drawn.

IFSECTIVORES

The Malagasy insectivores belong to the primitive family Centetidae, which shows considerable adaptive radiation. A number of these animals have habits like shrews and hedgehogs, some are mole-like in habits and appearance, and others are aquatic like muskrats. Of all these, only the hedgehog-like species, the tenrecs, and the so-called Madagascan hedgehog, have been examined for ticks. Nothing is known about the presence or absence of ticks on the others.

The 32 forms of Centetidae comprise about a third of the Malagasy land-mammal fauna exclusive of bats, and the tenrec and "hedgehog" are often very common locally though some of the other kinds are excessively rare or restricted in distribution.

Five of the nine haemaphysalid species of this area are insectivore parasites. Of these five, only one (*H. simplex*) has (rarely) been found on other hosts (*cf.* page 57). The only other tick known to parasitize these insectivores in *Ixodes lunatus* (*cf.* page 95), from Lt. Tipton's single collection.

The five species parasitizing insectivores live among the hosts' normal hairs and also among their spiny hairs. The circumference of these spines apparently necessitates special adaptations in order that the tick may obtain a firm grasp. This need is met by members of the *elongata* group (*H. elongata*, *H. tiptoni*, new species, and *H. subelongata*, new species) in extreme development of coxal and trochantal spurs *in both sexes* (*cf.* page 63). These spurs are also more or less well developed in the known immature stages, which are, however, small enough to slip among the hairs and spines without utilizing the basal segments of the legs for additional support. I amused myself in Madagascar by forcing *elongata* group ticks from their sites of attachment and watching them slip these spurs around adjacent spines when crawling about on the host. A rare and less specialized spiny-insectivore parasite, *H. theilerae*, new species, an exceedingly primitive representative of the genus, has an interesting and rather unusual continuous coxal groove which becomes gradually narrower and deeper from the fourth to the first leg; on leg I it is bounded by two spurs for additional support and trochanter I is ridged for support of the adjacent hair or spine. The fifth insectivore-parasite, *H. simplex*, shows these characters in only normal, not exceedingly developed form, but it is also the only one of these five ticks which is also known to attack non-insectivorous hosts. Possibly *H. simplex*'s range of host predilections is not so closely confined to these animals as are those of the other species. In addition, it appears from collecting notes that *H. simplex* prefers the ears of spiny hosts and seldom ventures among the spines on the body.

It may be worth noting that *H. numidiana* Neumann, 1905, an African and Asiatic hedgehog parasite, shows few of these specialized characters, although it does feed among the spines as well as on the somewhat exposed ears of the host. Perhaps not surprisingly, it is a rare tick in nature — and even rarer in collections. In less specialized characters to be enumerated below, *H. numidiana* does, however, follow the pattern of *leachii*-derived insectivore parasites.

The proximity and inflexibility of the hosts' spiny hairs, especially basally, obviously preclude feeding by a large tick. The *elongata* group is nicely adapted, in spite of an obviously hearty appetite, to reaching the hosts' skin. Each species has a narrow, elongate shape, unique posterior integumental bulging in males, convex scutum, rounded female body margins, and specialized manner of female integumental stretching when feeding (*i.e.* largely posteriorly until near the end of feeding, only then also laterally). *H. simplex* is also an elongate, rather narrow species and *H. theilerae* is comparatively so small that these adaptations are hardly necessary.

The various adaptations in four of these species for the wide palpi, which are a trademark of the *H. leachii* group, to move and fit over the scapulae and anterior leg, while far from unique, make an interesting study in functional anatomy. The combinations of basal palpal characters relating to distance from the scapulae and anterior legs, degree of inflation, and contours and emarginations can readily be discerned from the illustrations and descriptions. Primitive *H. theilerae* can be excluded from consideration in this respect because it has long, narrow palpi which obviously do not hinder its progress among the narrowly-spaced spines of the hosts.

The insectivores which have been examined for ticks are: the Madagascan "hedgehog" tenrec, *Setifer setosus*, the tenrec, *Tenrec ecaudatus*, and the streaked tenrecs, *Hemicentetes nigriceps* and *H. semispinosus*.

Ticks found on *Setifer setosus* were: *Haemaphysalis simplex, H. elongata*, and *H. theilerae*. Species from *Tenrec ecaudatus* were: *Haemaphysalis simplex, H. elongata, H. tiptoni, H. subelongata* (found on no other host), and *H. theilerae*. On *Hemicentetes semispinosus* occurred *Haemaphysalis elongata*, and *H. tiptoni*, but on *Hemicentetes nigriceps* only *Haemaphysalis tiptoni* was collected.

BIRDS

The birds of Madagascar show considerable endemicity and originate from both the African and Asiatic faunae (Rand 1936). It is not surprising that *Haemaphysalis hoodi madagascariensis*, the only known endemic avian tick, is so closely allied to both an African and an Asiatic (Singapore) avian parasite that its closest relationship is difficult to determine. *Haemaphysalis hoodi madagascariensis*, has been found only on the Madagascan coucal, *Centropus t. toulou* (*C. madagascariensis* of authors).

A normally mammalian parasite, *Haemaphysalis simplex*, has also been found on the crested wood ibis (*Lophotibis cristata cristata*).

Because of the paucity of our knowledge of avian ticks in this area it is not possible to discuss endemic bird-tick relations at greater length.

REMARKS

Considerably more tick and host collecting is necessary to elucidate many interesting lacunae in our knowledge of this subject in this fascinating area. Other tick species probably remain to be found, and many other hosts have escaped examination. The collections reported in this paper, although of moderate size, were made only from certain areas and incidentally to other major projects.

It is, unfortunately, not possible to determine the distribution of these ticks in the Archipelago within the biotic provinces of Madagascar or in relation to altitude and climatic conditions, as Rand (1936) has done so well for birds, because of the paucity of available data on these ticks.

V. ORIGINS OF MALAGASY TICK FAUNA

A brief recapitulation of the Malagasy tick fauna in relation to its apparent origins is of some interest.

Millot (1948; 1952) stated that Malagasy ticks are certainly all of African origin. This is entirely or almost entirely true for *introduced* species (pages 96 to 100). The *endemic* species show some affinities with African fauna, but many more with that of southern Asia.

The genus *Haemaphysalis* is much more highly developed in southern Asia than anywhere else in the world. As in Madagascar, haemaphysalid species form the bulk of the southern Asiatic ixodid ("hard") tick fauna.

The haemaphysalid ticks account for only a small proportion of the African tick fauna. The very important African genus *Rhipicephalus*, consisting of over forty species, is entirely unrepresented by endemic species in the Malagasy Faunal Region. *Amblyomma* ticks, represented in Africa by many more species than in Asia, are lacking in endemic species in the Malagasy Region except in the Seychelles. *Hyalomma* ticks, which appear to be North African or Near Eastern in derivation, have also failed to reach Madagascar except by recent importation in small numbers.

We have observed that *Haemaphysalis obtusa*, *H. fossae*, new species, and the three species of the *elongata* group are all derived from a *leachii* prototype of southern Asia. *H. theilerae*, new species, and *H. lemuris*, new species, have each evolved from distinctly Asiatic species. The status of origin of *H. simplex* is uncertain.

The bird-parasitizing *H. hoodi madagascariensis* is very closely related to avian parasites, *H. hoodi hoodi* of tropical Africa, and to *H. doenitzi*, *H. centropi*, and *H. minuta* of southern Asia, Ceylon, and the Philippines. It is difficult to say whether the Madagascan tick is more closely allied to its African or to its Asiatic relatives.

The single species of *Ixodes*, *I. lunatus*, which attacks both insectivores and rodents, is but slightly differentiated from an East African monkey-parasite, *Ixodes schillingsi* (*cf.* page 100). *I. schillingsi* however, is closely related to other species of Europe, New Guinea, and Australia.

It is of further interest to note that the two endemic ticks showing African affinities (*H. hoodi madagascariensis* and *I. lunatus*) are almost the same morphologically as their continental relatives, but the seven species showing Asiatic affinities differ widely from any other known species. It is therefore suggested that the Asiatic representatives of the Malagasy Faunal Region are of much more ancient origin (and more numerous) than are the endemic species or subspecies of African origin.

The relations of so many endemic tick species of Madagascar with the fauna of continental and insular southern Asia are so obvious that no conclusions other than the above can be drawn from our present knowledge. If these deductions are true, it is difficult to determine why they should be so diametrically opposed to Millot's (1952) conclusions for the origins of the entire fauna of Madagascar. Millot believes that this fauna is so strongly dominated by African elements that even the earlier proposed designation of Malagasy Faunal Region should be discarded. It is possible that subsequent search for other species will reveal enough endemic ticks of African origin to modify our conclusions in this respect. It seems advisable to put aside further discussion of this subject until additional collecting from endemic hosts has supplied enough material to adequately judge the Madagascan tick fauna.

If present evidence is eventually confirmed by further collections, the tick parasites of Madagascan mammals may prove valuable indicators of the origins of their hosts.

SUMMARY

1. The following information is furnished for the known haemaphysalid species of the Malagasy Faunal Region: *Haemaphysalis obtusa* Dönitz, 1910, redescription of male, original description of female and nymph, first "wild" records from Madagascar Island, new host records; *Haemaphysalis hoodi madagascariensis* Colas-Belcour and Millot, 1948, translation of original description into English; *Haemaphysalis simplex* Neumann, 1897, redescription of male, original description of female and nymph, new host and distribution records;

Haemaphysalis elongata Neumann, 1897, redescription of male and female, clarification of female characteristics, proposal of an *elongata* group to include *H. elongata*, *H. tiptoni*, new species, and *H. subelongata*, new species.

2. The following new species of *Haemaphysalis* ticks are described: *H. tiptoni* from tenrecs, *H. subelongata* from tenrecs, *H. theilerae* from tenrecs, *H. fossae* from carnivores, and *H. lemuris* from lemurs. *H. theilerae* is of special interest in that it is a primitive species related to the *Aponomma*-like *H. inermis* subspp. of Asia and southern Europe. The genus *Alloceraea*, erected by Schulze for *H. inermis* subspp., which would also include *H. theilerae*, is considered to be unnecessary and unnatural splitting.

3. The only other endemic tick (in addition to the nine endemic species of *Haemaphysalis* mentioned above) is *Ixodes lunatus* Neumann, 1907, for which new host and distribution records are furnished. The presence of an undescribed argasid parasite of bats, which is probably also endemic, is indicated.

4. Literature and unpublished records of introduced tick species are critically reviewed.

5. Host-tick relationships of the Malagasy Faunal Region are discussed in the light of composition of the mammalian fauna, structural peculiarities of mammal hosts, functional anatomy and adaptations of ticks, etc.

6. The endemic tick fauna of the Malagasy Region (excepting the Seychelles), so far as presently known, consists largely of species very obviously derived from continental and insular southern Asia. While maintaining the peculiarities of their Asiatic stock, these species are strongly separated by modification of basic characters. One species shows obviously African affinities and is but slightly different from its African relative. Another tick is a taxonomic subspecies of an African species but is almost equally closely related to an Asiatic species. These two African representatives appear to be of much more recent origin than those of Asiatic origin.

7. The apparent origins of this tick fauna are so different from recent conclusions about the origins of the Madagascan animal fauna as a whole that it is suggested that possibly numerous other endemic species showing African affinities await discovery.

8. The non-endemic tick fauna of this island group, established as the result of man's activities, particularly with importation of domestic animals, is entirely or almost entirely of African origin.

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CONTENTS

INTRODUCTION

Thanks to a generous grant from the Rockefeller Foundation, I was able in the spring of 1951 to spend four months on museum studies in the United States and Canada. The main task was to carry out the basic taxonomic work for a carabid fauna of Newfoundland. I started with the determination of my own material, collected in 1949 with a grant from the Arctic Institute of North America, and then proceeded with the study and revision of the Newfoundland material in the larger public and private collections, as far as available. Labrador and Nova Scotia records were listed at the same time. Eventually the study was enlarged to cover all carabid species common to Europe and North America with the purpose of making a revised list for publication. Occasionally other special taxonomic problems were attacked. Thus preliminary work was done for revisions of the North American species of *Diachila, Blethisa, Notiophilus, Pristodactyla,* and *Europhilus.* The results obtained will appear in a series of papers, in part regional (covering Newfoundland, Nova Scotia, and Labrador), in part purely taxonomic (on the genera mentioned above and on the Kirby types). It seems convenient, however, to present here a summary of all changes proposed in the nomenclature of North American Carabidae, especially as some of them are not concerned with the special investigations mentioned. In the latter cases full reasons for my opinions are given here, but in the others the reader is referred to the special papers mentioned above. As a rule, only new synonymies are listed, but in a few cases the confirmation of already accepted synonymies by re-examination of typical specimens is considered worth giving.

In three cases (*Bembidion concolor, Pterostichus mandibularis, Agonum affine*) the revised synonymy unfortunately requires that a name in use is transferred from one species to another within the same genus. In order to avoid hopeless confusion in these cases I have proposed to keep the name to be moved "in quarantine" for the time being, i.e. to regard it as a *nomen in praesens suppressum* until the name substituted for it in its old sense has become generally established.

Furthermore, I should like to point out that declarations of synonymy in this paper do not necessarily forbid the existence of *subspecific* differences. In some cases sufficient material was not available to decide about subspecies, and in such cases a statement of the *specific* identity is always the first and most important step.

The main part of my work was done at the Museum of Comparative Zoology, Cambridge, Massachusetts, where the foundation of North American coleopterology, the Leconte Collection, is preserved, supplemented in an excellent way by the admirable and modern Fall Collection. The Curator of Coleoptera at this museum, Dr. P. J. Darlington, Jr., gave me unlimited support not only from the museum's collections but also from his own vast experience of North American Carabidae.

At the National Museum, Washington, District of Columbia, where the Casey Collection was the most interesting subject, I was generously aided by Dr. E. A. Chapin and Dr. R. E. Blackwelder. In New York, Dr. M. A. Cazier placed the material of the American Museum at my free disposal. I am especially indebted to Dr. W. J. Brown, of the Department of Agriculture, Ottawa. Dr. Brown's great experience of the fauna of northern regions was of indispensable value to me. The very rich collection of Canadian-Arctic beetles in his charge at Ottawa revealed several Palæarctic species hitherto unknown in America.

Very useful was the examination of W. Kirby's types at the British Museum, and the C. G. Mannerheim types in the Museum at Helsingfors, Finland. I am most grateful to the officials of these two institutions for kind advice and assistance.

Most of the synonymies proposed below concern names given by Casey. It may therefore be of some interest to say a few words on his work and his collection, preserved at the United States National Museum in an excellent condition, thanks to the efforts of L. L. Buchanan (*vide* his paper of 1935, and Blackwelder 1950). This collection possesses a remarkable and unique quality: I was unable, in any case, to find two species confused under the same name label! This is characteristic of the positive side of the remarkable person Thomas L. Casey. He was an engineer by profession, but also as an entomologist. To him the members of a species had to show *absolute identity*, like the cogs of a machine. He made no allowance for intraspecific variation. Almost any deviation was described as a new species or, in some few cases, subspecies. Probably it never occurred to him that his rigid demand upon the species concept was contradictory to evolution, simply because he did not realize that his specimens had been living organisms. Perhaps he did not believe in evolution at all. Apparently he never allowed himself to work by instinct, to get a general idea of the "habitus" of a species. It appears from what I was told, that to identify a specimen he always put it directly under the microscope at high magnification. It is no wonder that many of Casey's "species" are simple aberrations or even anomalies, especially among those described in the last volume of his Memoirs (Vol. 10, 1924). His method of giving all revisions and most of his descriptions in the form of dichotomous tables was extremely unfortunate. Closely related species often became widely separated in this way, and the reader is usually completely denied the opportunity of making a comparative analysis of them. Only in exceptional cases can the student get an indisputable determination by using Casey's keys, and therefore, an examination of the typical specimens in his collection is usually the only reliable way to get definite determinations. The types must be examined in all groups treated by Casey before North American coleopterology can get a safe basis on which to build in the future. This will result in a complete rearrangement of Leng's Catalogue. Judging from my experience in Carabidae, I should guess that not more and perhaps less than 20 per cent of Casey's species will prove valid or worthy of being preserved even as subspecies.

In this connection I can not help regretting the rigid regulations of most American museums, forbidding any type specimen to be taken outside the building. At present it is impossible to have a Leconte and Casey type side by side for comparison. I dare say that a more liberal attitude would shorten by decades the way to stability in the coleopterological taxonomy of North America.

The male genitalia of Carabidae in most genera possess excellent specific characters. When male types were available, I therefore usually made a genital slide. This is indicated by an asterisk (*) after the species name.

It may be useful to describe briefly the simple method used for genital dissections. After the insect has been softened it is put under the microscope in a drop of water, the elytra are moved apart, and the penis is dissected out through the dorsum. It is cleaned in water, transferred for a minute to absolute alcohol, and finally put into clove oil, which makes the whole organ transparent and thus reveals the armature of the internal sac. Boiling in KOH immediately after the dissection removes muscles and ligaments and gives clearer details. The habit, prevalent in America, of killing and preserving beetles in alcohol is not good for specimens used for dissection: they get too fragile and, above all, the rapid infiltration of the alcohol into the living insect often causes a total or partial eversion of the internal sac, putting it in a position quite unsuitable for comparative study. Beetles killed in vapour of ethyl acetate give the best dissections.

The following abbreviations of museum names are used here.
AMN = American Museum of Natural History, New York.
BMN = British Museum, Natural History, London.
CMP = Carnegie Museum, Pittsburgh, Pennsylvania.
DAO = Department of Agriculture, Ottawa, Ontario, Canada.
MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts.
NMW = United States National Museum, Washington, D. C.
UMH = Zoological Museum, University, Helsingfors, Finland.

CHANGES IN SYNONYMY

The species are arranged according to Leng's Catalogue (1920), with species added in Supplements I–V (1927–1948) put at the end of each genus (with the number of the supplement in brackets). The Leng number of each species is given, and names listed by him as synonyms are marked "(syn.)". Species not listed in the catalogue or supplements are inserted without numbers in the proper places below.

115 *Trachypachys holmbergi* Mnh. 1853 (*inermis* Mtsch. 1864 [not 1845]), is not identical with *zetterstedti* Gyll. 1827, as maintained by Hatch (1933b, p. 117). The penis is quite different.

227 *Elaphrus obliteratus* Mnh. 1853. Types ♂* ♀ (Kadjak, Alaska, UMH) = *lapponicus* Gyll. 1810 (which is not a synonym of 230 *riparius*).

227(syn.) *E. obscurior* Kby. 1837. Type ♀ (BMN) = *lapponicus* Gyll. 1810 (227 *obliteratus* Mnh. 1853).

233 *E. ruscarius* Say 1834. I am unable to find any other difference from 230 *riparius* L. 1761 than the coarser and sparser punctuation of the prosternum. Outer and inner structure of penis seems identical.

The two forms are at least not specifically distinct.

235 *Diachila subpolaris* Lec. 1863. Type ♂* (Hudson Bay Territory, CMP) = *arctica* Gyll. 1808 sbsp. *amoena* Fald. 1835, described from southern Siberia. The species usually placed under the name "*subpolaris*" in American collections is *polita* Fald.

238 *Blethisa multipunctata* L. 1761 occurs in America only as sbsp. *aurata* Fisch. 1828 (*hudsonica* Csy. 1924).

239 *B. columbica* Csy. 1909. Type ♂* (British Columbia) = 240 *oregonensis* Lec. 1853, as already suggested by Hatch (1949, p. 114).

18582(I) *B. hudsonica* Csy. 1924. Type ♂* (Edmonton, Alberta) = *multipunctata* L. 1761 sbsp. *aurata* Fisch. 1828.

241(syn.) *Loricera neoscotica* Lec. 1863. Type ♀, paratype ♂* (Nova Scotia) = 241 *pilicornis* Fbr. 1775 (*coerulescens* auct. nec L.), contrary to Csy. 1920, p. 146.

248(syn.) *Notiophilus hardyi* Putz. 1866. Original example from Newfoundland in coll. Lec. (MCZ) = *aquaticus* L. 1761, in accordance with Fall 1906, p. 84, but contrary to Csy. 1920, p. 140, 143.

250(syn.) *N. evanescens* Csy. 1913. Type and 4 paratypes (Boulder, Colorado) = 250 *simulator* Fall 1906, as stated by Csy. himself (1914, p. 356), but later disputed by him (1920, p. 141).

18584(I) *N. sierranus* Csy. 1920. Single type ♀ (California) = 255 *nitens* Lec. 1857 (dwarf specimen).

18585(I) *N. coloradensis* Csy. 1920. Single type ♂ (Boulder, Colorado) = 247 *semistriatus* Say 1823.

18587(I) *N. parvus* Csy. 1920. Single type ♀ (New York) = 251 *novemstriatus* Lec. 1848.

N. lanei Hatch 1949. Paratypes ♂* ♀ (Pierce, Idaho) = 18586(I) *directus* Csy. 1920.

258 *Leistus nigropiceus* Csy. 1913. Paratype ♂* (Metlakatla, British Columbia) = 257 *ferruginosus* Mnh. 1843, as already suggested by Hatch (1949, p. 115).

276a *Nebria castanipes* Kby. 1837. Type ♀ = 276b *moesta* Lec. 1850. Kirby's name is valid. It is a subspecies of the Palaearctic *gyllenhali* Schh. (*rufescens* Stroem).

276b *N. moesta* Lec. 1850. The 4 types (Lake Superior) have nothing to do with 276 *sahlbergi* Fisch. 1821. The closest relative of *moesta* is the Palaearctic *gyllenhali* Schh. 1806, of which it may be regarded as a subspecies (Bänninger 1925, pp. 259, 279). Valid name is *castanipes* Kby. 1837 (see above).

18590(I) *N. labradorica* Csy. 1920. Type and 5 paratypes (West St. Modest, Labrador) = 276a *gyllenhali* Schh. 1806 sbsp. *castanipes* Kby. 1837 (*moesta* Lec. 1850) (see above).

18591(I) *N. prominens* Csy. 1920. Type and paratype (Mt. Washington, New Hampshire) = 276a *gyllenhali* Schh. 1806 sbsp. *castanipes* Kby. 1837 (*moesta* Lec. 1850).

18592(I) *N. curtulata* Csy. 1924. Type and 2 paratypes (West St. Modest, Labrador) = 276a *gyllenhali* Schh. 1806 sbsp. *castanipes* Kby. 1837 (*moesta* Lec. 1850).

18598(I) *N. nimbosa* Csy. 1920. Single type ♀ (Mt. Washington, New Hampshire) = 285 *suturalis* Lec. 1850.

323 *Dyschirius aeneus* Dej. 1825 is different from *integer* Lec. 1849 which has a very characteristic frontal sculpture. Apparently, as already suggested by Fall (1926, p. 130), the Palaearctic *aeneus* does not occur in America. I tried in vain to get a specimen of *frigidus* Mnh. 1853 for comparison; the type is not in UMH.

18603(I) *D. aureolus* Notm. 1920. Paratype ♂* (Schoharie, New York, Staten Island Museum) = *politus* Dej. 1825 from Europe and Siberia. *D. subpunctatus* Hatch, according to 2 paratypes*, is related but specifically distinct.

20696(II) *D. secretus* Fall 1926. Paratype ♂* (Anchorage, Alaska) = *helléni* Müll. 1922 (*norvegicus* Munst. 1923) from Siberia and Fennoscandia.

367(syn.) *Clivina collaris* Hbst. 1786 was regarded as a form of *fossor* L. 1761 by Jeannel (1941, p. 257; also by Hatch 1949, p. 118) but is specifically distinct as suggested by Brown (1950, p. 198). Jeannel originally failed to find males among *collaris* because there is no external sexual difference in this species. When, later, males were dissected (Jeannel 1949, p. 4) he regarded the two forms as specifically distinct but was unable to separate them on penis characters. A comparison of clove oil slides, however, reveals clear differences (fig. 1). The basal part of the penis is differently shaped, with stronger carinae in *fossor*, and also the apex. The spines of the internal sac are longer in *fossor*. The simplest external character separating the two species is the stronger, almost granulate microsculpture of the last ventral segment in *collaris*. This species apparently is constantly macropterous whereas *fossor* is dimorphic, in America as well as in Europe. I have seen both forms from Montreal and from Newfoundland.

367(syn.) *C. elongata* Rand. 1838, according to the description of colour and the locality (Massachusetts), belongs to *collaris* Hbst. 1786 and not to *fossor*.

411 *Bembidion littorale* auct. Amer., nec Ol. = 18612(I) *B.* (*Chrysobracteon*) *carrianum* Csy. 1924: type ♀ (Edmonton, Alberta), 2 paratypes ♂* (St. Albert, Alberta). See also 412 *lacustre*, below. The Palaearctic *litorale* Ol. does not occur in America.

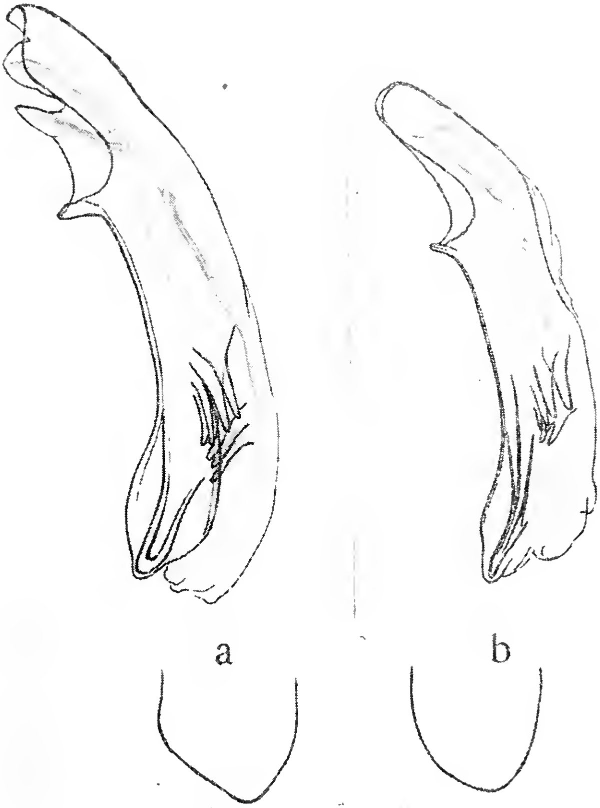


Fig. 1. Penis, side view, and dorsal view of apex: *a*, *Clivina fossor* L. (Montreal); *b*, *C. collaris* Hbst. (Stoneham, Massachusetts.)

412 *B. lacustre* Lec. 1848. Type ♀ (Lake Superior) = 408 *B.* (*Chrysobracteon*) *inaequale* Say 1823. Fall (1910, p. 94) was wrong in uniting *lacustre* and *littorale* auct. Amer.

474 *B. turbatum* Csy. 1918. Type and paratype, both ♀ (Colorado) = subspecies of the Siberian *B.* (*Plataphus*) *gebleri* Gebl. 1833 (*frigidum* J. Sahlb. 1880). And 475 *B. conflictum* Csy. 1918 is a synonym (see below).

475 *B. conflictum* Csy. 1918. Type ♂* (Colorado) = 474 *B.* (*Plataphus*) *gebleri* Gebl. 1833 sbsp. *turbatum* Csy. 1918. Penis is a little less arcuate than in *gebleri f. typ.* (fig. 11d; Lindroth 1943, p. 10), with inner armature almost identical. In DAO is 1♂ (Mabel Lake, British Columbia, H. Leech) which according to the penis apparently belongs to the same form. In NMW are 1♂ each* from National Park, Wyoming, and Banff, Alberta.

479 *B. bucolicum* Csy. 1918. According to Netolitzky (1931, p. 161), who examined types of both, this is a synonym of *B.* (*?Trechonepha*) *kuprianovi* Mnh. 1843 (Leng, p. 53, without a number). Another synonym is *ovipenne* Mtsch. 1845 from Sitka, Alaska (Netolitzky 1935, p. 23).

483 *B. solutum* Csy. 1918. Single type ♀ (California) = 482 *B.* (*Plataphus*) *planatum* Lec. 1848.

484 *B. adjutor* Csy. 1918. Type ♀, paratypes ♂* ♀ (California, 3 localities) = 482 *B.* (*Plataphus*) *planatum* Lec. 1848.

486. *B. simplex* Hayw. 1897 is not the manuscript name of Lec., to which the author refers. Leconte's "type" (Lake Superior) = 476 *B.* (*Plataphus*) *rusticum* Csy. 1918. None of the 4 "*simplex*" in coll. Lec. belongs to Hayward's species, a *Trechonepha*. Penis of *simplex* Hayw., figure 9e.

487 *B. planiusculum* Mnh. 1843. Types ♂* ♀ (Sitka, Alaska, UMH). This species, a true *Plataphus*, has been generally misidentified. Usually the name has been used for 476 *rusticum* Csy. (see Notman 1920, p. 185). Penis of *planiusculum*, figure 11a.

492 *B. flebile* Csy. 1918. Type ♀, several paratypes, ♂* ♀ (California) = *B.* (*Plataphus*) *complanulum* Hayw. 1897 (*nec* Mnh. 1853). The name *flebile* is valid for the small, light western form of the species (*cf.* 18623 *carolinense*, below).

493 *B. timefactum* Csy. 1918 (not *tumefactum*). Type ♀, paratype ♂* (California) = 492 *B.* (*Plataphus*) *flebile* Csy. 1918 (see above).

494 *B. decrepitum* Csy. 1918. Type ♂* (Colorado) = *B.* (*Plataphus*) *flebile* Csy. 1918 (see above).

498 *B. complanulum* Mnh. 1853. Type ♂* (UMH), paratype ♀ (coll. Lec., MCZ), both from Kadjak, Alaska. It is a true *Plataphodes* (see 18627 *parvulum,* below), whereas the *complanulum* of Hayward (1897, p. 65) and most other authors is a *Plataphus* (see 492 *flebile,* above). Only Fall, in his collection, recognized the true *complanulum.* Penis, figure 10a.

521 *B. concolor* Kby. 1837. Type ♀ = 529 *B.* (*Hirmoplataphus*) *longulum* Lec. 1848 and Kirby's name is therefore valid for this species. To avoid hopeless confusion, I propose to regard *concolor* as a name "*in praesens suppressum*", until *salebratum* Lec. 1848 has had time to become established as a substitute for *concolor* auct.

560 *B. nitens* Lec. 1850. Type ♂* (Lake Superior) = *B.* (*Peryphus*) *grapei* Gyll. 1827. Penis, figure 12b.

567 *B. militare* Csy. 1885. Single type ♂* (Long Island) = 572 *B.* (*Peryphus*) *lacunarium* Zimm. 1869 (*picipes* auct. nec Kby.) (see below).

572 *B. picipes* Kby. 1837. Types ♂* ♀ = 560 *B.* (*Peryphus*) *grapei* Gyll. 1827 (*nitens* Lec. 1850). *B. picipes* auct. must be changed to *lacunarium* Zimm. (see below).

572(syn.) *B. plagiatum* Zimm. 1869. Original ♀ (possibly the type, from Maryland) in coll. Lec. (MCZ) belongs to a species unknown to me and is not identical with *lacunarium* Zimm. (*picipes* auct. nec Kby.; see Hayward 1897; Fall 1926, p. 133).

572(syn.) *B. lacunarium* Zimm. 1869. Original ♀ (possibly the type, from New York) in coll. Lec. (MCZ) = *picipes* auct. nec Kby., and is therefore valid.

575(syn.) *B. sordidum* Kby. 1837. Type ♀ is a *Peryphus* distinct from *bimaculatum* Kby., well characterized in the original description and especially by the structure of the internal sac of the penis, as shown by males from Red River, Manitoba, compared with the type.

582 *B. canadense* Hayw. 1897. Type ♀ (Ottawa, Canada, MCZ) and a ♂* from Montreal, Canada (coll. Fall), both = *B.* (*Peryphus*) *stephensi* Crotch 1866, of western Europe.

583 *B. lepusculum* Csy. 1918. Single type ♂* (Colorado) = 584 *B.* (*Peryphus*) *petrosum* Gebl. 1833 (*lucidum* Lec. 1848).

584 *B. lucidum* Lec. 1848. Type ♀, paratypes ♂* ♀ (all Lake Superior) = *B.* (*Peryphus*) *petrosum* Gebl. 1833 (*substrictum* Lec. 1848). Under the label "*lucidum*" in coll. Lec. is represented also *rupicola* Kby. (*lucidum* auct.) from California, Colorado, and New Mexico.

584(syn.) *B. substrictum* Lec. 1848. Type ♀ (Lake Superior) = *B.* (*Peryphus*) *petrosum* Gebl. 1833 (*lucidum* Lec. 1848).

585 *B. castalium* Csy. 1918. Type ♀, paratypes ♂* ♀ (Las Vegas, New Mexico) = 584 *B.* (*Peryphus*) *petrosum* Gebl. 1833 (*lucidum* Lec. 1848).

588a *B. rupicola* Kby. 1837. Types ♂* ♀ = *B.* (*Peryphus*) *lucidum* auct. (nec Lec. 1848), as already stated by Fall (1926, p. 133), whose label is attached to the ♀ type. Fassati's opinion that *rupicola* Kby. is a synonym of *ustulatum* L. (*tetracolum* Say) is wrong.

588b *B. tetracolum* Say 1823 sbsp. *nactum* Csy. 1918. Single type ♀ (New York) = a pure synonym of *B.* (*Peryphus*) *ustulatum* L. 1758 (*tetracolum* Say 1823). See also Fassati 1950 (p. 43).

590 *B. dilatatum* Lec. 1848. Type ♀ (Pennsylvania) = large form of 592 *B.* (*Bracteomimus n. subg.*) *chalceum* Dej. 1831. Several ♂♂ from New England, Nova Scotia, and Newfoundland, completely agreeing with the type externally, have penis structure identical with normal *chalceum*.

599 *B. fuscicrum* Mtsch. 1855 (correctly *fuscicrus*) = *B.* (*Peryphus*) *obscurellum* Mtsch. 1845. It is a circumpolar species which has gone under several names (*cf.* Netolitzky 1935, p. 33; 1942–43, p. 116). The penis is identical in specimens from northeastern Europe, Siberia and North America, and there seems no reason to establish any subspecies on the rather inconstant colour characters.

620 *B. mobile* Csy. 1918. Single type ♀ (Metlakatla, British Columbia) = 681 *B.* (*Eupetedromus*) *incrematum* Lec. 1860.

621 *B. semotum* Csy. 1918. Single type ♂* (California) = 681 *B.* (*Eupetedromus*) *incrematum* Lec. 1860.

622 *B. nubiferum* Csy. 1918. Single type ♂* (California) = 681 *B.* (*Eupetedromus*) *incrematum* Lec. 1860.

623 *B. gulosum* Csy. 1918. Single type ♀ (Idaho) = 681 *B.* (*Eupetedromus*) *incrematum* Lec. 1860.

646 *B. monstratum* Csy. 1918. The 6 types (northern Illinois), all more or less immature = 648 *B.* (*Notaphus*) *posticum* Hald. 1843.

647 *B. fenisex* Csy. 1918. The 3 types (Indiana) = 648 *B.* (*Notaphus*) *posticum* Hald. 1843, but are a little larger than usual and with broader prothorax.

649 *B. plectile* Csy. 1918. The 2 types (Indiana; Wisconsin) = 648 *B.* (*Notaphus*) *posticum* Hald. 1843, the form with extended yellow markings.

652 *B. graphicum* Csy. 1918. Type ♂ (Bayfield, Wisconsin) = 612 *B.* (*Notaphus*) *nigripes* Kby. 1837.

654 *B. exclusum* Csy. 1918. Single type (Illinois) = 648 *B.* (*Notaphus*) *posticum* Hald. 1843.

655 *B. intermedium* Kby. 1837. Type ♀ = 651 *B.* (*Notaphus*) *patruele* Dej. 1831. Fall (1926, p. 133) was therefore right in regarding *rapidum* Lec. 1848 as the right name for *intermedium* auct.

657 *B. marcidum* Csy. 1918. Single type from New York, and additional specimen from Long Island, New York = 648 *B.* (*Notaphus*) *posticum* Hald. 1843, being unusually broad but otherwise typical.

679 *B. arcuatum* Lec. 1878. Type ♀, paratype ♂* (Marquette, Michigan) = 681 *B.* (*Eupetedromus*) *incrematum* Lec. 1860, type ♂* (Sitka, Alaska).

680 *B. graciliforme* Hayw. 1897. According to coll. Hayward (MCZ) it is a *Eupetedromus,* clearly different from 681 *incrematum* Lec. (*arcuatum* Lec.) (*cf.* Netolitzky 1931, p. 158). In coll. Casey it stands as "*arcuatum* Lec."

681(syn.) *B. nigripes* Mnh. 1852 (nec Kby. 1837). Three ♂ "types"* (Sitka, Alaska, UMH) = *B.* (*Eupetedromus*) *incrematum* Lec. 1860. Netolitzky (1942–43, p. 48) confused Mannerheim's species with *tinctum* Zett. (*cf.* Lindroth 1944).

681(syn.?) *B. dentellum* Thbg. 1785 does not occur in North America, since *B.* (*Eupetedromus*) *incrematum* Lec. is specifically distinct.

715 *B. tolerans* Csy. 1918. Type ♀, 6 ♂* ♀ paratypes (all Metlakatla, British Columbia) = 713 *B.* (*Furcacampa*) *decipiens* Dej. 1831, *sensu* Csy. 1918 (723 *versicolor* Lec. 1848).

723 *B. versicolor* Lec. 1848. Type ♀ (Lake Superior) and many additional specimens in coll. Lec. = 713 *B.* (*Furcacampa*) *decipiens* Dej. 1831, *sensu* Csy. 1918. But "*versicolor* Lec." in coll. Casey = *B.* (*Furcacampa*) *mimus* Hayw. 1897 (724 *pellax* Csy. 1918) (see below, unnumbered, at end of genus).

724 *B. pellax* Csy. 1918. Type ♂*, paratype ♀ (Rhode Island) = *B.* (*Furcacampa*) *mimus* Hayw. 1897 (p. 108) (see below, unnumbered, at end of genus).

731 *B. fraternum* Lec. 1857. Type ♀ (Georgia), paratype ♂* (Louisiana) = 648 *B.* (*Notaphus*) *posticum* Hald. 1843, according to an original ♂*, probably the type ("Middle States"), in coll. Lec.

754 *B. sulcatum* Lec. 1848. Type ♀ (Lake Superior) = *B.* (*Diplocampa*) *transparens* Gebl. 1829, circumpolar in distribution.

754(syn.) *B. trepidum* Lec. 1848. Type ♀ (Lake Superior) = 754 *B.* (*Diplocampa*) *transparens* Gebl. 1829 (*sulcatum* Lec. 1848).

767 *B. connivens* Lec. 1852. Type ♂* (California) = 772 *B.* (*Trepanedoris*) *cautum* Lec. 1848 (type ♀, Rocky Mountains; genital slide made from Leconte specimen from La Veta, Colorado). The penis apex is a trifle longer in *connivens*, possibly a subspecific difference.

18621(I) *B. notmani* Csy. 1924. Single type ♀ (New York) = 476 *B.* (*Plataphus*) *rusticum* Csy. 1918.

18622(I) *B. essexense* Csy. 1924. Single type ♂* (New York) = 486 *B.* (*Trechonepha*) *simplex* Hayw. 1897.

18623(I) *B. carolinense* Csy. 1924. Type ♂* (North Carolina) = 492 *B.* (*Plataphus*) *flebile* Csy. 1918, but is the larger eastern form, probably worthy of being retained as a subspecies.

18624(I) *B. keeneanum* Csy. 1924. Single type ♀ (New York) = 18623(I) *B.* (*Plataphus*) *flebile* Csy. 1918 sbsp. *carolinense* Csy. 1924 (see above).

18627(I) *B. parvulum* Notm. 1922 = 498 *B.* (*Plataphodes*) *complanulum* Mnh. 1853. The type ♂* of Mannerheim's species (UMH) and 1 ♂* of *parvulum* from the original locality (Paradise Park, State of Washington, coll. Fall) agree completely in penis characters. This synonymy is indicated by Fall in his collection. Penis of *parvulum*, figure 10a.

18641(I) *B. exiguiceps* Csy. 1924. Type ♀ (British Columbia) = 584 *B.* (*Peryphus*) *petrosum* Gebl. 1833 (*lucidum* Lec. 1848). Whether the narrow head and prothorax indicate a subspecies, I am unable to decide.

18642(I) *B. semiaureum* Fall 1922. Type ♀, paratype ♀ (Humboldt, California), additional ♂* (Snoqualme, State of Washington), all in coll. Fall (MCZ) = macropterous subspecies of 594 *B.* (*Peryphus*) *sejunctum* Csy. 1918 (single type ♂* from New Mexico). There are small but apparently constant differences in the internal sac of the penis.

18646(I) *B. oblectans* Csy. 1924. Single type ♀ (Edmonton, Alberta) = 681 *B.* (*Eupetedromus*) *incrematum* Lec. 1860.

18647(I) *B. fortunatum* Csy. 1924. Type ♀, paratype ♂* (Edmonton, Alberta) = *B.* (*Eupetedromus*) *incrematum* Lec. 1860.

18653(I) *B. edmontonense* Csy. 1924. Single type ♂ (Edmonton, Alberta) = 754 *B.* (*Diplocampa*) *transparens* Gebl. 1829 (*sulcatum* Lec. 1848). Casey overlooked the double frontal sulci.

18654(I) *B. contristans* Csy. 1924. Type and paratype (Rhode Island) = 648 *B.* (*Notaphus*) *posticum* Hald. 1843 (731 *fraternum* Lec. 1857), dark form.

18656(I) *B. lengi* Notm. 1919. Paratype ♂* (Ansable Lake, New York, AMN) = 681 *B.* (*Eupetedromus*) *incrematum* Lec. 1860.

18658(I) *B. terracense* Csy. 1924. Single type ♂* (Terrace, British Columbia) = 713 *B.* (*Furcacampa*) *decipiens* Dej. 1831 (723 *versicolor* Lec. 1848).

20704(II) *B. yukonum* Fall 1926. Single ♂* type (Dawson, Yukon Territory, Canada, coll. Fall, MCZ) = *B.* (*Peryphus*)*grapeioides* Munster 1930 (*sahlbergioides* Munst. 1932), from northern Scandinavia and Siberia. Fall's name is valid. The penis is identical with that of European specimens (fig. 12c). The metasternum is shown in figure 6. I have seen two additional American males*, from Mount McKinley, Alaska (F. W. Morand, 1932, NMW), and Reindeer Depot, Mackenzie Delta, North West Territory, Canada (W. J. Brown, 1948, DAO). The type is macropterous; the other two, brachypterous.

20705(II) *B. mckinleyi* Fall 1926. Types ♂* ♀ (Alaska, coll. Fall, MCZ) = *B.* (*Daniela*) *scandicum* Lindroth 1943 (northern Scandinavia). Fall's name is thus valid. The only external difference between American and Scandinavian specimens seems to be the more diffuse microsculpture of the prothorax in American ones. But the penis (fig. 12a) is almost identical, except that the tricorned piece distally in the internal sac is somewhat different in shape and the longest stylet is straight, not slightly curved, in the single Alaskan male. There seems no reason at present to attach even subspecific value to these small differences.

21695(III) *B. bryanti* Carr 1932 (preoccupied by *Peryphus bryanti* Andrewes 1921). Holotype ♂ in DAO, allotype and several paratypes in different museums (all from Mackenzie River, northwestern Canada). In the holotype the internal sac of the penis unfortunately is everted, preventing a comparison. Among the paratypes 1 ♂* (NMW), though immature, gave a tolerably good genital slide, showing complete agreement with the Palaearctic *B.* (*Chrysobracteon*) *lapponicum* Zett. 1840 (fig. 8a), which is the valid name. Another ♂* (Near Holy Cross, Lower Yukon, Alaska, NMW) gave a perfect slide, the penis differing from *lapponicum* (and probably also from *bryanti*) by its more slender form, the internal sac, however, being exactly the same. In external characters too the original *bryanti* are more like *lapponicum* than is the Alaskan example. The latter is more convex with more regularly and deeply punctured elytral striae, the 3rd interval less widened in front of the anterior "silver spot"; the eyes perhaps a little larger; the predominant colour of the upper surface brass green; the first antennal joint reddish brown with slight metallic reflection only above; the ground colour of the legs also (dark) reddish brown, with strong metallic lustre. In true *bryanti* only the base of femora is pale. The Alaskan form, judging from one single example, thus comes very close to the eastern Siberian subspecies *latiusculum* Mtsch. 1844 (see Lindroth 1939–40, p. 69).

B. mimus Hayw. 1897 (p. 108). This is a manuscript name of Leconte, also used in his collection ("type" ♀, Lake Superior). It was briefly but sufficiently characterized by Hayward, as a variety of *versicolor* Lec. It is a *Furcacampa*, identical with *versicolor* Csy. 1918 (nec Lec. 1848) and 724 *pellax* Csy. 1918, and is valid.

B. farrarae Hatch 1950. Paratype ♂* (State of Washington) = sbsp. of the Siberian *B.* (*Plataphodes*) *crenulatum* F. Sahlb. 1844 (penis, fig. 10c). Very closely related to 501 *quadrifoveolatum* Mnh. 1843 (fig. 10b).

B. wenatchae Hatch 1950. Paratype ♂* (Moses Coulee, State of Washington) = 584 *B.* (*Peryphus*) *petrosum* Gebl. 1833 (*lucidum* Lec. 1848, etc.).

B. fenderi Hatch 1950. Paratype ♂* (Ocean Park, State of Washington) = 18642(1) *B.* (*Peryphus*) *sejunctum* Csy. 1918 sbsp. *semiaureum* Fall 1922.

892 *Tachyta inornata* Say 1823 is different from *nana* Gyll., as originally stated in Leng (also in Csiki 1928, p. 184). The synonymy was wrongly re-established in Csiki's supplement (1933, p. 1650), probably on the authority of Andrewes (1925, p. 486). The armature of the internal sac of the penis is identical but *inornata* lacks the

rudiments of carinae at the hind angles of the prothorax, present in the Palaearctic *nana*. Therefore *inornata* must be regarded as a different subspecies. From Say's description of *inornata* (1823, p. 87) it appears that *angulata* Csy. is excluded by the form of the prothorax, and Say would probably not have overlooked the pronounced prothoracic carina of *falli* Hayw. Casey's interpretation of *inornata* (1918, p. 218) is therefore probably right. The "*Tachys nanus*" of Hayward (1900, p. 198) is a complex, apparently including *angulata* Csy., which is distinct.

892(syn.) *T. picipes* Kby. 1837. Types ♂* ♀ = *nana* Gyll. sbsp. *inornata* Say 1823, *sensu* Csy. 1918. The penis is quite different from that of *falli* Hayw. and *angulata* Csy. but agrees completely with the Palaearctic *nana*.

902(syn.) *Patrobus longiventris* Mnh. 1853. Two types ♀ (Kadjak, Alaska, UMH) = *fossifrons* Eschz. 1823 *f. typ.* (Darlington 1938, p. 162).

903 *P. fulvus* Mnh. 1853. 2 ♂, one marked as type (Kadjak, Alaska, UMH) = immature specimens of *fossifrons* Eschz. 1823 *f. typ.* (Darlington 1938, p. 162).

909 *Trechus borealis* Schffr. 1915. Type ♂ (Battle Harbour, Labrador, NMW) = 910d *apicalis* Mtsch. 1845 sbsp. *micans* Lec. 1848, as generally accepted.

910 *T. fulvus* Lec. 1848. Type ♂* (Lake Superior) = *apicalis* Mtsch. 1845 sbsp. *micans* Lec. 1848 (type ♂*, Lake Superior), as generally accepted.

Lyperopherus innuitorum Brown 1949. ♂*, det. author (Chesterfield, North West Territory) = *Pterostichus* (*Lyp.*) *vermiculosus* Men. 1850, from the Eurasian tundra.

1143 *Cryobius fastidiosus* Mnh. 1853. Type ♂* (Kenai, Alaska) = 1144 *Pterostichus* (*Cryobius*) *brevicornis* Kby. 1837 (*mandibularis* auct. nec Kby.).

1144 *C. brevicornis* Kby. 1837. Two types ♂* ♀ = *fastidiosus* Mnh. 1853, so the Kirby name is valid. This is the species known as *mandibularis* in Labrador, Newfoundland, and New England. Specimens from east of Hudson Bay differ by paler, more slender palpi and probably form a distinct subspecies. There are no constant differences in form and inner armature of penis.

1145 *C. mandibularis* Kby. 1837. Type ♂ (without abdomen) = a bright metallic species, quite different from what is regarded as *mandibularis* in northeastern North America (*i.e. brevicornis* Kby.). Kirby's "var. b" is different from both of them. Owing to the complete confusion in the nomenclature of subg. *Cryobius*, I am unable to state any possible synonyms of *mandibularis f. typ.* and its "*var. b*".

Page 58 (without number) *Cryobius arcticus* J. Sahlb. 1880. Type ♂* (Kola Peninsula, Russia, UMH) = 1144 *Pterostichus* (*Cryobius*) *brevicornis* Kby. 1837. Already placed as a synonym of 1143 *fastidiosus* Mnh. 1853 by Poppius 1906 (p. 192).

18702(I) *Omaseus brevibasis* Csy. 1924. Single type ♀ (New York) = 1174 *Pterostichus* (*Melanius*) *caudicalis* Say 1823 (dwarf specimen).

18703(I) *O. tenuis* Csy. 1924. Single type ♀ (New Jersey) = 1175 *Pterostichus* (*Melanius*) *luctuosus* Dej. 1828.

18704(I) *O. confluens* Csy. 1924. Type ♂ (Rhode Island) paratypes ♀ (no loc.) = *Pterostichus* (*Melanius*) *luctuosus* Dej. 1828.

18705(I) *O. aequalis* Csy. 1924. Single type ♀ (New Jersey) = 1176 *Pterostichus* (*Melanius*) *corvinus* Dej. 1828 (large specimen).

18706(I) *O. testaceus* Csy. 1924. Single type ♀ (Rhode Island) = 1175 *Pterostichus* (*Melanius*) *luctuosus* Dej. 1828 (immature).

18707(I) *Dysidius egens* Csy. 1924. Single type ♀ (New Jersey) = 1178 *Pterostichus* (*Dysidius*) *mutus* Say 1823 (dwarf specimen).

1181 *Pseudargutor erythropus* Dej. The subgenus- (or genus-) name "*Platysmatus* Lut." was introduced by Csiki (1933, p. 1666; Leng, II. suppl., 1933, p. 13) by mistake (*vide* Lutshnik 1929, p. 5), and in any case it cannot replace the earlier *Pseudargutor* Csy. 1918, as proposed by Leng (*loc. cit.*). Actually the American species belongs to *Lagarus*, and if this is regarded a subgenus of *Pterostichus*, as is usually done, the species name *leconteianus* Lut. 1921 becomes valid, with *erythropus* Dej. 1828 (nec Mrsh. 1802) and *nitidus* Kby. 1837 (nec Dej. 1828) as synonyms. The penis and parameres of the American species very much resemble those of the Palaearctic *vernalis* Panz. (very imperfectly figured by Jeannel 1941–42, p. 741). How Jeannel (*loc. cit.*) could join *Lagarus* with *Stomis*, I am unable to understand.

1182–1187. *Micromaseus* Csy. 1918 is preoccupied by Desbr. 1906 and is therefore changed to *Omasculus* Lut. 1929 (*Americomaseus* Cki. 1930). Actually these species belong to the Palaearctic subg. *Argutor* Steph. 1828 of *Pterostichus*.

1189 *Bothriopterus latescans* Csy. 1913. Types ♂ ♀ (California) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823, or possibly a subspecies, in which case, however, *oblongiusculus* Mtsch. 1859 (original example from California in coll. Lec.) seems to have priority.

1191 *B. sericeus* Csy. 1913. Single type ♀ (Clackamas, Oregon) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823. However 3 examples in MCZ (Creston, British Columbia), bearing the label "*sericeus*, comp. with type" (from coll. A. S. Nicolay) = *oregonus* Lec.

1193 *B. latebricola* Csy. 1913. 9 ex., ♂ ♀ (California) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1194 *B. luczoti* Dej. 1928. Described from Newfoundland. The author's remarks on the structure of the prothorax exclude *pensylvanicus* Lec. It therefore = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1195 *B. shastanus* Csy. 1913. Single type ♂ (Siskiyou, Colorado) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1196 *B. saxatilis* Csy. 1913. 8 ex., ♂ ♀ (Colorado; Idaho; Arizona) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1197 *B. laxicollis* Csy. 1913. 3 ex., ♂ ♀ (Colorado) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1198(syn.) *B. colligatus* Walk. 1866. Type ♀ (British Columbia, BMN) = *Pterostichus* (*Bothr.*) *oregonus* Lec. 1861, as already accepted.

1198(syn.) *B. obtusangulus* Mtsch. 1859. 1 ex. (probably original) in coll. Lec. = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1198(syn.) *B. motschulskyi* Maekl. 1857 (not 1859). The identification with *oregonus* Lec. is wrong; according to the description it = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1198(syn.) *B. sexpunctatus* Mnh. 1853. Types ♂* ♀ (Kadjak, Alaska, UMH) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

18709(1) *B. angusticollis* Csy. 1924. Single type ♂ (Canon, Utah) = 1192 *Pterostichus* (*Bothr.*) *adstrictus* Eschz. 1823.

1244 *Curtonotus rufimanus* Kby. 1837. Type ♂* = 1245 *Amara* (*Cyrtonotus*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878, etc.).

1244(syn.) *C. brevilabris* Kby. 1837. Type ♂* = 1245 *Amara* (*Cyrtonotus*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878, etc.).

1244(syn.) *C. lacustris* Lec. 1855. Type ♀ (Lake Superior). It is a distinct species and its penis (according to several males externally agreeing with the type) is quite different from that of 1245 *Amara* (*Cyrt.*) *torrida* Ill. (*rufimana* Kby., *brevilabris* Kby. *reflexa* Putz., *cylindrica* Lec., etc.).

1244(syn.) *C. reflexus* Putz. 1866. Original ♂ (Newfoundland, coll. Lec.) = 1245 *Amara* (*Cyrt.*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878, etc.).

1245 *C. cylindricus* Lec. 1878. Type ♂ (Colorado), paratype ♂* (Hudson Bay Territory) = *Amara* (*Cyrt.*) *torrida* Ill. 1798.

1247 *C. labradorensis* Csy. 1918. Type ♂*, 7 paratypes (W. St. Modest, Labrador) = 1245 *Amara* (*Cyrt.*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878, etc.).

1248 *C. scrutatus* Csy. 1918. Type ♂*, 2 paratypes (W. St. Modest, Labrador) = 1245 *Amara* (*Cyrt.*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878, etc.).

1251 *C. brunnipennis* Dej. 1831 is so closely related to the Palaearctic *Amara* (*Cyrt.*) *alpina* Payk. 1790, with which it is connected by intergrading forms, that it must be regarded as a subspecies.

1251(syn.) *C. obtusus* Lec. 1855. Type (Alaska) = *Amara* (*Cyrt.*) *alpina* Payk. 1790 sbsp. *brunnipennis* Dej. 1831.

1252 *C. rubripennis* Csy. 1918. 11 ex. (Colorado) in coll. Casey = 1251 *Amara* (*Cyrt.*) *alpina* Payk. 1790 sbsp. *brunnipennis* Dej 1831.

1253 *C. deficiens* Csy. 1918. Type and paratype ♀, both immature (New Hampshire) = 1251 *Amara* (*Cyrt.*) *alpina* Payk. 1790 sbsp. *brunnipennis* Dej. 1831.

1254 *C. argutus* Csy. 1918. Type ♂, 4 paratypes (New Hampshire) = 1251 *Amara* (*Cyrt.*) *alpina* Payk. 1790 sbsp. *brunnipennis* Dej. 1831.

1255 *C. inanis* Csy. 1918. Single type ♀ (New Hampshire) = 1251 *Amara* (*Cyrt.*) *alpina* Payk. 1790 sbsp. *brunnipennis* Dej. 1831.

1258(syn.?) *C. hyperboreus* Dej. 1831. Dejean's description (especially colour of antennae, form of prothorax) shows beyond doubt that his species = *Amara* (*Cyrt.*) *elongata* Lec. 1850. Dejean's name is consequently valid. Further synonyms are: *peregrina* Mor. 1863, *simulans* J. Sahlb. 1880 (*Harpalus*), *imperfecta* Brown 1930.

18712(1) *C. albertanus* Csy. 1924. Type ♂*, 3 paratypes (Edmonton, Alberta), 1 additional ex. (Husavik, Manitoba) = 1245

Amara (*Cyrt.*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878).

18714(I) *C. brevipennis* Csy. 1924. Single type ♀ (North West Territory) = 1245 *Amara* (*Cyrt.*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878).

18715(I) *C. manitobensis* Csy. 1924. Type and paratype ♀ (Manitoba) = 1244 *Amara* (*Cyrt.*) *lacustris* Lec. 1855.

18716(I) *C. durus* Csy. 1924. Single type ♀ (Edmonton, Alberta) = 1245 *Amara* (*Cyrt.*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878).

18717(I) *C. biarcuatus* Csy. 1924. Single type ♀ (Edmonton, Alberta) = 1245 *Amara* (*Cyrt.*) *torrida* Ill. 1798 (*cylindrica* Lec. 1878).

18718(I) *C. subtilis* Csy. 1924. Single type ♂ (Stupart Bay, Labrador) = 1251 *Amara* (*Cyrt.*) *alpina* Payk. 1790 sbsp. *brunnipennis* Dej. 1831.

20731(II) *C. imperfectus* Brown 1930. Type and paratype ♀ (Bradore Bay, Labrador, DAO) = 1258 *Amara* (*Cyrt.*) *hyperborea* Dej. 1831 (*elongata* Lec. 1850).

1260 *Stereocerus haematopus* Dej. 1828. *Boreobia strigicollis* F. Sahlb. 1844 is a synonym according to 2 ♂* from the Lena River and Tschuktsch Peninsula, Siberia (UMH). *Stereocerus* Kby. 1837 (*Boreobia* Tschitsch. 1896) must be regarded as a subgenus of *Pterostichus* (*cf.* Buchanan 1924; Leech 1935.)

1268 *Bradytus nainensis* Csy. 1918. Type ♂* and paratype ♀ (Nain, Labrador) = 1269 *Amara* (*Bradytus*) *glacialis* Mnh. 1853.

1270 *B. putzeysi* Horn 1875. Single type ♀ (St. Pierre-Miquelon, coll. Lec.) = 1267 *Amara* (*Bradytus*) *apricaria* Payk. 1790.

1285(syn.) *Celia inaequalis* Kby. 1837. Type ♀ = *Amara* (*Celia*) *patruelis* Dej. 1831, as generally accepted.

1285(syn.?) *C. interstitialis* Dej. 1828 is not identical with *Amara* (*Celia*) *patruelis* Dej. 1831 and occurs only in the extreme North West (Alaska, Yukon Territory), whereas *patruelis* is transamerican.

1298(syn.) *C. laevipennis* Kby. 1837. 2 ♂* types (one without abdomen). A species distinct from *Amara* (*Celia*) *erratica* Dft. 1825. I know of no synonym.

1304 *C. paganica* Csy. 1918. Type ♀ (Marquette, Michigan) = 1323 *Amara* (*Celia*) *discors* Kby. 1837 (*gibba* Lec. 1855). Casey's paratype is a little different but probably belongs to the same species.

1309 *C. remotestriata* Dej. 1828 = the Palaearctic *Amara* (*Celia*) *quenseli* Schh. 1806. I do not think it is possible to separate the American population even as a subspecies.

1309(syn.) *C. discors* Kby. 1837. Type ♀ = 1323 *Amara* (*Celia*) *gibba* Lec. 1855 and is thus valid.

18730(I) *C. columbiana* Csy. 1924. Single type ♀ (British Columbia) = 1285 *Amara* (*Celia*) *patruelis* Dej. 1831.

Isopleurus nitidus Kby. 1837. Type ♂* = 1350 *Amara* (*Celia*) *subaenescens* Cki. 1929 (*subaenea* Lec. 1855, nec Sturm nec Steph.). Kirby's name was omitted by Leng, as well as by Csiki (1927–33), but it is preoccupied by *Amara* (*s. str.*) *nitida* Sturm 1825.

1389 *Amara fallax* Lec. 1848. Type ♀ (Lake Superior) = 1385 *impuncticollis* Say 1823. The species is extremely variable.

1402 *A. marquettensis* Csy. 1918. Single type ♀ (Marquette, Michigan) = *lunicollis* Schioe. 1837 (*vulgaris* auct. p. p.).

18751(I) *A. neoscotica* Csy. 1924. Type ♂* (Halifax, Nova Scotia) = 1400 *cupreolata* Putz. 1866. The penis of the type has been compared with that of 1 ♂ from Ottawa (NMW) and this slide, in its turn, with the penis of "*cupreolata* 1" in coll. Lec., a specimen received from Putzeys and probably a cotype. "*A. cupreolata*" in coll. Casey is a different species, unknown to me.

18766(I) *A. carriana* Csy. 1924. Single type ♂ (Edmonton, Alberta) = *lunicollis* Schioe. 1837 (*vulgaris* auct. p. p.).

A. inepta Lec. 1855 (p. 351; omitted in Leng; *cf.* Horn 1875, p. 127; Csiki 1929, p. 435), according to the type ♀, is not a synonym of 1298 *A.* (*Celia*) *erratica* Dft. but a true *Amara s. str.*, unknown to me.

18775(I) *Rembus parallelus* Csy. 1920 = 1444 *obtusus* Lec. 1848. I did not study Casey's type (from Illinois) but the distinguishing characters mentioned by him are all inconstant in *obtusus*. In 1 ♀ from Truro, Nova Scotia, the scutellar stria is totally absent, in 1 ♂ from Halifax it is rudimentary on the left side, short but evident on the right. This specimen has a dorsal puncture on the 2nd stria of the right elytron only.

1471 *Badister pulchellus* Lec. 1848 et auct. is made up of two species, one of which was wrongly called "*bipustulatus* Fbr." (*vide* below).

1472 *B. bipustulatus* Fbr. 1801 does not occur in America. The name was wrongly used for *neopulchellus n. nom.* (*pulchellus* auct. nec Lec.). *Vide* below (p. 153).

1483 *Calathus ingratus* Dej. 1828 (*confusus* Lec. 1854, type ♂* from Lake Superior) is not a synonym of the Palaearctic *micropterus* Dft. 1812, as proposed by Hatch (1938, p. 146), but a clearly different subspecies characterized primarily by the slightly but apparently constantly deviating apex of the penis.

1483(syn.) *C. incommodus* Mnh. 1853. Two types ♂* (Kenai and

"Nikol. red.", Alaska) = *micropterus* Dft. 1812 sbsp. *ingratus* Dej. 1828, as generally accepted.

1483b *C. labradorinus* Csy. 1913. Type ♀, 3 paratypes ♂* ♀ (W. St. Modest, Labrador) = *micropterus* Dft. 1812 sbsp. *ingratus* Dej. 1828.

1484b *C. coloradensis* Csy. 1913. Type ♀ and paratypes ♂* ♀ (Boulder, Colorado), 1 paratype ♂* (Eldora, Colorado) = 1483 *micropterus* Dft. 1812 sbsp. *ingratus* Dej. 1828 (the large form).

18792(I) *C. planifer* Csy. 1920. Single type ♀ (Alaska) = 1483 *micropterus* Dft. 1812 sbsp. *ingratus* Dej. 1828.

18793(I) *C. beringi* Csy. 1920. Type ♂* and 10 paratypes (all from Alaska) = *micropterus* Dft. 1812 sbsp. *ingratus* Dej. 1828.

18794(I) *C. nanulus* Csy. 1920. Type ♂* and 10 paratypes (all from Alaska and all immature) = 1483 *micropterus* Dft. 1812 sbsp. *ingratus* Dej. 1828 (dwarf form).

18798(I) *C. aquilus* Csy. 1920. Single type ♂* (Colorado) = 1483 *micropterus* Dft. 1812 sbsp. *ingratus* Dej. 1828.

1487 "*Pristodactyla ambigens* Bates" from the United States, in all collections seen by me, is not a *Pristodactyla* and not *ambigens* Bates (compared with the type and numerous paratypes from Mexico in BMN). Whether the "*ambigens*" auct. is described or not, I have been unable to decide. The parameres of the ♂ are of the *Agonum* type.

1488(syn.) *P. mollis* Eschz. 1823 (nec Mrsh) Original ♀ (Alaska, coll. Mnh., UMH) = 1488 *Calathus advena* Lec. 1848, as generally accepted.

1488(syn.) *P. dulcis* Mnh. 1853. Original ♂* (Kadjak, Alaska) = 1488 *Calathus advena* Lec. 1848, as generally accepted.

1488a *P. levis* Mnh. 1853. Type ♂* (Kadjak, Alaska) = 1488 *Calathus advena* Lec. 1848. There seems no reason to maintain this form as a subspecies.

1489a *P. convexa* Csy. 1913. Single type ♀ (New York) = 1489 *Synuchus impunctatus* Say 1823, a large but otherwise typical specimen.

1491 *P. arizonica* Csy. 1913. Single type ♂* (Arizona) = 1490 *Synuchus dubius* Lec. 1854.

1492 *P. zuniana* Csy. 1913. Single type ♂* (New Mexico) = 1490 *Synuchus dubius* Lec. 1854.

18799(I) *P. neomexicana* Csy. 1920. Type ♀ (New Mexico), paratypes ♂* ♀ (Cloudcroft, New Mexico) = 1490 *Synuchus dubius* Lec. 1854.

18800(I) *P. binaria* Csy. 1920. Type ♀, 4 paratypes ♂* ♀ (S.

Arkansas) = 1488 *Calathus advena* Lec. 1848.

18801(I) *P. scolopax* Csy. 1920. Type ♂*, 8 paratypes (Colorado) = 1488 *Calathus advena* Lec. 1848.

18802(I) *P. juabitica* Csy. 1924. Single type ♀ (Trout Creek, Juab Co., Utah) = 1490 *Synuchus dubius* Lec. 1854.

1488b(III) *P. brunnescens* Mnh. 1852 (as var. of *mollis* Eschz.). Type ♂* (Atka, Alaska) = 1488 *Calathus advena* Lec. 1848.

1488c(III) *P. breviuscula* Mnh. 1852 (as var. of *mollis* Eschz.). Type ♂* (Atka, Alaska) = 1488 *Calathus advena* Lec. 1848.

1511a *Platynus octofoveolatus* Maekl. 1857. Type ♂* (Kadjak, Alaska, UMH) = 1511 *Agonum* (*Platynus*) *mannerheimi* Dej. 1828 sbsp. *stygicum* Lec. 1854. It is a common aberration, not worthy of being named.

1536 *P. clemens* Lec. 1863. Type and paratype (Nova Scotia) = 1576 *Agonum* (*Anchomenus*) *ruficorne* Gze. 1777 (*albipes* Fbr. 1796).

1541(syn.) *P. molestus* Lec. 1866 (nec Mtsch. 1844; *laevis* Lec. 1854, nec Dej. 1828). The type ♂* ("Middle States") has a penis (fig. 14) quite different from that of *Agonum* (*s. str.*) *mutatum* G. & H. 1868 (*atratum* Lec. 1850, nec Dft. 1812) which Leconte himself later (1879, p. 56) regarded as a synonym. Since both *molestum* and *laeve* are preoccupied names, the species must be known as 18910(I) *Agonum* (*s. str.*) *fidele* Csy. 1920 (*vide* below).

1546 *P. affinis* Kby. 1837. Type ♂* = 1547 *Agonum* (*s. str.*) *carbo* Lec. 1850 and is thus valid. *A. harrisi* Lec. 1848 (according to the type ♀) is a different species. In order to avoid hopeless confusion I propose that the name *affine* Kby. be treated as a "*nomen in praesens suppressum*" until *harrisi* has been generally adopted for the species hitherto regarded as *affine*.

1551 *P. metallescens* Lec. 1854. Casey (1920, p. 114, 122) changed this name into 18907(I) *Agonum* (*s. str.*) *lacustre* n. nom., because of the *metallescens* of Dejean (1837, p. 35). But this, as far as I can ascertain, is a *nomen nudum*, never described, and Leconte's name consequently remains valid.

1554 *P. hardyi* Lec. 1879. The 3 types (Newfoundland, coll. Lec.) = *Agonum* (*s. str.*) *mülleri* Hbst. 1784 (introduced from Europe).

1573(syn.) *P. strigicollis* Mnh. 1852. Type ♂* (Kaknu, Alaska, UMF) = *Agonum* (*Agonodromius*) *bogemanni* Gyll. 1813 (not 1808).

1583 *P. picicornis* Lec. 1860. Type ♂* (Jasper House, Alberta) and 4 additional ex. in coll. Lec. (1 ♂* "Nebraska etc.") = 1582 *Agonum* (*Europhilus*) *sordens* Kby. 1837 (dark specimens).

1583(syn.?) *P. similis* Kby. 1837. Two types ♀ belong to a distinct species of *Agonum* (*Europhilus*), related to *consimile* Gyll. (18925 *invalidum* Csy.).

1584(syn.) *P. gratiosus* Mnh. 1853. Two "types" seen, 1 ♀ in UMH, 1 ♂ in coll. Lec. (both from Kadjak, Alaska) = *Agonum* (*Europhilus*) *ruficorne* Lec. 1850, nec Gze. 1777, as generally accepted. Mannerheim's name is valid (*vide lenis*, below).

1586 *P. gemellus* Lec. 1879. Type ♂* (Vancouver, British Columbia) = *Agonum* (*Europhilus*) *thoreyi* Dej. 1828, widely distributed in the Palaearctic Region.

1587 *P. picipennis* Kby. 1837. Type ♀ = 1586 *Agonum* (*Europhilus*) *thoreyi* Dej. 1828 (*gemellum* Lec. 1879). Kirby's "var. d", type ♀ = 1584 *Ag.* (*Eur.*) *gratiosum* Mnh. (*ruficorne* Lec. nec Gze.), as generally accepted. For *Ag.* (*Eur.*) *picipenne* auct. (nec Kby.) the name *dilutipenne* Mtsch. 1864 seems available. The remark "oculis vix prominulis" in the original description seems to exclude *sordens* Kby. which, in addition, is not known to occur as far south as New Mexico.

1587(syn.) *P. lenis* Dej. 1828. According to the original description of the colour of the antennae this must be 1586 *Agonum* (*Europhilus*) *thoreyi* Dej. 1828 (*gemellum* Lec. 1879) (*cf.* Casey 1920, p. 130).

P. 64(without number) *P. exaratus* Mnh. 1853. Type and paratype ♀ (Kadjak, Alaska, UMH) = *Agonum* (*Europhilus*) *aldanicum* Popp. 1905, described from Lena River, Siberia; *exaratus* is thus valid.

18883(I) *Platynomicrus fragilissimus* Csy. 1920. Type ♂ (Toronto) = 1589 *Agonum* (*Platynomicrus*) *nigriceps* Lec. 1848 (brachypterous form).

18886(I) *Sericoda insulina* Csy. 1920. Single type ♂ (Edmonton, Alberta) = 1573 *Agonum* (*Agonodromius*) *bogemanni* Gyll. 1813 (not 1808).

18887(I) *S. invidiosa* Csy. 1920. Type ♀, paratype ♀ (Colorado) = 1573 *Agonum* (*Agonodromius*) *bogemanni* Gyll. 1813 (not 1808).

18888(I) *S. tacomae* Csy. 1920. Type ♀ ("Washington Territory"), 4 additional ex. (British Columbia) = 1573 *Agonum* (*Agonodromius*) *bogemanni* Gyll. 1813 (not 1808).

18908(I) *Agonum terracense* Csy. 1924. Single type ♂* (Terrace, British Columbia) = 1551 *metallescens* Lec. 1854 (18907 *lacustre* Csy. 1920).

18910(I) *A. fidele* Csy. 1920. Type ♂* and paratype ♀ (Rhode Island) = 1541(syn.) *laeve* Lec. 1854 (*molestum* Lec. 1866). Both the latter names are preoccupied and *fidele* Csy. is therefore valid. *A. mutatum* G. & H. (*atratum* Lec.) is a different species.

18911(I) *A. subinflatum* Csy. 1920. Type ♂*, 2 paratypes ♂ (Bayfield, Wisconsin) = 18910(I) *fidele* Csy. 1920.

18912(I) *A. humile* Csy. 1920. Single type ♂* (Kalispell, Montana) = 1543 *propinquum* G. & H. 1868 (*piceum* Lec. nec L.).

18913(I) *A. insuetum* Csy. 1920. Type ♀, 3 paratypes ♂* ♀ (Wilbur, Washington) = 1543 *propinquum* G. & H. 1868 (*piceum* Lec. nec L.).

18914(I) *A. amens* Csy. 1924. Type ♂*, paratypes ♂ ♀ (Edmonton, Alberta) = 1543 *propinquum* G. & H. 1868 (*piceum* Lec. nec L.).

18925(I) *A. invalidum* Csy. 1924. Single type ♂ (Edmonton, Alberta) = *A.* (*Europhilus*) *consimile* Gyll. 1810, widely distributed in the Palaearctic region.

18928(I) *Europhilus adustus* Csy. 1920. Type ♂ and 1 paratype (Indiana), 4 paratypes ("Levette coll.") = 1588 *Agonum* (*Eur.*) *lutulentum* Lec. 1854.

18930(I) *E. collusor* Csy 1920. Single type ♂ (Montana) = 1585 *Agonum* (*Eur.*) *retractum* Lec. 1848.

18931(I) *E. symmetricus* Csy. 1920. Type ♀ (Devil's Lake, North Dakota), 2 paratypes (Kansas; British Columbia) = 1584 *Agonum* (*Eur.*) *gratiosum* Mnh. 1853.

18932(I) *E. properans* Csy. 1920. Single type ♀ (New Hampshire) = 1584 *Agonum* (*Eur.*) *gratiosum* Mnh. 1853 (unusually dark).

18933(I) *E. facilis* Csy. 1920. Type ♀ and 5 paratypes (Rhode Island) = 1585 *Agonum* (*Eur.*) *retractum* Lec. 1848.

18934(I) *E. serenus* Csy. 1920. Type ♂ and 1 paratype (Bayfield, Wisconsin), 3 paratypes (Minnesota) = *Agonum* (*Eur.*) *retractum* Lec. 1848.

18935(I) *E. antiquus* Notm. 1922. Type ♂ (Connecticut, AMN) = 1584 *Agonum* (*Eur.*) *gratiosum* Mnh. 1853.

18937(I) *E. frosti* Csy. 1924. Single type ♀ (Maine) = 1582 *Agonum* (*Eur.*) *sordens* Kby. 1837.

1696 *Blechrus glabratus* Dft. 1812 (not 1825) is not the Palaearctic *Microlestes minutulus* Gze. 1777 (*glabratus* Dft.) but a composite, consisting of several purely American species (*cf.* Casey 1920, p. 268–271).

1732 *Cymindis evanescens* Csy. 1913, according to the ♂* type (Utah), is distinct from *cribricollis* Dej.

1735 *C. acomana* Csy. 1913. Single type ♂* (New Mexico) =

1738 *cribricollis* Dej. 1831.

1739 *C. rupimontis* Csy. 1913. Single type ♀ (Colorado) = 1738 *cribricollis* Dej. 1831.

1740 *C. marginata* Kby. 1837. Two types ♂* = 1738 *cribricollis* Dej. 1831. In Leng (3rd suppl., 1933) wrongly made a synonym of 1744 *brevipennis* Zimm. (*marginata* Chd. nec Kby.).

1741 *C. alticola* Csy. 1913. Single type ♂* (macropterous) (New Hampshire) = 1738 *cribricollis* Dej. 1831.

19022(I) *C. kirbyi* Csy. 1924. Single type ♂* (Colorado) = 1738 *cribricollis* Dej. 1831.

19023(I) *C. parowana* Csy. 1924. Type ♂*, paratype ♀ (Parowan, Utah) = 1736 *unicolor* Kby. 1837.

19024(I) *C. planifera* Csy. 1924 Single type ♂* (loc. unknown) = 1738 *cribricollis* Dej. 1831.

19026(I) *C. obliqua* Csy. 1924. Single type ♀ (Edmonton, Alberta) = 1738 *cribricollis* Dej. 1831.

19027(I) *C. sinuata* Csy. 1924. Single type ♀ (New Mexico) = 1738 *cribricollis* Dej. 1831.

19028(I) *C. alternans* Csy. 1924. Single type ♀ (loc. unknown) = 1738 *cribricollis* Dej. 1831.

1801 *Miscodera arctica* Payk. 1800 of North America is subspecifically distinct from the Palaearctic form and should be called sbsp. *americana* Mnh. 1853 (*hardyi* Chd. 1861). Hatch (1933a) wrongly united it with the Siberian sbsp. *erythropus* Mtsch. 1844.

1831a *Chlaenius cordicollis* Kby. 1837 is a valid species, not a subspecies of *leucoscelis* Chevr. 1834 (*cf* Darlington 1934). The penis is very different.

1903(syn.) *Harpalus convictor* Csy. 1884. Single type ♂ (Long Island) = 1903 *affinis* Schrank 1781 (*aeneus* Fbr. 1792, *viridiaeneus* Beauv 1805) Casey later suppressed his species (1914, p. 75), but re-established it in 1924 (p. 94).

1904(syn.), 19048(I) *H. rotundicollis* Kby. 1837. Type ♀ = *amputatus* Say 1834.

1920(syn.?) *H. longior* Kby. 1837. Type ♂* of *f. typ.* and type ♂* of "var. b", both = 1925 *H.* (*Pseudophonus*) *pennsylvanicus* DeG. 1752. *H. longicollis* Lec. 1848 thus remains valid.

1949 *H. foveicollis* Lec. 1848. Single type ♂* (Maine) = 1956 *herbivagus* Say 1823, with abnormally deep and large foveae of prothorax.

1950 *H. recensus* Csy. 1914. Type ♂* (W. St. Modest, Labrador)

= 1956 *nigritarsis* Sahlb. 1817 sbsp. *proximus* Lec. 1848.

1951 *H. aequabilis* Csy. 1914. Single type ♀ (Colorado) = 1944 *pleuriticus* Kby 1837.

1952 *H. lascivus* Csy. 1914. Single type ♂* (British Columbia) = 1944 *pleuriticus* Kby. 1837.

1953 *H. pumilio* Csy. 1914. Single type ♀ (Bayfield, Wisconsin), additional ♀ (Edmonton, Alberta), both immature, = 1944 *pleuriticus* Kby. 1837.

1954 *H. perspicuus* Csy. 1914. Single type ♂*, immature (Boulder, Colorado) = 1944 *pleuriticus* Kby. 1837.

1955 *H. lividulus* Csy. 1914. Type ♂*, paratype ♂ (Bayfield, Wisconsin) and 7 additional ex. = 1944 *pleuriticus* Kby. 1837.

1956a *H. proximus* Lec. 1848 is not a sbsp. of *herbivagus* Say, but of the Palaearctic *nigritarsis* Sahlb. 1817. The single type is a ♀ from Lake Superior.

1959 *H. placidus* Csy. 1884. Type ♂* (New Jersey) and 3 additional ex. = 1944 *pleuriticus* Kby. 1837.

1968 *H. opacipennis* Hald. 1843 is different from 1969 *plenalis* Csy. 1914, as assumed by the latter (p. 113), according to an original ex. of *opacipennis* (without loc., coll. Lec.), which can be regarded as the type.

1998(syn.?) *H. ochropus* Kby. 1837. The single type ♂* is different from *desertus* Lec. of which Dr. Darlington sent 1 ♀ from New Mexico agreeing in all essential characters with Leconte's ♀ type (MCZ).

2006(syn.?) *H. basilaris* Kby. 1837. Types ♂* ♀ belong to the species generally passing under this name or *obesulus* Lec. 1852. Kirby's name is valid.

2006(syn.) (III) *H. extensus* Walk. 1866 ("*Amara extensa*"). Type ♀ (British Columbia, BMN) = *basilaris* Kby. 1837 (*obesulus* Lec. 1852), as already accepted by Csiki (1932, p. 1180).

19078(I) *H. nivalis* Csy. 1924. Single type ♂* (Saskatchewan) = 1944 *pleuriticus* Kby. 1837.

19087(I) *H. modulatus* Csy. 1924. Single type ♀ (Quebec) = 1969 *plenalis* Csy. 1914.

19088(I) *H. leviceps* Csy. 1924. Type and 4 paratypes, all ♀ (Marquette, Michigan) = 1969 *plenalis* Csy. 1914, or possibly a different subspecies.

2091 *Anisodactylus interpunctatus* Kby. 1837. Types ♂*, 2 ♀ = 2090 *nigrita* Dej. 1829 (nec Lec.). The *interpunctatus* auct. (*lecontei* Chd. nec G. & H., *nigrita* Lec. nec Dej.) thus lacks a name and I propose for it **Anisodactylus kirbyi n. nom.** It differs from *nigrita* Dej. in having only one setigerous puncture each side of the clypeus and in the penis, which is more arcuate, more strongly pigmented in the apical half, and with a rough longitudinal sculpture of the surface. As holotype ♂ and allotype ♀ I designate a pair from Cheticamp, Nova Scotia, in DAO.

2146a *Trichocellus ruficrus* Kby. 1837. Single type = *cognatus* Gyll. 1827. There is no reason to regard the North American population as a different subspecies.

21723(III) *Trichocellus porsildi* Brown 1948 apparently belongs to the subg. *Oreoxenus* but differs from the Eurasian *mannerheimi* F. Sahlb. (*ponojensis* J. Sahlb., *setiporus* Reitt., *oreophilus* J. and K. Dan.) by the narrower, more pointed penis (*cf.* Lindroth 1943, fig. 21). I have seen *porsildi* from Alaska (NMW), Manitoba (DAO), Labrador (NMW, DAO) and Colorado, the latter specimen from Leavenworth Valley (10–11.000 ft.) 15. VI. 26, H. F. Wickham, 1 ♀ (MCZ).

20746(II) *Triliarthrus frosti* Fall 1930. Type ♂* (Natick, Massachusetts) = 2160 *protractus* Csy. 1914 (type ♂*, Massachusetts).

2163(syn.) *T. similis* Kby. 1837. Type ♀ of *f. typ.*, type ♂* of "var. b", both = 2261 *Agonoderus comma* Fbr. 1801.

2171(syn.) *Stenocellus flavipes* Kby. 1837. Types ♂* ♀ = *Bradycellus* (*Sten.*) *rupestris* Say 1823. Leng has this synonymy but at the same time incorrectly lists *flavipes* Kby. as a synonym of 915 *Trechus hydropicus* Horn 1883.

2213(syn.?) *Acupalpus immunis* Kby. 1837. Types ♂*, 2 ♀ = 2238 *Stenolophus conjunctus* Say 1823.

DISCUSSION OF CERTAIN SPECIES GROUPS

In the arrangement of species in his list Leng usually followed Casey, using the divisions into major groups proposed by that author. This usually involved splitting up the larger, old genera. On the other hand, there is a clear tendency among recent coleopterists — with the exception notably of Jeannel — *against* such splitting. How impractical "splitters" can make their nomenclature is shown by lepidopterists, and most of us would prefer to go in the other direction, to make the genera as large as possible and change the "modern" micro-genera into subgenera for the use of specialists. Also, among Carabidae, it is inconsistent to retain *Bembidion* and *Harpalus* as collective genera but to break up *Pterostichus*, *Amara*, and *Agonum*

(*Platynus*) into numerous small ones, as done by Casey.

Another trouble is that many subgeneric and several generic names have been used in different senses on opposite sides of the Atlantic. Sometimes, as in *Bembidion*, the American subgenera (created by Casey) show almost no correspondence with the names used for Old World groups. In order to encourage comparisons, I have tried in the list above to apply generic and subgeneric names used for Palaearctic fauna to appropriate American species.

1. BEMBIDION

In this genus, the largest in the family, agreement on the use of subgeneric names is particularly desirable. Some attempts to give North American species their proper place in Palæarctic subgenera have already been made by Netolitzky (especially in the important paper of 1942–43). Here follows a similar, more extensive review of the American species known to me, based largely on male genitalia.

Chrysobracteon Net. (*s. l.*): The species from 408 *inaequale* to 419 *punctatostriatum*, and 18612(I) *carrianum*, 21695(III) *lapponicum* (*bryanti*). The division of this subgenus into 6 new ones (Netolitzky 1942–43) was unfortunate and unnecessary.

Bracteon Bed.: 424 *bowditchi*.

Odontium Lec.: 420 *carinatum*, 421 *sculpturatum*, 426 *confusum*, 429 *coxendix*.

Ochthedromus Lec.: 431 *bifossulatum*, 432 *americanum*.

Bracteomimus n. subg. (type *chalceum* Dej.): 591 *honestum*, 592 *chalceum*.

Hydrium Lec.: 438 *nitidum*, 439 *obliqulum*, 440 *laevigatum*.

Metallina Mtsch.: 675 *dyschirinum*, *lampros* Hbst. (figs. 2, 9a), *properans* Steph. (figs. 2, 9b).

Actedium Mtsch.: 20700(II) *lachnophoroides*.

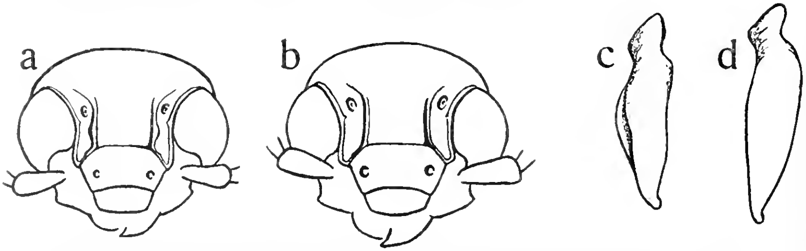
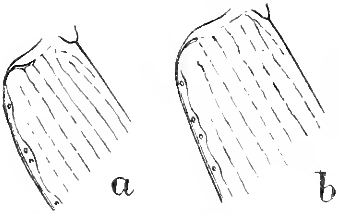


Fig. 2. *a*, *b*, head with frontal grooves; *c*, *d*, penis, seen from the convex dorsal side. *a* and *c*, *Bembidion lampros* Hbst., *b* and *d*, *B. properans* Steph.



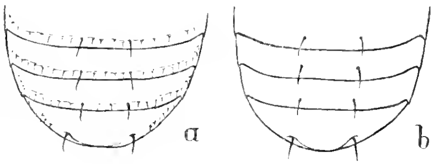


Fig. 3. At left. Left shoulder of: *a*, *Bembidion*, subg. *Plataphodes*; *b*, subg. *Plataphus* and *Blepharoplataphus*.

Fig. 4. At right. Last ventral segments of: *a*, *Bembidion*, subg. *Blepharoplataphus*; *b*, subg. *Plataphus s. str.*

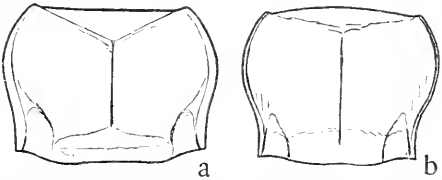
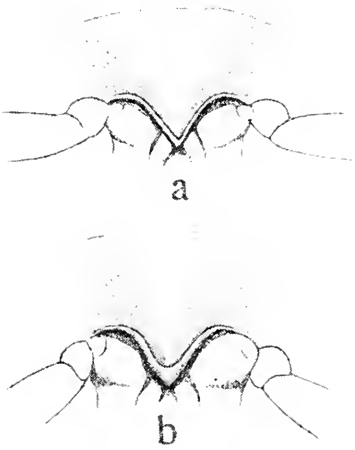


Fig. 5. Prothorax of: *a*, *Bembidion hyperboraeorum* Munst.; *b*, *B. hasti* Sahlb. Scandinavian specimens.



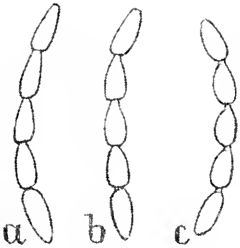


Fig. 6. At left. Metasternum between the middle coxae of: *a*, *Bembidion grapei* Gyll.; *b*, *B. yukonum* Fall. Scandinavian specimens.

Fig. 7. At right. Last 5 joints of antennae (tip down) of: *a*, *Bembidion yukonum* Fall; *b*, *B. grapei* Gyll.; *c*, *B. dauricum* Mtsch. Scandinavian specimens.

Trechonepha Csy. (*vide* Netolitzky 1942–43, p. 17): 460 *funereum*, 467 *iridescens*, 486 *simplex*.

Plataphodes Ganglb. (fig. 3a): 498 *complanulum*, 501 *quadrifoveolatum*, 502 *incertum* (penis, fig. 10d), 18620(I) *occultator*, *crenulatum* F. Sahlb. sbsp. *farrarae* Hatch.

Plataphus Mtsch. (fig. 3b): 474 *gebleri* sbsp. *turbatum*, 476 *rusticum*, 480 *gratiosum*, 482 *planatum*, 487 *planiusculum*, 492 *flebile* with 18623(I) sbsp. *carolinense*, *hyperboracorum* Munst., *lenense* Popp.

Blepharoplataphus Net. (if considered distinct from *Plataphus*): *hasti* Sahlb.

Hirmoplataphus Net.: 512 *nigrum*, 514 *quadrulum*, 521 *salebratum* (*concolor* auct.), 523 *recticolle*, 529 *longulum* (*concolor* Kby.), 530 *humboldtiense*.

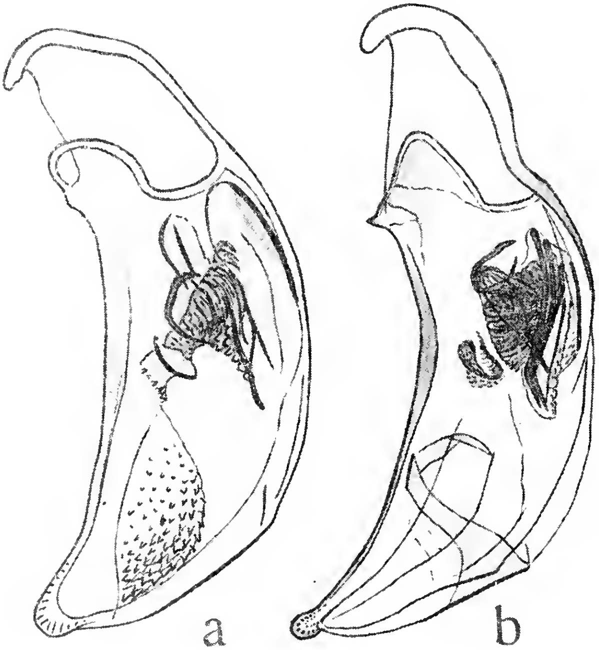


Fig. 8. Penis of: *a*, *Bembidion lapponicum* Zett. (*bryanti* Carr); *b*, *B. rupestre* L. Scandinavian specimens.

Trichoplataphus Net.: 533 *planum*, 536 *fugax*, 600 *grandiceps*.

Peryphus Steph.: 540 *transversale*, 547 *lugubre*, 560 *grapei* (figs. 6, 7, 12), 572 *lacunarium* (*picipes* auct.), 573 *scopulinum*, 575 *bimaculatum* and *sordidum*, 577 *postremum*, 579 *striola*, 581 *consanguineum*, 582 *stephensi* (*canadense*), 584 *petrosum* (*lucidum*), 586 *nevadense*, 588 *ustulatum*, 588a *rupicola*, 594 *sejunctum* with 18642(I) sbsp. *semiaureum*, 599 *obscurellum* (*fuscicrus*), 20704(II) *yukonum*, *dauricum* Mtsch., *rupestre* L.

Daniela Net.: 20705(II) *mckinleyi*.

Hydriomicrus Csy.: 552 *brevistriatum*, 553 *californicum*, 604 *semistriatum*, 18663(I) *quadratulum*.

Eupetedromus Net.: 680 *graciliforme*, 681 *incrematum*, *immaturum* n. sp.

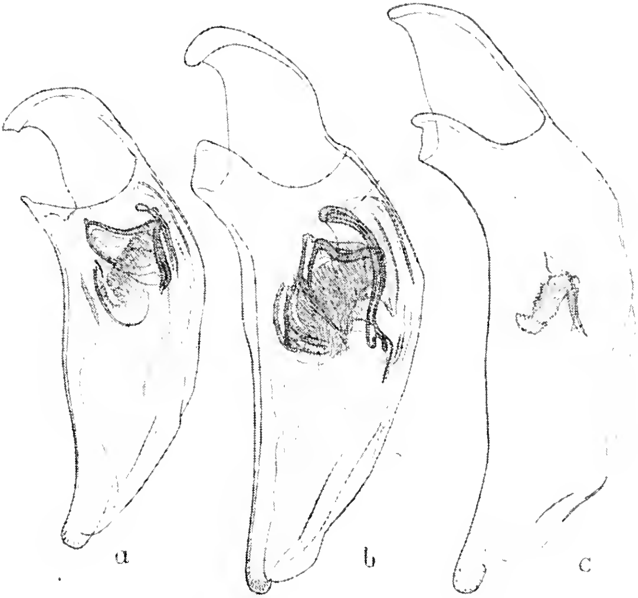


Fig. 9. Penis of: *a*, *Bembidion lampros* Hbst. (Finland); *b*, *B. properans* Steph. (Sweden); *c*, *B. simplex* Hayw. (Type, Mt. Washington, New Hampshire.)

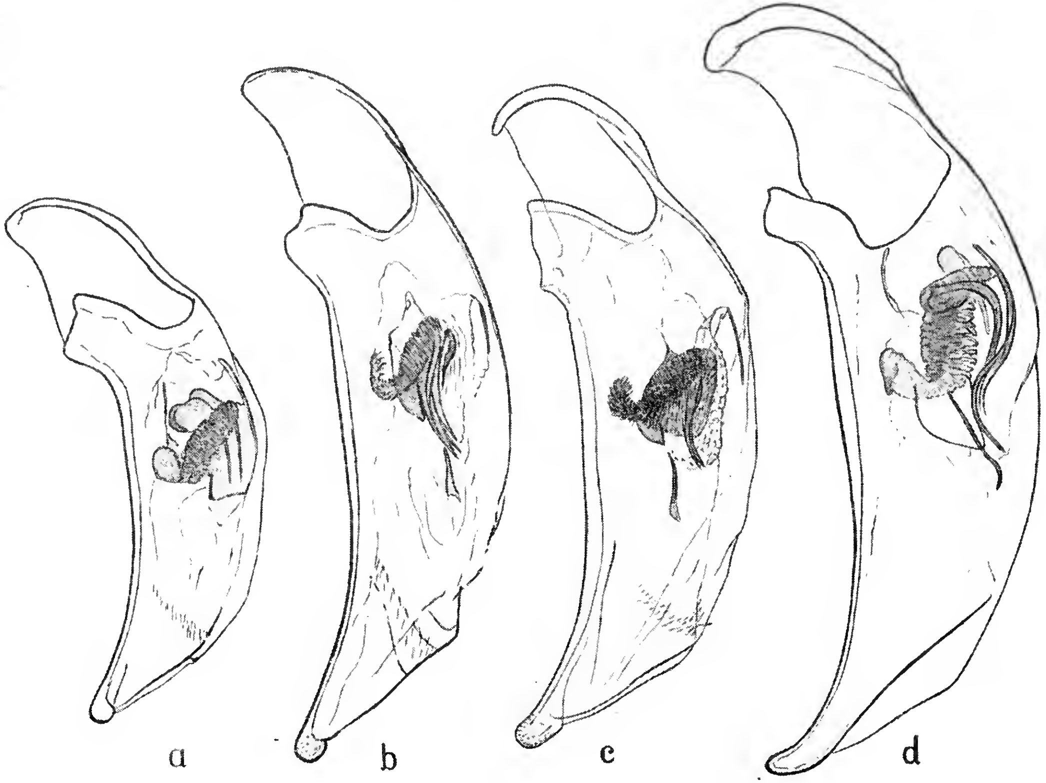


Fig. 10. Penis of: *a*, *Bembidion complanulum* Mnh. (penis compared with lecto-holotype; Paradise Park, Mt. Rainier, Washington, i.e. *loc. class.* of *parvulum* Notm.); *b*, *B. qudrifoveolatum* Mnh. (lecto-holotype, Sitka, Alaska); *c*, *B. crenulatum* F. Sahlb. (type, Ochotsk, Siberia); *d*, *B. incertum* Mtsch. (co-type of *tetraglyptum*

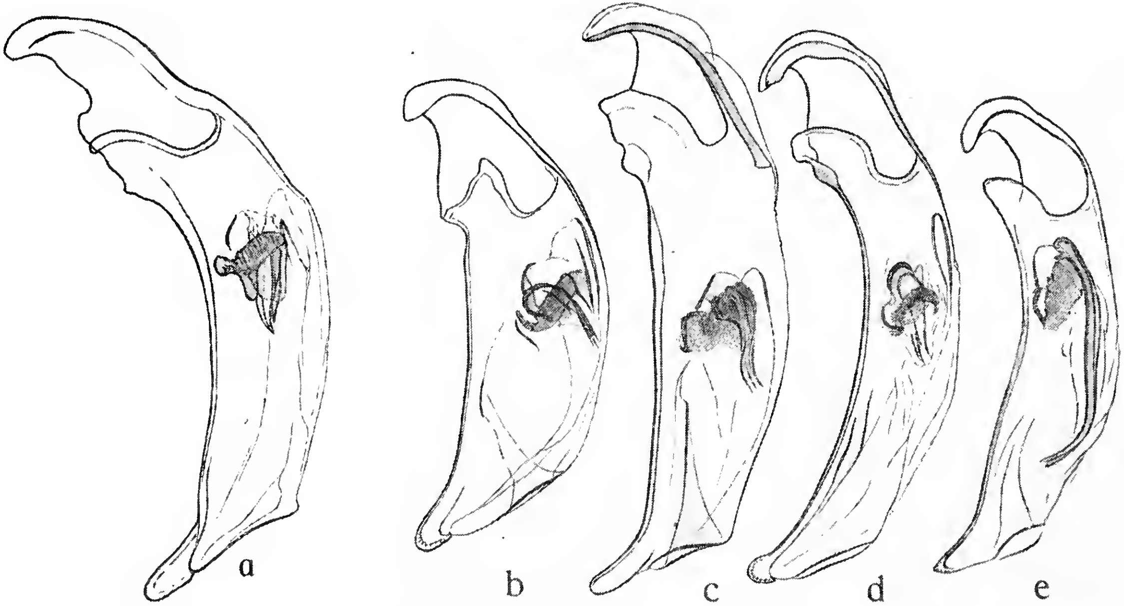


Fig. 11. Penis of: *a*, *Bembidion planiusculum* Mnh. (lecto-holotype, Sitka, Alaska); *b*, *B. hasti* Sahlb. (Norway); *c*, *B. hyperboraeorum* Munst. (Sweden); *d*, *B. gebleri* Gebl. (Siberia); *e*, *B. lenense* Popp. (Glenbournie, Benne Bay, Newfoundland).

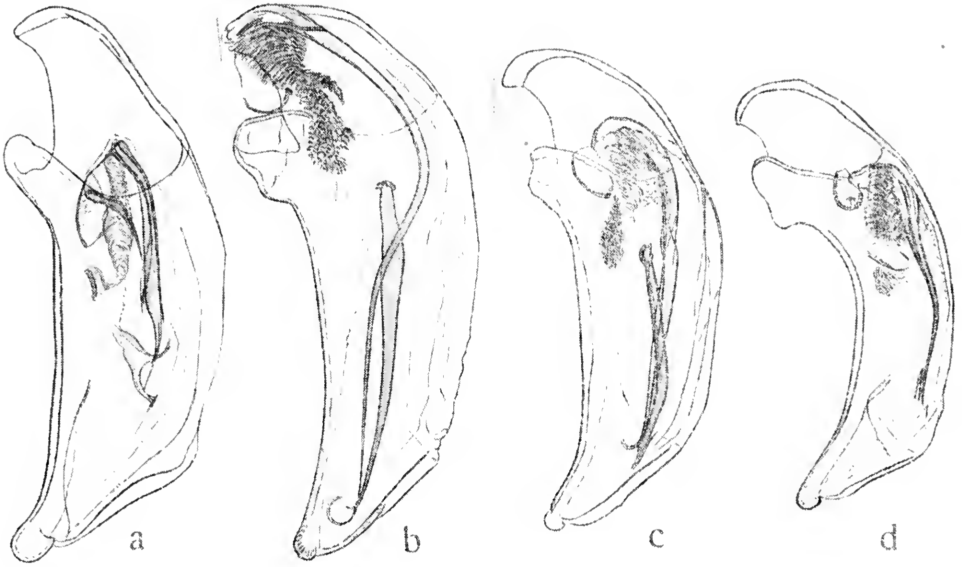


Fig. 12. Penis of: *a*, *Bembidion mckinleyi* Fall (*scandicum* Lindr.); *b*, *B. grapei* Gyll. (*picipes* Kby., *nitens* Lec.); *c*, *B. yukonum* Fall (*grapeioides* Munst.); *d*, *B. dauricum* Mtsch. All drawn from Swedish specimens.

Notaphus Steph.: 606 *coloradense*, 612 *nigripes*, 617 *variolosum*, 618 *umbratum*, 625 *approximatum*, 641 *indistinctum*, 648 *posticum*, 651 *patruele*, 655 *rapidum*, 659 *versutum*, 660 *variegatum*, 683 *insulatum*, 686 *viridicolle* (*cordatum*), 687 *nubiculosum*, 694 *contractum*, 695 *constrictum*.

Furcacampa Net.: 705 *affine*, 707 *impotens*, 713 *decipiens*, 724 *mimus* (*pellax*), and probably all species, as far as distinct, between 705 and 724. The subgenus was established on *affine* (Netolitzky 1931, p. 158) and named after the partially doubled frontal grooves. Though this fits *affine* only, the name must be applied also to the other members of the group, listed above, their close relationship with *affine* being shown by the inner armature of the penis. In any case the frontal grooves show a common external character: they are parallel between the eyes, with a more or less evident convergent prolongation on each side of the clypeus *inside* the setigerous puncture (lacking in *Notaphus*). Members of the Palaearctic subg. *Trepanes*, *e.g. octomaculatum* Gze., are generally similar but have straight frontal grooves, converging for their whole length. The armature of the internal sac of the penis is essentially different in *Trepanes* as well as in *Notaphus*.

Semicampa Net.: 725 *muscicola*, 755 *roosevelti* (*perconcinnum*), 18662(I) *semicinctum*, *browni* n. sp.

Bembidion s. str. (*Lopha* Steph.): 734 *quadrimaculatum* L., 741 *dubitans*, 744 *pedicellatum*, 747 *mutatum*, 749 *praecinctum*.

Diplocampa Bed. (nec Csy.): 754 *transparens* (*sulcatum*).

Trepanedoris Net. (*Diplocampa* Csy.): 759 *frontale*, 764 *acutifrons*, 772 *cautum*, 776 *anguliferum*.

Amerizus Chd.: 778 *oblongulum*, 779 *spectabile*.

2. Badister pulchellus group

The old record of the Palaearctic *bipustulatus* Fbr. from Vancouver (Leconte 1880, p. 165) has suggested a comparison between the bright, spotted *Badister* of America and of Europe. The two "*bipustulatus*" males in coll. Leconte prove, by a genital slide (fig. 13d), to be identical with the common American species usually known as "*pulchellus* Lec." But this is *not* the same as Leconte's type of the species (labelled "Western States", *i.e.* Evansville, Indiana, *vide* Leconte 1848, p. 418), which differs from all the rest of his specimens ("*pulchellus*" auct.). The original description states that the basal joints of antennae are pale, which fits the type specimen only. It is a small insect (5 mm.) with the elytra shorter and less parallel-sided than in the common

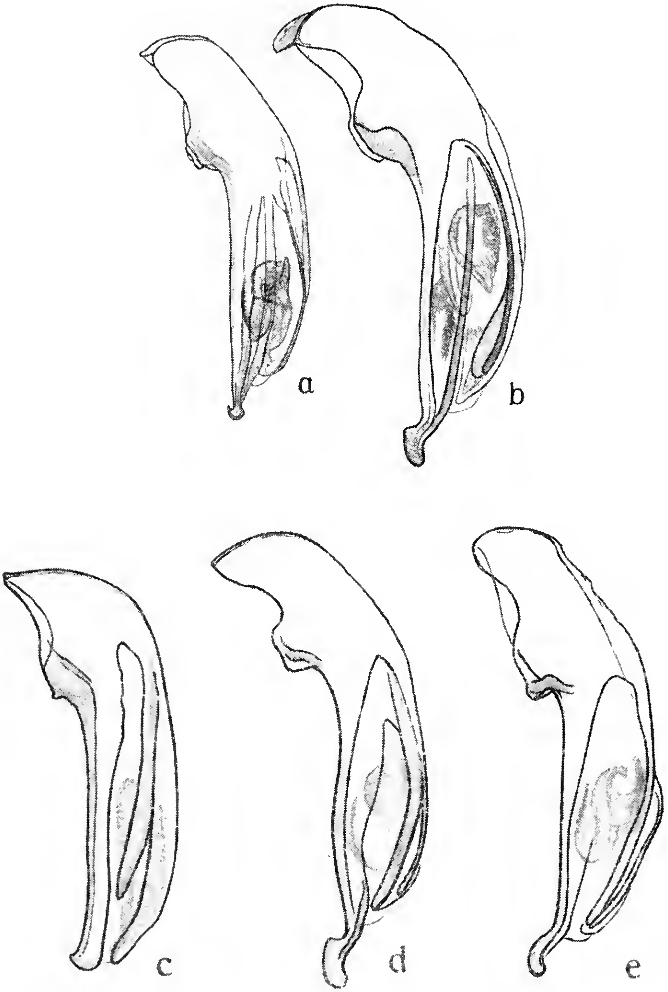


Fig. 13. Penis of: *a*, *Badister bipustulatus* Fbr. (Gotland, Sweden); *b*, *B. unipustulatus* Bon. (Öland, Sweden); *c*, *B. pulchellus* Lec. (type); *d*, *B. neopulchellus* n. sp. (Wayland, Massachusetts); *e*, *B. obtusus* Lec. (Isle Royal, Michigan; immature).

species, and with more arcuate basal margin inside the shoulders; the prothorax is not (or, in the second ex., *vide* below, very feebly) margined at base; and the antennae have three completely pale basal joints. The penis (fig. 13c) has a quite different apex which places the species near the Palaearctic *bipustulatus* (fig. 13a). In "*pulchellus* auct." the base of prothorax is evidently margined, at least laterally, and the second and third antennal joints, and usually also the first, are more or less darkened. The true *pulchellus* Lec. must be very rare. I have seen only one additional ex., a ♂ from Selma, Alabama (NMW), in which the antennae are still paler, the darkening from the fourth joint being inconspicuous.

The common species lacks a name, no synonym being available, and I propose to call it **neopulchellus n. sp.** As type locality I designate West Roxbury, Massachusetts (P. G. Bolster), from where 11 ex., including the holotype ♂ and allotype ♀, are in MCZ. Its nearest relative in North America is *obtusus* Lec. This species was described (1878, p. 594) as "unspotted" but the elytra of the single type ♀ show a clear, though feeble, trace of the characteristic pattern common to the other species here treated. A similarly coloured ♂ from Isle Royal, Michigan (coll. Fall, MCZ) and another from Aweme, Manitoba (NMW) have a penis (fig. 13e) closely resembling that of *neopulchellus* but with a slightly different apex. In the Palaearctic *unipustulatus* Bon. (fig. 13b) the penis is even more similar.

The easiest way to separate *obtusus* from *neopulchellus*, except on colour (which may be difficult in immature specimens), is by the elytral microsculpture which in *obtusus* (both sexes) is much stronger, forming evident, transverse meshes, whereas in *neopulchellus* it consists of extremely feeble transverse lines with no tendency to form meshes. This is apparently the reason why *neopulchellus* has iridescent elytra, *obtusus* not.

3. AGONUM MELANARIUM group

No carabids studied by me were found to be more utterly in confusion in North American museums than the species of *Agonum* (*Platynus*) listed in Leng's List as nr. 1538–1552, with several additional Casey species in the first supplement. Casey (1920, p. 111) named this group subg. *Melanagonum*, but a European coleopterist would treat them as belonging to *Agonum s. str.* The difficulties, no doubt, are due partly to the unimportant and largely inconstant

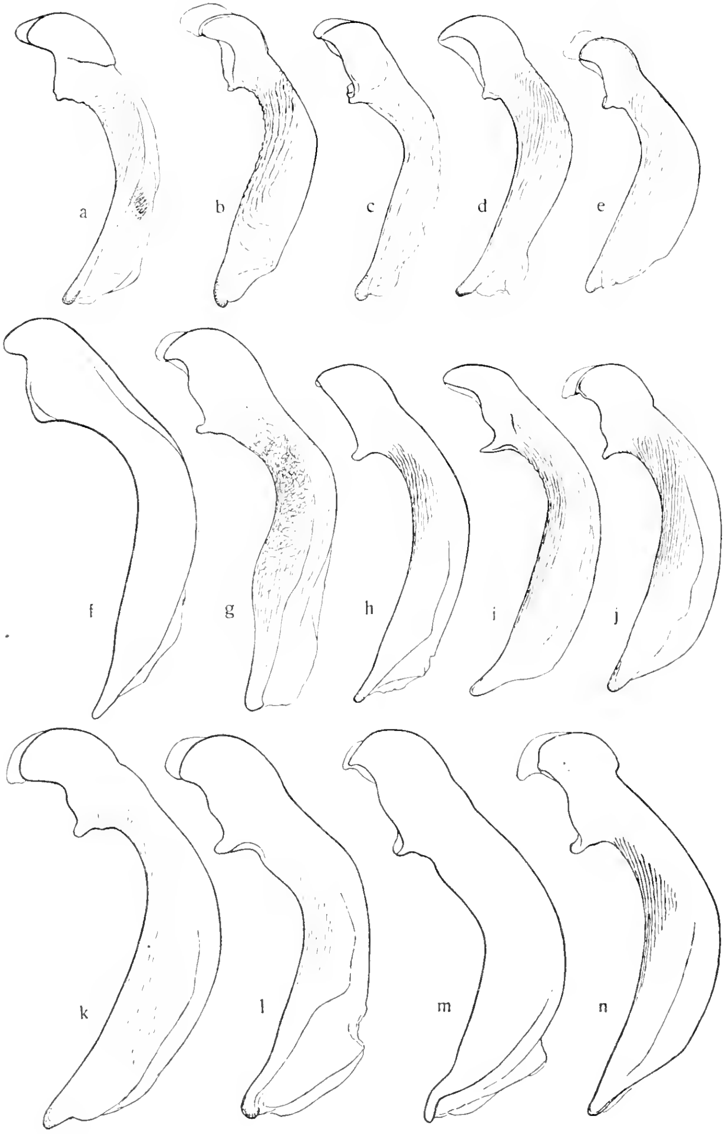

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Fig. 14. Penis (side view) of *Agonum s. str.* ("*b*" to "*e*" less magnified than the rest):

a, *collaris* Say (det. Darlington) Pennsylvania;
b, *mutatum* G. & H. (type of *atratum* Lec.) Lake Superior;
c, *fidele* Csy. (type of *laeve* Lec. and *molestum* Lec.) "Middle States";
d, *carbo* Lec. (original Leconte specimen) Lake Superior;
e, *metallescens* Lec. (original Leconte specimen) Hudson Bay Territory;
f, *arizonensis* Horn (det. Darlington) Arizona;
g, *moerens* Dej., Lec. (*tenue* Lec.?) Halifax, Nova Scotia;
h, *propinquum* G. & H. Deer Lake, Newfoundland;
i, *fraterculum* Lec. (det. Fall) Salmon Arm, British Columbia;
j, *deceptivum* Lec. (original Leconte specimen) Nova Scotia;
k, *harrisi* Lec. Cheticamp, Nova Scotia;
l, *trigeminum* n. sp. Halifax, Sackville, Nova Scotia;
m, *melanarium* Dej., Lec. Cheticamp, Nova Scotia;
n, *frater* Lec. (original Leconte specimen) California.

external characters separating these species, but in part also to the unfortunate way in which Leconte, in his synoptic table (1879), grouped them, mainly according to the position of the dorsal punctures of elytra, a character which is liable to considerable variation. Actually, because of the excellent characters in form and surface sculpture of the penis, the North American species can be more easily separated than those of the corresponding Palaearctic group of *viduum* Panz. etc., though the latter is less numerous in species. Therefore, as a starting point for interested students, drawings of the penis of the North American species known to me are here given (fig. 14).

Of the species figured, *collaris* Say and *arizonensis* Horn show little relation to the rest; *i.e.* the penis of *collaris* is the only one possessing chitinized parts (forming a group of teeth) in the internal sac. Casey (1920, p. 124) was therefore right in removing *collaris* from the "*melanarium*-group". The species most likely to be confused on penis characters are: *frater* Lec. with *deceptivum* Lec., and *melanarium* Dej. (& Lec.) with *trigeminum* n. sp. But within each pair of species a separation is easily made on external characters, for one species of each pair (*frater* and *melanarium* respectively) have well defined hind-angles of the prothorax.

The penis figured in fig. 14-l belongs to a species which I first considered identical with either *corvus* Lec. or *hyslopi* Csy. Of the former I have seen a ♀, checked with Leconte's ♀ type by Darlington. It is a different species, with slenderer maxillary palpi, deeper elytral striae, etc. I made a genital slide of the ♂ type of *hyslopi* in the Casey collection (NMW) but failed to draw it. A figure of the penis later sent by Blackwelder is essentially different. The species in question thus seems to be undescribed. I propose to call it

Agonum (s. str.) trigeminum n. sp.

Deep black without any trace of metallic lustre; tarsi and bases of tibiae sometimes slightly piceous.

Closely similar (related) to *fidele* Csy. (*laeve* Lec., *molestum* Lec., *subinflatum* Csy.) with which the female may be confused. The new species is slightly larger on an average, and its prothorax is broader with more broadly reflexed sides; the posterior setigerous puncture is a little removed from the side margin, and the depressed area surrounding this puncture usually does not (as in *fidele*) cause pronounced jag of the side margin (median view!); the maxillary palpi, especially their second joint, are more slender; and the microsculpture of elytra is more open than in *fidele* and its lines show a much clearer tendency to form meshes which are only slightly transverse, this difference being most evident in the female.

From *mutatum* G. et H. (*atratum* Lec.), to which also it is closely related and which agrees in elytral microsculpture, the new species is most easily separated by larger size and by the longer and, in proportion to the prothorax, much broader elytra. Furthermore the head is more narrowed forwards in *mutatum*, in which the side margins in front of the eyes are not parallel-sided as in *trigeminum* but closely convergent.

Length 8.3–10.0 mm.

The penis (fig. 14) is quite different in all three species. In *trigeminum* (fig. 14-l) it is stout, strongly arcuate, without conspicuous surface sculpture.

Holotype ♂ and allotype ♀: Sackville, Halifax, Nova Scotia, 20.V.1951 (Lindroth, DAO). 7 paratypes: same locality, 1 ♂; Waverley, Halifax, 21.V.1951, 2 ♂, 1 ♀; Riversdale, Truro, Nova Scotia, 22.V.1951, 1 ♂; Lapland, Lunenburg, Nova Scotia, 1.IX.1952, 1 ♂ (D. C. Ferguson); Rumney, New Hampshire, 13.VI.1924, 1 ♂ (P. J. Darlington). The paratypes are distributed among the following museums: MCZ, NMW, Nova Scotia Museum of Science (Halifax), Zoological Institute of the University, Lund (Sweden).

Ecology. In Nova Scotia *trigeminum* occurs in company with *fidele* at the margin of eutrophic ponds and pools with dense vegetation of Carices etc. It is very hygrophilus. In contrast, *mutatum* is a bog species, as a rule living in sphagnum.

SPECIES NEW TO AMERICA

The following 15 species, as far as I can judge, are not known previously under any name in North America. Four of them, apparently undescribed, are probably genuine, native American species. The rest are previously known from the Palaearctic region, and four of them (*Nebria brevicollis*, *Bembidion properans* and *rupestre*, *Pterostichus strenuus*) no doubt are recent introductions. Three of the new species will be described in my Newfoundland paper; the fourth (*Agonum darlingtoni*), is briefly diagnosed below and will be more fully described in connection with a revision of the subg. *Europhilus*.

Diachila polita Fald. 1835. Distinguished from *arctica* Gyll. sbsp. *amoena* Fald. (*subpolaris* Lec.) by the lack of a carina inside the hind angles of prothorax. The wings are constantly vestigial. Alaska (NMW! MCZ!), North West Territory (DAO!).

Blethisa eschscholtzi Zoubk. 1829. Large as *quadricollis* Hald., with a very characteristic prothorax, almost rectangular, with parallel sides in the posterior half, strictly rectangular hind angles, and strong, straight basal carinae, converging forward. Texas (Sanderson, 1 ♀, NMW).

Notiophilus intermedius n. sp. This species, to a certain degree intermediate between *simulator* Fall and *directus* Csy. (*lanei* Hatch), but well characterized by its penis, will be described in my Newfoundland paper. Known also from Labrador, Manitoba and Alaska.

Nebria brevicollis Fbr. 1792. This European introduction, known only from 1 ex. from the French island Miquelon (S. of Newfoundland), is at once distinguished from all indigenous North American species by the hairy upper surface of the tarsi, and belongs to the subg. *Helobia*.

Bembidion (*Metallina*) *properans* Steph. 1829. Differs from *lampros* Hbst. by the straight, not laterally dilated frontal grooves (fig. 2b) and by the quite different penis (figs. 2d, 9b). An introduced species, known from Nova Scotia only.

B. (*Plataphus*) *lenense* Popp. 1906. Similar to *rusticum* Csy. but averaging larger, with more parallel-sided elytra and more or less darkened legs. The penis (fig. 11e) is quite different and shows a close relationship to the Palaearctic *prasinum* Dft. There is complete agreement, including the penis, with Poppius' type specimen from River Lena, Siberia (UMH). Individuals with rufescent elytra are not rare. Alaska, Yukon Territory, British Columbia, Labrador, Newfoundland.

B. (*Pl.*) *hyperboraeorum* Munst. 1923. Similar to *rusticum* Csy. and *lenense* Popp., but with completely dark antennae and legs. Prothorax almost rectangular, with very feebly sinuate sides (fig. 5a). Differing from the similarly coloured *planiusculum* Mnh. by the broadly rounded tip of the elytra. Penis, fig. 11c. Alaska, North West Territory.

B. (*Blepharoplataphus*) *hasti* Sahlb. 1826. Distinguished from all true *Plataphus* by the fringe of minute hairs on each of the last ventral segments of the abdomen (fig. 4a) and therefore belonging to subg. *Blepharoplataphus*, of which I have seen no other representative from North America (*cf.* Netolitzky 1942–43, p. 80). Prothorax, fig. 5b. British Columbia, North West Territory, Manitoba, Quebec, Labrador.

B. (*Peryphus*) *dauricum* Mtsch. 1844. Externally similar to *grapei* Gyll. (*picipes* Kby., *nitens* Lec.) but easily distinguished by the oviform last antennal joints (fig. 7), the (especially in the ♀) network-like microsculpture at the tip of elytra, and the penis (fig. 12d). Alaska, North West Territory, Manitoba.

B. (*Per.*) *rupestre* L. 1767. Easily distinguished from all other four-spotted *Peryphus* (*ustulatum* L., *petrosum* Gebl., etc.) by the microsculpture of the prothorax extending over its whole disc. The femora are always darkened. Penis, fig. 8b. Quebec, New Brunswick, Nova Scotia, Newfoundland. Introduced.

B. (Eupetedromus) immaturum n. sp. Narrower than *incrematum* Lec., very pale, with apical part of penis much shorter. To be more fully described in my Newfoundland paper. New Hampshire, Quebec, Nova Scotia, Newfoundland.

B. (Semicampa) browni n. sp. A small, very dark species which will be described in my Newfoundland paper. Cooks Harbour, Newfoundland; Churchill, Manitoba.

Pterostichus (*Argutor*) *strenuus* Panz. 1797. Closely related to *patruelis* Dej. and the other species united by Casey (1918, p. 378) as genus *Micromaseus*, and like *femoralis* Kby. with coarsely punctured prosternum, but *strenuus* is smaller (6–7.2 mm.) with the prothorax with pronouncedly sinuate sides before the hind angles which are sharp and right, and with a more extensively punctured base. Newfoundland only. Introduced.

Agonum (Europhilus) darlingtoni n. sp. This small species, at once recognized by the densely transverse microsculpture of the elytra, will be described in a special paper. Connecticut, Massachusetts, Nova Scotia.

Harpalus fuliginosus Dft. 1812. Very characteristic in appearance, the prothorax being an exact copy of that of *Nestonotus lugubris* Dej., but the antennae being quite pale. Probably transamerican, from Newfoundland and Labrador to Alaska.

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By Donald Baird

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CHIROTHERIUM LULLI, A PSEUDOSUCHIAN REPTILE FROM NEW JERSEY

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No. 4.— *Chirotherium lulli, a Pseudosuchian Reptile from New Jersey*

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INTRODUCTION

In 1885 the vertebrate paleontologist and bibliographer John Eyerman, while examining Upper Triassic exposures in the Delaware River valley, discovered fossil footprints in the quarries of the Messrs. Clark near Milford, Hunterdon County, New Jersey. The series of footprint-bearing slabs which he collected was deposited in the geological museum of Lafayette College at Easton, Pennsylvania. Aside from a brief notice of the discovery by Eyerman (1886), curiously superficial descriptions of some of the species by C. H. Hitchcock (1889), and a redescription of *Chirotherium* [*Otozoum*] *parvum* by Lull (1904, 1915), the Lafayette footprint collection received little attention for 65 years. Recently Wilhelm Bock, while preparing a general treatment of Triassic reptilian tracks from the Newark basin of New Jersey and Pennsylvania, re-examined the collection and made good the previous neglect by describing and figuring the significant specimens. One of these, a small manus-pes set impressed in reddish-brown siltstone, became the type of the new species *Chirotherium lulli* Bock (1952).

During the same period a convergent series of events took place. An amateur fossil collector acquired (perhaps at an auction) a fine slab of fossil footprints reported to have come from Sanatoga, Pennsylvania. This slab of reddish-brown siltstone bore in relief the casts of four successive small tracks, the last overlapped by the birdlike footprint of a dinosaur. After the owner's death the slab was fortunately obtained for the Academy of Natural Sciences of Philadelphia by Wilhelm Bock, too late however for inclusion in his paper, and after the type of *Chirotherium lulli* had been returned to Lafayette College.

At this point, in the course of preparing a faunal study of the Milford reptile footprints in the Museum of Comparative Zoology, I visited Philadelphia and Easton and made latex molds of both specimens. On comparison of the molds it immediately became evident that, although the specimens are labeled as having come from different states, the type of *C. lulli* is the counterpart of the third manus-pes set on the Philadelphia slab. Every detail of the footprints and every furrow, rain-print, and exfoliated patch on the surface of the slabs corresponds exactly.

From this excellent new material so fortuitously brought to light we may draw a more precise understanding of the morphology and relationships of *Chirotherium lulli.* Its peculiar combination of primitive and advanced characters, its association with ornithoid dinosaur footprints, its bearing on problems of stratigraphic correlation, and its position as the youngest known member of an important genus justify the presentation of this supplementary note.

I am greatly indebted to Wilhelm Bock for his generous permission to describe the new specimen and for his hospitality during my stay in Philadelphia, as well as for his judgement on several controversial points. Without his cooperation in furnishing materials and photographs for study, this paper could not have been written. Hearty thanks are also due to Professor James L. Dyson of the Department of Geology, Lafayette College, for the loan of the type specimen; and to Drs. Joseph T. Gregory at Yale and Albert E. Wood at Amherst for their hospitality in facilitating my study of footprint specimens there. Dr. John C. Harper of the Department of Geology, University of Liverpool, has been most generous in furnishing data and literature on Keuper footprints in the Liverpool museums. Photographs for the plates were supplied by the Academy of Natural Sciences of Philadelphia through the courtesy of Dr. Horace G. Richards. My indebtedness to Professor Richard S. Lull for pleasant and stimulating discussions is gratefully acknowledged.

SOURCE OF THE MATERIAL

Obviously the type locality cannot be both Milford, New Jersey, and Sanatoga, Pennsylvania. It is suggestive to note that another specimen from the same private collection as the *C. lulli* trackway slab, the type of *Chirotherium copei* Bock, was labeled as having come from a quarry near Washington's Crossing on the Delaware River although internal evidence demonstrates beyond doubt that it actually came from the gray sandstone layer of the Smith Clark quarry at Milford. With this example of mislabeling in mind we may justifiably discount the Sanatoga label.

Although the source of the Lafayette College type cannot be proved, it is part of a collection made by John Eyerman, whose only recorded collecting of fossil footprints was done at the Milford quarries in 1885 and 1887. No reference is made to this specimen in the early reports on the Lafayette collection, but (as I will point out in a subsequent paper) grave ambiguities exist in both accounts. Bock (1952, p. 416) reports that a bed of red-brown shale bearing water-flow marks like those on the footprint slabs crops out in the Smith Clark quarry some 15 meters above the gray sandstone horizon which bears the *Chirotherium parvum* faunule. Thus it appears fairly probable that, as stated in the original description, the single known individual of *Chirotherium lulli* was found in the Smith Clark quarry near Milford, Hunterdon County, New Jersey. The type horizon (as determined by Bock) lies in the upper Brunswick formation some 5,100 meters above the base of the Newark series, Upper Triassic.

REDESCRIPTION OF THE SPECIES

Order THECODONTIA
  Suborder PSEUDOSUCHIA
    Family CHIROTHERIIDAE Abel, 1935
      Genus CHIROTHERIUM Kaup, 1835
        LARGE-MANUS GROUP of Peabody, 1948

CHIROTHERIUM LULLI Bock

Bock, Wilhelm, 1952. Jour. Paleontology, 26, p. 415, pl. 49, fig. 7.

Type. Lafayette College Geological Museum S491, a left manus-pes set (inadvertently cited as right in the original description). Academy of Natural Sciences of Philadelphia, Wilhelm Bock collection, four consecutive manus-pes sets in relief, the third of which is the counterpart of S491. As these specimens represent the same individual, both constitute the type in the sense of Simpson (1940); for the type of a zoological species is (at least in non-colonial forms) most reasonably regarded as an individual animal, the sum of all its parts however many museum specimens these may comprise.

Diagnosis. A diminutive species of the large-manus group. Trackway relatively wide with pace angulation of 150°; manus apparently elongate and prehensile; pes broad and strongly toed-out, characterized by oblique cross-axis, relatively long and subequal digits II and IV, and functionally posterior digit V with well-developed metatarsophalangeal pad. Measurements in Tables 1 and 2.

TABLE 1

COMPARATIVE MEASUREMENTS OF SMALL, LARGE-MANUS CHIROTHERIIDS

Data on the three Lower Triassic (Moenkopi) species from Peabody, 1948.

	C. lulli	*C. diabloensis*	*C. cameronensis*	*C. minus*
Stride, mm.	232	270	425	750
Pes length, mm.	44	53	50	85
Stride : pes length	5.3:1	5:1	8.5:1	9:1
Pace angulation	150°	140°	161°	164°
Pes divarication	29°	22°	13°	12°
Manus divarication	same	same	none	none
Angle, cross axis to digit III axis	*ca.* 68°	55°	55°	70°

Trackway. As body bulk has a definite effect on trackway pattern, the well-known smaller species of *Chirotherium* serve best for comparison with the diminutive *C. lulli* (see Table 1). From its proportions the type trackway appears to have been made by a walking rather than a running individual. The pace angulation and the ratio of stride to pes length are unexpectedly low for an Upper Triassic species, in which cursorial specializations might be expected; indeed these characters compare most closely with those of the primitive Lower Moenkopi species *C. diabloensis.* Perhaps these trackway proportions are as much a function of size as they are criteria of primitive organization.

The pes is toed-out to an unusual degree, the axis of digit III forming an average angle of 29° with the trackway midline. (The functional significance of this arrangement is discussed below.) Pes and manus are turned out at about the same angle. This is just the relationship found in *C. diabloensis* and contrasts with the situation in *C. cameronensis* and *C. minus*, in which the pes divarication is only about half that of *C. lulli* and the manus points directly forward. Large chirotheriids, however, in general have the manus turned out as far as the pes or (in *C. barthii*) even farther.

On the assumption that the animal's gait was alternating, i.e. that the left manus and right pes were implanted at essentially the same time, the gleno-acetabular length of the trackmaking reptile may be determined by the method used with primitive tetrapods (Baird, 1952, p. 834). This method is detailed below in the section on skeletal restoration. The agreement of figures, 142 and 145 mm., obtained from measurements over two segments of trackway is well within the limits of probable error. The slight overlap of the right pes onto the adjacent manus print might indicate that the manus print had previously been vacated, hence that the gait was not strictly alternating; but an overlap of this size could well occur with the manus still partially implanted but in the roll-off phase.

Manus. As may be seen from Plate 1, the left manus imprint lies nearly a centimeter ahead of the pes, with the axes of the third digits nearly in alignment. Though digits IV and V impressed only faintly, digits I–III recorded their full lengths. The right manus imprint, in contrast, lies just medial to the pes with its postero-lateral border slightly overlapped by the tip of pes digit II. Here digit impressions are wholly lacking and the imprint is ovoid, apparently representing the metacarpo-phalangeal pads and part of the adjacent sole. Whether this anomaly is caused by a malformed right manus or merely a normal variability in gait cannot be determined from this short trackway of a single individual.

For the details of manual anatomy we must rely almost entirely on the third manus-pes set which is fortunately preserved in counterpart. The imprint is incomplete, lacking digit V and much of IV, and is none too clear in the details recorded. Undue faith should not, therefore, be placed in the observations which follow.

The table of measurements compiled by Bock can now be supplemented on the evidence of the counterpart trackway (see Table 2).

TABLE 2

MEASUREMENTS OF *CHIROTHERIUM LULLI*, TYPE

Digit lengths include metacarpo- or metatarso-phalangeal pads; pes digit V measured along curved axis.

	MANUS	PES
Area, mm.^{2}	est. 180	360
Length, mm.	22	44
Width	est. 20	26
Length, I–IV group	19	30
Width, I–IV group	16	23
Length, digit I	8	17
II	15	22
III	19	27
IV	? 15	24
V	?	18
Pace (average of 3)	117	

As restored the manus has a surface area approximately half that of the pes. This ratio is high even for a member of the large-manus group, in which the manus area is more typically one-third to one-quarter that of the pes.

The manus is characterized by moderately divergent, elongate digits with distinct articular pads which indicate a phalangeal formula of 2–3–4–?–?. Peabody (1948, p. 401) has derived the same formula from rare specimens of *C. diabloensis* and deduces that the complete formula was probably 2–3–4–5(4?)–3. Digit I is offset laterally and set well back, suggesting that metacarpal I was unusually short. The proximal phalanges of digits II–IV seem to be united into a solid palm, so that the interdigital salients penetrate only to the level of the joint between phalanges 1 and 2. Digits II and III appear to be clawed; only the base of IV is preserved. Very little can be said about the fifth digit, as impressions which might be attributed to it bear different relationships to successive impressions of the left manus. (Considerable variation in the divarication of digit V in single trackways of *C. minus* has been noted by Peabody, 1948, p. 362). The position shown in Figures 1 and 2 is that indicated by the third manus-pes set, but the evidence is weak indeed.

No species of *Chirotherium* known to me has a less specialized manus than this; a closely comparable organ is found only in *C. cameronensis* from the Upper Moenkopi. The long, clawed digits with their individually padded joints indicate the retention of a grasping function which had been lost by all other chirotheriids except perhaps the small, primitive Lower Triassic species *C. diabloensis*, *C. cameronensis*, and *C. minus*, the Upper Triassic *Synaptichnium* (see Figure 1 B–E), and an unnamed Bunter species from southern France (Charles, 1949). Such a long-fingered, grasping manus is unique among Upper Triassic species of *Chirotherium*, for even in early Moenkopi (early Bunter) time the typical chirotherian manus had already become rather compact and inflexible, and a hoof-like manus characterizes all the other known Keuper species.

Pes. An optimum of information on pedal structure is revealed by the remarkably clear detail of the second pes imprint (Plate 2, figure 1), verified by the evidence of the other three. Digits I–IV form a relatively broad group, the posterior margin of which is not clearly defined, separated from digit V by a relatively wide sulcus. Metatarso-phalangeal pads I–IV are faintly separated by very shallow sulci; the curvature of the broad arc in which they lie is of course due both to transverse arching of the distal end of the metatarsal bundle and to differences in metatarsal length. The cross axis (drawn between pads I and IV) intersects the long axis of digit III at an angle which is less acute than in the primitive species *C. diabloensis* and *C. cameronensis* (see Table 1) but more acute than in most other species, in which the angle approaches 90°.

The first four digits are sub-parallel with a total divarication of less than 20°; they are separate rather than basally appressed, so that wide interdigital salients extend back almost to the level of the metatarso-phalangeal joints. All bear long sharp claws. Articular swellings, which are visible both in outline and as rounded, confluent elevations on the ventral surface, indicate a normal reptilian phalangeal formula. The digits as a group are rather short in relation to the width of the metatarsal bundle; IV is slightly shorter than III, and II is nearly as long as IV. This pattern of relative digit length

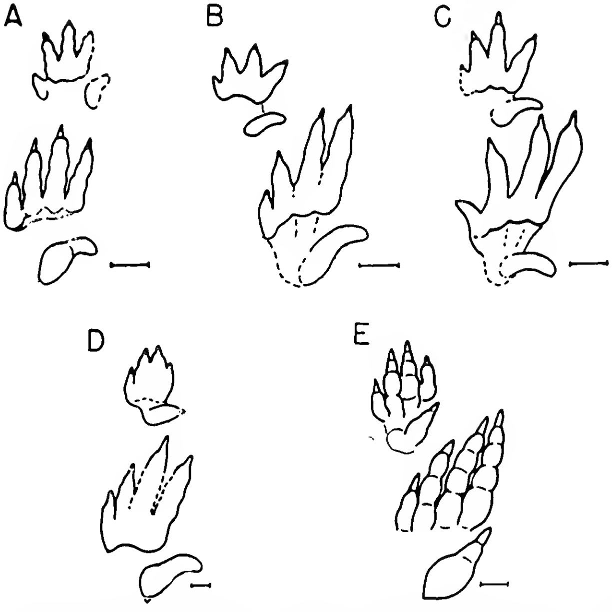

Fig. 1. Small chirotheriids of the large-manus group, similarly oriented for comparison. **A.** *Chirotherium lulli*; **B.** *C. diabloensis*; **C.** *C. cameronensis*; **D.** *C. minus*; **E.** *Synaptichnium pseudosuchoides*. **A C** x $^1/_2$, **D** x $^1/_4$, **E** x $^3/_8$. **B, C, D** from Peabody, **E** from Smith Woodward.

differs from that of other small chirotheriids (see Figure 1) but compares more closely with that of the large species *C. barthii*.

Digit V, unlike that of the other small species, bears a well-developed metatarso-phalangeal pad which impressed at every step. The digit as a whole is set rather medially so that the presumed position of its metatarso-phalangeal joint is in line with the long axis of digit IV; thus the phalangeal part, though of average proportions, projects laterally somewhat less than it does in the other small species. This phalangeal segment is clearly demarcated from the pad and shows (in the second imprint) faint constrictions and nodes which indicate the presence of three phalanges; the minute rudiment of a fourth may or may not have been present.

Here we have a foot in which the first four digits could apparently be flexed independently on the metatarsals like human fingers, and must have retained the primitive grasping ability which had been sacrified in most chirotheres to cursorial specializations. The thumb-like fifth digit, which primitively served to prop the chirotherian foot at right angles to the direction of movement, is fully developed and — when seen in the isolated footprint — appears to have lost little of this function. But this appearance is totally misleading, as the new-found trackway reveals. On the contrary, the foot in walking is toed-out so strongly that the entire length of digit V falls behind the pads of the first four metatarsals and medial to most of the free length of digit IV: the lateral propping function of the "thumb" has been entirely lost.

A striking parallel to this development is found in a British Middle Keuper chirotheriid designated as "form L" by Beasley (1904, p. 229, pl. 7) and named *Chirotherium beasleyi* by Nopcsa (1923, p. 144).[1] A trackway from Storeton, Cheshire (British Museum [Natural History] R.729) shows this to be a long-striding form rather similar in size and shape to *C. minus* (see Figure 1 D), though pes digit I is slender and almost non-functional and digits II–IV form a strong, symmetrical group. The pes is toed-out to about the same extent as in *C. lulli*, and digit V is (as Beasley observes) set well back and close to the middle line of the foot. Such a structure could readily have developed from that of the presumably ancestral *C. minus* by a medial shift of the distal end of metatarsal V.

Similar features are shown by another British Keuper form designated as footprints of *Rhynchosaurus* by Smith Woodward (1902),

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[1] *Non C. beasleyi* Peabody, 1948; the latter species is renamed in an appended note, page 189.

as form "D 3" by Beasley (1905, p. 277), and as *Synaptichnium pseudosuchoides* by Nopcsa (1923, p. 142; see also Abel, 1935, fig. 50). This species (Figure 1 E) is somewhat younger than the last and comes from Chillington, South Staffordshire. In form it is (as Nopcas concludes) more pseudosuchioid than rhynchosauroid, with the pes impressing behind the manus rather than beside or ahead of it. The whole aspect suggests a long-fingered small chirotheriid of the large-manus group, the chief difference lying in the straightness and sharp claws of manus and pes digits V.[2] In both manus and pes the fifth digit is set medially and entirely behind the other four; the pes is more toed-out than the manus but its exact divarication from the trackway midline is unknown.

In these two English species as in *Chirotherium lulli*, pes digit V can have acted only as a posterior, not a lateral prop. This fact in itself is no distinction, for partial or complete loss of the fifth digit's lateral propping function is so common among Keuper chirotheriids of both large-manus and small-manus groups as to be almost characteristic of the period. But the methods by which this modification of function was accomplished are varied. An examination of this variety in method offers us some insight into problems of pedal adaptation among late Triassic pseudosuchians as well as useful criteria for differentiating the various footprint species.

At least five processes are involved, either singly or in combination: *shortening* or virtual elimination of the phalangeal segment of digit V, *attenuation* of this segment, *straightening* it to reduce the lateral projection, *medial shift* of the distal end of metatarsal V and thus of the metatarso-phalangeal pad, and *toeing-out* to rotate digit V to the rear. The incidence of these processes in some of the better-known Keuper chirotheriids may be tabulated as follows. Parentheses indicate a slight modification; a dash, that the trackway is unknown.

Chirotherium lulli is unusual in having achieved such a modification without losing the primitive grasping ability of the foot. This ambivalence of pedal adaptation may well have been one of the factors which enabled *C. lulli* to survive all its relatives.

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[2] Discussion of the relationships of this remarkable form to *Chirotherium* and to such quasi-chirotherioid species as *C. angustum* Huene and *Thecodontichnus verrucae* (Tommasi) from the Verrucano of Italy, and *Gwyneddichnium minore* Bock from the Lockatong of Pennsylvania, is unfortunately beyond the scope of this paper.

	Shortening	*Attenuation*	*Straightening*	*Medial shift*	*Toeing-out*
LARGE-MANUS:					
C. lulli Bock				x	x
C. beasleyi Nopcsa				x	x
Synaptichnium pseudosuchoides Nopcsa		x	x		?x
C. angustum Huene	(x)			x	—
C. wondrai Heller		x	x	x	—
SMALL-MANUS:					
C. lomasi nom. nov.	(x)				x
C. parvum (Hitchcock)	x				—
GROUP UNCERTAIN:					
C. herculis Egerton (?=C. bipedale Abel)	x			x	
C. thuringiacum Rühle	x				—
Brachychirotherium hassfurtense Beurlen	x		x		—
Eyerman's chirotherium (Baird MS)	x				—

RELATIONSHIPS

Because of the equivocal nature of the footprint record it is necessary to examine the relationships of *Chirotherium lulli* as a member both of the form-family Chirotheriidae and of some family of the Pseudosuchia.[3] Comparison with skeletal remains may however be deferred for consideration in connection with an attempted reconstruction of the pedal skeleton.

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[3] Abel (1935, p. 67) proposed the Chirotheriidae as a family of the order Pseudosuchia, diagnosed both by footprint characters and by inferred skeletal structure. This treatment is however unworkable because of eventual overlap with some osteologically-based family of reptiles (if not several) — an overlap which cannot be resolved by the rule of priority because footprints and skeletons can almost never be correlated to the point of synonymy. A more realistic and practical procedure is to treat the Chirotheriidae as a form-family of footprints, diagnosed on observed characters only, and correlative with some part of the zoological order Pseudosuchia although taxonomically distinct. Such a procedure has ample precedent in the long-established use of form- and organ-categories in paleobotany and invertebrate paleontology. It preserves the proven advantages of the Linnaean system of nomenclature as contrasted with systems of formula-names or para-Linnaean categories.

Chirotherium lulli shows a curious assemblage of presumably primitive and specialized characters which are segregated in the tabulation below:

PRIMITIVE	ADVANCED
GENERAL	
Wide trackway (low pace angulation).	Pes V functional as posterior, not lateral prop.
Low stride-to-pes length ratio.	
Prehensile manus and pes.	
MANUS	
Elongate, clawed digits.	Metacarpal I apparently short.
PES	
Oblique cross axis.	Group I–IV broad.
Fairly long digit V widely separated from I–IV.	Long II; IV shorter than III but longer than II.
	Distinct metatarso-phalangeal pad on medially set V.

Comparisons with Lower Triassic chirotheriids of the large-manus group may be summarized by the statement that most of the characters listed fall within the range of specialization of species from the American Moenkopi and the European Bunter. *Chirotherium lulli* is readily distinguished from all of these, yet in morphology it is close to them; and were it not for the facts of stratigraphy and the associated tracks of dinosaurs, it might reasonably be assigned to the Lower Triassic. High in the Upper Triassic it is in many ways anachronistic.

The comparisons with European Keuper chirotheriids which were made in the preceding section indicate that while *Chirotherium lulli* resembles many of them in single characters or adaptive groups of characters it shows no close relationship to any. The other Upper Triassic chirotheriids from North America likewise offer few points of comparison. All the known specimens were found by the same collector in the same quarry near Milford, New Jersey, in a gray sandstone-over-shale sequence of the Brunswick formation some 15 meters below the horizon of *C. lulli.* Two basic structural types are present. The first, including *C. parvum* (C. H. Hitchcock) and *C. copei* Bock, represents a highly specialized lineage of the small-manus group and so does not concern us here. The second is an undescribed species known from a single deep pes imprint collected for the Museum of Comparative Zoology by John Eyerman in 1887. Preliminary examination indicates that this is a large-manus species of average size and not too different from *C. lulli* in general proportions. But in the structure of the fifth pes digit they are as unlike as possible, for *C. lulli* has a differentiated phalangeal segment of normal length while Eyerman's chirotherium has nothing but a compact, scale-bordered metatarso-phalangeal pad — the ultimate in digit reduction among Chirotheria.

Chirotherium lulli thus appears (on the evidence now available) to represent an independent lineage of the large-manus group which, though it paralleled other Keuper species in several respects, retained many characters more typical of Bunter species. Though probably not derived from any small, primitive Bunter form now known, it may have had ancestors in common with one or more of them.

SKELETAL RESTORATION

The skeletal restoration offered in Figure 2A is based on the assumption, supported by comparison with living reptiles and cursorial birds, that the toe joints correspond to the nodes and pads of the footprints. Except for manus digits IV and V, the form of which is conjectural, the basic skeletal pattern was restored entirely on the evidence of the footprints themselves and without reference to the pedal osteology of any fossil reptile. The result nevertheless conforms to the structure of known Triassic reptiles of the suborder Pseudosuchia, to which the Chirotheriidae have been referred for reasons succinctly stated by Peabody (1948, p. 395).

To find an approximate skeletal parallel for the pes of *Chirotherium lulli* we need look no farther than *Euparkeria*, a Lower Triassic genus of the family Ornithosuchidae. As may be seen in Figure 2B the pes of *Euparkeria* closely resembles the restored skeleton of *C. lulli* and is almost exactly the same size. Significant differences are, however, evident: in *Euparkeria* the metatarsal bundle is narrower and metatarsal I is decidedly shorter, so that the footprint of this genus is (as Peabody has pointed out) rather to be sought among the small Bunter chirotheriids with very oblique cross axes. A more striking difference lies in the position of the fifth metatarsal, the distal end of which in *C. lulli* must have lain directly beneath the shaft of the fourth: — the "thumb" was, if not apposable, somewhat apposed. Some experimentation with an enlarged model convinces me that the pes of *Euparkeria* cannot be made to conform to this pattern without doing violence to the articulation between metatarsal V and the calcaneum and tarsale. Here again the closest parallel to *Euparkeria* is to be

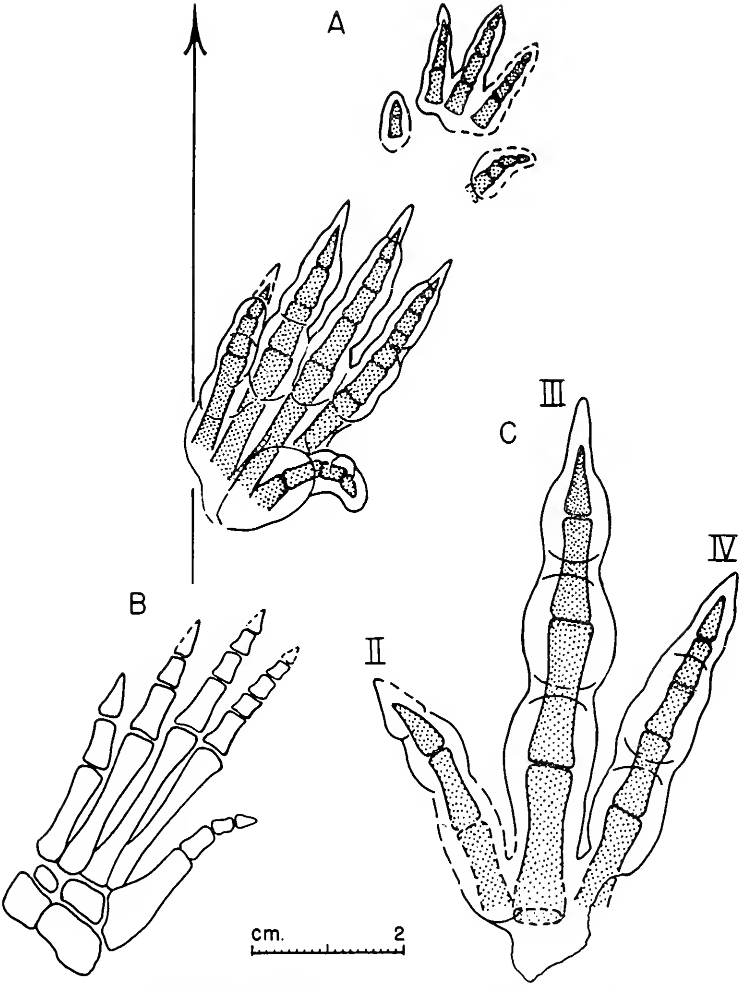

Fig. 2. **A.** *Chirotherium lulli* Bock, composite outline of right manus and pes with skeleton restored, x 1. Arrow represents midline of trackway. **B.** Pes of *Euparkeria capensis* Broom, x 1, modified from Broom after Schaeffer. **C.** Right pes imprint of the associated dinosaur, with phalanges restored, x 1.

found in a small Bunter chirotheriid such as *C. minus* (Figure 1D) in which the fifth metatarso-phalangeal pad is offset laterally.

The few Upper Triassic ornithosuchids whose feet are known are, like *Euparkeria*, only approximately comparable. *Saltoposuchus* may be eliminated as too far advanced in bipedality; the quadrupedal reconstructions by von Huene (1921, figs. 31, 32), in which the femora are essentially horizontal, cannot be manipulated to produce a chirotherioid trackway. The pes of *Ornithosuchus* (see Colbert, 1952, fig. 32B) differs significantly from the restored pes of *C. lulli*: digit I is the most robust and has a very short metatarsal, while metatarsal V is long and slender, lacking the proximal hook of *Euparkeria*, and bears a slender digit with elongate phalanges.

The pes of *Hesperosuchus* from the Chinle of Arizona, which has been restored after that of *Ornithosuchus* by Colbert (1952, fig. 31), is too incomplete for valid comparison with the restored skeleton of *C. lulli*. Its much larger size and proportionately longer phalanges appear to preclude any correlation. Although the manus is relatively large there is still no evidence to justify correlation of *Hesperosuchus* with the large-manus group of chirotheriids or (for that matter) with *Chirotherium* at all.

One Upper Triassic ornithosuchid in which the first four metatarsals correspond in relative length with those restored for *C. lulli* is *Pedeticosaurus* van Hoepen (1915, pl. 13) from the Karroo. Here no fifth digit or metatarsal is preserved, so comparison with *Chirotherium* is impossible.

Obviously there is insufficient material of both feet and footprints to permit valid or even tentative correlation between particular chirotheriid species and pseudosuchian genera. Nevertheless the body proportions of the reptile which produced the *Chirotherium lulli* footprints can be determined from the trackway and compared, in a general way, with those of ornithosuchids.

In computing the gleno-acetabular length of the trackmaker from the *Chirotherium lulli* trackway I assume that the gait was alternating as in living Archosauria, with the forelimb and hindlimb of opposite sides operating more or less simultaneously. Thus at one moment in each cycle of progression all four feet were in contact with the ground in such a manner that the left feet occupied a manus-pes set of footprints while the right pes was still implanted in the preceding set and the right manus had just impressed the first footprint of the next set. This situation is represented in Figure 3; a comparable stage in a

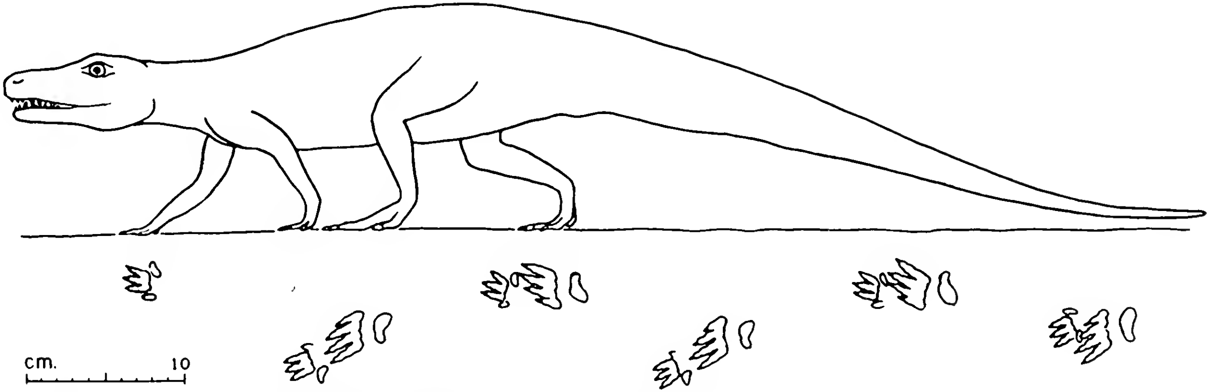

Fig. 3. A trackway of *Chirotherium lulli* Bock being made by an ornithosuchid pseudosuchian (restoration based on *Ornithosuchus* and *Euparkeria*).

walking sequence of *Alligator mississippiensis* is shown by Schaeffer (1941, fig. 17B) in a drawing made by projection from a motion picture.

At this moment in the cycle the center of the acetabular axis lies about midway between the tarsi, and that of the glenoid axis lies about midway between the carpi. To determine gleno-acetabular length from a trackway, therefore, we need only locate the midpoints between the carpal and tarsal areas, respectively, of four simultaneously-occupied footprints. The distance between these midpoints will represent a close approximation to the actual gleno-acetabular length of the trackmaker.

Quite a different method, it should be noted, has been used by Soergel (1925, p. 57) to determine the gleno-acetabular length of *Chirotherium.* The basic assumption of this method is that the movements of the opposite forelimb and hindlimb were one-half out of phase, so that at a moment when the center of the acetabular axis was midway between the implanted pedes, the glenoid fossa was directly above an implanted manus. Thus in his figure 51, where the left pes is in advance of the right, Soergel measures the "Rumpflänge" from the midpoint between the pedes to the next right manus imprint. The resulting measurement is exactly a quarter-stride longer than that obtained from the same trackway by my method.

We have observed that forelimb and hindlimb movement are essentially in phase in the Crocodilia, the closest living relatives of the Chirotheria. The wide straddle of *Alligator mississippiensis* and the nearly linear trackway of *Chirotherium barthii* are merely variants on the basic tetrapod trackway pattern, the differences between them being largely compromised in the trackway of *Chirotherium lulli.* Thus argument from analogy, though not conclusive, supports the interpretation offered here.

An out-of-phase pattern of limb movement such as that postulated by Soergel is characteristic not of reptiles but of mammals, whose physiology permits the development of gaits specialized for speed. Even the speed-adapted mammals, nevertheless, tend to revert to an alternating gait for leisurely progress. Whatever the appearance of the galloping, running, loping, pacing, or leaping trackways of such animals, the walking trackways in general consist of alternating left and right manus-pes sets. (Overlap or super-position of pes and manus imprints may obscure the basic pattern of sets. See Jaeger, 1948.) Although the mammal's opposite fore and hind feet may not move exactly synchronously at a walk, they are essentially in phase, and a reasonably close approximation of the animal's gleno-acetabular length may be determined from the trackway. Thus even if *Chirotherium* were capable of a rapid, out-of-phase gait, this would probably not be the gait at which it made a trackway of alternating manus-pes sets.

Having determined the basic body measurements of *Chirotherium lulli* we can now attempt to restore the trackmaker on the basis of an ornithosuchid of appropriate size and proportions. Dearth of skeletal material hinders the attempt, but by using *Ornithosuchus* as a model and modifying its proportions slightly after those of the more closely comparable but incompletely known *Euparkeria*, we may arrive at a fairly convincing restoration.

In the preparation of Figure 3 von Huene's reconstruction of *Ornithosuchus* (from Gregory, 1951, fig. 14.2) was enlarged until its gleno-acetabular length equalled that of *C. lulli*, and its feet were aligned with four simultaneously-occupied footprints of the trackway. The length of the fore limbs determined the shoulder height. As only the distal ends of the metatarsals impressed, the metatarsus had to be raised; the pelvis was also raised to give the femur the nearly vertical antero-posterior swing which is indicated both by its construction and by the narrowness of the trackway. The resulting figure is believed to represent with reasonable fidelity a small ornithosuchid in normal quadrupedal walking pose; it is also decidedly similar (with the exception noted) to the restoration of *Chirotherium barthii* which Soergel (1925, figs. 53, 54) derived from the trackways alone.

THE ASSOCIATED DINOSAURS

Slightly overlapping the fourth pes imprint of *Chirotherium lulli* (Plate 1 and Plate 2, figure 3) is the left pes imprint (reversed in the photograph) of a small tridactyl dinosaur. Most of the details are clear enough that a fairly reliable reconstruction of the form can be made from this single imprint. The slender digits bear triangular claws and well-defined articular nodes from which a normal theropod pedal skeleton may be reconstructed (Figure 2C).[4]

Digit II is shorter and more divergent than IV; both are placed well forward so that the joints between their first and second phalanges

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[4] My figure shows joints consistently reconstructed opposite nodes; in this respect it differs fundamentally from the reconstructions of Lull (1915) and slightly from those of Heilmann (1927, fig. 130 K) and Peabody (1948, fig. 37). A detailed critique of these various interpretations is included in my forthcoming study of the other reptile footprint faunules from Milford.

lie opposite the distal part of the first phalanx in digit III. If the lateral digits were rotated parallel, the tip of claw II would lie opposite the distal end of phalanx 2 in digit III; that of claw IV, the distal end of phalanx 3. The digits diverge almost from a common base: their long axes intersect just posterior to the metatarso-phalangeal pad of digit III.

Characteristic though it is, this type of foot is difficult to match among the well-known footprint genera of the Upper Triassic. The slender digits and pointed claws suggest the small, tridactyl coelurosaurs whose footprints comprise the family Grallatoridae, but the species of *Grallator* proper (one of which occurs in another Milford faunule) have lateral digits set well back on the foot with their claw-tips nearly opposite, claw II being slightly in advance. The Manchurian grallatorid *Jeholsauripus* (Shikama, 1942, fig. 1) more closely resembles the Milford form in position and divarication of digits but is proportionately shorter, with a relatively longer digit II and shorter IV.

Coelurosaurichnus toscanus Huene (1941, p. 14) from the Verrucano of Italy is more closely comparable to the Milford footprint in size and proportions, particularly in the length of digit IV. In the type imprint the base of the foot appears to be shod with a large, roughly circular "Metatarsalpolster," but this may be an artifact of impression: in another footprint of the same species (Fucini, 1936, pl. 76 near top) the lateral toes are less divergent and seem to have individual, oval metatarso-phalangeal pads of grallatorid form. Unfortunately, the genus *Coelurosaurichnus* is founded on inadequate material and has been loosely construed by subsequent authors to include any Keuper footprints of coelurosauroid type.

The Connecticut Valley pes imprints which are most similar in digit proportions and arrangement pertain to *Tarsodactylus caudatus* E. Hitchcock. This form, unlike the grallatorids cited above, is a quadruped with a broad trackway and a pentadactyl manus which is strongly toed-out and impressed lateral to and usually in advance of the pes. The Milford track may be interpreted as a *Tarsodactylus* whose manus imprint lay just beyond the broken edge of the slab; but in this case the next manus-pes set should appear on the surface. Another Massachusetts form in which digit IV is longer than II is *Anomoepus scambus* E. Hitchcock; but here disparity in digit length is much less marked than in the Milford imprint.

Closest comparisons are to be made with certain nameless footprints from beds of approximately equivalent age in south-central Pennsylvania. The cast of an imperfectly recorded pes imprint which is nearly identical in size and structure with the Milford track is preserved at Yale (YPM 3765). This specimen was collected at Hess' or Wentz's mill on Big Spring Run about 1 mile ENE of Yocumtown, New Cumberland quadrangle, York County, Pa., and is labeled as having come from the upper part of the Conewago formation (New Oxford of Stose). According to Stose and Jonas' (1939) map of York County, however, this locality lies not in the New Oxford but in the overlying Gettysburg shale. The label notes, "stride about 18 inches," but this cannot be verified.

Another footprint of this type, from an unspecified locality near Yocumtown, has been figured by Hickock and Willard (1933, fig. 6B). This track is interpreted as a left pes. The presence of three well-defined articular nodes in digit "II," however, is evidence that at least three phalanges impressed their full lengths. If the first articular node (like that of digit III) marks the joint of phalanx 2 with a proximal phalanx which sloped upward to its metatarsal, then at least four and probably five phalanges were present in digit "II": it must therefore be IV, and the foot a right pes.

In this imprint digits II and IV are shorter and digit II less divergent than in the Milford and Yale tracks, though it is similar in the other details recorded. The length and anterior position of digit IV debar this specimen from the species to which Hickock and Willard assigned it, *Anchisauripus sillimani*. Without examining the material I cannot agree or disagree with their generic assignment.

Although no name can at present be assigned to the New Jersey footprint, a better understanding of its affinities would seem to depend on a comprehensive study of dinosaur tracks from the Keuper of Pennsylvania.

On the back of the *Chirotherium lulli* slab, separated from the other tracks by a few millimeters of sediment, is a second small tridactyl footprint of quite another sort (Plate 2, figure 2). This track is even less determinable than the first, but because it is essentially a member of the same faunule let us dutifully but briefly examine its affinities. The foot, a left pes, is thick-toed and relatively broad. The slightly divergent lateral digits are set back from the base of a rather short digit III; IV extends a little beyond the tip of II and shows a faint metatarso-phalangeal pad.

This sort of foot is found in the Newarkian genera *Eubrontes*, *Anchisauripus*, and *Sauropus*. Gigantic *Eubrontes*, the smallest species of which is more than three times as large, can be omitted from consideration. Worthwhile comparisons narrow themselves to two species: *Anchisauripus gwyneddensis* Bock (1952, p. 406) from the Lockatong formation of Pennsylvania, and *Sauropus barrattii* (E. Hitchcock) from the Portland arkose of Massachusetts (Lull, 1915, p. 217). *A. gwyneddensis*, known from a single indistinct imprint, is very similar though half again as large and a little narrower in proportion. Equally poor preservation increases the similarity. One feature of both which may be significant is the concave medial margin of digit II, a feature which is more typical of the semi-biped *Sauropus* than of *Anchisauripus*. My conclusion from this meager evidence is that the second dinosaurian footprint probably belongs to the same genus as *A. gwyneddensis*, though whether that genus is really *Anchisauripus* remains to be seen.

Nearly all the forms cited require further study before their interrelationships can be determined. One potent source of confusion, I suspect, is that the Keuper "dinosaur" footprints were made not only by Saurischia and Ornithischia but by advanced bipedal Pseudosuchia as well. Cases of homeomorphism in foot structure among members of the three groups are to be expected, and the detection of such cases on the evidence of footprints alone will be nearly impossible.

The discerning reader has, I hope, winnowed one kernel of truth from the foregoing discussion: that a single imprint, in which individual anomalies of form and peculiarities of impression may be concealed, has no taxonomic value within so homogeneous a group as that of the ornithoid "dinosaur" footprints. This otherwise nearly profitless survey can at least serve to emphasize — it could hardly overemphasize — that ornithoid footprints cannot be diagnosed and classified without adequate quantities of well-preserved material, preferably trackways. To base new genera and species on isolated, poorly preserved footprints is useless; to base stratigraphic correlations on them is usually misleading.

SIGNIFICANCE OF THE FAUNULE

This reptile faunule, though it consists only of three essentially contemporaneous individuals which have a known geographic range of two square feet, presents some interesting problems in chronology and ecology. Associations of Keuper chirotheriids with dinosaurs in

England and on the Continent have been known for more than a century. (Heller, 1952, presents a useful tabulation of twentieth-century central European finds.) Such an association in this country was reported by C. H. Hitchcock in 1889 but not demonstrated until Bock's 1952 restudy of the New Jersey footprints; and the occurrence announced in this paper is only the second on record.[5]

Now this is very strange. Ornithoid dinosaurian trackways were found in the Upper Triassic of the Connecticut River valley as early as 1802, and in the subsequent century-and-a-half a rich series of faunas has been assembled from more than forty localities in Massachusetts and Connecticut. While footprints are not known from the New Haven arkose,[6] the lowest formation of the Connecticut Valley Newarkian sequence, they are abundantly represented in the overlying Meriden formation (the anterior and posterior shales and sandstones of earlier authors) and the upper series of sandstones and shales now known as the Portland arkose (Krynine, 1950). Specimens in museums must number at least 40,000.

Associated with the dinosaur footprints are several varieties of trackway, typically quadrupedal, resembling *Chirotherium* except for the absence of a functional fifth pes digit. *Batrachopus* is representative of this group. Most of these forms are small, having pes lengths ranging from 15 to 75 mm., and are logically correlated with the smaller varieties of Pseudosuchia. The single exception, *Otozoum*, is so large (490 mm.) that although its foot is merely a graviportal, bipedal modification of the *Batrachopus* type its affinities have previously been sought among dinosaurs rather than pseudosuchians.

But among these numerous and varied trackways of pseudosuchioid form no *Chirotherium* has ever been found. Although nothing can be said about New Haven time, the available evidence for the absence of chirotheriids from the Connecticut Valley basin in Meriden and Portland time is exceedingly weighty. On the other hand, the New Jersey-Pennsylvania basin, whose footprint faunas have been much less intensively collected and studied, has yielded eight specimens representing three clearly defined species of *Chirotherium*. If the *Chirotherium*-bearing Brunswick formation of New Jersey is a time equivalent of the Portland arkose, as Bock (1952, p. 430) has implied,

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[5] An association of possibly chirotherioid with possibly dinosaurian tracks from Virginia was described by Shaler and Woodworth in 1899. The second and fourth footprints in their rather diagrammatic figure 90 have a vague resemblance to *C. lulli* and its companion dinosaur, but the evidence is inconclusive.

[6] A New Haven find, unfortunately never collected, is mentioned by Lull, 1915, p. 94.

then some barrier — topographic, climatic, or biotic — must have prevented the spread of chirotheriids into the Connecticut Valley basin while it permitted the intermigration of small bipedal dinosaurs.

Such a barrier can hardly have been an upland, a permanent desert, or an impassable river. According to Krynine (1950, pp. 195–196):

> "Central and western Connecticut during Newark time can be pictured as a wide flatland, bordered on the east by the steep but relatively low hills of the Great Fault scarp and to the west merging insensibly into the somewhat similar flatland of southern New York and New Jersey. The interfluve between these two basins may have been so low as to lack any topographic expression, but it probably still was a divide between the two sedimentation basins of Connecticut and New Jersey. A master stream meandered over this flatland, probably flowing southward . . .
>
> "The climate was hot and seasonally very humid. During the wet season heavy, long-continued rains transformed the flatland into a vast, sticky, water-soaked morass . . . During the dry season a broiling sun was beating upon the Connecticut savanna, caking and cracking the red soils. However, dense and luxurious forests extended for several hundred yards on each side of the numerous watercourses, providing food and a cool shelter for the reptilian denizens of the Newark."

The cosmopolitan flora of the Triassic precludes any stringent climatic zonation. A biotic barrier which would affect cursorial, carnivorous pseudosuchians but not cursorial, carnivorous dinosaurs is of course possible but is very difficult to conceive.

Additional arguments for the distinctness of the Brunswick reptile faunas from those of the Meriden and Portland must await the description of new footprint types from the *Chirotherium parvum* horizon at Milford, now in manuscript. Nevertheless, it is not premature to state that the evidence of two *Chirotherium* faunas strongly suggests that the footprint-bearing sequence of the upper Brunswick formation which is exposed in the Smith Clark quarry at Milford, New Jersey, antedates not only the Portland arkose but the underlying Meriden formation as well, and more probably correlates with the New Haven arkose.

This conclusion is compatible with the tentative correlation by Colbert (1946, p. 267) in which the First Watchung, Second Watchung, and Hook Mountain extrusives of the upper Brunswick are shown as equivalents of the lower, middle, and upper lava flows of the Meriden (the anterior, main, and posterior traps of earlier authors), while the rest of the upper and the middle Brunswick are equated to the New Haven arkose. It is (so far as the evidence goes) entirely in harmony with the occurrence of *Stegomus arcuatus* in the New Haven arkose at New Haven and in the lower Brunswick shales near Neshanic, New Jersey (Jepsen, 1948). But the pitfalls and complexities of Newarkian correlation are many and the evidence is still inadequate for a positive, much less a dogmatic, statement on the relative ages of these beds.

Even less adequate than the data for stratigraphic correlation is our information on the extinction of the chirotheriids and the subsequent fate of the ecological niches which they had occupied. The problems here are comparable in complexity to those involved in the extinction of the dinosaurs — with the additional handicap that our whole understanding of adaptive relationships must be derived primarily from the pedal structure, trunk and limb proportions, and gait of the animals as revealed in the trackways; and secondarily (subject to much doubt) from our knowledge of the fossil reptiles with which we correlate the trackways. Difficulties in interpretation should not, however, deter us from listing the facts now available.

Chirotheriid footprints of a highly modified type, associated with those of coelurosauroid dinosaurs, occur as high in the European middle Keuper as the *Semionotus*-sandstone of Franconia (Beurlen, 1950), a formation which appears to have its age equivalent in the Lockatong formation of New Jersey (Bock, 1952, p. 425 ff.). The only Keuper chirotheriids known from North America occur at two horizons of the upper Brunswick formation, several thousand meters above the underlying Lockatong. *Chirotherium lulli* is the youngest of these species, and if the intercontinental correlations are correct it is also the youngest chirotheriid yet known.

If, as argued above, the *Chirotherium*-bearing beds of the upper Brunswick are older than the *Chirotherium*-barren beds of the Meriden, then extinction or at least extermination of the Newark chirotheriids must have taken place late in Brunswick time. *Chirotherium lulli* would thus appear to be nearly if not actually a terminal member of the group.

The causes underlying the extinction of the Chirotheriidae, a wide-ranging pseudosuchian lineage which originated sometime in the Permo-Triassic and flourished from Bunter until late middle Keuper time, are unknown. Competition with increasingly numerous and well-adapted dinosaurs has been suggested as a contributory factor (Peabody, 1948). The composition of Newarkian footprint faunas suggests to me that ecological replacement by better-adapted pseudosuchians may have been at least as influential. Of course I have no intention of drawing sweeping conclusions from such meager evidence, but propose rather to point out some facts which may be significant.

If any evolutionary trend can be said to characterize the Keuper chirotheriids it is the tendency toward elimination of the lateral propping function of the thumb-like fifth pes digit. The various means by which this end was approached or attained have been discussed on page 173. Such a shift from a pentadactyl pes with a lateral prop to an essentially tetradactyl pes with a postero-lateral digital "heel" must have had a high adaptive value to take place, for the most part independently, in so many different footprint species (each probably representing a reptilian genus).

Despite this modification the Newarkian chirotheriids were still osteologically pentadactyl, as were all the adequately known quadrupedal footprint genera of the New Jersey basin. In the Connecticut Valley basin, however, there were only three rare quadrupeds — *Shepardia*, *Sustenodactylus*, and *Arachnichnus* — which seem to have had a rudimentary but functional fifth pes digit. In all the other small pseudosuchioid footprint genera — *Batrachopus*, *Cheirotheroides*, *Palamopus*, *Exocampe*, *Orthodactylus*, and *Comptichnus* — the pes was functionally tetradactyl. Among these genera certain species of *Batrachopus*, *Palamopus*, *Exocampe*, and *Comptichnus* were decidedly similar to *Chirotherium lulli* in size and gait and in general body proportions as deduced from the trackways. What evidence there is suggests that they may have been its ecological equivalents.

Obviously it would be absurd to postulate and then account for a pattern of ecological replacement on the basis of footprints alone. Nevertheless, it is at least suggestive to observe that most of the pentadactyl-pes pseudosuchians of the Newarkian epoch seem to have evolved toward a functional pseudo-tetradactyly and then disappeared during Brunswick time; but the pseudosuchians with true functional tetradactyly are first seen in the Meriden and flourished in Portland time, persisting into the highest footprint-bearing beds of the Newark series.

NOTE ON NAMES OF BRITISH CHIROTHERIIDS

The name *Chirotherium beasleyi* was first proposed by Nopcsa (1923, p. 144) for the species known as "form L" in Beasley's terminology. Peabody (1948, p. 345) has through an oversight given the same name to the well-known small-manus chirotheriid designated as "A 4" by Beasley, a splendid trackway of which was described without name by Lomas (1908), and refigured by Soergel (1925, fig. 61) and Abel (1935, fig. 34) with the erroneous identification *Chirotherium storetonense*. In the absence of an available name for "A 4," Dr. Peabody has graciously delegated to me the necessary renaming of this form:

CHIROTHERIUM LOMASI Baird, nom. nov.

I designate as type the trackway of eight consecutive manus-pes sets described by Lomas, now in the Geology Department of the University of Liverpool (LU 8020). Specimens in this country include University of Cincinnati Museum 24831, a left pes; Yale Peabody Museum 3762, a right set; and Amherst College Geological Museum, Hitchcock cabinet 26/25, a right set and a manus from another trackway. The Amherst specimen has been figured by Lull, 1904 (pl. 72, figs. c–d) under the name *Chirotherium storetonensis*. This usage of Lull's was appropriate at the time, for "A 4" was not recognized as a form distinct from *C. storetonense* until 1906, when Beasley described it before the British Association at York (76th Report, p. 299).

SUMMARY

A trackway of four manus-pes sets from the Upper Triassic Brunswick formation of Milford, New Jersey, proves to be the counterpart of the type, a single set. This additional material shows *Chirotherium lulli* Bock to be a small, long-fingered member of the large-manus group of chirotheriids, primitive in many respects but specialized in the position and function of the thumb-like fifth pes digit. Affinities with ornithosuchid pseudosuchians are indicated by a skeletal restoration. Associated on the slab are two types of small tridactyl dinosaur footprint whose affinities, though uncertain, appear to lie with footprints from the Keuper of Pennsylvania.

Two American *Chirotherium*-dinosaur associations, from different horizons of the same formation and locality, are now on record.

The conspicuous absence of chirotheriids from the abundant Connecticut Valley footprint faunas, and the apparent lack of barriers between the New Jersey and Connecticut basins, suggest that the *Chirotherium* faunas in the Brunswick formation of New Jersey antedate the Meriden formation of Connecticut. *Chirotherium lulli*, the last known member of a widespread and long-ranging group of pentadactyl-pes pseudosuchian reptiles, appears to have been replaced ecologically by small, functionally tetradactyl-pes pseudosuchians such as *Batrachopus*.

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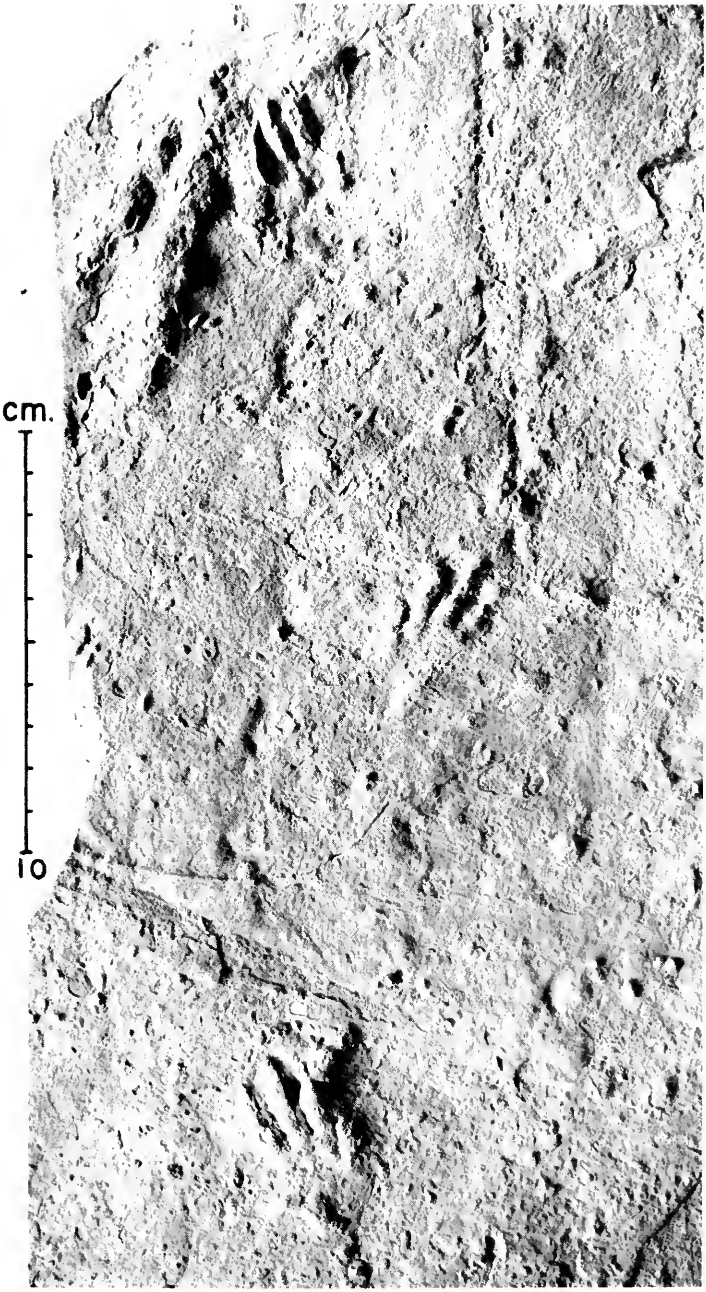
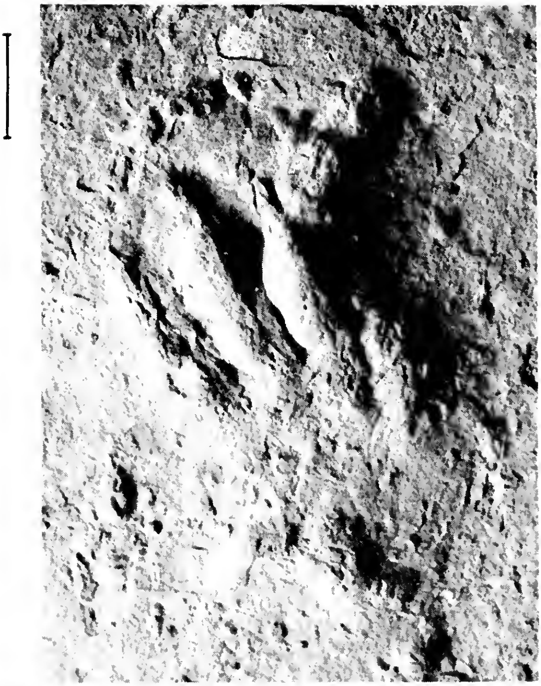


PLATE 1

Chirotherium lulli Bock, type, last three manus-pes sets of the ANSP trackway. Bock's type is the counterpart of the middle set. Dinosaur footprint at upper left.

1



2

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PLATE 2

Fig. 1. *Chirotherium lulli* Bock, natural cast of second (right) manus-pes set on the ANSP slab. Fig. 2. Dinosaurian left pes imprint, cf. *Anchisauripus gwyneddensis*, on back of slab. Fig. 3. Natural cast of dinosaurian left pes imprint enlarged from Plate 1. One centimeter scale (scale of fig. 2 approximate). Figures 2 and 3 lighted from right.

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THE SPIDER GENUS MANGORA (ARGIOPIDAE) IN PANAMA

By Arthur M. Chickering

Albion College, Albion, Michigan

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
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The two Cambridges (1889–1904) recognized a total of seven species of *Mangora* from Central America. Only one of these, *M. bimaculata* (O. P. Cambridge), was from Panama. Petrunkevitch (1925) believed that he had *M. trilineata* O. P. Cambridge from Barro Colorado Island (the Canal Zone Biological Area) and "the Wilcox camp on San Lorenzo River." As I shall indicate later, these records appear doubtful. Banks (1929) reported the collection of *M. bimaculata* (O. P. Cambridge), *M. picta* O. P. Cambridge, *M. spinula* F. P. Cambridge, and *M. trilineata* O. P. Cambridge from several localities in the Canal Zone. *M. spinula* is correctly placed but I am forced to regard the remaining three records as faulty. Chamberlin and Ivie (1936) described males and females of *M. dentembolus*, females of *M. pia*, and males of *M. belligereus* from my first collection, made in Panama during the summer of 1928. *M. dentembolus* Chamberlin and Ivie is, quite clearly, the same as *M. spinula* F. P. Cambridge. *M. pia* is the female of *M. belligereus* and, therefore, on the basis of page priority these will be known as *M. pia*. I have recognized three new species among my collections made since 1928 and a small number collected by others to whom credit is given in the appropriate places. For these new species I am proposing the following names: *M. candida* sp. nov.; *M. montana* sp. nov.; and *M. schneirlai* sp. nov. According to present knowledge, we are now able to recognize eight species, including one uncertainty, of *Mangora* in Panama. These may be listed as follows: *M. bimaculata* (O. P. Cambridge); *M. candida* sp. nov.; *M. mobilis* (O. P. Cambridge); *M. montana* sp. nov.; *M. pia* Chamberlin and Ivie; *M. schneirlai* sp. nov.; *M. spinula* F. P. Cambridge; *M. trilineata* O. P. Cambridge. Only females are known for *M. schneirlai* sp. nov. and *M. trilineata* O. P. Cambridge; both sexes are known for the remaining six species.

Acknowledgements are again gratefully extended to the following: Dr. A. S. Romer and Dr. P. J. Darlington, Jr. for their many courtesies and continued encouragement in the Museum of Comparative Zoology at Harvard College; Dr. W. J. Gertsch, American Museum of Natural History for the loan of specimens of *Mangora* from several localities in Panama; Dr. G. Owen Evans, E. Browning, and other members of the Department of Zoology of the British Museum (Natural History) for the loan of very valuable specimens from several localities in Central America; the donors of the Penrose Fund of the American Philosophical Society and The Society of Sigma Xi for grants which enabled me to spend the summer of 1950 in the collection and study of spiders in Panama.

Genus MANGORA O. P. Cambridge, 1889

Key to the known species of *Mangora* in Panama

Males

1. With special ventral spines on second tibia (*bimaculata, candida, pia, mobilis*) 2
1. Without special ventral spines on second tibia (*montana, spinula*) 5
2. Fourth coxa with a conical spur and small tubercles . . . . *M. mobilis*, p. 202
2. Fourth coxa without a conical spur and small tubercles 3
3. Tarsal bulb with a simple, curved, hook-like clavis; the embolus is of moderate length and a regularly curved spur . . . . . . *M. bimaculata*, p. 197
3. Tarsal bulb without a simple, curved, hook-like clavis but with either a pair of tooth-like apophyses or a broad plate with a single tooth-like apophysis; embolus either long, slender, and terminally lance-like or short, obscure, and hidden 4
4. Tarsal bulb with a robust clavis terminating in a pair of tooth-like apophyses; embolus swollen at base, then long and slender; terminating in a lance-like tip . . . . *M. candida*, p. 198
4. Tarsal bulb with a flat clavis terminating in a single tooth-like apophysis; embolus short, obscure, and hidden . . . . *M. pia*, p. 208
5. Fourth femur without a robust, ventral, basal spine . . . *M. montana*, p. 204
5. Fourth femur with a robust, ventral, basal spine . . . . *M. spinula*, p. 211

Females

1. Epigynum with a distinct, sometimes short, central tongue and a lateral lobe on each side (*bimaculata, candida, mobilis, schneirlai*) 2
1. Epigynum without any distinct central tongue and lateral lobes or with lateral lobes alone (*montana, pia, spinula, trilineata*) 5
2. Epigynum with a short central tongue and relatively long lateral convergent lobes (Fig. 1) . . . . *M. bimaculata*, p. 197
2. Epigynum either with relatively long central tongue and short lateral lobes or with both tongue and lateral lobes short 3
3. Epigynum with a broad plate deeply cleft in middle of anterior border (Fig. 22) . . . . *M. schneirlai*, p. 209
3. Epigynum without a broad plate deeply cleft in middle of anterior border . . 4

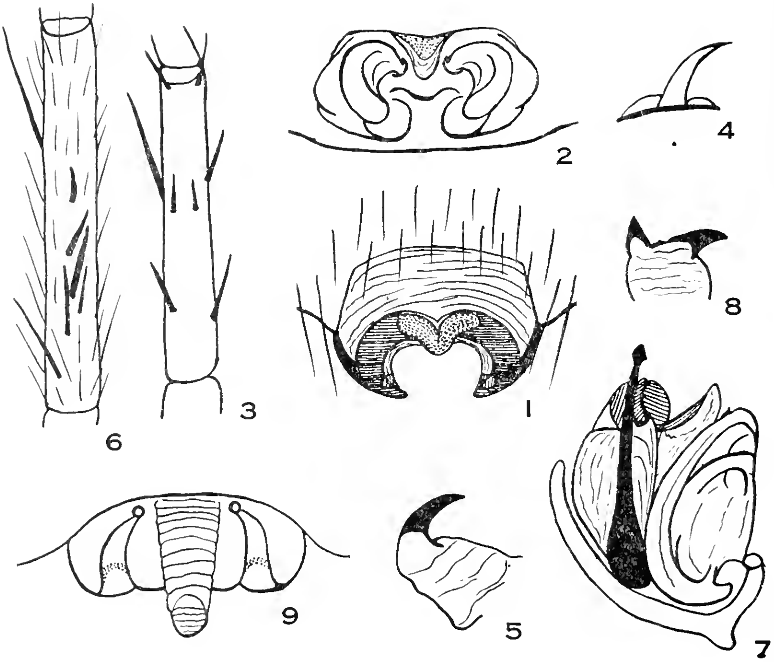
4. Epigynum with a relatively long central tongue arising from near anterior border of plate (Fig. 9) . . . . *M. candida*, p. 198
4. Epigynum with a very short central tongue arising from posterior border of plate (Fig. 13) . . . . *M. mobilis*, p. 202
5. Epigynum very simple; with a very short broad central lip; with a simple lateral lobe on each side (Fig. 17) . . . . *M. montana*, p. 204
5. Epigynum more complicated; without any distinct central lip; lateral lobes, if present, much more conspicuous 6
6. Epigynum with a deep, rounded, posterior notch; with a well defined lateral lobe on each side of notch; with two relatively large spermathecae much less than their radius apart (Fig. 27) . . . . *M. trilineata*, p. 213
6. Epigynum without a deep rounded posterior notch; without well defined lateral lobes; spermathecae relatively smaller and farther apart 7
7. Epigynum protruding as a massive, free extension turned ventrally at tip; deeply grooved just anterior to tip (Fig. 29) . . . . *M. pia*, p. 208
7. Epigynum protruding as a massive, free extension but not conspicuously turned ventrally at tip; divided apically into two inconspicuous lobes separated by a shallow cleft (Fig. 25) . . . . *M. spinula*, p. 211

MANGORA BIMACULATA (O. P. Cambridge), 1889

(Figures 1–5)

The Cambridges had this species from Veragua, Panama. Banks (1929) recorded the species from Barro Colorado Island, C. Z., but his specimens are all plainly females of *M. pia* Chamberlin and Ivie (1936). The species has not appeared in my collections and, to my knowledge, has not been collected since the originals were taken by Sarg and Boucard.

Notes taken from specimens loaned from the British Museum (Natural History): The epigynum (Figs. 1–2) has a concealing gummy mass attached to it and making it easy to confuse *M. pia* Chamberlin and Ivie with this species. The long slender branched prolateral hairs on the third tibia appear to be arranged in females in two oblique rows with seven in the first row and six in the second; in males they appear to be in two rows of three and four, respectively, although it is difficult to be certain because of the folding of the legs and the fragility of the specimen. Ventral spines on the second tibia of the male are as shown in Figure 3. The embolus of the male palp (Fig. 4) is of moderate length and like a slender spur; the clavis is a fairly robust hook (Fig. 5).



External Anatomy of *Mangora*
Figures 1–9

Fig. 1. *Mangora bimaculata;* epigynum from below.
Fig. 2. *M. bimaculata;* epigynum; a more posterior view.
Fig. 3. *M. bimaculata;* ventral spines, second tibia in male.
Fig. 4. *M. bimaculata;* embolus of male palp.
Fig. 5. *M. bimaculata;* clavis of male palp.
Fig. 6. *Mangora candida* sp. nov.; ventral spines, second tibia in male.
Fig. 7. *M. candida* sp. nov.; tarsus of male palp showing embolus, etc.
Fig. 8. *M. candida* sp. nov.; male palpal clavis.
Fig. 9. *M. candida* sp. nov.; epigynum from below.

MANGORA CANDIDA sp. nov.
(Figures 6–9)

Male holotype. Total length 2.67 mm. Carapace 1.43 mm. long; 1.08 mm. wide opposite second coxae where it is widest; .440 mm. tall and, therefore, about .40 as tall as wide; ascends regularly from PME to opposite interval between second and third coxae from where posterior declivity arches to posterior margin; longitudinal thoracic groove well developed.

Eyes. Eight in two rows, all dark. LE on slightly raised tubercles; AME project forward above clypeus. Viewed from above, posterior row slightly recurved, anterior row strongly recurved. Viewed from in front, anterior row slightly recurved, measured by centers. Central ocular quadrangle wider in front than behind in ratio of 3 : 2, about as long as wide in front. Ratio of eyes AME : ALE : PME : PLE = 10 : 7 : 8 : 7. LE somewhat angular, ME circular. AME separated from one another by 3/5 of their diameter, from ALE by one half their diameter. PME separated from one another by slightly less than one fourth their diameter, from PLE by their diameter. LE separated from one another only by a line. Clypeus receding from AME. Width of clypeus equal to seven tenths of the diameter of AME.

Chelicerae. Moderately well developed; parallel; basal segment .4 mm. long. Teeth along well developed fang groove difficult to see without serious damage to holotype but probably three on each margin.

Maxillae. Parallel; well developed; quite convex; with well dedeveloped serrula along distal margin and outer distal corner.

Lip. Reaches nearly to middle of maxillae; wider than long in ratio of nearly two to one. With a pair of black terminal bristles. Sternal suture gently procurved.

Sternum. Very convex; scutiform; only slightly longer than wide; widest between second coxae but nearly as wide between first; not continued between fourth coxae which are separated by 9/11 of the width of one of them.

Legs. 1243. Width of first patella at "knee" .198 mm., tibial index of first leg 8. Width of fourth patella at "knee" .190 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
1.	1.690	.520	1.820	1.820	.715	6.565
2.	1.462	.455	1.235	1.365	.709	5.217
3.	.975	.227	.585	.650	.455	2.892
4.	1.495	.400	1.170	1.170	.585	4.820
Palp	.286	.115	.110	——	.550	1.061

Spines. First leg: femur dorsal 1-1-1-1-0, prolateral 0-0-1-1-0, retrolateral 0-0-0-1-1-0, ventral 0; patella dorsal 1(weak)-1, retrolateral 0-1-0; tibia dorsal 0-1-1-1-0, prolateral 0-1-1-0, retrolateral

0-0-1-1, ventral 0-2-0-2 (right) and 0-2-1r-0-2(left); metatarsus dorsal 0, prolateral 0-1-0-0, retrolateral 0-1-0-0-0, ventral 0. Second leg: femur only dorsal 1(weak)-1-1-0, retrolateral 0-0-0-1-1-0; patella essentially as in first; tibia dorsal 0-1-1-1-0, prolateral and retrolateral 0-0-1-0, ventral as in Figure 6; metatarsus only prolateral 0-1-0-0-0 and retrolateral 0-1-0-0. Third leg: femur only dorsal 0-1-1-1-0 and retrolateral 1 near distal end; patella essentially as in first; tibia dorsal 1-0-1-0, prolateral 0, retrolateral 1-0-1, ventral 0-1r-2; metatarsus dorsal 0-1-0-1(weak), prolateral 0-1-0-1, retrolateral 0-1-0-1(weak), ventral and median 1-1-1. Fourth leg: femur dorsal 0-1-1-1-0, prolateral and retrolateral 1 near distal end, ventral 1-0-1; patella essentially as in first; tibia dorsal 0-1-1-0, prolateral 0-0-1-0, retrolateral 0-1-1-0, ventral 0-1p-0-2; metatarsus dorsal 1-1-0, prolateral 0-1-1-1, retrolateral 0-1-0-0, ventral 0. The long, slender, branched hairs on the prolateral side of the third tibia appear to be seven in number and somewhat irregularly arranged. The first coxa has a well developed ventral distal hook or spur and the second femur has a moderately well developed prolateral proximal groove and chitinized ridge. Three claws throughout as usual in the genus.

Palp. Patella with a single long distal spine; both patella and tibia short, the latter with a ventro-lateral extension. The embolus arises dorsally from near the base of the bulb where it is somewhat enlarged, and then extends in a gentle curve beyond the distal end of the bulb where it terminates in a lance-like tip (Figs. 7–8). The clavis is short, robust, and bifurcate; this term is continued from F. P. Cambridge.

Abdomen. Ovoid; moderately well supplied dorsally and laterally with recurved bristles tending to become longer and more spine-like toward the base; with a well developed colulus. Other features as usual in the genus.

Color in alcohol. Legs, mouth parts, and cephalothorax a fairly uniform yellowish color. Abdomen: nearly white; the posterior two-fifths of the dorsum bears a series of four pairs of elongate transverse black spots, the first three pairs more or less oval, the last pair hardly more than a line; in between the larger spots are rows of small and somewhat irregularly arranged black dots.

Female allotype. Total length 3.445 mm. Carapace 1.365 mm. long; 1.170 mm. wide opposite interval between second and third coxae; .715 mm. tall opposite third coxae where it is tallest and, therefore, about .61 as tall as wide; quite gibbous at greatest height.

Eyes. Central ocular quadrangle wider in front than behind in ratio of about 5 : 4; longer than wide in front in ratio of 12 : 11. Ratio of eyes AME : ALE : PME : PLE = 9 : 7.5 : 8 : 7. AME separated from one another by two-thirds of their diameter, from ALE by their radius. PME separated from one another by one-half of their radius, from PLE by slightly more than their diameter. LE separated only by a line. Otherwise essentially as in male.

Chelicerae. With three teeth along promargin of fang groove, the outermost one very minute; two fairly robust teeth along retromargin. Otherwise essentially as recorded for the male.

Maxillae, Lip, and *Sternum.* Essentially as recorded for the male.

Legs. 1243. Width of first patella at "knee" .2166 mm., tibial index of first leg 11. Width of fourth patella at "knee" .2058 mm., tibial index of fourth leg 13.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
1.	1.690	.585	1.430	1.182	.780	6.305
2.	1.495	.585	1.170	1.365	.690	5.305
3.	.975	.396	.638	.704	.440	3.153
4.	1.560	.528	1.100	1.300	.550	5.038

Spines. First leg: femur dorsal 1-1-1-1, prolateral 0-0-1-1-0, retrolateral only one near distal end; patella essentially as in male; tibia dorsal 0-1-1-1-0, prolateral 0-1-1-0, retrolateral 0-1d-0-1-0, ventral 0-2-1p-1p; metatarsus dorsal 1-0-0, prolateral and retrolateral 0-1-0-0, ventral 1r-0-0. Second leg: femur dorsal as in first, prolateral apparently only one near distal end, retrolateral 0-0-0-1-1-0, ventral 0; patella as in male; tibia dorsal as in male, prolateral and retrolateral as in male, ventral 0-2-1p; metatarsus dorsal 1-0-0, prolateral 1-0-0, retrolateral 0-1-0-0, ventral 0-1r-0-0-0. Third leg: femur only dorsal 0-0-1-1-1; patella essentially as in first and second; tibia dorsal 0-1-0-1-0, prolateral 0, retrolateral 0-0-1, ventral 0-0-2; metatarsus dorsal 0-1-0-0, prolateral 0-0-1, retrolateral 0, ventral median 0-1-1-1. Fourth leg: femur dorsal 0-1-1-1, prolateral and retrolateral 1 near distal end, ventral 0; patella as in other legs; tibia dorsal 1-0-0, prolateral 0-0-1-0, retrolateral 0-1-1, ventral 0-1p-2; metatarsus dorsal 0-1-0, prolateral 0-1-0-1, ventral and median 0-0-1-1. The long branched prolateral hairs on third tibia apparently arranged in two irregular rows of three each. Tarsal claws as usual in the genus. Palpal claw with three long slender teeth.

Abdomen. Essentially as in male except for sexual features.

Epigynum. Rather distinctive; nearly twice as wide as long, including the scape; the scape is long, transversely rugulose, turned ventrally at tip and originates near the anterior border of the epigynal plate (Fig. 9).

Color in alcohol. Similar to that of male. The series of black dorsal spots on posterior half of abdomen more fully developed than in male; these may be considered to occur in five instead of four pairs with the intermediate rows of black dots more pronounced than in male with the latter tending to join in narrow bands.

Type locality. Male holotype from Barro Colorado Island, Panama Canal Zone, June, 1950; female allotype from Canal Zone Forest Reserve, C. Z.; male and female paratypes from Madden Dam forest and Canal Zone Forest Reserve, C. Z., August, 1939; Canal Zone Forest Reserve, C. Z., July, 1950.

MANGORA MOBILIS (O. P. Cambridge), 1889

(Figures 10–14)

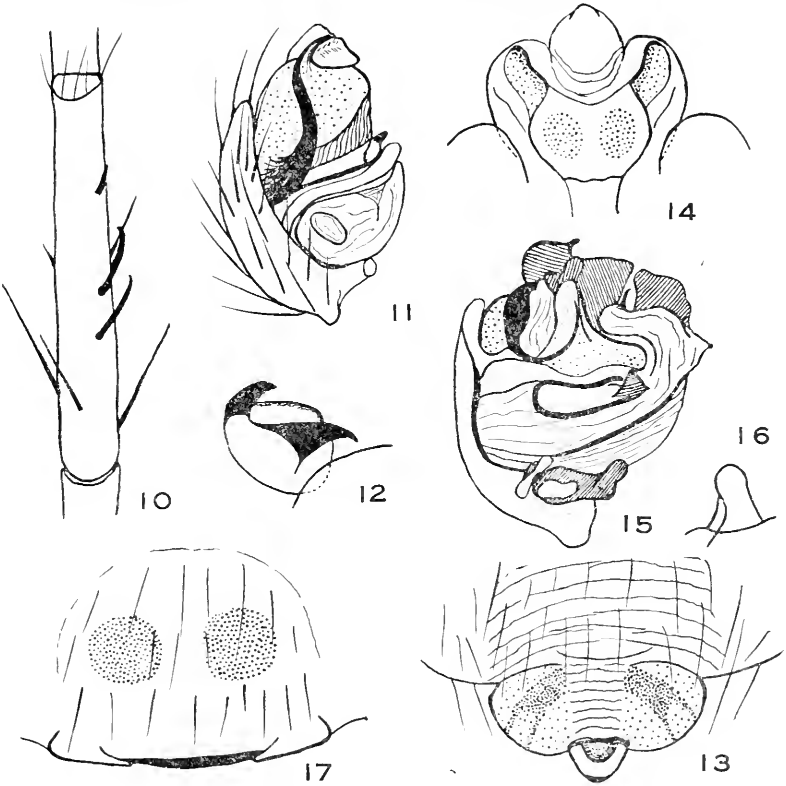
Epeira mobilis O. P. Cambridge, 1889
E. mobilis Keyserling, 1903
M. mobilis F. P. Cambridge, 1904
M. mobilis Petrunkevitch, 1911

Male. The special ventral spines on the second tibia appear as shown in Figure 10 although some variation has been noted. The fourth femur has a fairly robust ventral proximal spine much as in *M. spinula.* The fourth coxa has a prominent ventral spur together with two or three small tubercles. The usual ventral distal spur is present on the first coxa together with the usual prolateral proximal chitinous ridge and groove on the second femur. The male palp has a long sinuous embolus and a clavis terminating in two sharply pointed prongs (Figs. 11–12).

Female. The epigynum is nearly twice as broad as long; it has a short tongue arising from near the posterior margin (Figs. 13–14); there is a transversely rugulose median region with a somewhat convex lobe on each side.

The Cambridges had this species from Mexico and Guatemala. I now have it from the following localities in Panama: Barro Colorado Island,

C. Z., August, 1950; Madden Dam region, C. Z., August, 1939 and July, 1950 when it appeared to be abundant; Chilibre, C. Z., July, 1950; Summit, C. Z., July–August, 1950 when it also appeared to be abundant; El Cermeno, R. P., February, 1940 (Zetek).



External Anatomy of *Mangora*
Figures 10–17

Fig. 10. *Mangora mobilis;* ventral spines, second tibia in male.
Fig. 11. *M. mobilis;* tarsus of male palp to show embolus, etc.
Fig. 12. *M. mobilis;* male palpal clavis.
Fig. 13. *M. mobilis;* epigynum from below.
Fig. 14. *M. mobilis;* epigynum dissected and shown from dorsal surface.
Fig. 15. *Mangora montana* sp. nov.; left male palp to show embolus, clavis, etc.
Fig. 16. *M. montana* sp. nov.; full posterior view of palpal clavis.
Fig. 17. *M. montana* sp. nov.; epigynum from below.

MANGORA MONTANA sp. nov.

(Figures 15–17)

Male holotype. Total length 2.60 mm. Carapace 1.365 mm. long; 1.203 mm. wide opposite interval between second and third coxae where it is widest; .618 mm. tall and, therefore, about .51 as tall as wide; regularly arched from greatest height opposite third coxae to posterior border; with a scant covering of short procurved hair and a slender spinule behind each PLE.

Eyes. Eight in two rows, all dark; LE on slightly raised tubercles; AME protrude prominently over clypeus; viewed from above, posterior row gently recurved, anterior row strongly recurved; viewed from in front, anterior row slightly procurved, measured by centers; central ocular quadrangle wider behind than in front in ratio of about 5 : 4, slightly longer than wide behind. Ratio of eyes AME : ALE : PME : PLE = 7.5 : 5.5 : 10.5 : 6. AME separated from one another and from ALE by five-sixths of their diameter. PME separated from one another by about two-thirds of their diameter, from PLE by four-fifths of their diameter. Laterals separated from one another only by a line. Width of clypeus equal to slightly more than the diameter of AME. Clypeus with a weak spinule below interval between AME and a row of four spinules near ventral border, the outer well developed, the inner two very weak, all turned toward middle line.

Chelicerae. General features as usual in the genus. Teeth along fang groove difficult to see without serious damage to holotype but a paratype has three along promargin and two along retromargin.

Maxillae. Parallel or slightly convergent; with well developed and extensive serrula along distal margin and outer distal corner.

Lip. Deeply grooved at base; wider than long in ratio of 2 : 1; reaches little more than one-third of length of maxillae. Sternal suture procurved.

Sternum. Scutiform; strongly convex; depressed in the middle of anterior end; only slightly longer than wide opposite second coxae where it is widest; apparently continuous between fourth coxae which are separated by nearly four-fifths of their width; with numerous stiff dark bristles.

Legs. 1423. Width of first patella at "knee" .1949 mm., tibial index of first leg 12. Width of fourth patella at "knee" .1733 mm., tibial index of fourth leg 12.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
1.	1.430	.455	1.170	1.398	.748	5.201
2.	1.365	.455	1.040	1.250	.683	4.793
3.	.910	.325	.618	.683	.500	3.036
4.	1.430	.390	1.105	1.200	.683	4.808
Palp	.325	.128	.076	——	.650	1.179

Spines. First leg: femur dorsal 0-1-1-1-1-0, prolateral 0-0-1-0, retrolateral 0-0-1-1-0, ventral 0; patella only dorsal 1-1 and retrolateral 0-1-0; tibia dorsal 0-1-1-1-0, prolateral 0-1-1-0, retrolateral 0-0-1-1, ventral 0-2-1p-2; metatarsus dorsal 1-0-0, prolateral 1-0-0, retrolateral 0-1-0-0, ventral 0. Second leg: femur dorsal and retrolateral as in first, prolateral and ventral 0; patella as in first; tibia dorsal essentially as in first, prolateral 0-1-0-1-0, retrolateral 0-1-1(weak), ventral 0 (note absence of special spines such as occur on the second tibia of *M. candida* sp. nov.); metatarsus dorsal 1-0-0, prolateral 1-0-0, retrolateral 0-1-0-0, ventral 0-2-0-0. Third leg: femur only dorsal 0-1-1-1 and retrolateral 1 near distal end; patella essentially as in first; tibia dorsal 1r-0-1-0, prolateral and retrolateral 0, ventral 0-0-1r-1r; metatarsus dorsal 1-0-0, prolateral 0-1-0-1, retrolateral 0-1-0, ventral and median 1-0-1. Fourth leg: femur and patella as in third; tibia dorsal 1r-1-1-0, prolateral 0-1-0, retrolateral 0-0-1-1(weak), ventral 0; metatarsus dorsal 1-1r-0-0, prolateral 0-1-0-0-1, retrolateral 0, ventral and median 1-0-0. The long, slender, branched, prolateral hairs on the third tibiae are arranged in two oblique rows of three and five, respectively. There are also two ordinary trichobothria lying dorsal to the row of three branched hairs. The usual distal coxal spur is moderately well developed on the first coxa and the short prolateral proximal groove and chitinized ridge are also present on the second femur. Tarsal claws appear to be as usual in the genus.

Palp. Complicated; both patella and tibia very short, especially the latter; the tibia is transversely extended and trilobed, nearly three times as wide as long; patella with the usual long, slender, distal spine. The embolus is near the distal end of the bulb and is curved nearly into a circle. The clavis is a simple, thin, and somewhat triangular structure viewed as in Figure 15 but is a short, rounded plate as seen when viewed as in Figure 16. At the distal end of the bulb there is a massive, deeply grooved process as well as several other apophyses (Figs. 15–16).

Abdomen. Ovoid; longer than wide in ratio of 5 : 3; with a prominent colulus. Other features as usual in the genus.

Color in alcohol. All eyes on black spots. Cephalothorax, mouth parts, and legs various shades of light reddish brown. Abdomen: dorsally with a few scattered silvery subchitinous granules; posterior half of dorsum with an obscure folium; anterior half of dorsum yellowish with central dusty flecks outlining an obscure median stripe; lateral sides dusty brown; venter yellowish with an obscure central dusty brown stripe.

Female allotype. Total length 3.705 mm. Carapace 1.495 mm. long; 1.170 mm. wide opposite third coxae where it is widest; .715 mm. tall opposite interval between second and third coxae where it is tallest and, therefore, about .61 as tall as wide; somewhat more gibbous than in male. Otherwise essentially as in male.

Eyes. Ratio of eyes AME : ALE : PME : PLE = 8 : 7 : 10 : 7.5. AME separated from one another by nearly their diameter, from ALE by seven-eighths of their diameter. PME separated from one another seven-tenths of their diameter, from PLE by the same distance. Width of clypeus equal to five-fourths of the diameter of AME. Other features essentially as in male.

Chelicerae. Somewhat difficult to determine the teeth along the fang groove but apparently three along promargin and two along retromargin.

Maxillae and Lip. Essentially as in male.

Sternum. Essentially as in male except that posterior end is definitely not continued between fourth coxae.

Legs. 1243. Width of first patella at "knee" .2166 mm., tibial index of first leg 12. Width of fourth patella at "knee" .2166 mm., tibial index of fourth leg 14.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
1.	1.625	.585	1.200	1.495	.748	5.653
2.	1.495	.585	1.170	1.300	.715	5.265
3.	.960	.374	.660	.682	.520	3.196
4.	1.625	.455	1.105	1.300	.650	5.135

Spines. First leg: femur dorsal 0-1-1-1-1 on right, 0-1-1-1-1-1 on left, prolateral 0-0-1-0, retrolateral 1 near distal end, ventral 0; patella as in male; tibia dorsal 1-1-1-0, prolateral 0-1-1-1(weak), retrolateral 0-0-1-1(weak), ventral 0-2-0-0; metatarsus dorsal and median ?1-0-0, prolateral 1-0-0, retrolateral 0-1-0-0, ventral 2-0-0.

Second leg: femur only dorsal as in first and retrolateral 0-0-1-1-0; patella as in first; tibia dorsal as in first, prolateral and retrolateral 0-0-1-0, ventral 0-2-0-0; metatarsus dorsal and prolateral 1-0-0, retrolateral 0-1-0-0, ventral 1r-0-0. Third leg: femur only dorsal 0-0-1-1-1; patella apparently only dorsal 1-1; tibia dorsal 1-0-0, prolateral 0-1-1(weak), retrolateral 0-0-1, ventral 0-1r-1r; metatarsus dorsal 1-0-0, prolateral 0-1-0-1, retrolateral 0-1-0-0, ventral and median 1-1-1. Fourth leg: femur dorsal 0-0-1-1-1, prolateral and retrolateral 1 near distal end, ventral 1r near distal end; patella as in first; tibia dorsal 1-1-1-0, prolateral 0-1-1(weak), retrolateral 0-0-1-1(weak), ventral 0-1p-0-0; metatarsus dorsal 1-0-0, prolateral 0-1-0-1, retrolateral 0-1-0-0, ventral and median 1-0-1(weak). Special branched prolateral proximal hairs on third tibia arranged in two oblique rows of four and five, respectively. Palpal claw pectinate in a single row of several fine teeth. Palp with numerous stiff spines.

Abdomen. Overlaps carapace fully one-third of length of the latter. Except for sexual features, essentially as in male.

Epigynum. Simple; with two conspicuous spermathecae less than a diameter of one of them apart but apparently the distance varies somewhat in different individuals; with a posterior chitinized lip having a secondary lip in the center (Fig. 17).

Color in alcohol. Legs darker than in male and with color of segments more variable. Carapace with a median black stripe and another lateral black stripe on each side. Sternum dark gray. Abdomen: with a narrow central basal black mark connected to a broad central brownish variegated stripe extending through four-fifths of the dorsum; on each side of this central stripe there is a whitish stripe with silvery dots, narrowed at posterior end; each lateral side has a dark, nearly black stripe, narrow in front but widened behind; below this dark lateral stripe there is a narrow whitish stripe also with silvery dots; the venter has a central dark stripe with a narrower light stripe on each side; there is also a narrow dark ventrolateral stripe on each side. There are, therefore, five stripes on each side between the central dorsal and the central ventral stripes. This rather striking color pattern is highly variable among the paratypes and cannot be a reliable guide to the determination of species.

Type locality. Male holotype and female allotype from El Volcan, R. P., August, 1950. Several male paratypes from the same locality, February–March, 1936 (W. J. Gertsch). Female paratypes from the following localities in Panama: Boquete, July, 1939; El Volcan, February–March, 1936 (W. J. Gertsch) and August, 1950; Cerro Punta, March, 1936 (W. J. Gertsch).

MANGORA PIA Chamberlin and Ivie, 1936
(Figures 18–21)

Mangora bimaculata Banks, 1929
M. belligerens Chamberlin and Ivie, 1936 (males)

Some of the males and females collected by Banks on Barro Colorado Island and identified as *M. bimaculata* (O. P. Cambridge) quite clearly belong here. And it now seems certain that the females described by Chamberlin and Ivie go with the males described as *M. belligerens.* Hence, on the basis of page priority I am uniting them under the name *M. pia.* This is a relatively large species with females five to six millimeters long and males four to five millimeters long.

Males. The special ventral spines on the second tibia are shown in Figure 18. The fourth femur has a robust ventral proximal spine resembling that of *M. spinula;* a much weaker ventral proximal spine appears to be normal to each of the other femora. The usual distal spur is present on the first coxa together with the usual chitinized ridge and groove on the second femur. The long slender branched hairs on the third tibia appear to be arranged in two oblique rows of six each. Male palp: there is a small maxillary chitinized tooth just dorsal to the serrula which appears to work in opposition to a chitinized ridge near the base of the palpal femur; the tarsus is large and provided with several apophyses; the embolus appears to be small, obscure and more or less hidden; the patella has the usual long single distal spine; the clavis terminates in a relatively small plate with a single sharply pointed tooth (Fig. 19).

Female. The long slender branched hairs on the third tibia appear to be arranged in two oblique rows of seven each. Four promarginal teeth and three retromarginal show clearly along the fang groove; the groove itself has several minute denticles. Epigynum: extended free of the abdomen as a strongly chitinized body turned ventrally at the tip; deeply grooved at the point where it turns (Figs. 20–21).

Chamberlin and Ivie had this species only from Barro Colorado Island, C. Z. Records of the species now exist as follows: Barro Colorado Island, April–August, 1924, 1928, 1934, 1936, 1939, 1946 (Schneirla), and 1950; Madden Dam region, August, 1939; Canal Zone

Forest Reserve, August 1939 and July, 1950; France Field, C. Z., August, 1939; Summit, C. Z., November, 1946 (Krauss); Cocoli, C. Z., Sept., 1946 (Krauss); Taboga Island, R. P., August, 1946; Pedro Miguel, and Chilibre, C. Z., July, 1950.

MANGORA SCHNEIRLAI sp. nov.

(Figure 22)

Female holotype. Total length 4.875 mm. Carapace 2.015 mm. long; widest opposite third coxae where it is 1.495 mm. wide; very gibbous opposite interval between second and third coxae where it is .975 mm. tall and, therefore, about .65 as tall as wide; rises steeply from PME to apex of gibbosity and then descends steeply to posterior margin; with well developed longitudinal thoracic groove.

Eyes. Eight in two rows, all dark; LE on slightly raised tubercles; AME protrude over clypeus to a moderate degree; viewed from above, posterior row gently recurved, anterior row strongly recurved; viewed from in front, anterior row gently recurved, measured by centers. Central ocular quadrangle wider in front than behind in ratio of 27 : 22, only slightly longer than wide in front. Ratio of eyes AME : ALE : PME : PLE = 10.5 : 7.5 : 9.5 : 8. AME separated from one another by slightly less than their diameter, from ALE by nine-tenths of their diameter. PME separated from one another by slightly more than their radius, from PLE by nearly 1.4 times their diameter. Laterals barely separated. Width of clypeus about seven-tenths of the diameter of AME. Clypeus with a row of five spinules, the outermost in the row the most robust.

Chelicerae. Robust; basal segment .704 mm. long; vertical and parallel; with a rather poorly developed basal boss; fang well developed and evenly curved; fang groove with four promarginal teeth and three retromarginal teeth.

Maxillae. Parallel; robust; quite convex on retromarginal surface; with extensive serrula along distal border and outer distal corner; also with extensive scopulae along inner surfaces and inner distal corners.

Lip. Wider than long in ratio of about 4 : 3; reaches to less than the middle of maxillae. Sternal suture moderately procurved.

Sternum. Scutiform; slightly wider than long; widest at interval between second and third coxae; moderately convex; not extended between fourth coxae which are separated by nearly one third of their width.

Legs. 1423. Width of first patella at "knee" .330 mm., tibial index of first leg 14. Width of fourth patella at "knee" .308 mm., tibial index of fourth leg 15.

	Femora	Patellae	Tibiae	Metatarsi	Tarsi	Totals
		(All measurements in millimeters)				
1.	1.950	.700	1.593	1.755	.813	6.811
2.	1.875	.655	1.495	1.625	.813	6.463
3.	1.235	.455	.943	.902	.550	4.085
4.	2.080	.650	1.430	1.658	.845	6.663

Spines. Numerous irregularities in spination have been noted but are not recorded; right and left limbs often show marked differences on corresponding surfaces. First leg: femur only dorsal right 1-1-1-1-1, left 1-1-1-1, prolateral right 0-0-1-1-1-1-0, left 0-0-1-1-0, retrolateral only one near distal end; patella only dorsal 1-1, retrolateral 0-1-1-0; tibia dorsal 1-1-1-0, prolateral 0-1-1-1(weak), retrolateral 0-0-1-1, ventral 0-2-1p-2; metatarsus dorsal 0-1-0-0, prolateral 0-1-1-0, retrolateral 0-1-0, ventral 0-2-0-0. Second leg: femur dorsal right 0-1-1-0-1, left 1-0-1-1-0, prolateral and retrolateral only one near distal end; patella as in first; tibia dorsal 1-1-1-0, prolateral 0-1-1-1, retrolateral 0-1-1, ventral 0-1r-1p-2; metatarsus dorsal and prolateral 1-0-0, retrolateral 0-1-0-0, ventral 2-1p-1r-1p on right and 0-2-0-0 on left. Third leg: femur only dorsal 0-1-1-1, prolateral and retrolateral only one near distal end; patella as in first; tibia dorsal 1-1-1(weak), prolateral and retrolateral only one near distal end, ventral 0-1p-2; metatarsus dorsal 0-1-0-0, prolateral 1-1-1, retrolateral 0-1-0-0, ventral 2-1r-0-1r. Fourth leg: femur dorsal 0-1-1-1, prolateral and retrolateral only one near distal end, ventral 1r near distal end; patella dorsal 1-1, prolateral and retrolateral 0-1-0; tibia dorsal 1-0-1-1-0, prolateral 0-1-1-0-1, retrolateral 0-0-1-1, ventral 0-1r-1r-2; metatarsus dorsal and prolateral 0-1-0-0, retrolateral 0-1-1-1-1, ventral 0. The long branched prolateral proximal hairs on the third tibia appear to be arranged in two rows of five and six, respectively. Tarsal claws as usual in the genus. Palpal claw pectinate in a single row of numerous slender teeth.

Abdomen. 3.575 mm. long; 1.755 mm. wide; ovoid; other features as usual in the genus.

Epigynum. With a conspicuous, strongly chitinized plate divided anteriorly into a pair of lobes separated by a deep central cleft; a short broad median scape extends posteriorly and is flanked by a distinct notch on each side (Fig. 22).

Color in alcohol. Legs, mouth parts, and cephalothorax variable shades of yellowish and light reddish brown. Abdomen: with a series of four pairs of whitish spots extending along the middle of the dorsum and diminishing in size posteriorly; another series of four whitish spots on each lateral side; each of the white spots is made by a cluster of subchitinous granules; the posterior half of the dorsum also bears a series of three pairs of nearly black spots increasing in size posteriorly; the venter is yellowish with a pair of white dots anterior to the bases of the first pair of spinnerets.

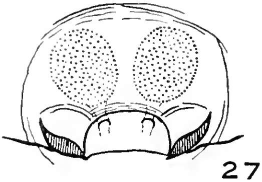
Type locality. Female holotype from Barro Colorado Island, C. Z., April, 1946. One mature female paratype and probably three immature females from the same locality, April–May, 1946. All of these were collected by Dr. T. C. Schneirla, American Museum of Natural History, for whom the species is named, and kindly loaned for this study by Dr. Willis J. Gertsch, American Museum of Natural History.

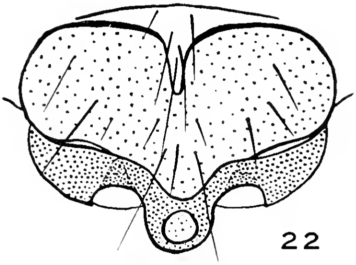
MANGORA SPINULA F. P. Cambridge, 1904

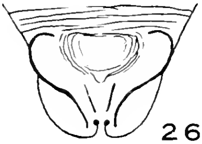
(Figures 23–26)

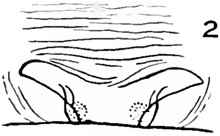
M. picta O. P. Cambridge, 1889 (females only)
M. picta F. P. Cambridge, 1904 (females only)
M. spinula F. P. Cambridge, 1904 (males only)
M. picta Petrunkevitch, 1911 (females only)
M. spinula Petrunkevitch, 1911
M. picta Banks, 1929
M. spinula Banks, 1929
M. trilineata Banks, 1929
M. dentembolus Chamberlin and Ivie, 1936

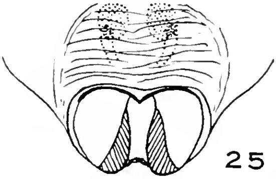
F. P. Cambridge found that the specimens regarded by the elder Cambridge as belonging to *M. picta* O. P. Cambridge were a mixture of several species but he retained females which he thought properly paired with the males. On the basis of my study of many specimens from Panama together with some on loan from the British Museum I have been forced to believe that the females of *M. picta* as recognized by both Cambridges are in reality the females of *M. spinula* which were not recognized by the author of the latter species. Chamberlin and Ivie had males and females properly paired but *M. dentembolus* is quite clearly the same as *M. spinula* F. P. Cambridge. Banks (1929) properly placed some of the males collected on Barro Colorado Island and nearby localities. Some of the females were, quite naturally,

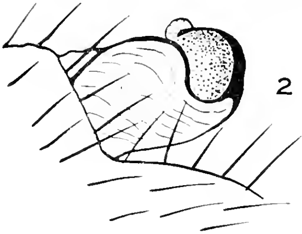


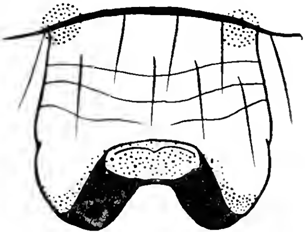












External Anatomy of *Mangora*
Figures 18–28

Fig. 18. *Mangora pia;* ventral spines, second tibia in male.
Fig. 19. *M. pia;* male palpal clavis.
Fig. 20. *M. pia;* epigynum from below.
Fig. 21. *M. pia;* epigynum in profile.
Fig. 22. *Mangora schneirlai* sp. nov.; epigynum from below.
Fig. 23. *Mangora spinula;* male palpal clavis to show shape from a different view than that usually shown.
Fig. 24. *M. spinula,* apophysis partly enclosed by curled embolus.
Fig. 25. *M. spinula;* epigynum as ordinarily seen in ventral view.
Fig. 26. *M. spinula;* epigynum; a more anterior view to show median depression.
Fig. 27. *Mangora trilineata;* epigynum from a ventral view.
Fig. 28. *M. trilineata;* epigynum; a more posterior view.

assigned to *M. picta* O. P. Cambridge; others he placed in *M. trilineata* O. P. Cambridge; he also assigned a few males to *M. trilineata*. The species seems to be widely distributed at least from Mexico to Panama and appears to be the most numerous of any of the species known from Panama.

Males. Many of the males are only two millimeters in length and some are even shorter than this. There are no special ventral spines on the second tibia. The fourth femur has a stout basal ventral spine which F. P. Cambridge considered the exclusive possession of males of this species among those from Central America. This is now known to occur on males of several species. The usual distal ventral spur on the first coxa is present and the usual prolateral proximal chitinized ridge and groove are also present on the second femur but they are small. Male palp: the apophysis, termed the conductor by F. P. Cambridge, is a long flat terminal hook; the clavis is also quite conspicuous proximal to the terminal curve in the embolus and is seen to be much broadened in the middle when properly viewed; the embolus originates near the distal end of the bulb, arches ventrally and then turns distally at the tip; there is also another characteristic process (Fig. 24) lying between the tip of the embolus and the median part of this structure.

Females. The fang groove appears to have four teeth along the promargin, the first and third relatively large, the second and fourth small; the retromargin seems to have only two relatively large teeth. Epigynum: extends for some distance free of the abdomen but it is not so strongly chitinized as in *M. pia*. Distally the extended part is divided by a groove into two lobes. Just anterior to the two lobes there is a relatively large depression (Figs. 25–26).

Hundreds of specimens are now in my collection from the following localities and extending over the period from 1924 to 1950: many separate localities in the Panama Canal Zone; Arraijan, El Valle, Boquete, El Cermeno, Porto Bello, El Volcan, and Cocoli outside of the Canal Zone in the Republic of Panama.

MANGORA TRILINEATA O. P. Cambridge, 1889

(Figures 27–28)

M. trilineata F. P. Cambridge, 1904
M. trilineata Petrunkevitch, 1911
M. trilineata Petrunkevitch, 1925

The Cambridges had only females from Mexico and Guatemala. Banks (1929) mistakenly reported this species from the Canal Zone as indicated under *M. spinula.* This is also true of the specimen from Costa Rica reported by Banks (1909). Petrunkevitch (1925) reported a female from Barro Colorado Island and two others from "the Wilcox camp on San Lorenzo River." I have had no opportunity to examine these specimens but on the basis of my experience with several hundred individual Mangoras from Panama I am obliged to regard this record as very questionable.[1] The species has not appeared in my collections and I am of the opinion that it has not been taken since the original collections upon which the work of the Cambridges was based. Because of the uncertainty of correct identification I am retaining the species among those known to occur in Panama and including it in the key to accompany this paper.

The long slender branched prolateral hairs on the third tibia appear to be arranged in two oblique rows with five in the first and four in the second row. The epigynum is quite characteristic; it has a central semicircular notch in the posterior margin and lacks a tongue; two large, somewhat oval spermathecae are separated by less than one half of the short radius of one of them (Figs. 27–28).

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[1] Through the courtesy of Dr. Petrunkevitch I have recently had the opportunity to examine the specimens from the Wilcox camp. In my judgment, both specimens belong to the species *M. spinula* F. P. Cambridge. The single female from Barro Colorado Island reported as *M. trilineata* O. P. Cambridge remains unavailable.

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EXOTIC EARTHWORMS OF THE UNITED STATES

By G. E. Gates

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
March, 1954

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EXOTIC EARTHWORMS OF THE UNITED STATES

By G. E. Gates

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PRINTED FOR THE MUSEUM
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No. 6 — *Exotic Earthworms of the United States*

By G. E. Gates

This contribution is concerned primarily with material of non-lumbricid and peregrine species that has been received for identification during the last six years since the author returned from the orient. Most of the material had been collected on the mainland, some in Porto Rico from which only two species (both peregrine) had been recorded, a little from various extra-American sources. All of the forms that have been identified as to species are known to be exotic but there is some uncertainty as to two others (*Ocnerodrilus* and *Trigaster spp.*) from Porto Rico. Additional records for localities outside the United States have been included for several species.

The author's thanks are extended to the following who kindly supplied material: Dr. Fenner Chace, Dr. C. W. Coates, Mr. Walter Harman, Mr. Stephen Haweis, Dr. Libbie Hyman, Dr. J. A. MacNab, Mrs. Dorothy McKey-Fender, Dr. C. W. F. Muesebeck, Dr. G. E. Pickford, Prof. H. J. Lutz, Mr. Ottys Sanders, Mr. Rudy Stinauer, Mr. B. T. Thompson, and to Profs. M. A. Miller and T. I. Storer for information as to certain earthworms of California.

Family GLOSSOSCOLECIDAE

Genus PONTOSCOLEX Schmarda 1861

PONTOSCOLEX CORETHRURUS (Fr. Müller) 1857

Chatham, New Jersey, greenhouses on Southern Boulevard, October 24, 1947, numerous juvenile and aclitellate specimens. Mr. B. T. Thompson. (All of a second lot, supposedly of the same species, were dead on arrival.)

Pana, Illinois, greenhouse, June 1948, 8 juveniles. Illinois Biological Survey per Mrs. McKey-Fender.

Luquillo Forest, Porto Rico, recreation area, 1,800 feet, in Caribbean National Forest, September 1, 1945, 6 clitellate specimens. Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

Mt. Joy, Dominica, British West Indies, "compost heap", June 19, 1949, 1 posterior fragment and 1 macerated clitellate specimen. Mr. Stephen Haweis.

Hog Harbor, Espiritu Santo, New Hebrides, native gardens, April 1927, 1 juvenile. Coconut plantation, at depth of a few centimeters in volcanic soil, *ca.* 100 ft. elevation and one half mile inland, 14.11.1927, 2 juvenile and 3 clitellate specimens.

14.3.1927, 5 juvenile and 4 clitellate specimens. Mr. J. R. Baker per Dr. G. E. Pickford.

P. CORETHRURUS?

Luquillo National Forest, Porto Rico, La Mina recreation area, 1,800 feet, Feb. 27, 1944, two specimens (one clitellate). Sept. 1, 1945, 38 specimens (4 clitellate). Sept. 16, 1945, 1 clitellate specimen. Sept. 22, 1945, 22 specimens (11 clitellate). Feb. 22, 1947, 29 specimens (8 clitellate). Dr. R. Kenk.

Barranquitas, Porto Rico, at 2,000 feet, 8/ix/1945, 8 specimens. Dr. R. Kenk.

Cidra, Porto Rico, "Treasure Island", 1,200 feet, Sept. 3, 1945, 3 specimens. Dr. R. Kenk.

Rio Piedras, Porto Rico, Sept. 16, 1945, 8 specimens. Mr. R. Cespo per Dr. R. Kenk. Farm on Trujillo Alto Road, 23/11/1947, 45 specimens (7 clitellate). Dr. R. Kenk.

St. Michel Plantation, Haiti, 1926, one posterior fragment. E. C. Leonard. (U. S. Nat. Mus. No. 91346.)

Jean Rabel, Haiti, Feb. 1929, 3 specimens. E. C. and G. M. Leonard. (U. S. Nat. Mus. No. 105088.)

Port de Paix, Haiti, 1.19–25.29, 1 fragment, E. C. and G. M. Leonard. (U. S. Nat. Mus. No. 105088.)

St. Thomas, D. W. I., hillside on north of island, July 18, 1915, 13 specimens. C. R. Shoemaker. (U. S. Nat. Mus. No. 58705.)

External characteristics. The apparent first segment is not as long as the next and its setae are only slightly behind its equator. The epithelium of the presetal portion does not have the smooth appearance of an external epidermis as does that of the postsetal portion.

Nephropores, on *c* lines, are recognizable from iv posteriorly on most specimens from the first four localities. A single nephropore is present on iii of one worm but on the other specimens nephropores could not be found on iii and ii.

Only one female pore is present (6 specimens), slightly in front of 14/15 and somewhat lateral to the *a* line, on the left side. The margin of the pore is very slightly tumescent and white (slight traction on the neighboring epidermis sometimes necessary to permit recognition of the actual aperture). A greyish translucent spot was noted at the expected site of a left pore but traction on the nearby epidermis of this as well as other specimens failed to reveal a definite aperture.

Tubercula pubertates are represented by a longitudinal band of grey translucence of the epidermis just lateral to the *b* line, on each side of the body.

Internal anatomy. Gizzard in vi (5). The ducts of the nephridia of iv, v and vi have been traced to the nephropores of those segments. The ducts from the two large clusters of nephridial tubules on the anterior face of 5/6 pass into the ventral face of the pharyngeal bulb.

Calciferous glands are directed laterally or dorsally so that the ducts pass from the mesial or ventral ends into the dorsal face of the gut. At the free end of the gland there may be recognizable a quite small, finely acinous lobe.

Remarks. Male pores again were not found. Seminal vesicles of each of the dissected clitellate specimens are juvenile and spermathecae are empty. External and internal characteristics of these specimens, except as indicated to the contrary above, are as previously noted (Gates, 1943, pp. 92–93).

Stephenson (1923, p. 490), Bahl (1942) and Gates (1943) disagree as to certain details of the excretory system in the anterior segments of this species. If the gizzard is in vi, as seems to be the case (Gates, 1943, p. 93, points out difficulties involved in segmental enumeration), then Bahl's segment numbering must be increased by one. The ducts of the large cluster of nephridial loops then would have opened on iii instead of ii. Stephenson and Gates, however, had found that the ducts of the large cluster pass into the pharynx. The condition of each of the present dissected clitellate specimens was such as to permit cutting of strands (muscular?) passing from the gut to the parietes so that the pharyngeal bulb could be lifted away from the body wall. When this had been done the ducts of the large nephridial cluster could be seen to pass into the tissues of the ventral portion of the pharynx. In the specimen with an apparent nephropore on iii, a translucent band of the same size and appearance as the nephridial duct passed into the body wall over the site of the nephropore, but the band had been broken and the point of emergence from the pharyngeal bulb was not found. In the other specimens, in which nephropores were lacking on ii–iii, no duct-like bands passed into the parietes at appropriate sites for nephropores. Presumably then there is some individual variation as to the manner of opening of the ducts of the nephridia belonging to iii. As no ducts were found between those of iv and those passing from the large cluster into the pharynx, it would appear that the large cluster usually is to be attributed to segment iii, and that nephridia of ii are lacking. This is in agreement with Bahl, after the necessary change in his segmental numbering. It seems doubtful that the membrane which Bahl calls septum 1/2 is a normal intersegmental septum. Presence of septal funnels of nephridia of three different segments on the anterior face of 5/6 (Bahl's 4/5) also seems anomalous.

One of Mr. Thompson's specimens was left in the dirt in which it had been received, without watering. About a month later, on Nov. 22, the worm was found to be rather sluggish. On Jan. 5, the worm was rolled up into a tight ball which was sprung apart in the opening of the chamber in which it had been contained. The worm remained quiescent until it was dropped into alcohol and then only made a few slight movements. The gut was empty. Obviously the worm was in a state of diapause.

As worms of this particular species had been regarded as unwelcome guests in the greenhouses, an explanation was requested from Mr. Thompson who kindly supplied the following report. As a result of the presence of these worms, in the rose benches of the greenhouses, the soil becomes so hard that one can scarcely shove his fingers down into it. The worms are very sluggish and when they have started in the end of a bench, the infestation progresses at the rate of only fifty lineal feet a year in the same bench. Where they have not as yet infested, the soil is friable and loose. A fine soil sifts every day through cracks in the boards of the benches where the worms are present. This soil does not sift through in other places. These worms are brought into the greenhouses from a bank of soil in the rear where they have been living for at least ten years (data supplied in 1947). The worms will consume straw and green grass when put into the soil.

P. corethrurus is originally from some part of the American tropics and is now common throughout the world in the tropics, presumably as a result of transportation by man. There are no previous records from the continental United States. Successful establishment of a colony of this species at Chatham some time prior to 1937 presumably resulted from escape of the species from greenhouses into which it had previously been introduced with plants.

Many of the worms from the localities listed under the interrogation mark are much macerated. Each specimen has the quincunx arrangement of setae posteriorly. External characteristics and internal anatomy, insofar as determinable without special treatment, are as in *P. corethrurus*, to which species they probably do belong.

Many of these specimens had lost posterior portions of the body. Several have a long and metamerically segmented tail regenerate with terminal anus. Others have a shorter metamerically undifferentiated regenerate also with terminal anus. A fragment from the intestinal region of the body has an unsculptured (imperforate) cicatrix anteriorly and a short, metamerically undifferentiated regenerate with terminal anus posteriorly.

II
Family EUDRILIDAE

Genus EUDRILUS Kinberg 1866
EUDRILUS EUGENIAE Kinberg 1866

Lake Geneva, Florida, from culture beds of an earthworm farm, April 1952, 1 aclitellate and 10 clitellate specimens. Mr. T. W. Baker per Dr. C. W. Coates.

Rio Piedras, Porto Rico, September 16, 1945, 15 specimens (8 clitellate). Mr. R. Crespo per Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

St. Michel Plantation, Haiti, 1926, 1 macerated specimen. E. C. Leonard. (U. S. Nat. Mus. No. 9136.))

Nova Friburgo, Brazil, near the Rio Parahyba northwest of Rio de Janeiro, May 9–13, 1935, 7 macerated clitellate specimens. Dr. Doris M. Cochran. (U. S. Nat. Mus. No. 13273.)

External characteristics. Length, to 185 mm. Diameter, in clitellar region, to 6+ mm. Segments, 193+, 211+ (2 longest specimens). The anus in the Florida specimens (one exception) is slightly dorsoterminal. Ventrally there are marked off, in the anal region, two to five U-shaped metameres (incomplete dorsally) on some of which setae and nephropores are recognizable.

Remarks. In spite of the unusual size of the Florida worms (cf. Gates, 1942, p. 137), and the presence of a normally developed clitellum, metameric differentiation (and possibly production of segments?) had not been completed in the anal growth region of the two largest specimens.

Although the size might be thought to be indicative of favorable cultural conditions there is evidence that some environmental factors had been less than optimal; the presence of one or more metameric anomalies in every specimen in some part of the intestinal region of the body behind xviii; presence on three of the eleven specimens of an extra caudal axis and on one of the three of a smaller tertiary caudal axis.

Bi- and trifid caudal regenerates have been obtained rarely in several species of earthworms (not including *E. eugeniae*), but the present monstrosities show no evidence that the extra axis or axes had resulted from regeneration.

Three anterior amputees were present in the West Indian lots. Amputation at some level behind 20/21, in one case, had been followed by healing without regeneration, the cicatrix unsculptured (imperforate). Loss of i–vi and part of the right side of vii had been followed by replacement of the missing portion of vii and development of a small conical bud without terminal invagination or other sculpturing. After loss of i–iii and parts of the left halves of iv–v, in the third case, the lost portions of iv–v had been replaced and a small bud had been developed with a blind (buccal?) invagination terminally. The nerve cord, somewhat widened, turns laterally in iv and passes up to the dorsal side where it is shortly bifurcated. A nerve cord thus bifurcated is found, at a certain stage of development, on the ventral side of a head regenerate. Perhaps the regenerate in this case would have developed into a dorsoventrally inverted head regenerate, a condition very rarely obtained.

The family Eudrilidae is purely African. *E. eugeniae*, the only species that is known outside of that continent, has been carried around the globe in the tropics, presumably by man, but had not hitherto been recorded from the continental United States. The species has been cultured for at least a year in New York City. Anglers, for whom these worms were raised in Florida, doubtless have been scattering them around the country and further records may perhaps be expected, presumably from the southern states.

E. eugeniae may have come originally from that part of Africa just north of the Gulf of Guinea.

III
Family MEGASCOLECIDAE

Genus PHERETIMA Kinberg 1866
PHERETIMA AGRESTIS (Goto & Hatai) 1899

New York City, in the aquarium building at the Bronx Zoo, September 1947, 2 clitellate specimens. July 2, 1949, 3 clitellate specimens. July 1950, 4 clitellate specimens. Dr. C. W. Coates. (These worms were being raised to feed the platypuses.)

Albany, New York, in leaf mold and peat moss of a florist's nursery, July 1948, 8 clitellate specimens. (U. S. Nat. Mus. No. 108057.)

External characteristics. Segments, 101, 102 (2), 103, 104, 105, 106 (3), 108 (1). Pigmentation red, more marked on the preclitellar portion, or becoming light brownish behind the clitellum and gradually fading posteriorly. Prostomium epilobous, tongue open.

Setae begin on ii and are more closely spaced in the ventrum. Setal circles are without marked and regular breaks middorsally and midventrally. The numbers in six specimens: 24, 32, 27, 27, 29, 28/ii; 35, 37, 40, 38, 34, 32/iii; 45, 45, 49, 38g, 43, 36/iv; 59, 64, 67, 54, 56, 53/viii; 61, 70, 76, 68, 62, 59/xii; 72, 67, 73, 63, 61, 55/xx; vi/23, 22, 24, 20, 21, 16g; vii/21, 26, 26, 16g, 23. 18g (g, one or more gaps with spaces for several setae).

Definite genital markings are again lacking but on vii (2), or viii (1), or vii–viii (4), there are paired areas of finely wrinkled epidermis on which setae may be lacking (in the latter case one or two setae may be present midventrally). These areas had a slightly brownish appearance, on at least one of the worms when alive, but after preservation coloration was no different from that of surrounding epidermis.

Internal anatomy. The intestinal caeca have 6–8 secondary caeca of which the dorsalmost sometimes has one or two small ventral pockets posteriorly. Dorsal sacculations of the intestine, in the caecal segment forward to xx, are not as marked as in *P. hilgendorfi.* The typhlosole is lamelliform in only about fifteen postcaecal segments, then gradually becoming more irregular, flattened and translucent. The ventral typhlosole is flat and ribbon-like but with a median groove. On the roof of the intestine along the mid-dorsal line, in specimens in which contents are not adherent to gut wall, there is recognizable a longitudinal series of pit-like depressions. Each pit is close to region of a septal insertion and has an opaque, whitish, tumescent margin. These pits, which may be well formed even after the typhlosole is no longer recognizable, were noted at the following sites: 48/49–68/69, 44/45–75/76, 50/51–68/69.

The last hearts are in xiii (17). Left heart of ix present (5), right heart (10), both hearts equally developed (2). Commissures of x apparently are lacking (17). The ventral trunk bifurcates anteriorly, the two branches uniting dorsally to form the dorsal trunk. Between those bifurcations and septum 4/5 only two pairs of vessels (ventral portions of commissures of iv and iii?) pass out from the ventral trunk.

The testis sac of xi, in several worms, is u-shaped. Male funnels are plicate and medium-sized. Testes are mammiform to spheroidal. The testis sac, vesicles and hearts of xi may be bound to each other and to the septa by delicate connective tissue. Rudimentary pseudovesicles are present on the posterior face of 13/14 (17) just above the ovaries but no vesicles or sacs were found in xiv.

Spermathecae are large enough to reach well up onto gizzard. The duct is not as bulbous ectally as in some specimens of *P. hilgendorfi*.

Remarks. Worms with 69, 79, 90, 96, and 97 segments are unregenerate posterior amputees. Healing had been slightly asymmetrical, in one case, so that the anus was mostly on the left side. The elongated last segment of one amputee had lost all of its setae but sites of apertures of setal follicles were still recognizable in a complete circle.

The cuticle turns into the buccal cavity and in some much macerated specimens (from the Calif. Acad. Sci. labelled "Japan, 1877. Shigermoto. Gustav Eisen. No. 4547") was recognizable as far back as x or xi. In the gizzard the cuticle was much thickened. The postgizzard collar of these Japanese worms is unusually large and deeply lobed. (There are numerous parasites in the coelomic cavities of iii–x).

P. agrestis has been reported from Baltimore and was recently found in the Arnold Arboretum at Boston (Gates, 1953b, pp. 5–8).

PHERETIMA CALIFORNICA Kinberg 1866

New Orleans and vicinity, La., logs, moist river bottom forest, Dec. 31–Jan. 1, 1931–32, 3 clitellate specimens. J. M. Valentine, per Dr. G. E. Pickford.

New Orleans, La., Jan. '42, 2 clitellate specimens. E. Liebman, per Dr. G. E. Pickford.

Poughkeepsie, N. Y., leaf pile below greenhouses of Vassar College, Aug.–Nov. 1 clitellate specimen. V. L. Fogerson, per Dr. G. E. Pickford.

Poughkeepsie, N. Y., pile of dirt in unheated greenhouse of Vassar College, 1 clitellate specimen. V. L. Fogerson, per Dr. G. E. Pickford.

Waterral Baven, eastern Transvaal, South Africa, 16.iv.'27, 1 juvenile and 1 clitellate specimens. Dr. G. E. Pickford.

As the name suggests this species must have become established in the United States more than a century ago.

PHERETIMA DIFFRINGENS (Baird) 1869

New Orleans and vicinity, Louisiana, logs, moist river bottom forest, Dec. 31–Jan. 1, 1931–32, 3 clitellate specimens. J. M. Valentine, per Dr. G. E. Pickford.

New Haven, Conn., Yale Botanic Garden at Prospect Street, Aug. 19, 1943, 2 aclitellate and 1 clitellate specimens. Dr. G. E. Pickford.

Uvalde, Texas, rotten log, June 1938, 3 aclitellate and 5 clitellate specimens. John Robinson, per Ottys Sanders.

Boone's Cave, N. C., July, 1946, 1 clitellate specimen. Dr. C. D. Howell.

Lincoln, Nebraska, soil near University greenhouses, August, 1927, 1 aclitellate and 5 clitellate specimens. Dr. J. A. Macnab.

Anniston, Alabama, humus in marshy places, June, 1949, 5 clitellate specimens. Wilfred W. Staples, per Dr. Libbie Hyman. (These worms were reported to be known locally as "black wrigglers".)

Fayetteville, Arkansas, wet soil with large admixture of bark from walnut and other lumber in grounds of Brower Veneer Mill, August 17, 1949, 3 clitellate specimens. Dr. W. J. Baerg, per Dr. C. W. F. Muesebeck. (Dr. Baerg reported an attempt to rear this species for sale as fish bait.)

Gainesville, Florida, grounds about agricultural college, Sept. 30, 1914, 1 aclitellate specimen. F. E. Watson, per Am. Mus. Nat. Hist. (Acc. No. 5007, Field No. 3612).

Ruston, Louisiana, yard of apartment house, March 1951, 14 clitellate specimens. Mr. Walter Harman.

Dayton, Oregon, under flats in greenhouses, March 17, 1951, 1 aclitellate and 2 clitellate specimens. Mr. Ray Albright per Mrs. Dorothy McKey-Fender.

Dayton, Oregon, under flats in Albright Greenhouses, March 18, 1951, 1 clitellate specimen. Mrs. Dorothy McKey-Fender.

McLean, Virginia, in "deep woods", August 1953, 1 clitellate specimen. Mr. A. D. Cushman per Dr. C. W. F. Muesebeck.

Chapulhuacan, Mexico, 7/12/37, 1 clitellate specimen. Ottys Sanders. (Posterior fragments of two other specimens probably are of the same species.)

Nova Friburgo, Brazil, near the Rio Parahyba northwest of Rio de Janeiro, May 9–13, 1935, 1 macerated clitellate specimen. Dr. Doris M. Cochran. (U. S. Nat. Mus. No. 13273.)

Kirstenbosch, South Africa, on grass near pond, 2.iii.'27, 1 clitellate specimen. Dr. G. E. Pickford.

Salisbury, South Africa, in bank of Makabusi River, 3/7/27, 4 clitellate specimens. Dr. G. E. Pickford.

Remarks. The gut of the Nebraska specimens (straight and in a splendid condition rarely available) is strongly sacculated in xx–xxvi but there is no indication of demarcation into dorsal and ventral pockets as in *P. hilgendorfi.* The typhlosole (scarcely represented anterior to the caecal segment, xxvii) is low, straight, opaque, rather thin and lamelliform to the region of l–liv. From thence posteriorly it is slightly thicker, lower, rather translucent and regularly interrupted. Just in front of each level of septal insertion the ridge bifurcates, each branch decreasing rapidly in height as it passes diagonally and posteriorly to the midventral line. A pit comparable to those found in *P. hilgendorfi* is present on the roof of the gut middorsally just behind each bifurcation. The typhlosole ends abruptly in lxxxii (worms of 109, 114 and 116 segments), lxxxiii (worms of 109 and 115 segments) but in lvi of an autotomized worm (of 77 segments), in lxix and lxxiii in worms with tail regenerates (at 95/96 and 94/95 respectively).

Both testis sacs are above the nerve cord. The ventral blood vessel is imbedded in testicular coagulum within the posterior sac at least. Prostates are lacking in the Nebraska specimens but prostatic ducts are well developed.

The anterior pair of spermathecae is lacking in two of the Ruston specimens and the spermathecae of the other segments lack ampulla, diverticulum or both. The spermathecae of one of those worms are covered with parasitic cysts.

Maximum number of segments found in tail regenerates is five.

This species probably has been established in the United States at least as long as *P. californica.* Although it had been collected in California prior to 1867 the earliest record yet found to the East (Illinois) that is likely to have been of this species is 1888.

PHERETIMA HAWAYANA (Rosa) 1891

New Orleans and vicinity, La., logs, moist river bottom forest, Dec. 31–Jan. 1, 1931–32, 1 clitellate specimen. J. M. Valentine, per Dr. G. E. Pickford.

New Orleans, La., Jan. '42, 2 clitellate specimens. E. Liebman, per Dr. G. E. Pickford.

Pana, Illinois, greenhouse, June, 1948, 1 clitellate specimen. L. L. English, per Ill. Biol. Survey.

Nashville, Tenn., Jay's greenhouses, Jan. 1947, 1 aclitellate and 4 clitellate specimens. Lester Eck, per Ill. Biol. Survey.

Auburn, Alabama, Farm Ponds Laboratory, May, 1947, 1 aclitellate and 5 clitellate specimens. E. E. Prather, per Ill. Biol. Survey.

Lutz, Florida, spring of 1950, 8 clitellate specimens. Dr. H. S. Hain, per Dr. C. W. Coates. (These worms were being raised for sale as bait, in a bed of muck and manure on white sand, in the shade of cypress trees.)

Lutz, Florida, March 1951, 8 clitellate specimens. Dr. C. W. Coates.

Dayton, Oregon, under flats in Albright Greenhouses, March 18, 1951, 1 clitellate specimen. D. McKey-Fender.

Los Angeles City College, California, June 15, 1951, 2 aclitellate and 19 clitellate specimens. Prof. A. W. Bell, per Mrs. Dorothy McKey-Fender.

Jackson, Michigan, 4 clitellate specimens. Rudy Stinauer. (These worms were secured from a bait dealer who was said to have obtained them from Florida.)

Nova Friburgo, Brazil, near the Rio Parahyba northwest of Rio de Janeiro, May 9–13, 1935, 2 macerated clitellate specimens. Dr. Doris M. Cochran. (U. S. Nat. Mus. No. 13273.)

Madeira, Funchal, 9.viii.1928, "wet vegetable mould," 1 clitellate specimen. Dr. G. E. Pickford.

A spiral abnormality involves viii–x of one Florida specimen.

A tail regenerate of about 14 segments, at 49/50 also has spiral abnormalities in the proximal portion. A tail regenerate at 63/64 has 9 (+?) segments, the proximal metamere with setae ventrally, complete circles on the next five segments followed by three which are clearly demarcated but without setae. The anus is terminal.

P. hawayana may have been one of the species that had become established in Illinois prior to 1888.

PHERETIMA HILGENDORFI (Michaelsen) 1892

Kingston, Ulster County, New York, September 13, 1948, 5 clitellate specimens. T. P. Weyhe, per New York State Museum and the U. S. Nat. Mus.

Bronxville, Westchester County, New York, September 1950, 7 clitellate specimens. Dr. Wm. J. Robbins per Dr. C. W. Coates.

Michigan, beside Ox Creek, just north of Benton Harbor, Berrien County, October 21, 1950, 2 clitellate specimens. Mr. Rudy Stinauer. (7 aclitellate and 1 clitellate, much macerated specimens, received earlier in the year presumably were from the same locality.)

Middleburg, Virginia, October 24, 1950, 1 clitellate specimen. December 12, 1950, 4 clitellate specimens. (U. S. Nat. Mus. Nos. 188565 and 189104) Miss June Badger. (These worms were said to be "extremely lively". Used for food for certain animals in the National Zoological Park.)

External characteristics. Length, of complete specimens, 109–130 mm. Diameter, 6–8 mm. Segments, (87, 1 specimen), 98 (2), 105, 107, 108 (2), 109 (2), 110 (2), 111, 113 (3), 114, 116. Pigmentation, red, restricted to dorsum (unrecognizable in Kingston specimens, alcoholic preservation). Prostomium epilobous, tongue open.

The setae begin on ii, the circles with no marked, regular break middorsally or midventrally, gaps when present irregular and mostly slight. Setal circles of xvii–xx, as well as of more posterior segments, are uninterrupted. Setal numbers are shown below.

Variation in number of setae in *Pheretima hilgendorfi*

Segment	ii	iii	viii	xii	xx	vii/sp
	17	18	50	51	56	23
	20	28	49	54	58	12*
	22	27	54	56	55	22
	23	30	51	60	59	26
	23	34	56	58	62	23
	26	31	55	54	59	24
	24	32	55	61	61	25
	27	30	59	56	61	22
	26	38	60	66	57	26
	22	34	47	56	50	22

sp setae between spermathecal pore lines.

* gaps present in circle.

On the macerated specimens number of setae between spermathecal pore lines varies between 24 and 28.

The first dorsal pore is apparently on 11/12 (8, including seven macerated specimens), 12/13 (13, but with an apparently non-functional marking on or near 11/12 in 6), 13/14 (2, but with an apparently non-functional marking on 12/13 on one) The clitellum (annular) reaches to 13/14 and 16/17 but with pores of those furrows not occluded, intersegmental furrows and setae unrecognizable, dorsal pores of 14/15 and 15/16, except on one specimen, occluded.

Quadrithecal, spermathecal pores very small (but larger than female pore) transverse slits with slightly whitened margins, nearly ½C apart, on 6/7–7/8. The female pore is median (10).

Genital markings small, clearly demarcated, circular tubercles, each with a minute central aperture, in unpaired median presetal patches on viii (32), viii–ix (6), viii–x (1, with a single marking on xii), viii–xi (1). The patches are closer to the intersegmental furrows than to the setal circles and the tubercles are in 1–5 rather irregular transverse rows of 3–5 each, a patch containing 3–24 tubercles.

Internal anatomy. Septa 8/9–9/10 lacking, none markedly thickened though 11/12–12/13 are more opaque than the others and obviously with some slight muscularity (7). Postgizzard glandular collar on the oesophagus markedly iridescent and deeply lobed. Intestinal origin in xv (10). Intestinal caeca manicate, with 7–9 secondary caeca; the dorsalmost the longest and thickest, reaching into xxii, xxiii or xxiv, the ventralmost shortest and only about 2–3 mm long. The gut from the caecal segment through xx is markedly sacculated, two dorsal rows of sacculations extending from the middorsal to midlateral levels, a row of still more marked sacculations extending from midlateral to midventral levels. Typhlosole low but lamelliform, decreasing in height and flattening out irregularly passing posteriorly, ending in lxxix (specimen of 113 segments). Pits are recognizable (December Middleburg specimen) at levels of 47/48–69/70 (typhlosole ends in lxxi). Ventral typhlosole flat and ribbon like, from first, second or third postcaecal segment through 16–17 segments.

Last hearts in xiii (11). Left heart of ix present (5), right present (5), both hearts of ix present but that of left side much smaller (1). Commissures of x lacking (10) or represented by a pair of small blood-filled vessels passing ventrally from the supra-oesophageal (1). Subneural trunk continued into iii, bifurcating anterior to the subpharyngeal ganglion. The dorsal trunk passes under the brain.

Testis sacs unpaired and ventral, above the nerve cord, the ventral trunk apparently included and just below the roofs. Testes rather mammiform, the protuberant central nipple-like portion brownish. Male funnels plicate, medium-sized. Seminal vesicles rather small, low down in coelomic cavities, those of xi bound by connective tissue to the testis sac, those of xii sometimes marked off into distinct ampulla and lamina. Pseudovesicles in xiii (8) may be as large as the vesicles of xii. Ovisacs or vesicles of any sort were not found in xiv (7). Vasa deferentia apparently end usually in a slightly pear-shaped swelling, in xvii, xviii, even xix or xx though a filament may pass from the enlargement into the parietes. The ducts of the Kingston specimen were continued into xxiii or xxiv where they ended without any terminal swelling.

Spermathecae fairly large, reaching well up onto the gizzard. The duct, which may have an obvious muscular sheen, is more or less widened towards the parietes so as to have a rather flask-shaped appearance but is much narrowed just at or within the parietes. The diverticulum is longer than the main axis and comprises a stalk portion with muscular sheen and a slightly thicker seminal chamber of variable shape and thin translucent wall. The diverticulum passes into median face of the duct close to the parietes.

Genital marking glands have long coelomic stalks.

Remarks. A 96 mm. worm of only 87 segments, the last of which has a complete circle of setae, appears to be a posterior amputee. The penultimate segment has no setae (7 specimens), or about eight on the right side only (specimen of 108 segments). A complete circle of setae is present on the penultimate segment of three Kingston worms (of 98, 98 and 113 segments). The last segment of specimens having 70 and 72 segments has a complete circle of setae, the small anal regenerate not marked off from substrate by an intersegmental furrow.

The oesophagus, including the pharyngeal bulb, contained no soil but the gizzard lumen in each of the dissected specimens was filled with earth. The lumen of the oesophagus in x–xiii of several specimens was filled with a reddish translucent material of jelly-like consistency. A piece of a midrib of a leaf, about nine mm. long, with small bits of the lamina still attached, was found in one intestine. The cuticle turns into the gut at the anus and in favorable conditions can be recognized for some distance forward.

Each spermathecal pore of some of the worms is on a hemispheroidal tubercle with smooth, greyish translucent surface. The tubercle usually is slightly sunk into the body wall so that its periphery is covered by a slight preputial-like protuberance. The region around each spermathecal pore of the December Middleburg worms is whitened and tumescent, with greyish translucent spots similar in appearance to those of the genital marking patches. No stalked glands corresponding to these areas were found internally though they could have been concealed from view in the muscular layers. The narrowed parietal portion of the duct, after dissecting the spermatheca out of the body wall, appears as a shortly conical protuberance from the ventral face of the thickened ectal section of the duct.

Two conjoined masses of tissue that protrude from the posterior margin of the brain are clearly distinguished from the rather greyish and smooth ganglion by a rough surface and strong iridescence.

Lymph glands of posterior segments are enlarged and filled with a brown, granular debris and small cysts of some parasite. Similar cysts were also present, in some cases, in the coelomic cavities.

These worms are "extraordinarily rich in vitamin B_{12}" (*in litt.*) according to Dr. Wm. J. Robbins (also 1951) who supplied some of them.

Spermatozoal iridescence is lacking on male funnels, in vasa deferentia and spermathecae, though the clitellum is sufficiently developed to indicate full sexual maturity. Even if sperm had been produced there would have been no normal way for it to be passed out of the body. The seminal vesicles have a rather juvenile appearance and the testes showed no evidence of discharge of sperm. All this, together with the fact that every specimen is completely anarsenosomphic, would seem to indicate that reproduction, in American individuals of the species, is parthenogenetic instead of sexual. The presence of normally developed spermathecae, as well as of seminal vesicles, may then indicate, in accordance with the principal of evolutionary economy, that the acquisition of parthenogenesis has been recent.

P. hilgendorfi was erected on seven specimens. One was sexthecal (No. 6) and one was monothecal (No. 7, with pore on 6/7), and both, as well as one quadrithecal worm, were without genital markings. Subsequently, sexthecal specimens, as well as dithecal (pores on 6/7–7/8), were referred to this species by its author. *P. hilgendorfi*, in agreement with various Japanese investigators, is considered to be primarily quadrithecal. Partial or complete disappearance of the spermathecal battery would not however be unexpected though apparently unrecognized hitherto by Japanese students. If genital markings also disappear along with the spermathecae, distinction of such individuals of *hilgendorfi* from similar mutants (without spermathecae and genital markings) of *P. agrestis* and *levis* will be impossible until new criteria for specific identification have been developed.

P. hilgendorfi, except for a Korean record (Koryo and Keijo in Keiki-do), had not hitherto been recognized outside of Japan.

PHERETIMA HUPEIENSIS (Michaelsen) 1895

New Orleans, La., Jan. '42, 3 aclitellate and 1 clitellate specimens. E. Liebman, per Dr. G. E. Pickford.

New York City, deer corral in Zoological Park, spring of 1951, 21 medium-sized to large juveniles, 10 aclitellate (at least five postsexual) and 1 clitellate specimens. July 2, 1951, 8 medium-sized to large juveniles, 11 aclitellate and 2 clitellate (one early) specimens. Dr. C. W. Coates.

A greenish coloration mentioned by the collector was no longer recognizable externally when the New York worms were examined after formalin preservation but traces were still visible internally. The mid-dorsal longitudinal band was red. Spermathecal pore protuberances were lacking and sex organs were juvenile in the clitellate New York specimens. Rudiments of genital markings are recognizable even on the smallest juveniles and one had an extra pair on 16/17.

The typhlosole is a low lamelliform ridge less than one mm. high, beginning in the caecal segment and ending in lxxxviii (a clitellate specimen of 126 segments). A pre-typhlosolar ridge in xvi–xxvi is scarcely recognizable.

P. hupeiensis has been reported as a nuisance, because of casting deposition above ground, in "many" golf courses and country clubs but attempts to secure more data as to specific localities involved have been futile. Methods of control have been worked out at the Conn. Agr. Exp. Sta., New Haven (Schread, 1952).

The species has been established in the United States for forty years at least. It was collected in the District of Columbia in 1910.

PHERETIMA LEVIS (Goto & Hatai) 1899 ?

New York City, in the aquarium building at the Bronx Zoo, September 1947, 4 clitellate specimens. July 1950, 1 clitellate specimen. Dr. C. W. Coates. (From the tanks where worms were being raised to feed the platypuses.)

External characteristics. Length, 75–100 mm. Diameter, 5–7 mm. Segments, 88–97 (see under regeneration below). Dorsum pigmented, pigmentation red in the 1950 specimen, others reddish, brownish or even grayish. Prostomium epilobous, tongue open.

The setae begin on ii, the circles with no marked, regular break mid-dorsally or midventrally: 28/ii, 30/iii, 35/iv, 48/viii 47/xii, 48/xx, viii/20. First dorsal pore on 12/13 (5). Clitellum (annular) probably reaches to 13/14 and 16/17 but the dorsal pores of those furrows are not occluded.

Spermathecal pores minute and superficial, nearly ½C apart; on 6/7–7/8, two pairs (2 specimens), on right side only (1), on right side of 7/8 only (1). One specimen is athecal. The female pore is median (5).

Genital markings are quite small, circular tubercles, each with a single, central minute aperture. Two markings are usually close to each spermathecal pore, one in front and one behind, the posterior slightly more median to the spermathecal pore than the other. Postclitellar markings are present on two specimens, in the setal circle of xviii and on the left side; one marking (athecal specimen), two markings (specimen with spermathecae on right side only).

Internal anatomy. Septa 8/9–9/10 lacking, none especially muscular. Intestinal origin in xv (5). Intestinal caeca manicate, dorsalmost secondary caecum the longest. Typhlosole low, lamelliform, with a few slight lateral ridges, gradually disappearing posteriorly, definitely lacking behind xlii (specimen with 88 segments), xlvii (92 segments), xlviii (94 and 97 segments), continued anteriorly from caecal segment into xx but gradually decreasing in size. Ventral typhlosole flat, ribbon-like and with a slight median groove, from first, second or third postcaecal through 15, 16, or 17 segments.

Last hearts in xiii (5). Left heart of ix present (3), right present (1), both hearts of ix present but that of the left side larger (1). Hearts of x lacking (5).

Testis sacs unpaired, the ventral blood vessel in roof of the sacs which are above the nerve cord. The sac of xi is U-shaped, with seminal vesicles of that segment apparently included (1, uncertain in other specimens). Testes disc-shaped to spheroidal. Seminal vesicles small and with primary ampullae. Vasa deferentia usually with a vesicular swelling in region of xv–xvii from which a filiform continuation is recognizable on or in the parietes for varying distances.

Spermathecae are fairly large. The duct has a marked muscular sheen, is about as long as the ampulla and is narrowed ectal to diverticular junction, which may be at the parietes or quite obviously more entally. The diverticulum is usually at least as long as the main axis. The stalk is slightly slenderer than the duct and at least as long. The seminal chamber is of about the same length as the stalk, sausage-shaped or variously widened but never looped. The seminal chamber, and occasionally the ampulla also, contains an opaque material without iridescence.

Genital marking glands are stalked, the stalks short and confined to the parietes or longer and markedly protuberant into the coelomic cavities.

Regeneration. Short tail regenerates are present on four of the specimens: of two segments at 86/87, 90/91, and 94/95, of three segments at 91/92. The penultimate and antepenultimate segments of the other worm are about as long as those in front but are markedly narrower and have no setae. If these two segments were not regenerated they must have been recently developed in normal growth.

Remarks. Each specimen is anarsenosomphic and, being clitellate, presumably mature. As there is no indication of production of spermatozoa in any of these worms, reproduction probably would have to be parthenogenetic. Nevertheless, the opaque material present in spermathecal ampullae and seminal chambers may indicate that these particular individuals had, in spite of their inability to exchange sperm, gone through the form of copulating.

P. levis is known only from the original brief description of the Japanese types (number?, present location?). The species can be distinguished, for the present, from *P. hilgendorfi* by the absence of unpaired median patches of genital markings and by the presence of discrete markings near the spermathecal pores.

P. levis, hilgendorfi and *agrestis* are but three examples of species of the genus *Pheretima* in which evolutionary tendency has been in direction of obligatory parthenogenesis. With acquisition of ability to reproduce parthenogenetically most organs of the hermaphroditic reproductive system — the prostates and their ducts, copulatory chambers and associated porophores, penes and glands, the male porophores, male deferent ducts and their funnels, seminal vesicles, testis sacs, testes, spermathecae, and perhaps also genital markings and the glands associated therewith — presumably became almost or completely useless. In *P. diffringens,* which may prove to be parthenogenetic, prostate glands frequently are lacking (as in Nebraska specimens) though the ducts of such glands may be more or less normally developed. In American colonies of *P. agrestis, hilgendorfi* and *levis* all of the male terminalia are, usually at least, lacking. In other species (in Japan, Burma, etc.) spermathecae are lacking, in some cases as well as the male terminalia.

The taxonomy of the genus *Pheretima* has been concerned mostly with reproductive structures. If then, along with such organs as spermathecae and male terminalia, characteristic genital markings also disappear in parthenogenetic forms, specific identification, in the present state of our knowledge, becomes impossible. Just that kind of a taxonomic puzzle has been presented by 18 specimens from three places: New York City (supplied by Dr. Coates), Kingston, and a New Jersey locality (supplied by Mr. Harold Davies). Each of these worms has manicate intestinal caeca. The only species of *Pheretima* with such caeca that are now known to be established in the continental United States are *agrestis*, *hilgendorfi* and *levis*.

PHERETIMA sp. I

Athecal and anarsenosomphic specimens are all rather small. Most are posterior amputees.

PHERETIMA sp. II

One anarsenosomphic worm has a single spermatheca that appears not to be normally developed. The aperture is located on 6/7 on the left side, but was invisible until after the cuticle had been peeled off. The long stalk of a coelomic gland passes into the parietes near the spermatheca but no genital marking is recognizable externally even after removal of the cuticle. This gland permits tentative identification of the worm as *P. levis*.

PHERETIMA sp. III

A transversely elliptical male porophore is present in the setal circle on the left side of xviii. A prostate gland is present on the left side and is unusually large, extending through segments xv–xx! The prostatic duct is bent into a hairpin loop the ectal limb of which is much thicker, but both limbs have a marked muscular sheen. The vasa deferentia of the left side pass into the ental end of the prostatic duct.

If this specimen had been in a pure culture it could have provided interesting information as to characteristics of the male terminalia in the ancestral form from which the anarsenosomphic type has been evolved.

PHERETIMA MORRISI (Beddard) 1892

Poughkeepsie, N. Y., leaf pile below greenhouses of Vassar College, Aug.–Nov., 2 clitellate specimens. V. L. Fogerson, per Dr. G. E. Pickford.

Poughkeepsie, N. Y., pile of dirt in unheated greenhouse of Vassar College, January, 8 clitellate specimens. V. L. Fogerson, per Dr. G. E. Pickford.

Lutz, Florida, spring of 1950, 1 clitellate specimen. Dr. H. S. Hain, per Dr. C. W. Coates. (These worms were being raised for sale as bait, in a bed of muck and manure on white sand, in the shade of cypress trees.)

Lutz, Florida, March 1951, 1 clitellate specimen. Dr. C. W. Coates.

Negritos, Peru, Nov. 16, '39, 1 clitellate specimen. Mrs. H. Exline Frizzell per Dr. G. E. Pickford.

PHERETIMA RODERICENSIS (Grube) 1879

Lutz, Florida, spring of 1950, 1 clitellate specimen. Dr. H. S. Hain, per Dr. C. W. Coates.

Lutz, Florida, March 1951, 5 clitellate specimens. Dr. C. W. Coates.

Sta. Anasco, Porto Rico, (probably in the western part of Aguadillo province), 1/20/99, 1 clitellate specimen. Porto Rico Expedition, Steamer Fish Hawk, 1898–99. (U. S. Nat. Mus.)

Rio Piedras, Porto Rico, Sept. 16, 1945, 16 large juvenile and aclitellate specimens, 12 partially clitellate or clitellate specimens. (17 juveniles and posterior fragments presumably also of the same species.) Mr. R. Crespo per Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

Mt. Joy, Dominica, British West Indies, March 18, 1949, 4 clitellate specimens. Mr. Stephen Haweis.

Mt. Joy, Dominica, British West Indies, compost heap, June 19, 1949, 1 juvenile, 1 aclitellate and 2 clitellate specimens. Mr. Stephen Haweis.

Grahamstown, Eastern Cape Province, South Africa, "dug by gardener from lands above gardens, rich soil", 8/3/26, 4 clitellate specimens. Dr. G. E. Pickford.

External characteristics. Segments, 92, 95 (2), 96 (2), 97 (2), 98, 99 (2). Prostomium epilobous, tongue open. Setae begin on ii. The circles have no marked or regular breaks mid-dorsally or midventrally. Numbers (Florida specimen): 21/ii, 32/iii, 35/iv, 36/viii, 49/xii, 48/xx. The clitellum (annular) of the Florida specimen did not quite reach 13/14 and reached to just behind the equator of xvi. Each spermathecal pore is at the center of a clearly demarcated, transversely elliptical, greyish translucent area and is in line with an intersegmental furrow but the translucent area appears to belong to the segment in front (Florida specimens).

Genital markings are lacking on three specimens, the posterior markings present on 30, the anterior only on one. The markings in some of these specimens appear to be squarely and equally across 18/19 but in others, especially in an early stage of development, appear to be definitely segmental and postsetal on xviii.

Internal anatomy. The typhlosole is lamelliform, about 1½ mm. high, gradually decreasing in height posteriorly, ending abruptly in lxvi (worm of 92 segments), lxvii (95, 96, 96, 97 segments), lxix (97 segments), lxxi (99 segments), lxxii (95 segments). A lower ridge continues the typhlosole from the caecal segment into xv. From 52/53, in one specimen, the ventral margin of the typhlosole is scalloped and with definite pits under septal insertions as in *hilgendorfi*. A ventral typhlosole apparently is lacking. Hearts of x are present (3 specimens).

Regeneration. A tail regenerate at 88/89 is metamerically abnormal but with about five segments. Another tail regenerate, of two segments, is at 59/60. A small regenerate at 55/56 is metamerically undifferentiated and with terminal anus. The typhlosole of this worm is high from xlix anteriorly but rudimentary in l–liv and lacking in lv, and presumably has regressed, since amputation, in those segments. Several other worms probably have a tail regenerate of two or three segments only.

Remarks. The penultimate segment of several specimens has only a few setae ventrally, differentiation not yet having been completed. The anal segment of one worm has a well developed intersegmental furrow in the ventrum but setae are not yet visible in front of it.

P. rodericensis has not been reported previously from the mainland of the United States but probably has been widely distributed throughout the country in earth around greenhouse plants (Gates, MS). The center or centers of such distribution have not yet been discovered.

With addition of *P. bicincta* (E. Perrier) 1875, which probably has been similarly distributed with greenhouse plants, ten species of *Pheretima* are now known to have become established within the limits of continental United States.

Genus PONTODRILUS E. Perrier 1874

PONTODRILUS BERMUDENSIS Beddard 1891

Boca Chica, Texas, 4/2/38, 2 clitellate specimens. Mr. Ottys Sanders.

?

Marquesas, Florida, sand, June–July 1914, 51 specimens. A. L. Treadwell. (Am. Mus. Nat. Hist. No. 2181.)

External characteristics. Length, 59–62 mm. Diameter, 2.5 mm. (clitellar region and xvii). Segments, 98, 104. Spermathecal pores exactly on *b* lines, on tips of slightly conical protuberances. The left male pore is on xvii of one of the worms, the right on xix and the genital marking on 20/21 but xvii–xix may be involved in a spiral abnormality (intersegmental furrows not definite in the region involved).

Internal anatomy. Lamellae which may be calciferous are present in xiv–xvi and are especially pronounced in xv. The gut is widened in xvii but no definite valve was found. A sacculation of the intestine in xviii, on each side, is so marked as to have the appearance of a caecum. Nephridia of xiv are lacking. Those of xiii, xv–xvii are large, the surfaces with a finely granular appearance. The caliber of the nephridial tube decreases in xviii–xx, and from xxi posteriorly the large flattened sac is recognizable. The spermathecal diverticulum apparently passes into the body wall some distance from the point of entry of the duct.

External characteristics (Marquesas specimens). Spermathecal and male pores are on the *b* lines.

A pair of small, circular, greyish translucent areas is present in *aa* on xviii (except in two worms), the areas nearly symmetrically placed across the setal arc. Both areas, on some of the specimens, are on a single transverse area of marked tumescence. The grey areas of another specimen are in contact mesially and on a ridge which also includes the slightly depressed male pores. The whole median region (of *aa*) of two specimens (with indications of clitellar glandularity) is greyish translucent, slightly depressed and surrounded by a rather conspicuously protuberant white rim.

A median genital marking is present on 19/20 on at least 41 of the specimens, and is clearly marked off into an opaque marginal band and a grey, translucent central portion.

Internal anatomy. The deferent duct passes into the ental end of the prostatic duct. The latter has no muscular sheen and is in two short, u-shaped loops which are bound to the parietes. The single, shortly digitiform diverticulum passes into the median face of the spermathecal duct well above the parietes and may have several translucent spots suggestive of discrete but empty seminal chambers.

Remarks. None of the Marquesas specimens is sexual and the spermathecae appear to be in various stages of late juvenile development.

The spermathecal pores are in the *bermudensis* rather than the *gracilis* location but the diverticulum passes into the spermathecal duct well up from the body wall in the coelomic cavity as in *gracilis*. Grey areas on xviii presumably represent an early stage of development of a median part of the male field.

PONTODRILUS GRACILIS Gates 1943

Punta Garda, Florida, 3 juvenile and 2 aclitellate specimens. J. C. Galloway per U. S. Nat. Mus. (1 long intestinal fragment and 8 tail pieces may be of the same species.)

Spermathecae are fairly well developed in the two aclitellate specimens, the single, median diverticulum passing into the duct quite definitely ental to the parietes.

These specimens were labelled as, "Found in beach sand between tides, putting up castings after the fashion of *Lumbricus*".

IV
Family MONILIGASTRIDAE

Genus DRAWIDA Michaelsen 1900
DRAWIDA BAHAMENSIS (Beddard) 1892

Cidra, Porto Rico, "Treasure Island", 1,200 feet, September 3, 1945, 1 aclitellate specimen. Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.) A posterior fragment of another individual may be of the same species.

External characteristics. Length, *ca.* 20 mm. Diameter, *ca.* 1½ mm. Segments, *ca.* 110. Pigmentation lacking (? alcoholic preservation). Prostomium probably prolobous, deeply retracted. Setae begin on ii; closely paired, *ab ca.* = *cd*, *aa* slightly < *bc*, *dd ca.* = ½C. Nephropores large and readily recognizable from iii posteriorly, in *cd* or on *d* lines.

Spermathecal pores just median to *c* lines, on 7/8. Female pores on xii, just behind 11/12, about on *b* lines. Male pores on 10/11, in middle portion of *bc*.

Genital markings are two pairs of indistinctly demarcated, transversely placed areas of tumescence, with smooth surfaces and no indication of differentiation of central and marginal portions, in *ad.* postsetal on x and presetal on xi.

Internal anatomy. Septa 5/6–8/9 thickly muscular. Gizzards in xii–xiv. Gut valvular in xviii.

Testis sacs apparently are restricted to x (?) The vas deferens. probably fairly long, and entirely in x (?), is coiled into a tight ball of loops that is of about the same size as the sac immediately above it. The prostate comprises a quite small, spheroidal, acinous mass into which the vas passes, connected by a very short and slender neck to a larger, thick-walled spheroidal body that is protuberant into the coelom. This body, which has a muscular sheen, has on its roof a shortly digitiform penis.

The spermathecal duct is looped and passes into the ental end of a shortly digitiform atrium erect in viii that is about twice the thickness of the duct. The ovarian segment probably is reduced to a horseshoe-shaped ovarian chamber. Ovisacs are juvenile and confined to xii.

Remarks. This species has been known hitherto from two specimens supposedly imported to Kew from the Bahamas.

The family Moniligastridae is oriental. Very few cases of transportation have been recognized and all have been in the genus *Drawida.* As yet there have been no records of any species from the continental United States.

D. bahamensis may have come originally from some part of China.

V

Family ACANTHODRILIDAE

Genus DICHOGASTER Beddard 1888

DICHOGASTER sp.

Luquillo National Forest, Porto Rico, April 4, 1943, 1 small juvenile. Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

Rio Piedras, Porto Rico, September 16, 1945, 1 juvenile and 2 clitellate specimens. Mr. R. Crespo per Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

Remarks. Juveniles of *Dichogaster* sp. have been intercepted, on various occasions, in shipments of plant material into the United States.

Two species have been recorded from California: *D. bolaui* (Michaelsen) 1891 (San Francisco) and *D. saliens* (Beddard) 1893 (Del Monte and San Francisco). Peregrine species of *Dichogaster* are all small and may have been overlooked in other localities.

Genus MICROSCOLEX Rosa 1887

MICROSCOLEX DUBIUS (Fletcher) 1887

Ruston, Louisiana, yard of apartment house, March 1951, 3 clitellate specimens. Mr. Walter Harman.

Canberra, Australia, drainage ditch between row of poplars and Cupressus hedge, 1 clitellate specimen, per Dr. N. Tebble.

Remarks. These worms are fairly large for this species, 47–65 mm. long, 3–4 mm. thick. Segments, 114–116. The cuticle turns into the gut at the mouth and is recognizable back to level of 6/7. A supra-oesophageal trunk is recognizable in ix–xiii but no subneural was found. The dorsal trunk passes forward under the brain. Hearts, in x–xii, are large and apparently latero-oesophageal. Commissures of ix–v are lateral. There are no spermathecae but on 6/7–8/9, on the *a* lines, a minute greyish marking is present which was thought, until after study of internal anatomy, to represent a rudimentary spermathecal pore.

This is the first record from Louisiana, but the species has been reported from California (San Francisco, Berkeley, Santa Rosa, Santa Barbara, Mt. Diablo) and North Carolina (Raleigh). Other records: Mexico, Chile, Argentina, Uruguay, France, Cephalonia, Balearic Is., Madeira, Canary Is., Algiers, Tunis, South Africa, Australia (Southwest Australia, South Australia, New South Wales, Tasmania), Norfolk Island, New Zealand.

MICROSCOLEX PHOSPHOREUS (Duges) 1837

New Orleans, Louisiana, park, June 1942, 1 clitellate specimen in poor condition. Mr. E. Liebman per Dr. G. E. Pickford.

Bangor, Maine, greenhouse, February 28, 1953, 2 clitellate specimens.

Remarks. Genital markings are postsetal, on xi, the centers about on the *a* lines. The gut is valvular in xv, moniliform in ix–xiv, the sections in xiii–xiv small but larger than that in xv, much larger in ix–xiii. On the floor of the gut in ix–xiii there is a low longitudinal ridge with a slight groove at the median plane (2). Each spermatheca (Bangor specimens) has two diverticula, one to the median and the other to the lateral side of the duct.

This species had previously been recorded from Washington (D. C.), North Carolina (Raleigh), Florida (Quincy), and California (San Francisco, Coulterville, Redding, Santa Barbara, Santa Rosa, Lake Chalot, Alameda County). Other records: Mexico, Brazil, Paraguay, Argentina, Chile, Germany, Switzerland, France, Italy, Sardinia, Algiers, Canary Is., South Africa, New Zealand.

M. phosphoreus, like *M. dubius*, may have come originally from the extreme southern part of South America.

Genus TRIGASTER Benham 1886

TRIGASTER sp.

Luquillo Forest, Porto Rico, 1,800 feet, September 22, 1945, 1 juvenile. Sept. 22, 1947, 1 specimen. Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

External characteristics. Length, *ca.* 40 mm. (juvenile specimen). Diameter, *ca.* 1.5 mm. Pigmentation red (not leached in spite of alcoholic preservation, but formalin fixation). Prostomium tanylobous. Setae begin on ii; *ab* much smaller than *cd* throughout, *dd ca.* = ½C(?). First dorsal pore on 5/6.

Internal anatomy. Gizzards, three, possibly in vi–viii. Gut in next segment but one behind last gizzard, and through two or three segments widened, with numerous, closely crowded, white, circular, thin and lamelliform ridges on inner wall. Excretory system micronephridial.

A bundle of (penial?) setae is conspicuously protuberant into the coelomic cavity on each side of xvii (?) and xix (?). The setae are not sigmoid and taper to a rather pointed tip and appear to be unornamented.

Remarks. Genital organs were not found. The specimen is in too poor condition to permit further characterization.

The 1947 specimen is 155 x 5 mm. In spite of anesthesia and preservation in alcohol the red pigmentation is still recognizable. Maceration is too advanced to permit determination of other external characteristics. Two pairs of fairly large nephridial clusters are present in segments in front of the first gizzard. Four pairs of hearts are present behind the last gizzard segment.

Species of *Trigaster* have been recorded hitherto only from St. Thomas and Mexico. All of the species are in need of more adequate characterization. The Porto Rican form is distinguishable from the Mexican by the presence of a third gizzard, and from the St. Thomas species by the bright pigmentation, presence of penial setae, and a more anterior location of the first dorsal pore. Little importance can be attached, at present, to any of these distinctions, since nothing is known as to intraspecific variation in gizzard number in the genus and penial setae have occasionally been said to be absent in species (of other genera) that do have them. If, however, presence of a third gizzard, and of penial setae, prove to be valid criteria of specific distinctness the exotic label (implied by inclusion in this contribution) may have to be removed.

VI

Family OCNERODRILIDAE

Genus EUKERRIA Michaelsen 1935

EUKERRIA PEGUANA Gates 1942

Rio Piedras, Porto Rico, September 16, 1945, 2 clitellate specimens. Mr. R. Crespo, per Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

Remarks. Because of the poor condition the relative size of setal intervals *aa* and *bc* could not be determined. The genital marking is on xxi (1, lacking on the other specimen).

The spermathecal duct (coelomic portion) is about as long as the ampulla and is widened ectally. This widened portion contains an ovoidal mass of spermatozoa.

The finding of this species (hitherto known only from Burma) in Porto Rico confirms a prediction implicit in the inclusion of the original description in a contribution on peregrine forms.

The original home of this species presumably is somewhere in the southern part of South America.

EUKERRIA SALTENSIS (Beddard) 1895

Dayton, Oregon, hopyard, gravel bar below woods, Willamette River, June 4, 1948, a number of specimens. Mrs. Dorothy

McKey-Fender.

Remarks. These well preserved specimens had already been identified by Mrs. McKey-Fender.

This is the first record of this species from the continental United States. "In origin it is undoubtedly South American" (Pickford, 1928, p. 379). It has been recorded from the following places: Chile (Salto, Quillota, Coquimbo, Valparaiso). Easter Island. South Africa: Cape Province (Stellenbosch), Natal (Durban, Horwick), Transvaal (Pretoria, Johannesburg). Burma (Pyinmana, Monywa). Australia: New South Wales (Sydney, Paramatta, Mt. Victoria). New Caledonia (Oubatch).

Genus GORDIODRILUS Beddard 1892

GORDIODRILUS PEGUANUS Gates 1942

Rio Piedras, Porto Rico, September 16, 1945, 5 clitellate specimens. Mr. R. Crespo per Dr. R. Kenk. Several other specimens may be of the same species. (U. S. Nat. Mus. No. 184700.)

Remarks. The condition does not permit determination of relative sizes of setal intervals *aa* and *bc*. The clitellum apparently extends only between the setal arcs of xiii and xix. Male and prostatic pores are unrecognizable.

Although testes are present in both x and xi, seminal vesicles again are present only in xii and are small. Several transparent chambers are present about at the middle of the coelomic portion of each spindle-shaped spermathecal duct but, as in the Burmese and Indian specimens, are empty.

This record confirms a prediction implicit in the inclusion of the original description of this species in a contribution on peregrine forms (Gates, 1942).

G. bonacanus Cernosvitov 1942 is distinguished from *peguanus* only by characteristics that may be explainable as due to incomplete development, individual variation, or misinterpretation of conditions in rather difficult material. *G. peguanus* has priority (February over June).

Although *G. peguanus* is known today only from Burma (Amherst, Thaton, Hanthawaddy, Insein, Minbu and Katha districts), India (Bangalore), Bonaco Island (in the Caribbean) and Porto Rico, the original home of the species must be somewhere in Africa.

OCNERODRILUS sp.

Luquillo Forest, Porto Rico, Recreation area, 1,800 feet, September 1, 1945, 8 specimens. Dr. R. Kenk. (U. S. Nat. Mus. No. 184700.)

External characteristics. Length, to *ca.* 35 mm. Diameter, *ca.* 1 mm. Pigmentation unrecognizable (alcoholic preservation). Prostomium epilobous, *ca.* $\frac{1}{2}$, tongue narrowed posteriorly. Setae begin on ii; *ab ca.* = *cd*, *aa* < *bc*, *dd* < $\frac{1}{2}$C, *a* and *b* of xvii apparently lacking. Clitellum, on xiv–xviii (+?), apparently saddle-shaped, lacking in *cc* ventrally or a smaller portion of that interval.

Spermathecal pores were not seen but apparently are on 8/9 in region of *ab*. Female pores on xiv, on *b* lines. Male pores (?) on xvii, about on *b* lines. The immediate margin of each pore may be slightly tumescent and whitened.

Internal anatomy. Septa 7/8–8/9 rather thickly muscular, 6/7 with less marked muscularity. No gizzard. Calciferous glands paired, in ix, elongately ellipsoidal, the anterior end of each attached by a short cord to the posterior face of 8/9, the posterior end attached to the ventral face of the gut just in front of 9/10, the walls rather thick, the lumen central and longitudinal. Intestinal origin in xii. No typhlosole. Hearts large, in x and xi.

Holandric, testes and funnels apparently free in x and xi the coelomic cavities of which are however narrowed by approximation of the septa. The coelomic cavities of x and xi are filled with a white material apparently composed of compacted coelomic corpuscles. Seminal vesicles are acinous, those of ix small, those of xii united into a rather horseshoe-shaped mass (3 specimens).

The prostates are of variable length, confined to xvii, extending into xviii, long enough to reach through three or four segments. The deferent duct lies just lateral to the ectal end of the prostatic duct and apparently passes into the parietes on the posterior face of the prostatic duct without widening.

The spermathecae are small. The ampulla is nearly spheroidal but with small lobulations entally. The duct is very slender and much shorter than the ampulla.

Remarks. The condition is only fair and does not permit certainty with respect to some important external characteristics. As only one pore was recognized on each side of xvii, it is assumed that the prostatic and deferent ducts unite in the body wall. Although clitellar glandularity was recognizable on certain segments no spermatozoal iridescence was noted anywhere. Accordingly, it is uncertain whether the clitellum and certain other organs such as the prostates and spermathecae are fully developed.

The species clearly belongs to a group that has been recognized (Stephenson, 1930) as of subgeneric status, *Ilyogenia* Beddard 1893. in which specific distinctions rest largely on characters such as: presence or absence of ventral setae of xvii, presence or absence of clitellar glandularity on ventrum, segmental extent of clitellum, size of prostates, *i. e.*, characters that either are known to change during growth, or that may be suspected of undergoing such changes. In these circumstances, and in absence of certainty that development had been completed in the Porto Rican specimens, specific identification scarcely seems feasible. However, the single horseshoe-shaped seminal vesicle of xii now appears to be unique in the genus.

The only species of *Ocnerodrilus* previously known from the West Indies, *O. calwoodi* Michaelsen 1899, has been reported from two localities, St. Thomas and Havana, Cuba. (Thirteen of the eighteen North American species are known only from the original descriptions of fifty or more years ago, or only from the original specimens, in either case from a single locality.) Another "American" species, *O. occidentalis* Eisen 1878 has been carried around the world. The Luquillo form, whatever it may eventually prove to be, is regarded tentatively as an exotic in Porto Rico.

VII

Family HORMOGASTRIDAE

Genus HORMOGASTER Rosa 1887

HORMOGASTER REDII Rosa 1887

In "soil with citrus tree, in baggage from Italy arriving on S/S La Guardia at New York, Nov. 8, 1950, 2 clitellate specimens. Dr. C. W. F. Muesebeck.

External characteristics. Length, 112–122 mm. (+? posterior end lacking?). Diameter, 10–12 mm. Segments, *ca.* 254–317 (+?). Segment length increases through i–ix, decreases through x–xv, is very short from xvi and from xxviii posteriorly still shorter. Numerous furrows extend from the anterior end of the body to 2/3 and are about equally spaced in both dorsum and ventrum. A well marked secondary furrow, on the dorsum only, is present on each of ix–xii. The dorsum has a grey or slate color that is darker in the clitellar region. The prostomium is prolobous (2 specimens). (No dorsal pores.)

Setae are small: on iii–x *a* and *b*, when recognizable, are very closely paired, from xi *a* is increasingly more median until greatest separation is reached on xiv or xv; *c* and *d*, usually lacking (?) on ii–xvii or xviii, are very closely paired throughout the rest of the body. Behind the clitellum *ab* is somewhat smaller than *bc* which is smaller than *aa*, *dd* $<\frac{1}{2}$C. Apertures of the *a* and *b* follicles of xviii–xxviii are enlarged, slit-like or comma-shaped, diagonally placed. The apertures of the *a* and *b* follicles of xii–xiv are also somewhat enlarged.

Nephropores are large, first recognizable on iii (2) and are slightly above the *b* lines, in a regular longitudinal rank on each side, probably close to the midlateral line.

The clitellum has rather indistinct boundaries but apparently is annular, extending from the posterior half of xii to 27/28 (or 28/29?), or the posterior half of xiii to 26/27 (+?). The epidermis is not much thickened and intersegmental furrows are not obliterated (grooves containing the furrows apparently as deep here as posteriorly).

Spermathecal pores are minute, three pairs, on 9/10–11/12 (2), dorsal to the nephropore ranks. An extra pore, on 10/11 of one specimen, is median to the normal location. The female pores, about as large as the nephropores, are on the posterior half of xiv, about in line with the male pores and somewhat median to the nephropore lines. Male pores are almost as small as the spermathecal and are on 15/16, slightly median to the nephropore lines. The male tumescences are well developed, horseshoe-shaped, transversely placed on xv–xvi, with open end laterally, 15/16 obliterated on the median portion.

A broad band of whitening (and especial epidermal tumescence?) extends along xviii–xxviii from just median to the *a* lines to just lateral to the nephropore lines. Midway between *a* and *b* lines the whitening may be less obvious or lacking (1). The lateralmost portion on xviii or xix to xxiv or xxv is slightly more protuberant and marked off by a slight median groove as an intersegmentally interrupted, low, rounded ridge possibly equivalent to a tuberculum pubertatis.

Internal anatomy. Septa 6/7–9/10 are thickly muscular. The gizzards are large, in vi, vii, viii, separated from each other by much weaker sections of the gut. The post-gizzard portion of the oesophagus has a white wall, rather smooth internally, is bent (almost looped) and irregularly contracted, definitely and gradually widened in the last two segments (xix–xx or xx–xxi?). A very short portion just in front of the last two segments apparently is valvular. Calciferous lamellae were recognizable in the terminal portion of the oesophagus, in one specimen, in an intramural gland that was nearly circumferential (no openings into gut recognized). The typhlosole begins in the region of xxiii, completely fills the gut lumen, and ends abruptly in the region of cxcv (1). Anteriorly the typhlosole is composed of seven thick lamellae, of which the lateral three on each side join dorsally before uniting with the median lamella. Posteriorly the ventral margin of the typhlosole is rounded, smooth, and with no trace of longitudinal lamellation but the tissues are separable into very thin transverse lamellae.

The dorsal blood vessel is single and passes into the tissues of the pharyngeal bulb slightly behind the cerebral ganglia. The ventral trunk bifurcates just above the suboesophageal ganglia. The supra oesophageal trunk passes into the tissues of the pharyngeal bulb near the posterior margin and is free from the gut in v–ix or x, immediately underneath the dorsal trunk. Hearts of ix–xi are lateral and moniliform. The commissures of viii are nearly as large and moniliform dorsally but, like the smaller commissures of vi–vii, become very slender ventrally, the length of the slender portion increasing from viii anteriorly. Just beneath the boundary between the thick and the slender portions a fairly large vessel passes off and along the mesentery from the heart to the posterior septum. (The mesenterial vessels pass directly into the ventral trunk in x, but in ix into the hearts just prior to the junction with the ventral trunk). Commissures of v are present and a small vessel from the dorsal trunk on each side may represent a portion of commissures belonging to iv.

Holandric, testes and funnels in x–xi, the funnels rather large and polyplicate. Seminal vesicles are acinous, in xi and xii.

Spermathecal ampullae are nearly spheroidal, the duct practically restricted to the parietes. Oviduct funnels are transversely elliptical discs flattened against 13/14. A small organ on the posterior face of 13/14 just behind each oviducal funnel presumably is an ovisac (containing a small brown body).

Remarks. The depth of the grooves between the segments externally, and the looping of the nerve cord show that both of these worms are strongly contracted. This contraction would then be responsible for the irregularities and bending of the postgizzard portion of the oesophagus, as well as of divers portions of the intestine. The gut was completely empty. If these specimens had been taken in diapause they must have straightened out during preservation. Hearts, ventral and dorsal trunks were filled with blood, as was the supra-oesophageal back into ix or x. Subneural and other trunks were unrecognized, like a posterior portion of the supra-oesophageal, presumably because they were empty. Nephridial bladders were collapsed and empty.

A grey-translucent marking on the intersegmental furrow (5/6–7/8) just below the nephropore lines, looks very much like a pore but no aperture was recognizable under the highest power of the binocular.

The foramen between the circumoesophageal nervous commissures measured 1.5 (dorsoventrally) by 1 (right–left) mm.

Both specimens had copulated, as was indicated by marked spermatozoal iridescence in the spermathecal ampullae but none was visible on the male funnels nor was there any coagulum in the coelomic cavities of x–xi.

The longitudinal white band present ventrally on each side of the clitellum apparently comprises genital tumescences surrounding modified setae, as well perhaps (laterally) as a tuberculum pubertatis. Such structures, together with the indistinctly demarcated but well developed tumescences around the male pores, are common in the Lumbricidae. In fact, Stephenson (1930, pp. 720–721) was inclined to believe that *Hormogaster* should be included in the family Lumbricidae because of the presence of "characteristic grooved genital setae" and since it is distinguished merely by "the multiplication of gizzards" which was regarded as "only of generic or at most of subfamily importance". The location of the gizzards in the oesophagus instead of the intestine, the strict metamerism of the gizzards[1], the posterior extension of the oesophagus behind xiv, absence of calciferous glands in xi–xiii (where they are located in the Lumbricidae), presence of a calciferous gland (in xx?) at the hind end of the oesophagus, perhaps also the peculiar typhlosole and the peculiar nephridial vesicles, should be taken into consideration as well as grooved setae.

Two species usually have been recognized, each with varieties, forms or subspecies. None of them seems to have been available in long series to permit study of variation. Some doubt has been expressed as to the distinctness of the two "species".

Hormogastrids have been reported from Italy (Samnium, Rome,

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[1] The gizzard muscularity frequently extends through two or three segments in the Lumbricidae, but without separation into distinct metameric components

Naples), Corsica, Sardinia (Cagliari and Siliqua), Sicily (Taormina, Palermo), Spain (provinces of Tarragona, Lerida, Basedona), Tunis, Algeria.

VIII

Family CRIODRILIDAE

Genus CRIODRILUS Hoffmeister 1845

CRIODRILUS LACUUM Hoffmeister 1845

Remarks. This species was collected some years ago, according to information kindly supplied by Mrs. Dorothy McKey-Fender, from some locality in the eastern states. This should indicate that the species already had become established in this country prior to that time, and presumably after transfer from some part of that area where it is known: Germany, Austria, Hungary, Italy, south Russia, Syria and Palestine. Increased pollution of waters in which the worms were living, resulting in extermination of the entire colony, may explain, in part, absence of any records in the literature.

C. lacuum is one of the few species that can replace, in anterior regeneration, the entire pre-intestinal portion of the body and including functional gonads of both sexes.

IX

Family LUMBRICIDAE

Peregrine species of this family probably have been established in the United States for 150 years or more. Accordingly, it is not surprising that by 1832 four of them were so common around Bangor, Maine, as to be considered "native" there. More recently, however, some of these same species have been characterized as "native" or "endemic" in scientific publications[1].

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[1] *Lumbricus rubellus* "is, in the writer's opinion, our most common endemic earthworm west of the Cascade Mountains. It is found in almost every location in this section where any earthworms are found." (Altman, 1936, p. 95)

The lumbricid earthworms of Connecticut, none of them endemic there, are collectively distinguished from the more recently recognized "oriental earthworm", *P. hupeiensis*, as "native". (Schread, 1952)

Eighteen lumbricid species are exotic anywhere on the continent of North America.

Allolobophora arnoldi Gates 1952
" caliginosa (Savigny) 1826
" chlorotica (Savigny) 1826
" limicola Michaelsen 1890
" longa Ude 1885
Dendrobaena mammalis (Savigny) 1826
" octaedra (Savigny) 1826
" rubida (Savigny) 1826
" subrubicunda (Eisen) 1874
Eisenia foetida (Savigny) 1826
" rosea (Savigny) 1826
" hortensis (Michaelsen) 1890
Eiseniella tetraedra (Savigny) 1826
Lumbricus castaneus (Savigny) 1826
" rubellus Hoffmeister 1843
" terrestris L. 1758
Octolasium lacteum (Orley) 1881
" cyaneum (Savigny) 1826

Allolobophora iowana Evans 1948, considered by its author to be endemic in Iowa, is difficult to distinguish from the long-known *caliginosa*, and may have been the form primarily responsible for the conclusion that there really are no old species in the United States but only recently introduced forms "rapidly changed from their European progenitors" (Muldal, S. 1952. The chromosomes of the earthworms. Heredity, 6, p. 56.)

Among these lumbricid exotics probably are included those species most frequently introduced deliberately, in the past, into previously unentered areas. Records of several such introductions have been found in non-scientific as well as scientific publications, but for each of those instances there must be others about which information would be as welcome as that just received from Prof. Miller. According to this report, which was taken from Prof. Storer's file: "In 1913 Dr. J. O. Snyder sent about 100 specimens of the common large earthworm of the eastern United States from Washington, D. C. and the animals were planted in the Memorial Court at Leland Stanford Junior University. The species was still present there, in living condition, in 1931."

Colonization, in the United States, by three of the species, *A. arnoldi* (Gates, 1952a), *A. limicola* (Gates, 1953a) and *D. mammalis* (Davies, 1954) has been recognized only recently. Already, however, two of the three have been obtained at additional localities some distance from the site of the original find (Davies, 1954 and Gates, 1952b). Several species that might have been expected, as well perhaps as others, possibly are awaiting discovery.

ALLOLOBOPHORA CALIGINOSA (Savigny) 1826

Juneau, Alaska, about ten miles to the north, in soil of an abandoned Indian village site (locally known as the Auke village site, in Auke Bay), September 11, 1950, 3 clitellate specimens. (11 juveniles of similar habitus presumably are of the same species.) H. J. Lutz and R. F. Taylor.

These earthworms, and those mentioned below, were the only ones found, according to Dr. Lutz, while sampling soils in Alaska. The site was covered with a very rank vegetation, mostly nettles (*Urtica* sp.) six to seven feet tall, and the soil was rich and gravelly.

LUMBRICUS RUBELLUS Hoffmeister 1843

Juneau, Alaska, about ten miles to the north, in soil of an abandoned Indian village site (locally known as the Auke village site, in Auke Bay), September 11, 1950, 1 clitellate specimen. (3 juveniles of the same habitus presumably are of the same species.) H. J. Lutz and R. F. Taylor.

Earthworms have not hitherto been recorded from the mainland of Alaska, though there has been one record of quite another species from Behring Island.

Presence of *L. rubellus* and *A. caliginosa* in Alaska undoubtedly is the result of an accidental introduction, and presumably involving transfer of soil containing live worms and/or cocoons.

X

DISCUSSION

Earthworms probably have been imported accidentally into this country ever since the first permanent European settlements. These animals are being so imported still, according to data secured in an investigation that has been under way for several years. In addition, they are being deliberately introduced, if certain advertisements are truthful, from various foreign sources. Many of the accidentally imported species probably never became established and, except in quite unusual circumstances, will remain unknown. Nevertheless, a total of forty-five species in eighteen genera, belonging to nine of the twelve families (Table) are now known to have reached the United States

Table

Exotic species of earthworms already found in the United States, including Porto Rico

Family	Genus	Number of species	Remarks		
Alluroididae					[1]
Moniligastridae	Drawida	1	Porto Rico only.	+?	
Ocnerodrilidae	Eukerria	2	1 from P. R. only.		
	Gordiodrilus	1	Porto Rico only.	+?	
	Ocnerodrilus	2		+?	
Acanthodrilidae	Microscolex	2			
	Dichogaster	2		+?	
Megascolecidae	Pheretima	11	1 from P. R. only.	+?	[5]
	Pontodrilus	2		+?	
Eudrilidae	Eudrilus	1			
Glossoscolecidae	Pontoscolex	1			
Sparganophilidae			Species endemic in North America.		
Microchaetidae					[2]
Hormogastridae	Hormogaster	1			[3]
Criodrilidae	Criodrilus	1			[4]
Lumbricidae	Allolobophora	5		+?	
	Eisenia	3		+?	
	Eiseniella	1			
	Dendrobaena	4			
	Octolasium	2			
	Lumbricus	3		+?	

+? Other species of the genus known to be peregrine and possibly to be expected either on the mainland or in the Caribbean possessions.

[1] The Alluroididae has not been recorded from any place outside of Africa.

[2] One species of the Microchaetidae, *Glyphidrilus papillatus* (Rosa) 1890, has been regarded as peregrine but outside of Burma, where it may be endemic, has been reported only from India (Lucknow and Saharanpur) and the island of Hainan.

[3] No evidence has yet been found to indicate that *H. redii* was ever established in the United States or anywhere outside of the Mediterranean lands.

[4] *C. lacuum* may have become extinct in this country.

[5] *P. elongata* (E. Perrier) 1872, has not yet been found on the mainland.

The families are those of Michaelsen's classification of 1921 (Arch. Naturg. 86-A) except for omission of the Syngenodrilidae (probably belongs in the Alluroididae) and elevation of the acanthodrilid Ocnerodrilinae to independent status. Only six families were recognized in "The Oligochaeta" (London, 1930) though Stephenson was inclined "to regard the Ocnerodrilinae as more entitled to independent status" (p. 720).

(including Porto Rico) from sources ultimately in Europe, Africa, Asia, and South America, all the continents except Australia. Most of those species appear to be permanently established on the mainland.

Some of the exotic forms are being raised every year in hundreds of thousands, perhaps millions (if the claims of the "earthworm farmers" are correct), for sale to "organic" gardeners and farmers (for cultivating and enriching the soil) and to anglers who can be expected to scatter them even more widely. Some exotic forms have been distributed through the mainland from Maine to California with greenhouse plants and must have escaped frequently from retail greenhouses, occasionally at least to work their way from urban centers into more rural areas and thence even into the forests. Adherents of the "organic" cult of gardening and farming have been urged for several years to make use of techniques that are claimed to result in increase in number of earthworms. but only, so far as is known, of the exotic kinds. These species, rigorously selected from so many different generic types, have been in competition, in much of the country, with native forms.

The endemics of the mainland, all the way from the Mexican border to the Arctic, belong to *Sparganophilus* (Sparganophilidae), *Eisenia* and *Bimastos* (Lumbricidae), *Plutellus* and *Megascolides* (Megascolecidae, and Pacific coast area only), *Diplocardia* (Acanthodrilidae) — only six genera of four families. Species of *Diplocardia* have never been found outside of this continent, even as a result of accidental transportation. Yet one way restriction on accidental transportation seems highly improbable. Failure of any of our American species to colonize those foreign regions to which they were transported must then have been due to lack of some or all of those characteristics that enable exotic forms to become established here.

SUMMARY

Eukerria saltensis (Ocnerodrilidae), *Pheretima bicincta, hilgendorfi, levis* and *rodericensis* (Megascolecidae), *Eudrilus eugeniae* (Eudrilidae), *Pontoscolex corethrurus* (Glossoscolecidae), *Hormogaster redii* (Hormogastridae), *Criodrilus lacuum* (Criodrilidae), are reported for the first time from the mainland, *P. hilgendorfi* and *levis* for the first time outside of Japan–Korea, *H. redii* for the first time outside of Mediterranean lands. *Drawida bahamensis* (Moniligastridae), previously known only from the types, *Gordiodrilus peguanus, Eukerria peguana, Ocnerodrilus* sp. (Ocnerodrilidae), *Trigaster* sp. (Acanthodrilidae), *E. eugeniae* and *P. corethrurus* are reported for the first time from Porto Rico, seven of the nine species now known from there certainly exotic.

Among further new records are those of *Microscolex phosphorcus* in New England, and of two lumbricid species in Juneau, the first earthworms reported from the Alaskan mainland. Two-tailed specimens of *Eudrilus eugeniae* are reported for the first time and a record of one with a third caudal axis is the first for any adult, unregenerate earthworm. *P. agrestis, hilgendorfi* and *levis* being anarsenosomphic must reproduce parthenogenetically, as perhaps *P. diffringens* may also. Athecal, anarsenosomphic individuals of these species are not at present identifiable. Forty-five species of eighteen genera of nine of the twelve families of earthworms are now known to have reached the United States, presumably during the last 350 years, from sources ultimately in Europe, Africa, Asia and South America. Most of these species are now permanently established on the mainland. American endemics apparently lack those characteristics that enable the exotics to become established here.

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By John A. McGowan and Ivan Pratt

Oregon State College and
Oregon Institute of Marine Biology

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No. 7 — *The Reproductive System and Early Embryology of the Nudibranch Archidoris montereyensis (Cooper)*[1]

By John A. McGowan[2] and Ivan Pratt

INTRODUCTION

Most of the earlier works on nudibranchs are essentially of a taxonomic nature. But since the arrangement of the reproductive tract is frequently used as a taxonomic character it has been described for many species. These descriptions, however, seldom give a very clear idea of the functions of the various organs described. Because the reproductive processes in nudibranchs are fairly complex it was thought desirable to provide a detailed account of the entire phenomenon. Observations on the development and hatching of the larvae are included.

Eliot described the anatomy of the reproductive tract of *Doris tuberculata* in the supplement to Alder and Hancock (1845-1910), although he apparently did not make histological preparations. He pointed out that Alder and Hancock had designated the tube into which the sperm are introduced during copulation as the androgynous duct, but noted that unless self-fertilization occurred, this was an incorrect designation. Although self-fertilization does not occur, we shall use this name rather than introduce a new term.

Chambers (1934) reviewed the reproductive systems of nudibranchs and described the hermaphrodite valve of *Embletonia fuscata*, family Eolidae. O'Donoghue (1922) and Costello (1938) described the form and color of the egg mass of *Archidoris montereyensis*, and listed the months when egg masses were found at Vancouver Island, British Columbia, and Monterey, California, respectively. Casteel (1904) gave a classic description of cell lineage and fate of the germ layers of the eolid, *Fiona marina*. Thorson (1946) described larval stages, types of larval shells, and duration of pelagic life of certain Danish nudibranchs. Ostergaard (1950) studied size and type of ova of several tropical nudibranchs in Hawaii.

Archidoris montereyensis was selected for the present study because information on the functions of the reproductive organs

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[1] Published with the approval of the Oregon State College Monographs Committee. Research Paper No. 242, Department of Zoology, School of Science.

[2] Now at Scripps Institution of Oceanography, La Jolla, California.

of dorids is particularly sparse and because it is one of the commonest nudibranchs of the Pacific Coast of North America.

MATERIALS AND METHODS

Archidoris montereyensis is easily obtained throughout the year along the central and southwestern coast of Oregon. It is found most commonly below mean lower low water levels of protected rocky, outer coast regions.

Specimens collected about the middle of June were placed in aquaria through which fresh, cold sea water was constantly circulated. No difficulty was experienced keeping these animals through the middle of August. Spawning under laboratory conditions was frequent and apparently normal.

Care of the Egg Mass and Larvae

As soon as the animal had spawned, the egg mass was removed from the aquarium and placed in a petri dish of fresh sea water, which in turn was placed in a shallow pan through which sea water, varying not more than 2°C from ocean temperature, was constantly circulated. The water and egg mass in each dish was aerated with a fine jet of air, which served also to agitate the egg mass. Water in the dishes was changed daily.

Technique of Observation

The developmental stages were observed and recorded every 1 to 2 hours for a period of 2 days after spawning. During the third day examinations were made at 4-hour intervals, and subsequently 2 or 3 times a day for the remainder of the incubation and larval period.

Small portions of the egg mass were cut off and placed in a depression slide with sea water and examined under low and high powers of the microscope, using both transmitted and reflected light. Reflected light gave better visibility during the early cleavage stages, for the large amount of yolk made the eggs opaque. Observations were recorded with camera lucida drawings. After study of the living material it was fixed in Kleinenberg's picro-sulfuric mixture.

Adult animals to be studied were fixed in Bouin's mixture at the following periods of the reproductive cycle: copulation, egg laying and during the interval between the above. Serial sections of 10 microns thickness were made of the gonads and other parts of the reproductive system and stained with Heidenhain's iron hematoxylin. Careful gross dissections were also made. Smears of living gonad and other parts of the reproductive system were examined.

THE REPRODUCTIVE SYSTEM

A. *The Hermaphrodite Gland* (Plate 1, fig. 1). This structure consists of a layer of ovarian and testicular tissue covering the "liver." The reproductive tissue is composed of numerous lobes which subdivide many times until they ultimately become small follicles. Sections taken from anterior to posterior showed a gradual transition from an area consisting entirely of sperm producing follicles to one made up chiefly of ovarian follicles. However, serial sections of an hermaphrodite gland taken from an animal that was killed while laying eggs contained mature ova in the lumina of the anterior male follicles. This fact was taken as evidence that the sperm and egg follicles intercommunicate. The follicles eventually join one of two tubes which come together at or near the surface of the gland to form the hermaphrodite duct.

B. *The Anterior Genital Mass* (Plate 1, fig. 1). This mass includes all of the parts of the reproductive system except the hermaphrodite gland. The hermaphrodite duct leaves the hermaphrodite gland at its right anterior tip, and is the only connection between the hermaphrodite gland and the rest of the reproductive system. The wall of the duct is made up of a single layer of ciliated, cuboidal cells covered with a thin layer of smooth muscle. The duct gradually widens into the ampulla (Plate 1, fig. 1 *a*), which is convoluted as it passes toward the anterior. Where it enters the albumen gland it bifurcates and gives rise to the much twisted vas deferens.

A valve is located at the bifurcation of the hermaphrodite duct (Plate 1, fig. 1 *v*; Plate 2, fig. 7). It consists of a conical extension of the hermaphrodite duct into the vas deferens. The cells making up the epithelia of the two branches are quite different. Within the valve the epithelium changes abruptly to the rather poorly defined ciliated, columnar type characteristic of the lining of the vas deferens. It is thrown into folds and often appears to be a stratified columnar type. Vacuoles are numerous, indicating that it has a secretory function. The cilia probably assist in the transport of sperm.

The valve and vas deferens are surrounded by heavy muscle layers. The muscles around the valve are oriented in such a way as to effect the closing of the valve. The vas deferens is surrounded by a thin inner layer of longitudinal muscle and a thick, outer circular layer. Some parts of the duct lack the longitudinal layer. The vas deferens gradually widens as it approaches the body wall until it forms a conical bag-shaped structure, the intromittent organ (Plate 1, fig. 1, *in*). No accessory glands emptying into the vas deferens were found. Sperm are carried from the hermaphrodite gland down the hermaphrodite duct, through the valve and along the vas deferens and out the opening of the intromittent organ.

The female branch of the hermaphrodite duct (oviduct) bifurcates again a short distance from the hermaphrodite valve. One branch, the androgynous duct, serves to conduct incoming sperm from the copulatory orifice to the unfertilized ova. The other branch enlarges and becomes the complicated and convoluted albumen gland. The fertilized ova pass through this portion during spawning. The albumen gland has been divided by some students into albumen and mucous secreting parts. Grossly it appears as a single large organ, the mid-anterior region of which is yellower than the rest. It could not be determined whether the duct was a simple tube, much convoluted, or one with numerous caeca off the main channel. The epithelium is of a tall, simple, columnar type throughout, the cells of which are usually greatly distended with secretion products. Serial sections taken from an animal in the process of laying eggs revealed that by the time the ova had reached the "mucous" part of the gland, the outermost coating, the case membrane, had been secreted over the eggs.

The androgynous duct consists of a muscular tube leading from the point of branching from the oviduct past a pear-shaped caecum, the spermatocyst, to a large, thin walled sac, the spermatotheca. The duct leaves this sac at a point very near where it entered and passes toward the genital aperture, where it widens slightly to join with the sac of the intromittent organ anterior to it and the oviduct posterior to it. The three ducts join at the inner body wall to form a single opening to the outside, the external genital pore. This is situated at the junction of the under surface of the mantle and the foot, about one-third of the way from the anterior end, on the right side.

During copulation non-motile sperm are deposited in clumps by the copulating partner into the distal portion of the androgynous duct. They are passed along the tube probably by ciliary action and muscular contraction of the duct into the spermatotheca. This caecum is almost spherical; it is lined with a simple columnar epithelium surrounded on the outside by a thin layer of connective tissue (Plate 2, fig. 8). The cells are apocrine secretory cells, indicating that the spermatotheca is glandular in function. In fixed material the lumen is usually filled with a granular substance which stains poorly with haematoxylin. Although non-motile sperm were seen in fresh smears from the spermatotheca, they were not present in the sections of this organ. The sperm probably pass through only the basal region of the spermatotheca and then are carried along another short region of the androgynous duct to the spermatocyst. Here they become oriented so that the heads of the sperm are imbedded in the epithelium, while the tails project straight out into the lumen of the organ (Plate 1, fig. 6). Sperm taken from the spermatocyst were motile.

The epithelium lining the lumen of the spermatocyst is a simple columnar type. Several rank of spermatozoa lie with heads embedded in the free surface of the epithelial cells. Sperm leaving the spermatocyst join the eggs at the juncture of the androgynous duct with the oviduct.

C. *Gametogenesis.* Although gametogenesis was not studied in great detail it does appear to differ from that found in other gastropods.

The wall of the male follicles of the hermaphrodite gland consists of a thin outer covering of connective tissue and of spermatogonia. No nurse cells could be identified. All stages of spermatogenesis could be seen in any one section of the hermaphrodite gland, but any one male follicle usually contained only 3 or sometimes 4 of the stages. No follicle was seen in which all of the cells were in the same stage of spermatogenesis. The spermatogonia develop into spermatocytes in small groups. The spermatids and maturing spermatozoa remain in clumps until the follicle contains mostly sperm and the cellular detritus incidental to their development. Both the male follicles and the hermaphrodite duct contained morphologically mature sperm in an animal killed after spawning but before any subsequent copulation. The presence of sperm in the hermaphrodite duct indicates that the animal is potentially capable of copulating immediately after spawning. It also shows that ripe eggs of an individual may be in contact with its own sperm during spawning. That self-fertilization does not occur is demonstrated by the facts that spawning never takes place unless preceded by copulation, and that these sperm are not motile and are probably physiologically immature. The sperm (Text Fig. 1) is approximately 205 microns in length. There was no evidence of the atypical spermatogenesis and size polymorphism of sperm that have been reported for other gastropods by Bowen (1922) and Hyman (1923), respectively.

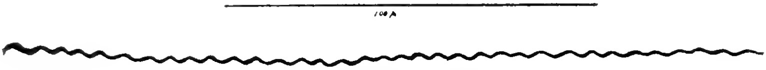

Fig. 1. Spermatozoön of *Archidoris montereyensis.*

The ova begin their development as small spherical cells about 12.5 microns in diameter in the walls of the female follicles, but are soon released into the lumen, where they continue to grow to about 81.5 microns. After copulation the nuclei reach the first reduction division and remain in the metaphase stage until spawning. The eggs remain in the follicles until they move out at the time of spawning.

D. *Fertilization.* This process is internal and takes place during spawning, which usually occurs 5 to 7 days after copulation. The ova passing into the hermaphrodite duct collect in the enlarged ampulla region of that tube, and are joined by a mass of sperm released from the spermatocyst. In material taken from an animal in the process of egg laying, sperm and eggs were in contact along a large part of the length of the ampulla. Sperm became scarcer in the ampulla in the vicinity of its bifurcation into vas deferens and oviduct; only a few sperm were found in the oviduct between the hermaphrodite valve and the junction of the androgynous duct. None was found distal to that point in the mucous-albumen gland portion of the oviduct. There is then no special "fertilization chamber" and fertilization takes place all along the ampulla of the hermaphrodite duct. Eggs and motile sperm removed from the ampulla of a nudibranch during spawning were examined. No fertilization membrane was found on the eggs.

E. *Spawning.* The fertilized eggs enter the albumen gland and pass singly down its convoluted duct, but by the time they reach the mucous secreting portion, they are arranged into long cords of eggs. It may also be seen here for the first time that the eggs are surrounded with their encapsulating membrane. A moderate polyvitelliny, 2 or 3 eggs per capsule, was seen in sections of the mucous gland before the ribbons were formed. The duct of the mucous gland widens and flattens as it approaches the external genital orifice, and it is probable that in this portion the cords of egg capsules are arranged into the flat ribbon that make up the egg mass.

In the laboratory, egg laying began at about 9 o'clock in the morning, and continued from 4 to 6 hours. The egg ribbon (Plate 1, fig. 2) coming from the genital opening is in the form of a pleated sheet, with the pleats running parallel to the long axis of the ribbon. The bottom edge of the ribbon is attached to the substrate and the rest of the mass floats free. The animal moves in a counter-clockwise direction very slowly until it has completed 3 spirals. Toward the end of the last spiral the egg mass decreases in size and becomes disorganized. Within a few minutes after the egg ribbon comes out of the genital opening, the pleats unfold and the ribbon comes to resemble a flat, coiled watchspring laid on its side. A record was kept of the weights of 3 individuals for several days before they spawned and immediately after spawning. Although the egg masses were large, there was no detectable weight loss.

In an attempt to determine the length of the breeding season, animals were brought into the laboratory during the months of February, April, June, July, August, September and December. They were kept in aquaria which were thoroughly aerated and maintained at temperatures within a few degrees of their normal environment during these months. Copulation and spawning in laboratory occurred during every month listed above. Development occurred in every egg mass.

The structure of the ribbon making up the egg mass may be divided into 3 components. First, the egg capsule is a clear, spherical structure ranging in size from about 160 to 290 microns. It contains from 1 to 18 eggs. There is a relationship between the size of the animal laying the egg mass and the number of eggs in each capsule. Capsules from animals less than 6 cm. in length usually contained 1 or 2 ova; those from animals 6 to 12 cm. in length usually enclosed 3 or more eggs.

Second, the capsules are arranged into a flattened cord, generally 3 capsules wide (Plate 1, fig. 2). The capsules are maintained in this relationship by a coating of clear jelly-like material. The flat cords are then bent back and forth upon themselves thousands of times until they form a flat sheet.

Third, the entire sheet is covered with a second coating of mucus which holds the cords in place and serves also to hold the ribbon erect. One such egg mass laid by an animal 8 cm. long was 2 cm. wide and 25 cm. long. It was estimated to contain almost 2 million eggs.

F. *Type and Rate of Development.* Because fertilization is internal it is impossible to date the age of the embryo from the time of fertilization. Therefore age was counted as number of hours after a particular area of the egg ribbon had come from the genital aperture.

During the first 12 to 18 hours of development all the embryos in any one small portion (about 2 $cm.^2$) of the egg mass undergo cleavage in unison. Later, those in the center regions lag behind the embryos in capsules situated in the margins of the ribbon.

About 4 hours after laying, a small protrusion begins to arise at the surface of the egg membrane. This first polar body gradually rounds into a 10 micron sphere and is cast free of the egg, undergoing a second division and later degenerating. In the meantime a second polar body is being formed by the egg in a similar manner and reaches a similar size, but it is not set free from the surface of the egg.

Within 6 hours after laying, the nucleus becomes indistinct and the egg begins to elongate and a cleavage furrow forms in the center of the egg. Two spherical daughter blastomeres of equal size are formed. Soon they flatten together and the nuclei become visible. Following the interphase of about 3 hours, the second cleavage occurs about 10 hours after laying and results in 4 cells of about equal size. The spindles of the second cleavage are at right angles to that of the first, and nearly parallel to each other. The resulting 4-cell stage is typical of the molluscan type of spiral cleavage.

The spindles which precede the appearance of the first quartet of micromeres lie at first nearly radial, their proximal ends being distinctly higher than the distal ones. These spindles make their appearance 12 hours after laying. As division proceeds they turn in a dexiotropic direction and with associated cytoplasmic constrictions, 4 small cells are given off toward the animal pole. This first quartet of micromeres are each about 25 microns in diameter; the macromeres are about 50 microns. As the micromeres round out in shape, they come to project high above the macromeres beneath them, briefly, and then as they are moved further to the right, they come finally to lie in the furrows to the right of the cells from which they arose.

The fourth division occurs some 14 hours after the eggs have been laid. The second quartet arises laeotropically, being pushed strongly to the left as they divide off. This second quartet of micromeres is made up of cells about half the size of the macromeres from which they divided, and all 4 are about equal in size. There is no increase in size in the D quadrant, as there is with many annelids and some mollusks.

Before the macromeres divide again, the first quartet begins cleavage. This results in 8 cells of nearly equal size. The spindles which precede division are laeotropically directed, and the lower cells are pushed downward and outward between the second quartet cells and just above the macromeres. These "primary trochoblasts" do not divide again until about 60 cells are present, as illustrated by Casteel (1904) on his Plate XXV, figures 33 and 38. The formation of the primary trochoblast occurs about 16 hours after egg laying.

No further observations were made on the cell lineage of the embryo due to the difficulties encountered because of the excessive yolk content of the cells. It was considered sufficient to establish the fact that *Archidoris montereyensis*, at least in the early stages of its development, shows the typical molluscan spiral cleavage pattern.

The remaining stages of development will be described from external appearance only. However, during the later stages in the development of the larva, the yolk decreases and the entire animal becomes almost transparent.

Approximately 6 days after laying, the embryos are no longer spherical, but have a rather flattened oval appearance. At this time a darkened depression occurs in the posterior half of the embryo. From its resemblance to similar structures in other opisthobranch larvae, it was considered to be the blastopore (Plate 1, fig. 3). At the widened end of the 6-day larva, 2 symmetrically placed clear protrusions appear. These were weakly ciliated and were subsequently identified as the developing velar lobes. Another unidentified clear area was observed at the narrow end.

At some time during the period from the sixth to the eleventh day the ciliary movements of each embryo become strong enough to set it spinning within the case. This spinning movement continues almost constantly until hatching.

By the eleventh day the larva was a well defined veliger. The velum is still small and not yet bilobed and the foot anlage has just made its appearance. No internal structures are discernible because of the heavy yolk content.

Between days 11 and 13 two transitory structures make their appearance at the right postero-ventral end of the larva. They resemble 2 small, clear bubbles joined together at their base. No reference has been found to these structures in the literature of molluscan development. However, the shell of many veligers originates in this area, and in some forms shell glands have been identified at this locus.

The veliger is fully developed at 20 days. There is very little yolk remaining in the interior, and the movements of some organs can be seen. The following internal structures could be identified (Plate 1, fig. 5): the central part of the gut (*g*) which is ciliated (no mouth or anus could be seen); the heart (*h*) which pulsated regularly; a small area of yolky cells (*y*) in the ventral region (this is sometimes called "larval liver"); the heavily ciliated foot (*f*); and velar lobes (*v*). There is also the shell (*s*) which forms from ¾ to 1 entire whorl and has a diameter of 135 microns. This shell is an example of Thorson's (1946) type B larval shell. No "eyes" could be found.

By the time the egg mass is from 20 to 25 days old, the layers of jelly become soft and begin to disintegrate. The larvae in the marginal regions meanwhile are very active, spinning rapidly in their capsules. Upon slight agitation of the egg mass, the veligers break out of their capsules and swim actively about the container. The larvae in the inner portions, because of their slower rate of development are not yet ready to hatch, and the jelly of the central area remains firm enough to hold the egg capsules in place. It appears that the degeneration of the jelly of the egg mass is related in some way to the state of development of the larvae in the area where the degeneration takes place.

The larvae have a very short free-swimming life, then settle to the bottom of the dish in a matter of a few hours. Here they crawl actively over the surface of the glass. No attempts were made to rear the larvae beyond this stage.

Table 1

Rate of Development of *Archidoris montereyensis* in sea water at 17°C.

Stage	*Elapsed Time After Laying*
2 polar bodies	4 hours
2-cell stage	6-7 hours
4-cell stage	10 hours
8-cell (1st quartet)	12 hours
12-cell (2nd quartet)	14 hours
18-20 cell (primary trochoblast)	20 hours
Early trochophore (gastrula)	6 days
Foot and velum formation	11 days
Early veliger	14 days
Late veliger	20 days
Hatching	20-24 days
Settle to bottom	1-2 hours after hatching

DISCUSSION

The arrangement of the male and female follicles of *Archidoris montereyensis* is similar to that described by Alder and Hancock (1845-1910) for *Doris tuberculata*. But the statement that "the ultimate lobes consist of a central portion containing spermatozoa, round and about which are smaller globular ovarian follicles, opening into the central portion" could not be verified in this species. These workers did not mention the existence of a valve at the bifurcation of the hermaphrodite duct into vas deferens and oviduct. A related type of structure was described by Chambers (1934) for *Embletonia fuscata*. Although the organ as illustrated by Chambers differs greatly from the one found in *Archidoris montereyensis*, the two appear to have the same function. It is considered probable that this valve in the present instance serves to shut off the vas deferens from the hermaphrodite duct during egg laying. This would prevent the eggs from entering the vas deferens. During copulation, however, this valve remains open to allow the flow of sperm into the vas deferens. The entry of an individual's own sperm into its oviduct is prevented by the small flap of tissue that projects down into the lumen of the oviduct at this time (Plate 2, fig. 7). The structure described by Chambers was merely a simple sphincter muscle surrounding the oviduct near the juncture of this duct with the hermaphrodite duct and the vas deferens.

Eliot (1910) in the supplement to Alder and Hancock's monograph, concluded that the spermatotheca functions as the first resting place for sperm after being transferred during copulation. That may be so, but in addition it is a glandular structure and spermatozoa are not motile until they have passed through it and have been oriented in the spermatocyst. Therefore, it may be that the secretion of the spermatotheca contributes to the physiological maturation of the sperm.

As was pointed out above, the sperm after leaving the spermatotheca enter the spermatocyst and become oriented so that their heads are imbedded in the lining epithelium of this structure. This appears to be the typical sperm-nurse cell relationship except that the nurse cells nourish sperm received from another animal, and not their own. Since it is in the spermatocyst that the sperm first become motile it may be assumed that it is in this organ that the final steps of physiological maturation are completed.

The rate of development of *Archidoris montereyensis* in the early period compares with that of *Doris bifida* as reported by Reid (1846), but the rate from gastrula on is slower in *A. montereyensis*. Ostergaard (1950) reported that several tropical nudibranchs developed to hatching in 6-10 days, in contrast to the 20-24 days required in these studies.

It is evident from a study of the hermaphrodite gland of any sexually mature specimen of *Archidoris montereyensis* that the sperm and eggs are maturing at the same time in adjoining follicles. Mature eggs in the arrested metaphase stage were found in the same follicle with morphologically mature sperm. The lack of motility of sperm in the hermaphrodite gland of the donor as compared with those leaving the spermatocyst of the recipient probably is the important factor in preventing self-fertilization.

From a consideration of the reproductive processes, it is apparent that this animal is not, as others have suggested, a protandrous hermaphrodite. The egg and sperm are produced at the same time, but while the eggs mature in the individual that produces them, the sperm never mature until introduced into the androgynous duct of another individual. According to Coe (1944) this would be functional hermaphroditism.

SUMMARY

1. Individuals of the dorid nudibranch, *Archidoris montereyensis* (Cooper) were collected at Cape Arago and Yaquina Head, Oregon, and established in aquaria in the laboratory where they copulated and spawned repeatedly.

2. Fresh smears and fixed material taken at 3 stages of their reproductive cycle were examined. These stages were: during copulation, during egg laying, and in the period between egg laying and copulation. A study was made of the gross and microscopic anatomy of the reproductive system. Functions of the various organs were determined or suggested.

3. The spermatotheca and the spermatocyst were found to be the storage organs for the incoming sperm. The epithelium lining the lumen of the spermatotheca was secretory and it was suggested

that this secretion plays an important part in bringing about the physiological maturity of the incoming sperm. The cells of the lining of the spermatocyst acted as nurse cells. It was found that in this organ the sperm first became motile.

4. A valve at the juncture of the hermaphrodite duct, vas deferens and oviduct was described. The function of the valve is to shunt the sperm into the vas deferens and to prevent the sperm from entering the oviduct as they pass out during copulation.

5. The egg mass of *Archidoris montereyensis* consists of a flat, white, ribbon-like band, attached along one edge to the substrate and coiled in a counter clockwise direction through 3 revolutions. The egg capsules are arranged in a long cord, which is bent back and forth upon itself to form the main ribbon. Each egg capsule contains from 1 to 18 eggs, 3 being the usual number. The capsules at the ends of the band contain fewer eggs than those in the center.

6. The eggs of this nudibranch undergo the typical molluscan spiral cleavage for at least the first 24 hours of development. Larvae incubated under laboratory conditions hatch out of their capsules in 20-24 days. Hatched veligers swam for a period of 30 minutes to 2 hours before settling to the bottom. Larvae were not maintained beyond the settling stage.

7. *Archidoris montereyensis* is not a protandrous hermaphrodite, but produces sperm and eggs at the same time. However, the sperm do not become motile until after they have been transferred to the reproductive tract of another individual.

8. Either one or both animals may spawn in from 5 to 7 days after copulation.

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PLATE 1

Fig. 1. Diagram of the organs of reproduction of *Archidoris montereyensis.* Abbreviations: *a*, ampulla; *ad*, androgynous duct; *ag*, albumen gland; *ep*, external genital pore; *hd*, hermaphrodite duct; *hg*, hermaphrodite gland; *in*, intromittent organ; *mg*, mucous gland; *sc*, spermatocyst; *st*, spermatotheca; *v*, hermaphrodite valve; *vd*, vas deferens.

Fig. 2. Diagram of the egg mass of *Archidoris montereyensis.* The width of the cord containing the egg capsules has been exaggerated for illustrative purposes. Abbreviations: *ec*, egg capsule; *jl. 1*, inner jelly layer; *jl. 2*, outer jelly layer.

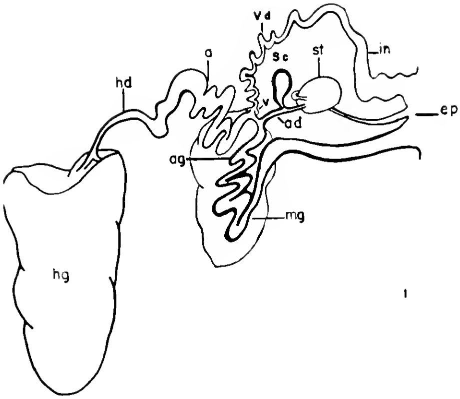
Figures 3, 4, and 5 are camera lucida drawings of living embryos.

Fig. 3. Gastrula. Abbreviations: *BP*, blastopore; *VA*, velum anlage.

Fig. 4. Young veliger. Abbreviations: *f*, foot; *v*, velum; *vh*, visceral hump.

Fig. 5. Fully developed, free-swimming veliger. Abbreviations: *f*, foot; *g*, gut; *h*, heart; *s*, shell; *v*, velum; *y*, yolk mass or "larval liver."

Fig. 6. Wall of spermatocyst, drawn by camera lucida under oil immersion. Sperm oriented with heads against simple columnar epithelium and tails free in lumen.



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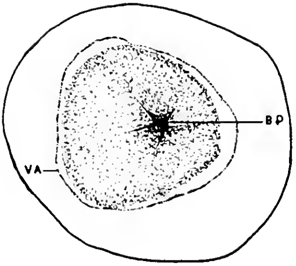

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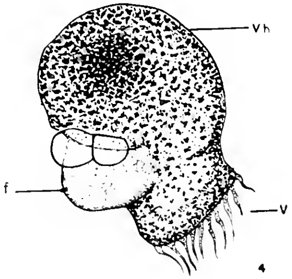

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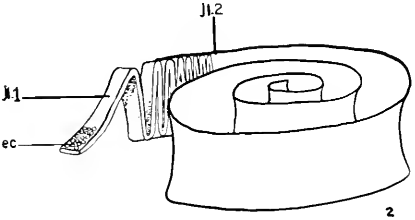

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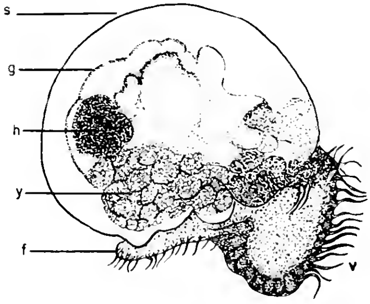

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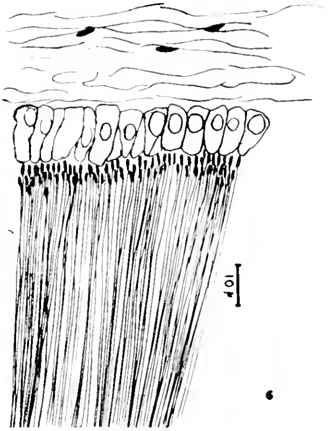

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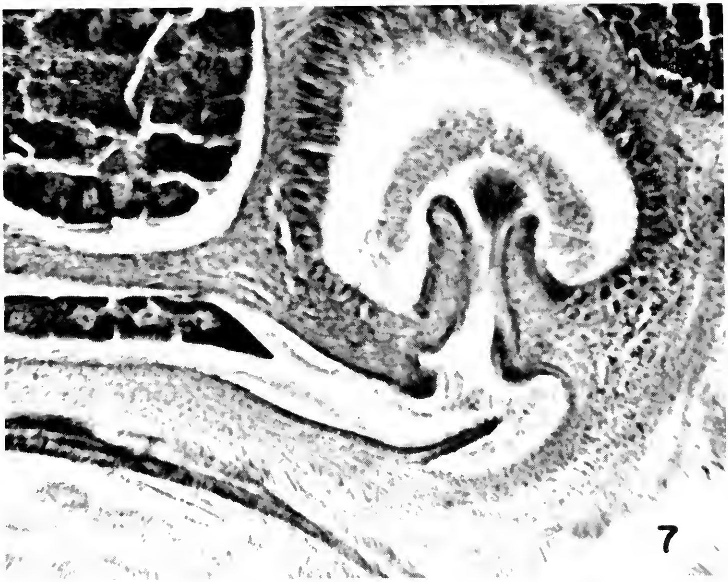
PLATE 1

PLATE 2

Fig. 7. Hermaphrodite valve, showing the junction of the hermaphrodite duct with the vas deferens. 200X. Taken through the region of the valve, *v*, diagrammed in Plate 1, fig. 1.

Fig. 8. Epithelium lining the spermatotheca, showing apocrine secretory cells. 520X. Wall of spermatotheca, *st*, in Plate 1, fig. 1.



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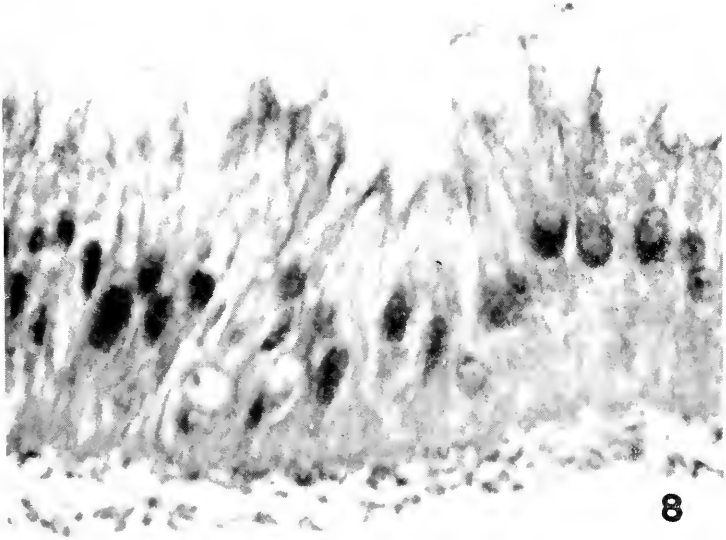

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PLATE 2

Bulletin of the Museum of Comparative Zoology
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Vol. 111, No. 8

A KEY AND DESCRIPTION OF THE LIVING SPECIES OF THE GENUS *PODOCNEMIS* (*SENSU* BOULENGER) (TESTUDINES, PELOMEDUSIDAE)

By Ernest Williams

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AT HARVARD COLLEGE

Vol. 111, No. 8

A KEY AND DESCRIPTION OF THE LIVING SPECIES OF THE GENUS *PODOCNEMIS* (*SENSU* BOULENGER) (TESTUDINES, PELOMEDUSIDAE)

By Ernest Williams

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No. 8 — *A Key and Description of the Living Species of the Genus Podocnemis (sensu Boulenger) (Testudines, Pelomedusidae)*

By Ernest Williams

Although *Podocnemis* (*sensu* Boulenger) is a genus of exceptional interest because of its distribution (South America and Madagascar), and because of the long fossil record ascribed to it (extending back to the Cretaceous), it has received little taxonomic attention since the review of the living species by Siebenrock in 1902. The need for such attention is well known. The keys provided by Boulenger (1889) and by Siebenrock (1902) are generally admitted to be unsatisfactory. Indeed in 1935 Lorenz Mueller, on the occasion of describing a new species *Podocnemis vogli* (thus raising the number of included species to eight), attempted a new key. This, however, has proved no more successful than the keys which preceded it.

At the urging of Mr. Llewellyn Price I have begun a study of the living species. I have thus far seen the material in the Museum of Comparative Zoology, the American Museum of Natural History, the United States National Museum, the Carnegie Museum, the Museum of Zoology of the University of Michigan, and the Chicago Natural History Museum, and I have also examined the material in the British Museum (Natural History), the Rijksmuseum, Leiden, the Senckenberg Museum, Frankfurt, the Museum für Naturkunde, Stuttgart, the Zoologische Staatssammlung, Munich and the Muséum d'Histoire Naturelle, Paris. I have seen also certain material from the Departamento de Zoologia, Sao Paulo, Brasil.

The revisionary task which I have set myself will be of interest to several sorts of individuals — to the naturalist in South America who desires to identify the forms he sees, to the museum worker in North America and in Europe concerned with labelling his specimens, to the student interested in the phylogeny, relationships and ancient migrations of these animals, and to the anatomist to whom some of the peculiarities (especially of the skull) in this and related genera will seem especially remarkable.

It will not be possible to satisfy these diverse interests in a single paper, and as a first step I am presenting here only a key to the species. I am hopeful that the key will really permit ready recognition of all eight species, but I am hopeful also that a new and better key may stimulate interest in the genus and perhaps result in the acquisition of additional specimens of certain species (*cayennensis*, *vogli*, *lewyana*) which are all too rare in collections and which in consequence are incompletely known. Because of the inadequacy of our knowledge of these species the present is a preliminary and provisional effort.

The present key is unusually elaborate, and it is in effect a condensed description of the eight species presented in the form of a key. I have felt this to be desirable for several reasons.

First, the great individual variability of the members of this genus makes a simple key depending upon a few supposedly invariable characters nearly or quite impossible. The keys of Boulenger, of Siebenrock, and of Mueller have all failed because of the variability of supposedly diagnostic characters. I have indeed found some characters more constant than others, but I am unwilling to prophesy that *any* single character that I cite will not vary. The eight species of *Podocnemis* should be identified on the totality of the descriptions given.

Secondly, the fullness of the key should lessen errors due to any ambiguity of phrasing or to mere unfamiliarity with the characters in this genus. To still further decrease these opportunities for error I have included simple diagrams of certain key characters.

Finally the extreme fullness of the key is intended to permit recognition of juveniles as well as adults and of skeletons, or at least skulls, as well as alcoholics.

NOMENCLATORIAL REMARKS

The recent action of the Copenhagen Congress in adopting a 50-year rule in regard to preservation of commonly accepted specific names relieves this genus of its only nomenclatorial problem — the applicability of certain of the Schweigger names. In 1953 with the aid of M. Jean Guibé, I endeavored to discover the Schweigger types at the Paris Museum, but it quickly became evident that these types are now lost or mislabelled. Though Schweigger (1812) gives measurements for certain individuals of the species he names (and I would therefore regard these measured individuals as the holotypes), in no case do the measurements check with any Paris specimen. The names therefore rest upon Schweigger's descriptions which, as is usual with descriptions of so early a period, are insufficient. It is fortunate to have available Siebenrock's 1902 paper as a fiat decision on the debatable Schweigger names.

Siebenrock's identification of *dumeriliana* Schweigger with *tracaxa* Spix is, in any case, quite certainly correct, and his adoption of the name *cayennensis* Schweigger for *erythrocephala* Spix is possible although not demonstrable. It is in some degree unfortunate that the Schweigger names now without types must be used in preference to those associated with the still extant and quite recognizable Spix types (seen at the Zoologische Staatssammlung, Munich), but if the Copenhagen rules are firmly adhered to, this situation will offer no real difficulty.

It must be stated that Siebenrock was in error in believing that *dumeriliana* of Boulenger was equivalent to his *cayennensis* = *erythrocephala* Spix. There is no *cayennensis* in the collections of the British Museum, and Boulenger recorded under this name some of the specimens of *unifilis* Troschel.

Bartlettia pitipiti Gray (type seen at the British Museum) is unquestionably a synonym of *P. sextuberculata* Cornalia.

Not having seen the type, I do not regard *P. coutinhii* Goeldi as assignable on the basis of the published description and figure (Goeldi 1886). Siebenrock's action in synonymizing this form with *P. lewyana* is unfortunate, since it extends the range of *P. lewyana* to the Amazon on grounds which seem quite inadequate.

I have examined the cotypes of *P. lewyana* A. Duméril in Paris. The two specimens belong to two species. The figured specimen (A. Duméril, 1852) from Bogotá, Colombia, presented by M. Lewy, is necessarily the holotype of *P. lewyana*, while the Venezuelan specimen belongs to *P. vogli* Mueller.

The species which I recognize are listed below with their most important synonyms:

1. *Podocnemis expansa* (Schweigger)
   Synonyms: *Emys expansa* Schweigger 1812[1]

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[1] The Boulenger citation of the original publication of the Schweigger names is incorrect. See references cited below.

Emys amazonica Spix 1824
Podocnemis expansa Wagler 1830, Boulenger 1889, Siebenrock 1902

2. *P. cayennensis* (Schweigger)
Synonyms: *Emys cayennensis* Schweigger 1812
Emys erythrocephala Spix 1824
Podocnemis cayennensis Siebenrock 1902

3. *P. dumeriliana* (Schweigger)
Synonyms: *Emys dumeriliana* Schweigger 1812
Emys tracaxa Spix 1824
Emys macrocephala Spix 1824
Peltocephalus tracaxa Duméril et Bibron 1835
Podocnemis tracaxa Boulenger 1889
Podocnemis dumeriliana Siebenrock 1902

4. *P. unifilis* Troschel 1848
Synonyms: *Chelonemys dumeriliana* Gray 1870
Podocnemis dumeriliana Boulenger 1889
Podocnemis unifilis Boulenger 1889, Siebenrock 1902

5. *P. sextuberculata* Cornalia 1849
Synonyms: *Bartlettia pitipiti* Gray 1870
Podocnemis sextuberculata Boulenger 1889, Siebenrock 1902

6. *P. lewyana* A. Duméril 1852
Synonyms: *Podocnemis lewyana* Boulenger 1889, Siebenrock 1902

7. *P. madagascarensis* (Grandidier)
Synonyms: *Dumerilia madagascarensis* Grandidier 1852
Erymnochelys madagascarensis Baur 1888
Podocnemis madagascarensis Boulenger 1889, Siebenrock 1902

8. *P. vogli* L. Mueller 1935

I have seen very unequal numbers of these several species: over 300 *P. expansa*, over 100 *P. unifilis*, nearly 40 *P. sextuberculata*, about 20 *P. dumeriliana*, over 20 *P. madagascarensis*, 12 *P.*

lewyana, 15 *P. vogli*, and only 2 *P. cayennensis* — one of the latter the type of *Emys erythrocephala* Spix, the second a stuffed specimen in the Paris Museum. I have also notes on 5 additional specimens of *P. cayennensis* and 4 additional specimens of *P. dumeriliana* which have been examined for certain of their characters by Dr. J. Eiselt of the Naturhistorisches Museum, Vienna, for whose generous and courteous diligence I am deeply grateful.

It should readily be understood that our knowledge of certain of these forms still leaves much to be desired. I have not been able to see a skull of *P. cayennensis*, for example, and our information on the skull of this species is limited to a few remarks by Lorenz Mueller based on the skull of the type of *erythrocephala* Spix — a part of that type which was destroyed by fire during the Second World War. I have further not seen any of the forms in life, and my statements on color, taxonomically important at least in the young, are correspondingly limited. Information on species differences in habits and habitats is also much to be desired.

EXPLANATION OF TERMS USED

I have provided diagrams which should explain many of the terms used.

Thus certain of the most important types of head scalation are shown in Figure 1 A-H. I use the terminology of Siebenrock (1902).

For interpretation of the median notching of the upper jaw, see Figure 2 A-C.

The two principal conditions of the enlarged scales on the posterior borders of the hind feet are shown in Figure 3 A-B.

For the dorsal and ventral emargination of the temporal region of the skull see Figure 4 A-C. These figures show also the condition of the cavum tympani in three species — the size of the whole cavum tympani as compared with the orbit, the presence or absence of a precolumellar fossa, the relative size of the entrance to the post-otic antrum and the shape of the columellar foramen.

Figures 5-6 and 8-9 show palatal views of the seven species in which I have seen the skull. These views show the foramina incisiva, the maxillary ridges, the presence or absence of inter-

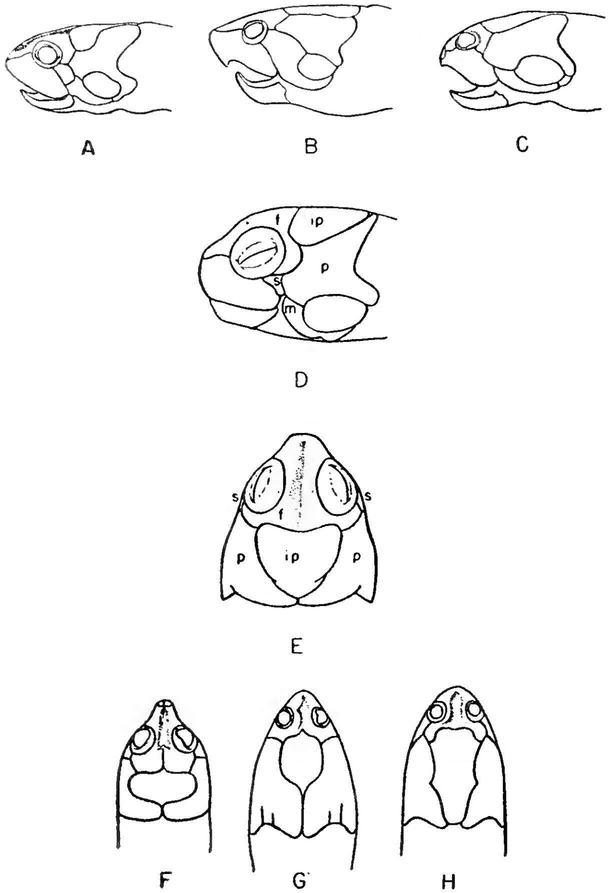

Fig. 1. Diagrams to show different conditions of the head scales. *A, P. unifilis* adult, lateral view — subocular present; *B, P. dumeriliana,* lateral view — masseteric reaching orbit; *C, P. expansa,* lateral view — frontal meeting maxillary; *D, P. unifilis* juv., lateral view. *E, P. unifilis* juv., dorsal view. *F, P. lewyana,* dorsal view — interparietal very broad, heart-shaped. *G, P. unifilis* adult, dorsal view — interparietal moderately elongate but parietals meeting behind it. *H, P. sextuberculata,* dorsal view — interparietal separating parietals. *D* and *E* original. *A-C, F-H* after Siebenrock (1902). Abbreviations: *f,* frontal scale; *ip,* interparietal; *m,* masseteric; *p,* parietal; *s,* subocular.

choanal bars, and the shape of the choanal opening.

Figure 7 shows the shape of the anterior lobe in four species and the length-width relations of the intergular scute in the same forms.

All figures are from specimens, except Figure 1, A-C and F-H which are after Siebenrock (1902).

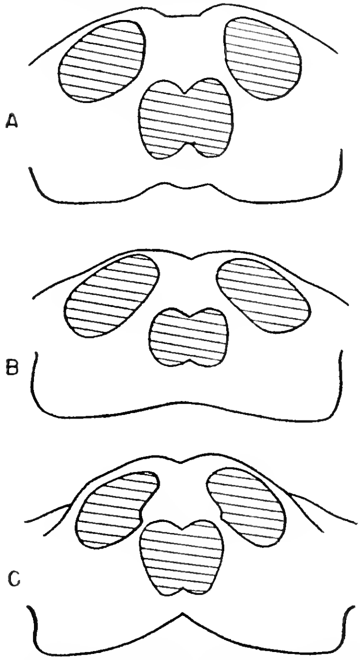

Fig. 2. Diagrams to show median notching of upper jaw. *A, P. expansa* — squared off, not rounded or notched. *B, P. lewyana* — rounded. *C, P. unifilis* — notched.

It is a pleasure to acknowledge the kindness of the authorities of the many museums listed above who have permitted me access to their collections or who have generously loaned specimens. I am indebted to Dr. Paulo Vanzolini and Mr. Benjamin Shreve who have tested my key and have pointed out some weaknesses in the original versions. Miss Patricia Washer is to be credited with the original sketches which illustrate this paper.

The opportunity to study the material in European collections was provided by a Guggenheim Fellowship 1952-1953.

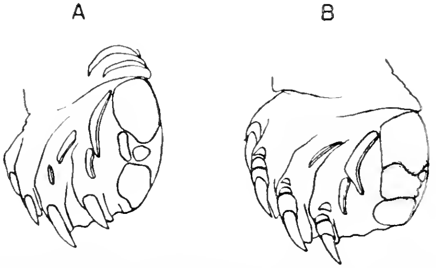

Fig. 3. Enlarged scales on posterior border of hind foot. *A*, *P. sextuberculata* — two scales. *B*, *P. unifilis* — three scales decreasing regularly in size.

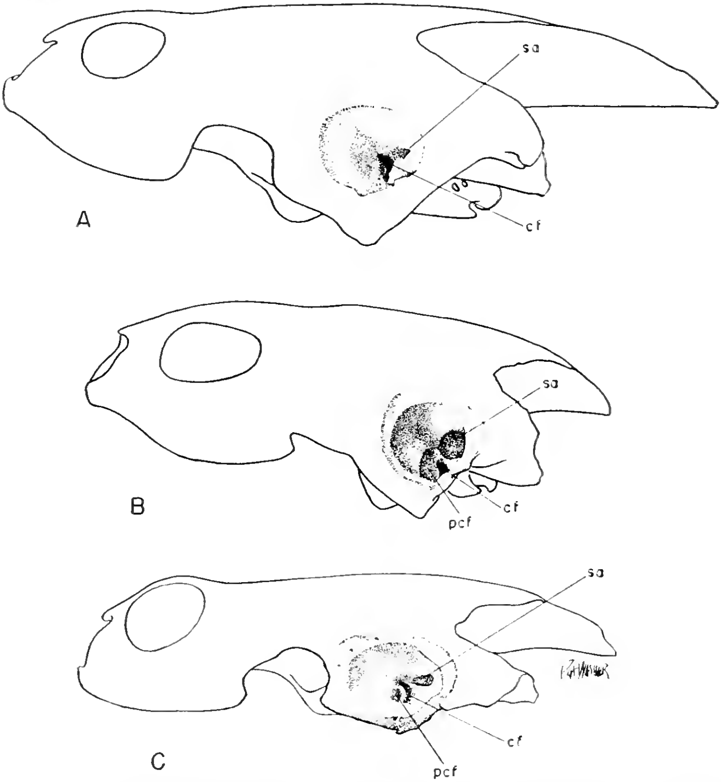

Fig. 4. Diagrams to show skull shape and ear region. *A*, *P. expansa* adult. *B*, *P. madagascarensis*. *C*, *P. unifilis*. Abbreviations: *cf*, columellar foramen; *pcf*, precolumellar fossa; *sa*, post-otic antrum.

Key and description

1. Forehead grooved; masseteric scale not reaching orbit; dorsal surface of marginal six more than half as wide as long; jugal bone meeting parietal bone; quadrate bone not meeting jugal bone; temporal region of skull emarginate from below or not 2

Forehead convex; masseteric scale usually reaching orbit; dorsal surface of marginal six less than half as wide as long; jugal not meeting parietal; quadrate usually meeting jugal; temporal region of skull never emarginate from below 7

2. Upper jaw notched medially, if feebly notched the interparietal scale elongate; shell more or less convex 3

Upper jaw not notched medially, instead gently rounded or squared off; shell more or less flat 6

3. Notch of upper jaw continued to the nostril as a groove; interparietal scale very broad, heart-shaped even in adults; the first marginal scute long anteroposteriorly, as long or longer than wide.. 5

Shell distinctly convex, much expanded posteriorly; vertebral keel distinct, most prominent on vertebral two or three. No nuchal indentation.

Skull elongate with two parallel longitudinal ridges on surfaces of the maxilla (*fide* L. Mueller, 1935).

Head scales: suboculars present.

Barbels: two.

Foot scales: two.

Color: Head reddish brown in individuals of *ca.* 250 mm. carapace length. Juvenile coloration unknown.

Size to 275 mm. (carapace length) ....*P. cayennensis* Schweigger
(Guianan and Amazonian regions and the Orinoco)

Notch of upper jaw not continued to nostril as a groove; interparietal elongate, if at all heart-shaped only so in the very young; the first marginal scutes wider than long 4

4. Vertebral keel sharply raised into a swelling at the posterior margin of vertebral two; shell always smooth, concentric lines of growth if present few and usually lines of pigment only, not ridges on the horny shields. Hatchlings with three pairs of prominent swellings on the sides of the plastron, the axillary pair often still indicated in the adult.

Shell much expanded posteriorly. A nuchal indentation present, sometimes feeble.

Skull broad, a single feeble ridge on the triturating surface of the maxilla. Premaxillae separating maxillae and reaching the choanal margin. Vomer absent. No precolumellar fossa in cavum tympani. Width of cavum tympani about equals width of orbit. Interorbital width less than height of orbit.

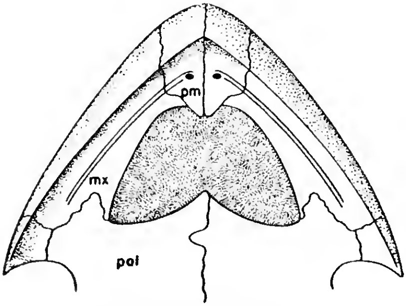

Fig. 5. Palate of skull in *P. sextuberculata.* Abbreviations: *mx,* maxilla; *pal,* palatine; *pm,* premaxilla.

Head scales: Interparietal scale usually widely separating parietal scales. Large suboculars present.
Barbels: two.
Foot scales: Three.
Size to 310 mm. .... *P. sextuberculata* Cornalia
(Amazonian region)

Vertebral keel never raised into a swelling at the posterior margin of vertebral two, shell often with concentric ridges. Hatchling never with three pairs of lateral swellings on the plastron 5

5. Vertebral keel usually distinct, typically most prominent on vertebral three; posterior shell margin somewhat expanded; shell commonly concentrically ridged. Size known to exceed 600 mm. Upper jaw distinctly notched. Skull elongate with two ridges on the triturating surface of the maxilla, the internal ridge not sharply dentate. Temporal region of skull strongly emarginate both dorsally and ventrally. Vomer usually absent.

Shell with a distinct nuchal indentation. Hatchlings with vertebral two usually only as long as vertebral three and with the plastron completely yellow or without a definite plastral pattern.

Skull more or less elongate. A deep precolumellar fossa in the cavum tympani. Width of cavum tympani as great as or greater than the width of the orbit. Interorbital width less than height of orbit. Premaxillae not separating maxillae, not reaching choanal margin. Foramina incisiva well within the borders of the premaxillae. The interchoanal bar, if present, formed from the palatines.

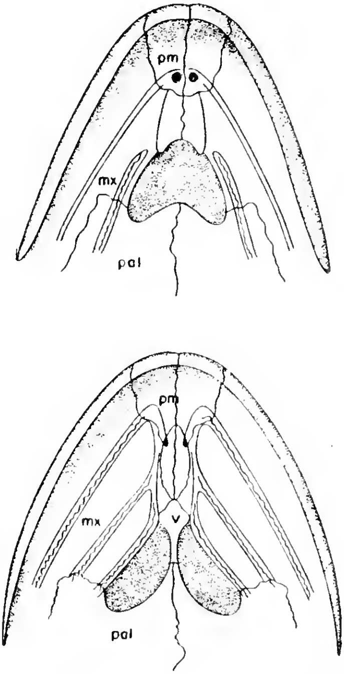

Fig. 6. Palates in *P. unifilis* (above) and *P. vogli* (below). Abbreviations as in Figure 5, with *v*, vomer.

Head scales: Interparietal scale very elongate but parietal scales usually meeting behind it. Suboculars usually present, usually not large. Maxillary scale light in color anteriorly and posteriorly, dark in the middle.

Barbels: Usually one.

Foot scales: Usually three.

Size to 680 mm. . . . . *P. unifilis* Troschel
(Guianan and Amazonian regions)

Vertebral keel feeble or absent; posterior margin of shell not expanded. Shields smooth or nearly so. Size not known to exceed 300 mm. Upper jaw feebly notched. Skull rather broad with three ridges on the triturating surface of the maxilla, all ridges roughened or dentate. Temporal region of skull well-covered, only slightly emarginate dorsally or ventrally. Vomer present, tending to form part of choanal septum.

Shell with only a feeble nuchal indentation. Hatchlings with vertebral two large, exceeding vertebrals three or four in length and with black quadrangular blotches on each plastral scute.

Skull rather broad. A precolumellar fossa present. Width of cavum tympani equals width of orbit. Interorbital width less than height of orbit. Premaxillae not reaching choanal margin but joining vomer to separate maxillae.

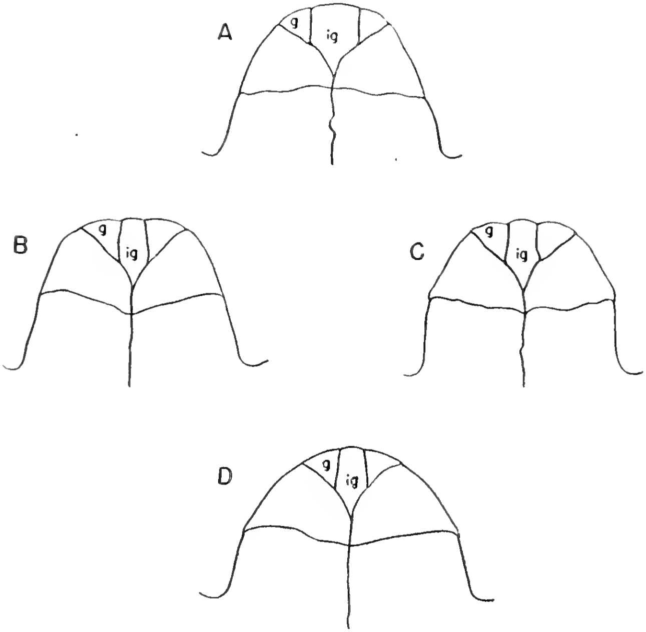

Fig. 7. Diagrams to show shapes of anterior lobes and of intergular scutes. *A*, *P. lewyana*. *B*, *P. vogli*. *C*, *P. unifilis*. *D*, *P. expansa*. Abbreviations: *g*, gular; *ig*, intergular.

Foramina incisiva well within margins of premaxillae but almost concealed from ventral view by extensions of the parachoanal triturating ridges.

Head scales: Interparietal scale elongate, but parietal scales meeting behind it. Suboculars large. Maxillary scale light only posteriorly, dark in middle and anteriorly.

Barbels: Two.

Foot scales: Three.

Size to 275 mm. . . . . *P. vogli* L. Mueller
(Venezuela, Orinoco drainage)

6\. Intergular broad, gulars not longer than intergular is wide anteriorly. Head never with yellow spots on the interparietal scale, always with sides of head light in color.

Shell with vertebral keel barely or not at all visible. No nuchal indentation.

Skull moderately elongate, upper jaw rounded, not notched at middle. Two parallel ridges on the triturating surface of the maxilla. Width of cavum tympani equals width of orbit. Interorbital width less than height of orbit. Premaxillae not separating maxillae and not reaching choanal margin. Foramina incisiva well within the borders of the premaxillae. A vestigial vomer may be present.

Head scales: Interparietal scale heart-shaped. Suboculars present.

Barbels: Two.

Foot scales: Three.

Size to 411 mm. . . . . *P. lewyana* A. Duméril
(Colombia: Magdalena drainage)

Intergular narrow, gulars longer than intergular is wide anteriorly. Head at least in juveniles showing yellow spots on the interparietal scale.

Shell distinctly flattened, very large in adults. Vertebral keel usually not visible in adults, if visible most prominent on vertebral two very rarely most prominent on vertebral three. Horny shields weakly or not concentrically ridged. No nuchal indentation. Hatchling with vertebral three extremely broad and short, up to three times as broad as long, always shorter than vertebrals two or four. Vertebral two as long as or longer than vertebral four. Sometimes first marginals as long as wide, usually wider than long.

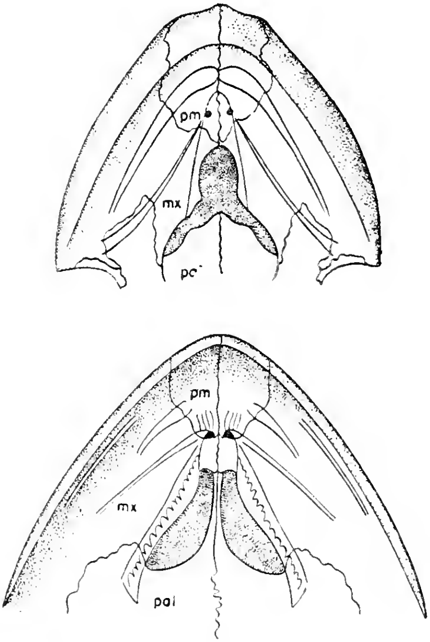

Fig. 8. Palates in *P. lewyana* (above), and *P. expansa* (below). Abbreviations as in Figure 5.

Skull broad in adults, less so in young, upper jaw squared off at tip rather than rounded or notched. Two or three ridges on the triturating surface of the maxilla, the first very short, originating from the premaxilla, the second much longer but parallel to the first, the third, if present, parachoanal, diverging strongly from the other two. Another very feeble ridge placed on the inner side of the outer vertical cutting surface of the maxilla. Width of cavum tympani greater than width of orbit. Interorbital width less than height of orbit. Premaxillae not separating maxillae, not reaching choanal margin. Foramina incisiva at caudal margin of premaxillae, a small area of bone anterior to the foramina wrinkled. Vomer absent. Palatines usually forming choanal septum and reaching maxillae anteromedially. Precolumellar fossa in cavum tympani absent or feebly indicated, except in young in which it may be well developed. Entrance to post-otic antrum narrowed in adults.

Head scales: Interparietal scale tapering posteriorly, separating the parietal scales or not. Usually frontal scale in contact with maxillary scale and suboculars absent.

Barbels: Usually two.

Foot scales: Usually two, if three, middle scale smallest.

Size to 820 mm. . . . . *P. expansa* Schweigger
(all northern South America east of the Andes, and the Magdalena drainage)

7. Interparietal scale expanding posteriorly. Upper jaw strongly hooked. Femoral median sulcus longest. Humeral usually about as long as pectoral. Intergular usually larger than gulars.

Shell convex, vertebral keel strong on last two vertebrals. First marginal not wider than long. Shields with numerous concentric growth rings, sometimes also with radiating striae. Supracaudals sometimes united.

Skull triangular. A single feeble ridge on the triturating surface of the maxilla. A deep anterior premaxillary fossa. Premaxillae usually separating maxillae and reaching choanal margin. Foramina incisiva well within the borders of the premaxillae. Vomer absent. A vertical poorly defined precolumellar fossa. Width of cavum tympani equal to or greater than width of orbit. Interorbital width greater than height of orbit.

Head scales: Interparietal scale widely separating parietal scales. Masseteric scale so far as known always reaching maxillary.

Barbels: One.

Foot scales: Three.

Size to 480 mm. . . . . *P. dumeriliana* Schweigger
(Guianan and Amazonian regions)

Interparietal scale tapering posteriorly. Upper jaw feebly hooked. Abdominal median sulcus longest. Humeral much shorter than pectoral. Intergular very small, gulars uniting behind it.

Shell convex, a vertebral keel not discernible in adults. First marginal broader than long. Shields with numerous concentric growth rings and radiating striae.

Skull broad. A single feeble ridge on the triturating surface of the maxilla. Premaxillae separating maxillae and reaching choanal margin narrowly or maxillae barely meeting and separating premaxillae from choanal margin. Foramina incisiva well within the borders of the premaxillae. A vertical precolumellar fossa present in cavum tympani. Width of cavum tympani less than width of orbit. Interorbital width about equal to height of orbit.

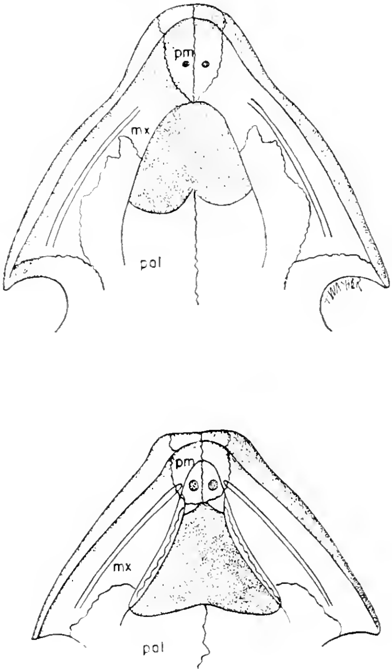

Fig. 9. Palates in *P. dumeriliana* (above), and *P. madagascarensis* (below). Abbreviations as in Figure 5.

Head scales: Interparietal scale tapering posteriorly, parietal scales meeting behind it. Usually masseteric scale reaching maxillary scale, but sometimes suboculars present.

Barbels: One, rarely two.

Foot scales: Three.

Size to 435 mm. . . . . *P. madagascarensis* Grandidier (Madagascar)

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ON BOLOSAURUS AND THE ORIGIN AND CLASSIFICATION OF REPTILES

By D. M. S. Watson

With One Plate

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By D. M. S. Watson

With One Plate

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No. 9 — *On Bolosaurus and the Origin and Classification of Reptiles*

By D. M. S. Watson

INTRODUCTION

For very many years it has been believed that the classification of reptiles should express, even if remotely, the evolutionary history of these animals. If one considers palaeontological text books one finds that Richard Owen's "Palaeontology" (2nd edition, 1861) gives a systematic treatment of fossil reptiles in general, including within the class Labyrinthodontia *Archegosaurus*, *Trematosaurus*, etc. The group is then divided into ten orders, with an additional order Batrachia including the frog, and the giant fossil salamander of Oeningen. Owen makes no attempt to group the orders, though he does suggest that the Pterosauria have affinities with birds, and the Deinosauria with mammals.

In 1871 T. H. Huxley brigaded together as Sauropsida the Reptilia and Aves, the Reptilia being divided immediately into nine orders which are not further grouped.

In 1898 A. Smith Woodward divided all reptiles into nine orders whose mutual relations were not further discussed.

In 1902 C. R. Eastman, in the American translation of Zittel's "Grundzüge", follows the same plan, as in effect does Broili in the later editions of Zittel.

H. F. Osborn in November 1903 divided the reptiles into two groups—subclasses Synapsida and Diapsida—all the then known reptiles being allotted to one or the other group, the Synapsida giving rise to the mammals, the Diapsida to the birds. These groups are further divided into branches presumably to be regarded as orders, and the separation was based essentially on the nature of the temporal arches, though many other structural features were considered. The Synapsida contains Cotylosaurs, Anomodontia (including Placodonts), Testudinata and Sauropterygia. The Diapsids include Phytosaurs, Ichthyosaurs, Crocodiles, Deinosaurs, Squamata, Pterosaurs and a superorder Diaptosauria with Pelycosaurs, *Procolophon* and *Sphenodon* in addition to many other things. The list of characters which were held to distinguish the Synapsids from the Diapsids do not do so because in very many cases they were known only in single species (or even specimens) and were assumed without evidence to occur in a great variety of animals, believed to be related, which do not in fact exhibit them. It follows therefore that it is undesirable to use the term Synapsida and Diapsida in classification on the grounds that each group is so complex that it is false and unrecognisable.

The first real attempt to lay a foundation for a fundamental classification of reptiles was E. S. Goodrich's paper in the Proceedings of the Royal Society, 1916. In this he shewed that the structure of the ''ventral aorta'' in all living reptiles and birds differed fundamentally from that found in mammals. It seemed evident that the whole group of reptiles back to its establishment (or even before it arose from the Amphibia) was divided into two — the Theropsida ending in mammals, and the Sauropsida in birds. In this paper Goodrich pointed out that the living reptiles, and many of those fossils clearly related to them, shewed a ''hook-shaped'' 5th metatarsal, whilst the mammal-like reptiles did not. At that time Goodrich proceeded no further with the classification, and his paper, published in the middle of the war, attracted little immediate attention. (A further treatment of this matter will be found on page 427 of the present paper.)

In 1917 I published a classification of pre-Jurassic reptiles which paid no attention to Goodrich's classification, of which I had then no knowledge, and was in the main a division into three superorders, each further subdivided. In effect these superorders consisted of one including all the mammal-like reptiles, another including all the immediate relatives of the living reptiles other than the Rhynchocephalia and Chelonia, whilst the third was the Cotylosauria, including the Seymouriamorpha.

S. W. Williston, in a posthumous work published in 1925, divides the reptiles into five major groups (superorders): Anapsida, containing Cotylosaurs (including *Seymouria* and *Pantylus* now regarded as Amphibia), Eunotosauria, and Testudinata; Synapsida, containing Theromorpha (=Pelycosauria) and Therapsida; Synaptosauria, containing Sauropterygia and Placodontia; Parapsida, containing *Mesosaurus, Ichthyosaurus,* Protorosauria (*Araeoscelis* and *Saphaeosaurus*), and Squamata; and Diapsida, including all patently two-arched reptiles. This grouping uses Synapsida and Diapsida (Osborn's terms of 1903) in a modified form, no longer as representing a complete dichotomy of the reptile stocks. This use is not desirable, owing to ambiguity. Synaptosauria is a device to put together two groups of aquatic reptiles clearly related to one another, and to avoid a decision on their origin. Parapsida, introduced for the first time in 1917, includes *Mesosaurus*, *Ichthyosaurus*, *Araeoscelis*, *Protorosaurus*, *Saphaeosaurus*, *Pleurosaurus*, lizards and snakes. It is extremely unlikely that these animals have any close relation to one another, the only common diagnostic character alleged being the existence of an upper temporal vacuity in isolation. Ichthyosaurs and *Araeoscelis* are in all probability mammal-like reptiles; *Saphaeosaurus* and *Pleurosaurus* clearly are not.

In 1930 Goodrich in his "Structure and Development of Vertebrates" gave a very full classification of all vertebrates, without any definitions; but the genera included under each group make his intentions evident. In this, certain groups perhaps Amphibia — the Microsauria for instance — are included in reptiles, but the old division into Theropsids and Sauropsids which he had set up fourteen years before had been reduced in rank, and we find a group Synapsida (or Reptilia Theropsida) for the mammal-like reptiles. Parapsida makes its appearance for Mesosaurs, Plesiosaurs, Pleurosaurs and Ichthyosaurs; and the Reptilia Sauropsida now becomes the Eusauria, including Chelonia and all the Diapsids and lizards. Thus Goodrich here leaves the reptiles with a closed temporal region in three groups, Cotylosaurs, Pariasaurs and Procolophonids, as part of a major group, Anapsids, which also includes Microsaurs and *Seymouria;* and the new group of Parapsids is really an artificial device for the inclusion of a whole series of aquatic reptiles of uncertain position.

In the 14th edition of the Encyclopaedia Britannica, 1929-32, I gave an account of reptiles which includes a classification not differing materially from that of 1917.

A. S. Romer in the 1933 edition of his textbook has a subclass Anapsida including Cotylosaurs and Chelonia; doubtful subclasses for the Ichthyosaurs and Plesiosaurs; a doubtful Lepidosauria for the Eosuchia, Rhynchocephalia and the Squamata; and then a subclass Archosauria for the Pseudosuchia, Crocodilia, Deinosauria, etc. Finally a subclass Synapsida includes all the mammal-like reptiles. This classification of Romer's thus adopts as a basis the fenestration of the temporal region of the skull and carries it through systematically. How far such a basis is valid is clearly disputable and I shall deal with that problem later in this paper. In 1945 Romer much elaborates his earlier classification, changing it a good deal.

Finally in 1952 F. von Huene has a ''Ramus Reptiliamorpha'' including the embolomerous Anthracosaurs, *Seymouria*, Microsaurs (characterised by *Microbrachis* and *Pantylus*), Ichthyosaurs, Diadectomorphs, Procolophonids, and so on, everything being divided into orders without any higher grouping.

Thus the most recent classifications of the class Reptilia have placed all the known reptiles in a series of orders, usually undefined and with their mutual relationships unexplored. The only way of testing the usefulness of such a classification is to try to determine the place it provides for an animal whose structure can be described in some detail, but which has not been very much discussed and has no determined systematic position. The animal so used should be represented by materials sufficiently extensive to enable much of its structure to be determined, and should be of early date so that the criteria which can be used in determining its position are those on which major groups are recognized. *Bolosaurus* from the Lower Permian, Wichita formation of Texas is such an animal.

ON BOLOSAURUS

HISTORY OF MATERIAL

The genus *Bolosaurus,* with a type species *B. striatus,* was established by Cope in 1878, the original description being reprinted by Case in his monograph of Cotylosauria in 1911. Meanwhile in 1907 Case had collected, prepared, and described (1907a) two crushed but well preserved skulls and associated vertebrae and limb-bones which he referred to this species, and the morphological account of *Bolosaurus* in the 1911 monograph is almost entirely based on this new material. In 1913 Broom pointed out the differences between Case's new skulls and skeleton parts and Cope's original materials of *Bolosaurus*, establishing the genus *Ophiodeirus* for Case's material, and giving a short account of the most complete of Cope's skulls. In this description he recognized the presence of a ''lower temporal vacuity'', and of a very large flat tabular behind the squamosal. But the description which began by giving an account of a skull of *Bolo-*

saurus then passes on to describe an occipital condyle which is evidently that of *Ophiodeirus*. Thus Broom believed that *Bolosaurus* and *Ophiodeirus* belonged to the same family and after an inconclusive discussion concluded that the "family" so established was a group of primitive "Theromorphs."

In 1917 I placed *Bolosaurus* in a separate superfamily of the Pelycosauria, with possibly *Glaucosaurus* and *Palaeohatteria*. *Araeoscelis,* which is close to *Ophiodeirus,* was placed with doubt into the doubtful order Protorosauria. No further work has been published on *Bolosaurus*, but Romer and Price (1940) suggest that the lower temporal bar has no real existence and leave the animal unplaced.

Thus it is desirable to have further work on what is evidently an unusual animal.

The material which I have used includes at any rate the greater part of that so far discovered and is as follows:

Cope Collection, American Museum of Natural History. All specimens appear to have been collected near Mt. Barry, Wichita Co., Texas.:

4320. Type specimen, a skull and lower jaw lacking the anterior end, laterally and obliquely crushed, occiput jumbled up, temporal region nearly complete though distorted on left side. Dentition poor. Sclerotic plates shown in each orbit. This specimen is a red brown calcareous nodule containing a skull which has been prepared mechanically with a needle. All the compact bone is broken by rectilinear cracks into areas seldom more than a millimeter across. A small nodule containing vertebrae, ribs, and a patch of abdominal ribs is supposed to be part of the type and is under the same number.

4327. Skull and lower jaw in natural articulation, obliquely crushed so that the left lower jaw, left side of the skull, and dorsal surface are visible on the left side; the right lateral surface of the skull and articulated lower jaw and the inner surface of the left lower jaw are visible on the other side. The whole is contained in a nodule about 5.0 x 3.35 x 1.4 cm. Coll. Boll and Isaac, 1878, probably from the same place as Nos. 4320-4326.

4321. Skull and jaws similar in condition to the type but less useful; shows the quadrate and articular on the left side. Coll. Boll and Isaac, 1878.

4462. The anterior part of a skull and lower jaws obliquely crushed, and crossed on the right side by part of a flattened humerus and ulna. This specimen differs in physical state from those previously listed in that the matrix was not a distinct nodule but a hardened mud, cemented by calcium carbonate but penetrated all through by very thin sheets of silica. It was entirely etched out by acetic acid. The specimen shows more of the dentition than any other. ''Cope Collection.'' From the same place as Nos. 4320-4326.

4324. The anterior part of a large skull with the mandible in position, crushed dorso-ventrally. Similar in condition to No. 4462 and certainly found with it. Prepared by acid. Also two dentary and one maxillary fragment with imperfect teeth. Boll. and Isaac, 1878.

4322. Partial dentary figured by Case, 1911, pl. 7, figs, 4, 5, 6. String of four vertebrae.

4326. Fragment showing left maxilla and dentary in position. Two specimens showing the symphysis of the lower jaws; four dentary fragments; one maxillary fragment. String of five vertebrae. Boll. and Isaac, 2-9-'78 (=Feb. 9, 1878), Wichita Co., Texas.

Nothing in the character of these specimens renders it unlikely that they were found together, and the first description of *Bolosaurus* founded on this material is said to have been given at a meeting of the American Philosophical Society on April 5th, 1878.

The Museum of Comparative Zoology contains:

1436. The anterior end of a left dentary with perfect teeth, the hinder end of a left maxilla with four perfect teeth, and a fragment of a right dentary with three teeth. These came, presumably in association, from Godwin Creek, Archer Co., Texas, probably lower part of Belle Plains formation, Wichita Group.

2089. Fragment of left dentary with three teeth. Geraldine.

1910. A perfectly preserved and prepared right maxilla and separated premaxilla from the Geraldine Bone Bed.

2088. Partial left mandibular ramus; twelve complete vertebrae and fragments. South side of Godwin Creek, Boone Ranch, Archer Co., Texas.

2090. Section of jaw and fragment of maxilla. Briar Creek Bone Bed.

2087. Scrap including a maxilla and dentary in natural apposition, other jaw bones, limb bones, phalanges, etc., all crushed and incomplete and covered with an unremovable film of matrix. Locality Briar Creek Bone Bed.

It is evident that this material does not suffice to give a full knowledge of the skeleton and that even the skull can only be understood by making a careful reconstruction from the whole material. This I did, making a series of drawings which conform to one another and to the material, by assuming that no changes in proportion took place during the 10 or 15 per cent growth represented in the material. The drawings were made by measuring the specimens with needle-pointed screw dividers under a binocular microscope. The measurements were read on a steel scale divided in 64ths of an inch. They were then transferred to a drawing made on 1/10th inch squared paper, each 1/10th inch representing 1/64th of an inch in the measurement. Measurements on other specimens were similarly made and then multiplied by a figure representing their size relation to that of the most complete specimen.

DESCRIPTION OF STRUCTURE

Braincase

Basioccipital. The only basioccipital forms part of the type, 4320. Weathering has removed the very thin outer layer of dense bone from the condyle and the posterior parts of the upper and lower surfaces but seems to have left the shape quite evident.

The condyle is shallow, wide, and apparently not very protuberant. It may well have been added to by additional faces on the exoccipitals. The ventral surface is nearly flat, the upper bears a median depression lateral to which lie rather rounded faces for the articulation of the exoccipitals.

The lateral surface is rounded, but toward the anterior end gives origin to an outstanding process, with flattened dorsal and ventral surfaces, coated with dense bone. The outer end of the process ends anteriorly in a dorso-ventrally rounded surface, which behind passes abruptly into a cup-shaped hollow which faces outward and backward and has a margin of dense bone. I can offer no interpretation of this remarkable structure.

Basisphenoid. The basisphenoid, or rather the inseparable complex of that bone and the parasphenoid, is partially shown in A.M.N.H. 4320, from below and from the right side; the basipterygoid processes are seen from above in 4324. The bone is long and narrow, nearly parallel sided, but with its ventral surface expanded below the basipterygoid process, then narrowed to a single rounded ridge which behind splits into a pair of deep rounded ridges ending at the tubera and separated by a deep groove narrowing in front to an abrupt rounded end. The basipterygoid facets are rather widely separated. Nothing is seen of the region where the parasphenoid processus cultriformis should lie.

Exoccipital. An exoccipital is shewn from behind in 4320 and 4327 as a large bone with obvious articular faces above and below, with an extensive concave admesial border, shewing that, as the small size of the animal makes necessary, the foramen magnum was large.

Supraoccipital. 4327 shews rather more than one half of a large symmetrical bone, clearly a substitution bone, which can only be a supraoccipital. Its size and general character are shown in Figure 1.

Opisthotic. The same specimen shews another very much damaged bone with a foramen passing into its substance which appears to be a semicircular canal. This may be a paroccipital. Its size may be judged from Figure 1B. (*Par. Oc.*)

No trace of any sphenethmoid is to be seen.

The membrane bones which are associated with this cranium are shewn in many specimens differently distorted and the arrangement they have in the figures represents a reconstruction drawn from many specimens.

Dermal Skull Bones

Premaxilla. The premaxilla is shewn in A.M.N.H. 4327, 4324, 4462, and M.C.Z. 1910. It is a small bone, meeting its fellow in an extensive contact in the middle line where it extends up as an internarial process to meet the nasal. The outer surface of the bone is exposed for a very small distance on the rounded anterior end of the skull, and appears as a very narrow strip below the nostril above the maxilla. But the greater part of this surface is a flat face overlapped by the anterior end of the maxilla. The anterior part of the palatal surface is completely occupied by the two laterally compressed teeth, but the bone is continued back for an unknown distance mesial to the palatal nostril.

Septomaxilla. The upper surface of the premaxilla within the nose is covered by the septomaxilla, well shown on the right side of 4327. This bone, usually extensive, seems to have no exposure on the face.

The ventral part of the bone is a sheet of some thickness which rests upon the upper surface of the palatal part of the premaxilla, extending outward nearly to the border of the nostril. This sheet ends mesially at an abrupt margin where a deep rounded groove passes antero-posteriorly to penetrate the bone behind. The inner side of this groove lies on the upturned inner part of the bone, which stands up in the nose, its concave anterior part swinging round until it seems to reach the middle line, where it presumably met its fellow.

The hinder end of this inner part of the septomaxilla has a special process which passes outward above the groove to complete the foramen from which this groove leads. Dorsal to this foramen the bone leans outward nearly to touch some bone of the face, with which it forms another more dorsally placed opening leading forward from the nasal chamber.

Presumably the upper and larger of these holes transmitted the duct of Jacobson's Organ, the lower the anterior end of the lachrymal duct.

Maxilla. The structure of the maxilla is perfectly known from isolated examples as well as by articulated skulls.

The bone consists of a thin delicate sheet, whose upper border overlaps the lachrymal and is itself overlapped by the jugal, with a feather edge. This superficial bone arises from a very massive tooth bearing region. This has an outer surface directly continuing that of the dorsal lamina which rolls gently round to

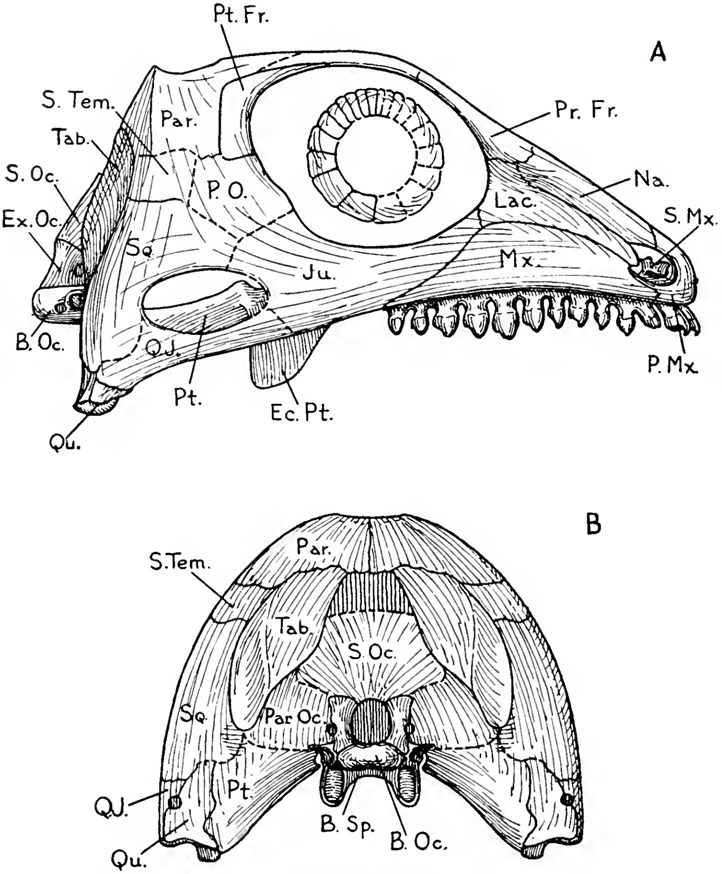

Fig. 1. *Bolosaurus striatus* Cope. Reconstruction of the skull, founded on A.M.N.H. 4327, with additions from other materials, x 2. *A*, lateral aspect; *B*, occiput. Reference letters: *B.Oc.*, basioccipital; *B.Sp.*, basisphenoid; *Ec.Pt.*, ectopterygoid; *Ex.Oc.*, exoccipital; *Ju.*, jugal; *Lac.*, lachrymal; *Mx.*, maxilla; *Na.*, nasal; *P.Mx.*, premaxilla; *P.O.*, postorbital; *Par.*, parietal; *Par.Oc.*, paroccipital; *Pr.Fr.*, prefrontal; *Pt.*, pterygoid; *Pt.Fr.*, postfrontal; *Qu.*, quadrate; *Q.J.*, quadratojugal; *S.Mx.*, septomaxilla; *S.Oc.*, supraoccipital; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Tab.*, tabular.

the very slightly hollowed palatal surface. The outer half of this surface is occupied by the single row of teeth, the remainder forming a smooth surface, directly continued onto the palate bones. Posteriorly the palatal surface narrows to a point.

The thickened lower part of the maxilla has a horizontal upper surface which passes abruptly into the inner surface of the dorsal lamina, but the inner surface of this part of the bone is diversified. Anteriorly it has a flat articulation with the premaxilla. Behind this for a distance of some three teeth the bone has a rounded smooth margin to the palatal nostril.

The inner surface, here at an angle of some 45° to the vertical, has a wide scarfed attachment surface for the palatine bone. Behind this a nearly vertical surface is attached to the anterior end

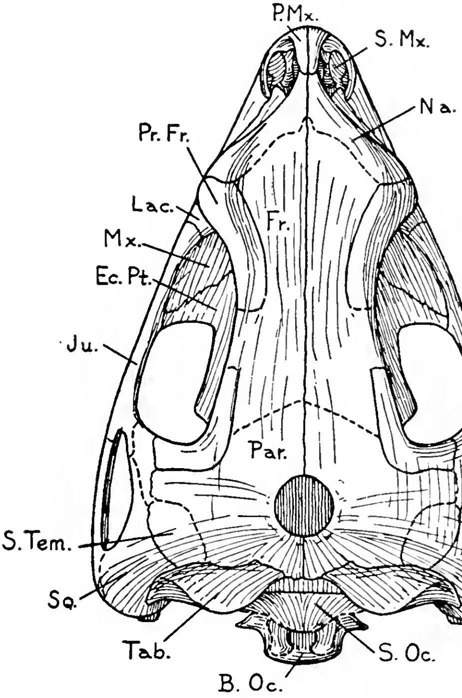

Fig. 2. *Bolosaurus striatus*, Cope. Reconstructed as in Fig. 1. x 2. Dorsal aspect. Reference letters as before, with *Fr.*, frontal.

of the ectopterygoid, the two bones being in contact along an oblique surface passing out to the area overlapped by the jugal.

Lachrymal. The lachrymal is well shown in 4327 and 4320 which shows its intraorbital portion. It is a thin bone stretching from orbit to nostril, overlapped below by the maxilla throughout its length, and in turn resting on a rabbet on the outer face of the nasal, and having some connection to the prefrontal posteriorly. The bone is thin but posteriorly thickens and forms a quite wide front wall to the orbit (jointly with the prefrontal).

This surface is perforated by two foramina, one near its upper edge, the other far back below the orbit, each of which lies very superficially. These are for the lachrymal ducts or canaliculi.

Prefrontal. The prefrontal is well shewn in 4327 and 4320 as a bone which has a long suture with the lateral border of the frontal, apparently ending before it meets the postfrontal. The bone is pushed outward as a rounded boss (actually a hollow shell) above the anterior border of the orbit, and ends by a suture with the nasal and lachrymal.

Postfrontal. The postfrontal is completely shewn only in 4327. Here it is a purely superficial bone with a dorsal part ending anteriorly at a transverse suture with the frontal, a straight, antero-posterior suture with the frontal and parietal, turning rather abruptly at right angles to pass outward and downward where the narrow ventral part of the bone lies on an oblique articular facet on the front border of the lateral part of the parietal.

Postorbital and *Jugal.* It is impossible to distinguish the suture between the postorbital and jugal though their relation to other bones is reasonably well determined.

The jugal meets the lower end of the lachrymal on the orbital margin, and there lies in a recess on the outer face of the maxilla (4327; 4324, right side; 4320). It then forms the lower border of the skull and of the orbit for some distance, and here has a contact with the ectopterygoid. The bone is thin throughout the whole of its extent, very much cracked and its limits are uncertain. But it seems certain, from specimen 4320 left side, that it meets the squamosal above the temporal vacuity, and that it only extends for a very small distance, if at all, into the quadratojugal arch.

The postorbital, certainly present, is a featureless bone whose borders cannot be determined. There seems to be reason for believing that the shape and position of the bone cannot differ materially from those in Figure 1.

Quadratojugal. The quadratojugal is shown in 4327, 4320, and 4321. It is a rather large bone attached to the outer surface of the quadrate by a face of considerable vertical extent, which continues until it is interrupted by the quadratojugal foramen, whose border seems to be completed by an inturning of the quadratojugal onto the posterior surface of the quadrate. The bone extends forward on the outer surface of the skull as a bar below the temporal fossa until, apparently at the extreme anterior end of the fossa, it meets the jugal.

This sub-fossal bar is shewn by an impression of its inner surface on the right side of 4327 to have thickened but rounded upper and lower borders and hence not to come into suture with any other bones in those regions; thus confirming the existence of the temporal vacuity.

Squamosal. The squamosal is shown in 4327 and in 4320. The hinder part of the bone is wrapped round the quadrate and quadratojugal, forming a part of the occipital surface where it is overlapped by the very large tabular. From this surface the bone rolls round, so that there is no occipital margin, onto the outer surface. The bone extends forward to meet the postorbital, and presumably the jugal, above the temporal fossa.

Dorsally the squamosal is shewn in 4327 to have (near its tabular attachment) an obliquely truncated margin overlapped by the supratemporal.

Supratemporal and *Parietal.* These bones are shewn in intelligible form only in 4327. In this specimen the external surface of the left parietal is shown essentially completely, and seems to have retained its original shape, as it is very little cracked. It was however damaged presumably by weathering and certainly by the original preparation, which seems to have been done by scraping the whole outer surface of the specimen with a knife.

Cracking, weathering, and scraping make it impossible to say where the parietal and frontal meet, but it is evidently somewhere in the flat, horizontal interorbital region. This surface ends behind at the relatively very large pineal foramen. The whole half border of this opening made by the left parietal is well shewn, and from it the parietal passes horizontally forward to the frontal, nearly horizontally outward from the front border of the pineal foramen to the knee in the border of the postfrontal.

Passing directly outward from the midpoint of the pineal to the end of a long projection behind the postfrontal, the bone is bowed outward but is inclined downward at about 40°. From the midpoint of the pineal foramen the parietal passes backward and downward at an angle of some 60° with the horizontal.

The ventral border of the bone seems to meet the postorbital for a short distance, and then overlaps the supratemporal, until both bones are overlapped by the tabular.

The upper margin of the supratemporal is shown by an excavation made where damage had removed a formerly present piece of parietal. It is evident that the parietal overlapped the outer surface of the more laterally placed bone.

Frontal. The frontals are shewn in 4320 and 4327, in each case damaged by weathering and cracking. Their general nature is however evident. Each is a narrow bone, having a sutural attachment to its fellow throughout its length, and with it forming a surface which is nearly flat between the eyes and very gently convex in the preorbital region. The suture with the parietal is not visible but the mode of attachment of the pre- and postfrontals is very well shewn.

In front of an oblique facet for contact with the prefrontal the right frontal of 4327 ends at a border which limits a sharply marked depression, a rabbet, in which the admesian border of the nasal must have lain. This extends forward until the border of the frontal suddenly turns in transversely and then projects forward so as to make with its fellow a very narrow process in the middle line.

Nasal. The nasal is thus a rather small bone whose posterior end rests in a transverse rabbet on the anterior border of the frontal. The anterior end has a narrow contact with the internarial process of the premaxilla and the lateral border extends forward as a rounded edge from the prefrontal to the nostril.

The lateral or lower border of the nasal is itself recessed to be overlapped by the upper edge of the lachrymal.

Palate

The palate is only very incompletely seen, but is here described.

Quadrate. The quadrate bone is well shewn from behind and below in 4320 and 4321.

Its ventral surface is entirely occupied by an articular face which is divided into two condyles, the outer being short, rather flattened, and facing downward and a little forward; it is separated by a shallow groove from a larger, more rounded inner condyle which lies at a lower level and a little more posteriorly.

From this extremity the posterior face of the bone rises, sloping a little forward but soon becoming vertical. The lateral border is notched by a rounded incision, above which its border continues vertically. This border is attached to the quadratojugal, which

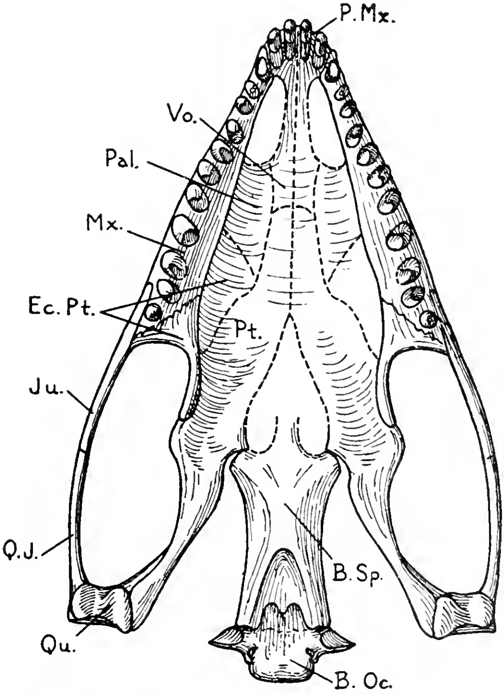

Fig. 3. *Bolosaurus striatus* Cope. Reconstructed as in Fig. 1. x 2. Ventral aspect. Reference letters as before, with *Pal.* palatine; *Vo.*, vomer.

seems to be attached to the outer border of the bone, without resting in a step over the outer condyle.

The inner part of the quadrate (seen broken across on the right side of 4320) continues as a pterygoid ramus, with a rounded lower border, on the outer surface of the pterygoid.

Pterygoid. The pterygoid is seen, very imperfectly as to its quadrate ramus, in 4320 where it is crushed inward and exposed from its admedian side, and in 4324 where a small area round the articulation with the basisphenoid is seen from below.

The articulation seems to be placed a little obliquely, in the plane of the hinder border of the deep transverse flange. This scarcely forms a separate ramus, for though deep, it lies only a little laterally of the basipterygoid articulation.

The quadrate ramus is rather broad seen from below, its border there being out-turned so that the ventral exposure of the bone is cylindroid.

Nothing is known of any epipterygoid.

Ectopterygoid. That part of the ectopterygoid which passes behind the maxilla to meet the jugal is shewn from above and behind in 4324; the forward extension of the bone is shewn by the facet for its attachment on the maxilla.

Palatine and *Vomer*. No part of either the palatine or vomer is shown by the materials available to me, but their general character as suggested in Figure 3 is obvious, for maxilla M.C.Z. 1910 shews the smoothly rounded external border of the nostril perfectly.

Lower Jaw

Both rami of the lower jaw are shewn in 4327, but generally the preservation is inadequate, though the inner surface is well though incompletely shewn on the left side. 4321 is useful for the articular, as is 4320, which also shews the enormous coronary eminence better than any other specimen; 4462 and 4324 are also useful and there are many valuable fragments of dentaries.

Dentary. The dentary meets its fellow in a small symphysis notched behind by the anterior end of the cavity of the jaw. This symphysis covers a small area and is spheroidal, so that some movement may have been possible.

The bone has a wide and deep upper part in which the teeth are inserted and to which they are fixed. From this thin sheets of bone descend to form the outer surface of the jaw and to be covered by the coronoid and probably other bones on the inner surface.

The tooth-bearing upper surface is nearly flat, and widens as it is followed back from the symphysis, where the two bones together are rounded into a semicircular border.

Behind the last tooth the dentary suddenly rises to form the anterior border of an immensely exaggerated "coronoid process."

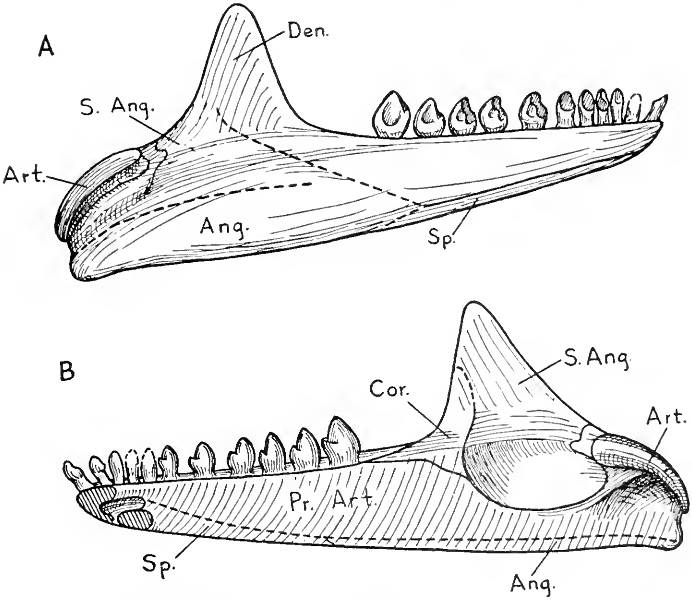

Fig. 4. *Bolosaurus striatus* Cope. Reconstructed as in Fig. 1. x 2. Lower jaw. *A*, outer, *B*, inner aspect. *Ang.*, angular; *Art.*, articular; *Cor.*, coronoid; *Den.*, dentary; *Pr.Art.*, prearticular; *S.Ang.*, surangular; *Sp.*, splenial.

Splenial. The splenial is a small bone at its anterior end where it has a symphysis with its fellow; from here it extends backward as a small shell of bone forming a rounded lower border of the jaw, overlapped by the dentary, and by the prearticular on the inner surface.

Articular. The articular is a bone with a widened upper surface, the whole of which is occupied by the articular face for the quadrate. This is much longer from back to front than the corresponding condyle on the quadrate, and is as wide. It is divided into two by a rather deep ridge, running antero-posteriorly, whose upper edge forms a considerable convex segment of a circle, and evidently moved in a groove in the cartilaginous quadrate condyle.

The two hollows so separated, which articulate respectively with the two quadrate condyles, are less notably rounded from back to front so far as can be seen. Below this articulation the bone is a narrow sheet clasped between the surangular, angular, and prearticular bones, with a free hinder surface which is certainly not carried backward in the usual way into a postarticular process but may be drawn out into a knob at the ventral end of its hinder exposure.

Surangular. The surangular is best shown in 4320, right side. It sheaths the outer surface of the articular, not reaching the articular border, and it swings inward in front of the articular surface to stretch forward and upward to form part of the immense ''coronoid process''. Here the outer surface of the bone lies much mesial of its position lower down, so that the whole of the process is, as it were, ''set back'' from the general outer surface of the jaw. This arrangement allows a large and thick external element of the temporal musculature to extend downward to its insertion mesial to the quadratojugal arcade.

The bone ends by being overlapped by the hinder end of the dentary and its lower border is overlapped by the angular.

Angular. The angular lies mainly on the outer surface but rolls round the lower border of the jaw to end at an overlap, apparently not broken by any fenestra, on the prearticular.

Prearticular. The prearticular is tightly applied to the concave mesial surface of the articular. From here it extends forward certainly for more than three quarters of the total length of the jaw. The bone is a thin sheet throughout its length, overlapped by the angular and splenial for a very small extent at its lower border. Its upper edge forms the lower and inner border of the supra-meckelian vacuity, in front of which it is attached to the inner surface of the coronoid bone, ultimately reaching the dentary.

Coronoid. A coronoid bone is seen forming the anterior border of the supra-meckelian fossa, extending up in contact with the elevated "coronary" part of the dentary for a considerable distance, and having an anterior continuation wedged in between the prearticular and the dentary

Hyoid. A slender cylinder of thin and badly surfaced bone, broken into short lengths, lies below the ventral border of the right lower jaw of 4327. It is essentially a straight rod extending from a point below the anterior end of the articular surface of the jaw to the front end of the supra-meckelian fossa.

Dentition

The teeth of *Bolosaurus* are unique in character, and as they are very well preserved it is necessary to discuss them in some detail.

The tooth rows are essentially straight, the sides of the face and of the two dentaries being also straight, the whole forming a wedge with a rounded point

The mature dentition, as it is shown in 4327, consists of two teeth in each premaxilla and eleven in each maxilla, the dentary housing ten or eleven only

There is evidence that the more posterior teeth were cut in succession as the animal grew larger over a considerable time, and there is evidence that teeth in the front of the mouth were worn out, shed, and replaced.

The teeth have elaborate crowns and are to some extent individualized.

All the teeth agree in some general characters:—The crown is coated with an unusually thick enamel whose outer surface is ridged to a very variable extent. It may be almost smooth, but it usually bears a series of low, rounded ridges passing down from the summit of the crown, toward but not to the termination of the enamel at the gum. These ridges may be straight and continuous, or they may be interrupted, or they may anastomose with one another. They are usually sparse, or even absent from the small anterior teeth, becoming better developed on the large posterior teeth. The difference in degree of development of the ridges seems to be an individual matter, teeth being uniform in this respect throughout whole dentitions.

The mode of development of a tooth seems to have been the same throughout the jaws. The tooth-bearing bone becomes excavated into a rounded cavity with a narrow opening (M.C.Z. 1910) onto the tooth-bearing surface. In the cavity so formed the enamel organ, still in connection with the epidermis by a string passing through the small foramen, secretes the enamel crown. The arrangement is exactly similar to that found in mammals or in the cynodont *Diademodon*.

There is evidence to show that the tip of the cusp is the first formed part of the enamel, and that the cap was gradually completed while in the cavity.

It is not evident when the formation of dentine begins, but apparently about at the stage when the complete enamel crown is finished, a lining of dentine exists and the formation of a root begins. The tooth must then cut, an increasing length of root holding it in position. This root contains a large cylindroid pulp cavity which remained open for a long time. The gum by which the tooth is held in position then begins to ossify, giving to the root a vertically ridged and striated appearance which extends throughout its depth (see M.C.Z. 1436). Ultimately the gum becomes completely bony, though when broken across it may still show a series of radial slits crossing the cylinder which surrounds the root; these die away where a thin surface of dense bone fairs off the surface connecting the neck of the tooth with the tooth-bearing surface of the bone by a smoothly curved ring.

Several maxillae and dentaries show a condition where a continuous series of teeth is followed by an empty alveolus, or by a formative cavity with a tooth crown still lying in it. These make it probable that additions were made at the hinder end of the tooth row throughout the growing period of the animal. The only exception to this arrangement is that in a maxilla, M.C.Z. 1910, a minute peglike eleventh tooth is present although the tenth (a large tooth) has its incompletely formed crown still in the formative chamber, lying on its side and visible only through a very small opening through which passed the epidermal string to the enamel organ.

There are several cases in both maxilla and dentary where a tooth placed anteriorly to one which is very heavily worn is itself little touched by wear. These suggest that a very worn tooth could be shed by resorbtion of the ossified gum and then replaced. That this was so is confirmed by the occasional occurrence in the anterior part of a jaw of an empty alveolus between teeth which are themselves completely co-ossified with the jaw. Finally the left premaxilla of 4462 shows an admesial tooth crown in the alveolus, whilst the neighboring tooth is in use, and both the teeth in the other premaxilla are fused onto the bone in the normal manner.

This individual (4462) has an essentially complete dentition with maxillary tooth No. 10 still incomplete. It seems quite evident that the crown of the first left premaxillary tooth is that of a replacement.

It thus appears that a tooth change, of an occasional nature at any rate, took place in the remarkably specialized dentition of *Bolosaurus*.

The complete dentition of *Bolosaurus* is as follows:—

The two teeth in the premaxilla are similar, lie close together, and incline forward in front of the skull. The crown is laterally flattened, produced into a backwardly turned cusp in front with a posterior extension of the crown behind. The teeth are evidently prehensile hooks, placed tightly together and projected forward as if to lay hold of some small object as food.

The root is flat, oval in section, and fused into the bone.

The first maxillary tooth is a laterally compressed and forwardly directed structure, whose crown is injured in all known cases; it lies only little behind the lateral premaxillary tooth.

The second tooth in the maxilla is best shewn on the left side of 4462, from which it is evident that teeth nos. 2-4 are all very similar, their structure changing a little so that 5 merely continues its direction of change.

In each case the root, if broken across, appears as an oval, obliquely placed so that its long axis lies at about 30° to the median plane of the skull.

The outer and anterior part of the crown is bulbous, and ends in a blunt point directed inward and backward. This cusp is truncated by a face which lies in general very nearly transversely on the skull. This surface is divided into two shallow depressions which are separated by a low rounded rib beginning at the summit of the cusp. The surface of these depressions becomes horizontal toward the root of the tooth and ultimately ends in a ridge which cuts them and forms a cingulum round the inner and hinder sides of the cusp.

From this point backward to the ninth tooth there is no real change in structure but the whole tooth becomes larger, though very little higher, and the outer surface more bulbous. The line where the outer surface of the cusp meets the anterior border of the front depression on the inner surface becomes a ridge, which develops until its base forms a marked rounded swelling just above the neck of the tooth, separated by a notch from that which lies behind it.

The tenth tooth is usually smaller than the ninth; the eleventh is variable in structure, sometimes a rather simplified and smaller version of the tenth, in some cases a mere peg.

This remarkable maxillary dentition wears in a unique manner. Each tooth first shows signs of wear in the form of a flat facet lying at an angle of about 45° to the horizontal, the admesial end being the higher, whilst a horizontal line on the facet runs in the general direction of the tooth row and not parallel to the principal plane of the skull.

The anterior end of each wear facet lies a little admesial of the hinder end of the facet on the next anterior tooth. The wear begins on the anterior ridge of the cusp and on the horizontal ledge of the inner depression, an L-shaped area. It spreads ultimately to the rounded hinder surface of the cusp and ultimately becomes continuous from the summit of the cusp to the cingulum, with a central unworn area the deepest point of the depression on the cusp.

The lower dentition consists of eleven teeth. The anterior teeth in the dentary are best shown in 4462. The first tooth is placed very nearly at the tip of the bone and is directed upward and forward; it has a blunt anterior cusp, a little backwardly turned, and a concavity behind it.

The second tooth, still in the symphysis, is similar but upright and smaller. The third tooth has the structure found with some modification throughout the rest of the series.

The fifth tooth has a crown of oval section, the long axis being directed from outward and in front, to inward at the back.

A bluntly conical cusp rises from the hinder and inner part of the crown, which has a low ridge separating two flatter surfaces on the front and outer face. The base of this cusp rises from a large cingulum in front, whilst a mere trace of a cingulum surrounds its inner and posterior side.

The posterior cingulum is only seen in the tooth just described; in general, teeth farther back in the series have bulbous crowns without anything to break the curved inner face of the great cusp.

The anterior and outer cingulum is widened so that the tooth crown comes to have a rhomboidal horizontal section. The wear facet begins on the outer side of the tip of the main cusp, then cuts into the edge of the cingulum, extending with time until these two facets join exactly as in an upper tooth, and finally forming a large, nearly flat surface.

Jaw Mechanism

The dentition as a whole has in the front teeth — two or perhaps functionally three pairs above and one below — a prehensile apparatus, narrow from side to side, projecting well forward in front of other parts of the head, and shewing so little sign of wear that it evidently formed only a mechanism for picking up and making accessible to the tongue some type of food.

The rest of the dentition is a cutting device, divided into short lengths as is the cutter bar of a hay mower. Each tooth has its own wear facet, which maintains a sharp, scissor-like cutting edge anteriorly and sometimes on other borders.

This is clearly a cutting mechanism adapted to relatively small food masses. But it is also a grinding mechanism of an unusual kind.

There is no real parallel to this remarkable arrangement amongst mammals, but such a lizard as *Uromastix*, or even in a modified form *Sphenodon*, affords a parallel. Unfortunately whilst *Uromastix* is said to be completely vegetarian, *Sphenodon* eats only animals, so that it is evidently impossible to determine the diet of *Bolosaurus*. But the delicacy of the anterior teeth, both those in the premaxillae and in the dentary, is such that it is difficult to believe that they can ever have been used to detach parts of plants. On the other hand, they seem well adapted to seize and hold firmly small animals, insects and their larvae, earthworms or snails.

Thus it is not impossible that *Bolosaurus* was an "insectivore."

Further light might be shed on the feeding habits of *Bolosaurus* by a discussion of jaw movements and musculature.

The jaw articulation much resembles that of *Dicynodon* in that the articular possesses an articular face, very much elongated from back to front, presenting to the quadrate a surface convex along its length, and with a central ridge separating the two condyles on each quadrate, which prevents disarticulation whilst leaving a possibility of free movement.

There seems no doubt that two separated cartilaginous condyles, convex when seen in side view, completed the quadrate bone.

Such a structure allows the lower jaw to slide backward and forward with respect to the upper jaw, while the mouth is open or closed. It permits of nice adjustment of the upper and lower anterior teeth for holding a possibly moving piece of food, and it allows the cheek teeth of the lower jaw to be pulled to and fro in contact with the upper teeth so that obliquely placed wear facets may cut against those on the other jaw.

In discussion of the musculature these possibilities must be kept in mind.

The other peculiar structure of the lower jaw is the high "coronoid" process projecting very much above the line of insertion of the dentary teeth.

This process is set back from the outer surface of the jaw so that not only does it lie mesial of the temporal arch, but leaves between these two bones a space of some width which ends below at a cylindroid out-turning of the jaw surface to which muscle may well have been attached.

The first interpretation of the coronoid process which presents itself is that it served as an attachment to pennately arranged muscle fibers, which would have given a very powerful bite. But such an arrangement seems improbable because: (a) it is apparently impossible to arrange such muscle so as to allow use to be made of the sliding movement that the jaw articulation makes provision for; (b) it is impossible to so arrange the muscles as to allow the mouth to be opened to any reasonable extent; (c) such a distribution of muscles provides no explanation of the existence of the temporal vacuity. It follows therefore that some other arrangement of muscles must have existed. The simplest explanation is to suppose that large temporal muscles, attached as they must have been to the inner surface of the temporal region of the skull roof, converged on the summit of the coronary process. Such an arrangement is impossible because muscles so attached would be too short to lengthen sufficiently to allow the mouth to open to a reasonable amount; and they again provide no explanation of the temporal vacuity.

It therefore seems probable that the main jaw-closing musculature arose from the lower surface of the bones of the temporal region, the fibers passing directly downwards nearly parallel to one another in two sheets: one on the inner side of the process, inserted in effect in the supra-meckelian fossa; the other, a masseter, being attached to the curved outer surface of the base of the process. Such an arrangement allows the mouth to be so far opened that a centimetre or so separated the tips of the anterior upper and lower jaw teeth when the mouth was fully open.

Furthermore such an arrangement of muscles allows the jaw to be slung up in such a way that an independent musculature could draw it forward and backward, inducing a rocking motion determined by the shapes of the articular surfaces of the quadrate and lower jaw.

And such a masseter muscle would extend over the whole area of the temporal vacuity, which would allow it to thicken in contraction, even although it rests against a vertical sheet of bone, the coronoid process.

Thus neither the temporal muscle nor its derivative the masseter is attached to the coronoid process, and some other explanation of its function must be found. The longitudinal movements of the jaw made possible by the nature of the articular surface of the articular, and shewn by the wear of the teeth to have occurred, must have been made by the action of muscles. The jaw could be pulled forward by the contraction of anterior pterygoid muscles, but the shape of the temporal region is such that it is difficult to imagine how it could be moved backward. The temporal muscles seem to have been vertically placed. But it may well be imagined that a special muscle might arise as a slip from the temporal muscle primordium whose origin migrated ventrally along the posterior wall of the temporal space, so that its horizontally directed fibres came to be attached to an upgrowing coronoid process, and thus brought about the backward movement of the jaw which is shewn to have occurred.

The only remaining necessary muscles are some which pull the jaw as a whole forward, and provide some mode of opening the mouth.

In other contemporary reptiles the jaw is pulled forward by an anterior pterygoid muscle which, arising from the pterygoid or from the dorsal surface of the palate anterior to its articulation with the basisphenoid, extends downward and backward internal to the lower jaw until it passes below the hinder part of that structure and is attached to its outer surface.

The muscle thus runs antero-posteriorly nearly parallel to the lower jaw and by its contraction pulls it forward.

A posterior pterygoid muscle is usually present in early reptiles. Arising from some part of the palatoquadrate cartilage or bones in its vicinity, it passes out to the hinder part of the lower jaw, and its action includes a component whch pulls the jaw forward.

Early reptiles generally include a hyoidean musculus depressor mandibuli, inserted on a definite retroarticular process of the articular bone of the lower jaw. As no such process is known in *Bolosaurus*, it is probable that no such specialized muscle existed, and that the mouth was opened by the activity of a series of muscles of hyoidean and hypoglossal innervation.

Sclerotic Plates

Sclerotic plates are preserved in both orbits of specimens 4320 and 4327. In three of these cases from 15 to 17 individual plates can actually be counted, and in each case it is evident that not much more than half the circumference of the eye is accounted for.

The left eye of 4320 shows the plates surrounding the anterior half of the eye ball practically uncrushed and in what was apparently their original position, surrounding a circular space for the cornea and otherwise lying in an outer hemisphere of an approximately spherical eye. From this specimen it seems certain that the upper plates were much narrower than those of the lower half of the eye, and the arrangement in Figure 1 is based on this specimen.

Vertebral Column

Vertebrae occur in association with characteristic teeth of *Bolosaurus* in A.M.N.H. 4320, 4326, M.C.Z. 2088 and M.C.Z. 2087. The last association is in a tight-packed mass of more or less articulated material where there is no real doubt that the vertebrae belong to the teeth: the bones are however crushed and covered with a thin but irremovable film, and the vertebrae serve only to confirm the determination of two small strings of vertebrae in 2088. These, with two damaged intermediate vertebrae, make a total of 14 not including either axis or sacrals; their total length is approximately 95 mm. The number of presacral vertebrae in Lower Permian reptiles varies from 27 in pelycosaurs to some 21 in cotylosaurs. Thus the series in *Bolosaurus* represents more than half the presacral region. An associated dentary is large, probably bigger than 4327 by 10 or 15 per cent: the skull length being *circa* 45 mm., + 15 per cent=51.8 mm. Twenty-one vertebrae would be 142.5 mm.=2.75 times skull length. This is of the order of proportion said by Romer to be common amongst primitive pelycosaurs and reptiles in general.

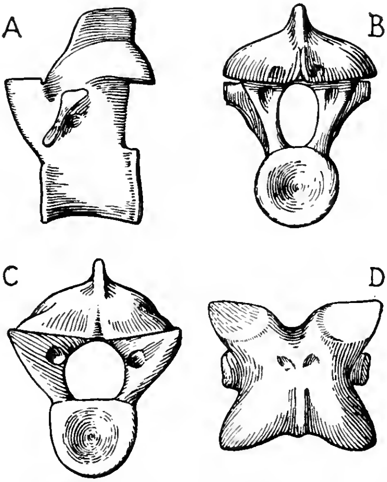

Fig. 5. *Bolosaurus striatus* Cope. M.C.Z. 2088. x 2. Trunk vertebra. *A*, left lateral, *B*, posterior, *C*, anterior, *D*, dorsal aspect.

The structure of an individual vertebra, based on the second of this series, is shewn in Figure 5.

The centrum has a nearly circular posterior surface, with a conical pit continuous with that at the front end. The pit leaves a definite articular ring, largely carried out laterally on special out-turnings of the lateral surface. The upper surface is little notched by the spinal cord. The anterior end of the centrum has its articular surface drawn outward and upward to the foot of the neural arch, but the central conical pit is similar to that at the other end of the bone

The ventral surface is nearly straight from front to back, is a little flattened and passes smoothly into the rather concave side. In adults no trace of the neurocentral suture remains, but separated bones shew that as in early reptiles in general a wedge-shaped base of the pedicel of the neural arch fits into a deep depression on the upper surface and side of the centrum, toward the front.

The neural arch of the vertebra figured is considerably higher than that of smaller specimens, but the straight, nearly vertical front border of the centrum from below the prezygapophysis to the ventral margin occurs in essentially the same form in smaller specimens. The canal for the spinal cord is large, as in all small animals, but the thickened upper parts of the pedicels and their excavation by pits below the zygapophyses are unusual.

The swollen upper surface of the posterior zygapophyses, the nearly horizontal articular surfaces, and the great width across the zygapophyses are familiar features of the cotylosaur vertebrae, found also in a less extreme form in the pelycosaur *Varanosaurus*, and in a more extreme form in *Seymouria*. The rib facet is carried at the end of a considerable transverse process extending downward and forward as a rather narrow face a little hollowed, not covered by a perichondral layer, and not invading the centrum. There are no intercentra.

The vertebrae have essentially the same structure throughout the series of fourteen, but the width across the postzygapophyses of the most anterior of these vertebrae is 9.55 mm., that in the tenth vertebrae 7.93 mm. The neural arch thus becomes more slender posteriorly in contrast to the condition in *Seymouria*, but in agreement with Broili's figure of a vertebral column of *Labidosaurus*.

Ribs

Small fragments of ribs exist in connection with the Boone Ranch string and with skull A.M.N.H. 4320. They are all badly preserved, short lengths and shew nothing notable.

Abdominal Ribs

Specimen 4320 retains, in part as bone and in part only as impression, a small patch of abdominal ribs in the form of tight-packed slender rods, each itself built up from many series (perhaps four or five) of very short, almost scale-like elements. These rods meet their fellows of the opposite side at an acute angle, about 45°, the points of the V's so made being forwardly directed. There are about six or seven rods to each vertebra.

Limbs

No intelligible remains, other than a very badly preserved shoulder girdle and an ilium, of either of the limb girdles exist.

The humerus is represented by a flattened, much broken distal end crushed onto skull 4462. This shows that the bone is narrow, with a well formed radial condyle facing at right angles to the shaft; there is a trace of an ulnar surface on the end of the bone, and a well developed but rounded entepicondyle with a large foramen. The ectepicondylar region is lost. The bone is an unusually slender version of the common Basal Permian reptilian type, owing its characters merely to its small size.

The shoulder girdle shews only the presence of both precoracoid and coracoid.

The acetabular part of a left ilium lacks the dorsal extension and is of common form, unusual only in the rather marked boundaries of the dorsal articular surface on the "wedge". A fragment presumably of an ischium shows nothing characteristic.

The upper ends of a pair of femora belong to M.C.Z. 2087. The bone is long, slender, with the proximal articular surface set directly at right angles to the shaft, and much wider than deep. There is an internal trochanter very near to the head, forming the truncated end of a deep ridge which runs obliquely across the shaft.

The M.C.Z. No. 2087 includes what is apparently a knee with the lower end of the femur lying nearly parallel to a tibia and fibula. The tibia which is nearly twice the diameter of the fibula at the middle of its shaft has a widely expanded head. It seems to be certain that both femur and tibia are longer than the cranial length.

A series of ungual phalanges probably of a hand are also preserved in this material. They have a concave articulation from which they narrow to a point, the ventral surface being flattened proximally and sometimes bearing a raised tendon insertion.

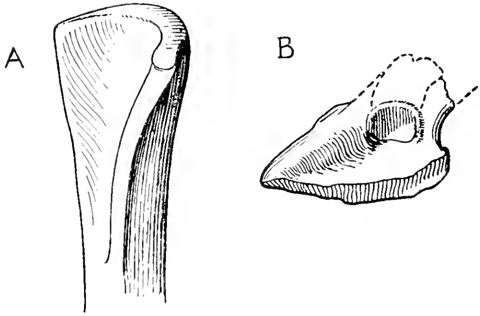

Fig. 6. *Bolosaurus striatus* Cope. M.C.Z. 2087, x 2. *A*, proximal end of right femur. *B*, acetabular part of left ilium.

Systematic Position

Case in his early work confused *Bolosaurus* with the animal which Broom subsequently named *Ophiodeirus*. Somewhat earlier Williston had described *Araeoscelis*, and Broom, rightly as it now appears, regarded *Ophiodeirus* as a related but different animal. *Araeoscelis* has been discussed by von Huene, Broom, Romer and the present writer, and both it and *Ophiodeirus* are now being described in detail by Mr. P. Vaughn.

For my immediate purpose all that is necessary is to point out that comparison of the drawings of this paper with any of those of the *Araeoscelis* skull published by Williston (1913), von Huene (1944), Broom (1931), and Watson (published in Parrington 1937) will shew that there are no real resemblances other than size between *Bolosaurus* and *Araeoscelis*. The structures throughout differ; the temporal fenestra, for example, is in a different place, and has different bordering bones.

We can therefore deal with *Bolosaurus* as an independent form, without any recognized relatives. It is of Lower Permian age, known only in the Wichita beds. It is evidently a reptile. Thus the only great groups which need be considered (in the first instance) are those which have contemporary members. These are Cotylosaurs of each of the two divisions Diadectomorpha and Captorhinomorpha, Pelycosaurs, and *Mesosaurus*. European long-limbed Lower Permian reptiles, *Aphelosaurus*, *Kadaliosaurus* for example, are so incompletely preserved that no useful comparisons are possible.

The vertebrae of *Bolosaurus* lack intercentra, but are otherwise of Cotylosaur type, with relatively small centra, with deeply conical ends, and perforate. The neural arches are heavy with nearly horizontal zygapophysial articular faces, widely separated, and with swollen, rounded upper surfaces of the postzygapophyses. The neural spine, though a definite structure, is low. The neural canal is, in large individuals, higher than it is wide, the neural arch being exceptionally elevated. There is a long rib articulation at the end of a sheet-like process, which passes downward and forward toward the place where an intercentrum might be anticipated. The differences are insignificant and imply that some origin from Cotylosaurs lay not very far back.

The Cotylosaurs are divided into two groups, the Diadectomorpha, in which there is a large otic notch, the lower end of the quadrate standing almost vertically some way in front of the occipital condyle, and the Captorhinomorpha, in which there is no otic notch (or only a completely vestigial one), the cheek ending behind at a straight vertical border, which lies essentially along the hinder edge of the quadrate, little, if at all, in front of the occipital condyle.

The simplest comparison shews that although the occipital condyle of *Bolosaurus* is visible in side view behind the hinder border of the cheek, there is no vestige of such a Diadectomorph structure, the hinder border of the cheek, quadratojugal, squamosal and tabular forming essentially a continuous slightly waved line. Thus the Cotylosaur relatives of *Bolosaurus* may have lain amongst the Captorhinomorphs.

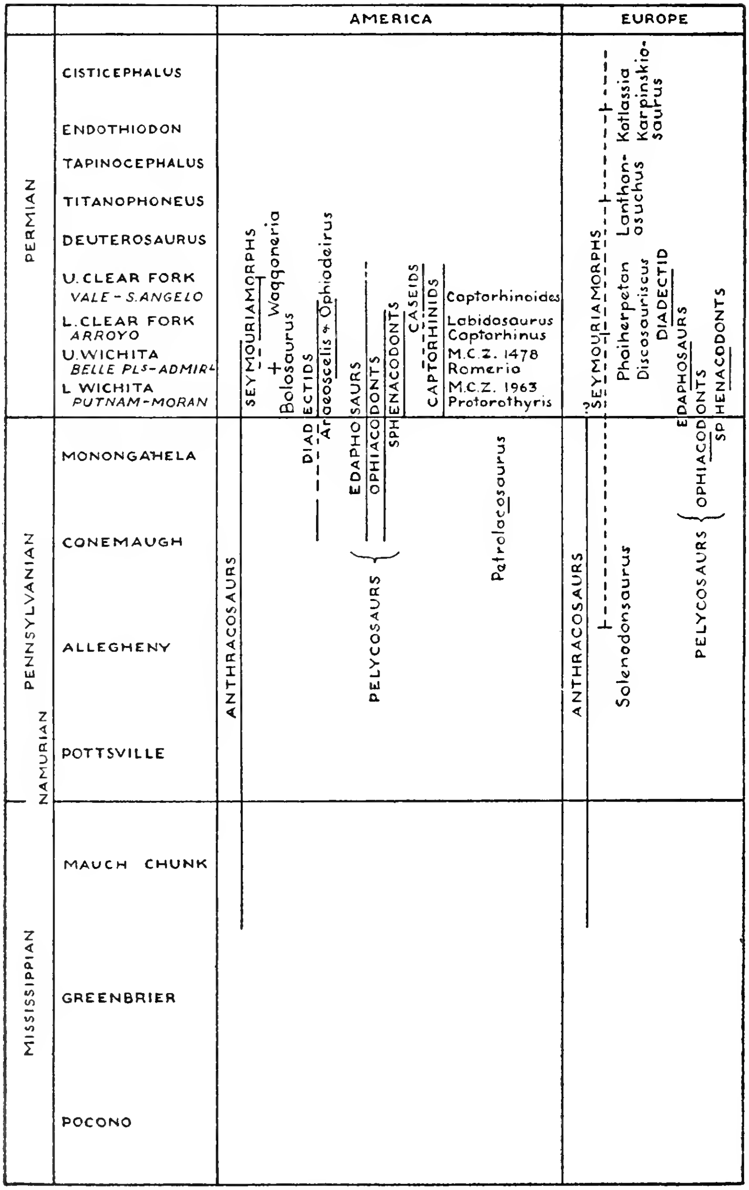

Table of Horizons

THE CAPTORHINIDS

The only well known Captorhinomorphs are *Captorhinus* and *Labidosaurus*, closely allied forms, both of late date, leading on to a series of less well known animals found by Professor Olson in the still higher beds of the Texan Permian.

L. I. Price was the first to find and describe Captorhinomorphs of earlier date and more primitive structure than *Captorhinus*, and his two genera, *Romeria* and *Protorothyris*, were correctly identified by him as exhibiting an approximation of structure to the more primitive Pelycosaurs. Recently the Museum of Comparative Zoology has collected four more individual skulls and parts of the skeleton of *Protorothyris*, and other skulls of different ages which connect that form with *Captorhinus* itself. Figures 7, 8 and 9 shew dorsal, lateral and posterior views of the skulls of the animals so represented in the form of very careful reconstructions, made by measurements at a large magnification, from all this material so far as it is at present prepared.

The *Protorothyris* material comes from Cottonwood Creek in the Moran formation of the Wichita. From the same horizon there is a single skull (M.C.Z. 1963) well preserved and apparently little distorted, except that the cheek, at least on one side, is pressed somewhat inwards. This skull, which I do not propose to name, comes from the same locality and horizon as that of *Protorothyris* but is quite obviously of more advanced character. The preservation is good though some structures are difficult to see.

The next stage is *Romeria*, still represented only by the type skull described by Price. This comes from the Archer City bone bed in the Putnam formation which overlies the Moran. The skull is well preserved, little distorted, and shews nearly all the sutures admirably; but the postparietal and tabular (if they were present) have been lost.

In the succeeding Admiral formation there comes from Rattlesnake Canyon the skull M.C.Z. 1478, perfectly preserved, uncrushed and complete. This is very evidently an immediate forerunner of *Captorhinus*, which again I leave without a name in the expectation that someone will carry out a further preparation and give a complete account of the whole structure, including the palate.

Finally *Captorhinus* itself, represented by a large amount of material from the Arroyo of the Clear Fork division of the Texan Permian, which still awaits a complete description.

Description of New Forms

Protorothyris

Protorothyris is a small reptile whose skull is about 50 mm. in length. Of the five known skulls in the Museum of Comparative Zoology three are dorsoventrally compressed so that the cheeks have spread out laterally, and in the type specimen there is some displacement of bone in front of the parietal. The other two skulls look at first sight quite different, for in them the top of the head is a comparatively wide, flat surface, and the cheeks stand very nearly vertically, their posterior portions having been pressed inwards so that the outer surface of their upper and posterior parts lies mesial to the supratemporal lateral border. This displacement implies the lack of a firm sutural attachment between the supratemporal and the squamosal, and the existence of a firm attachment between the anterior part at any rate of the postorbital and the postfrontal and some portion of the lateral border of the parietal.

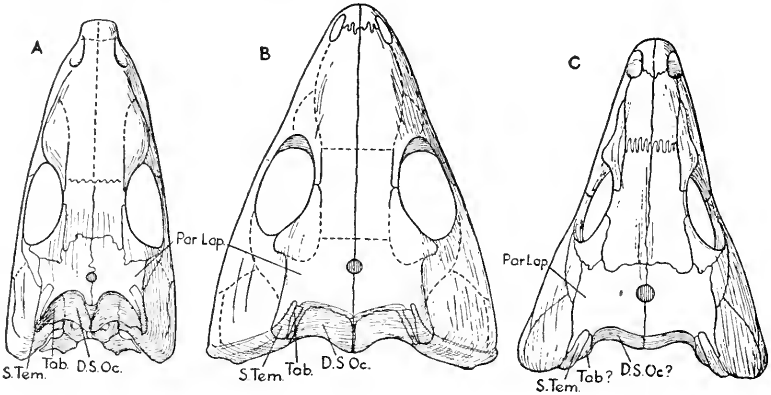

Fig. 7. A.B.C.

The skull, restored from the whole of the material, is high in proportion to its width, and it is markedly square cut in transverse section in the region of the pineal foramen. This shape is confirmed by an undistorted, articulated clavicular arch belonging to one of the skulls. Anteriorly the prefrontals form a bulge over the lachrymal on the side of the face, which below it stands almost vertically. The occiput has been partially exposed and is well preserved in one of the new specimens, and is of extraordinary interest. The basi- and exoccipitals are not preserved, but the supraoccipital and the paroccipital are well exposed from the occipital surface, and are very remarkable indeed in structure.

There is no real difficulty in making a tentative restoration of the basi- and exoccipital bones, which are indeed preserved in skulls still unprepared. The supraoccipital forms the upper half

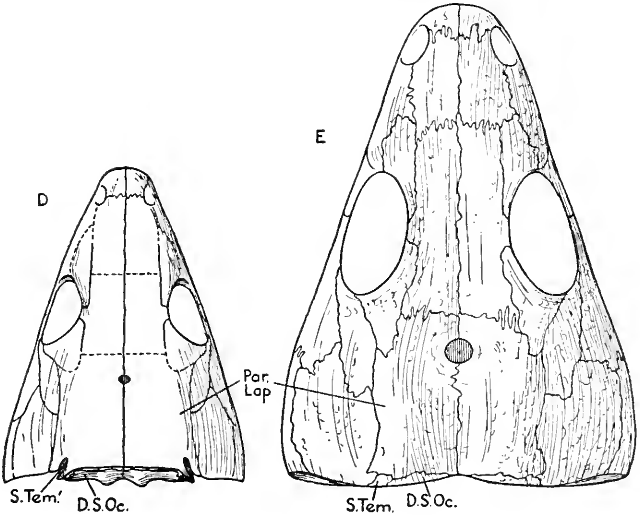

Fig. 7a. D.E. Dorsal aspect of a series of Captorhinid skulls, in order of time. A little less than natural size. *A*, *Protorothyris archeri* Price, Moran Formation; *B*, M.C.Z. 1963, Moran Formation; *C*, *Romeria texana* Price, Putnam Formation; *D*, M.C.Z. 1478, Admiral Formation; *E*, *Captorhinus* sp., Clear Fork Formation. The originals of *A* — *D* are in the Museum of Comparative Zoology, that of *E*, in Mr. Parrington's collection. Reference letters: *D.S.Oc.*, dermosupraoccipital; *D.S.Oc.?*, facet for dermosupraoccipital. *Par.Lap.*, parietal lappet; *S.Tem.*, supratemporal; *S. Teḿ.*, incision formerly occupied by a lost supratemporal; *Tab.*, tabular; *Tab.?*, a facet to which a tabular was probably attached.

of the border of the foramen magnum. It has an extremely narrow contact on the occipital surface with the exoccipital, a straight suture with the paroccipital passing outward and up-

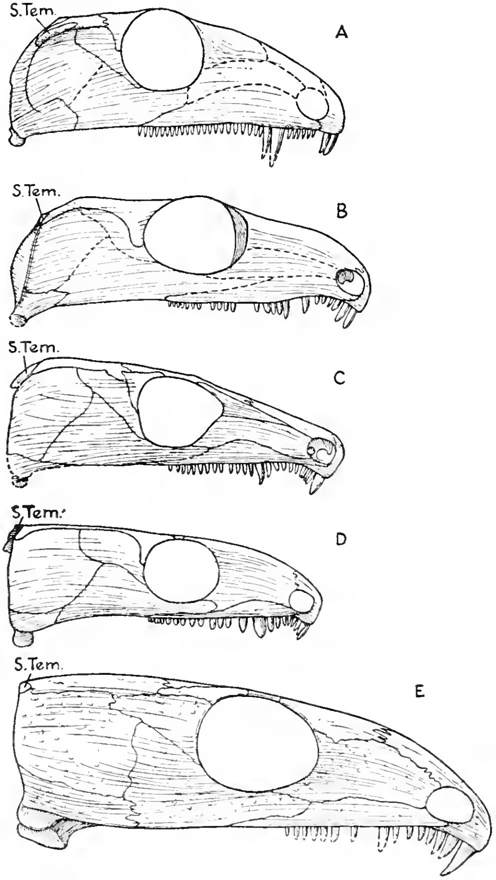

Fig. 8. Lateral aspect of the series of Captorhinid skulls shown in Figures 7 and 7a, same magnification. Lettering as in Figure 7.

ward to the border of the temporal fossa. Above this level the supraoccipital forms a thin pent house over the brain, its dorsal surface stretching upward and forward except for a narrow median ridge whose posterior surface rises directly upward to join the extreme posterior process of the dermosupraoccipitals. A deep groove passes forward for an unknown distance on each

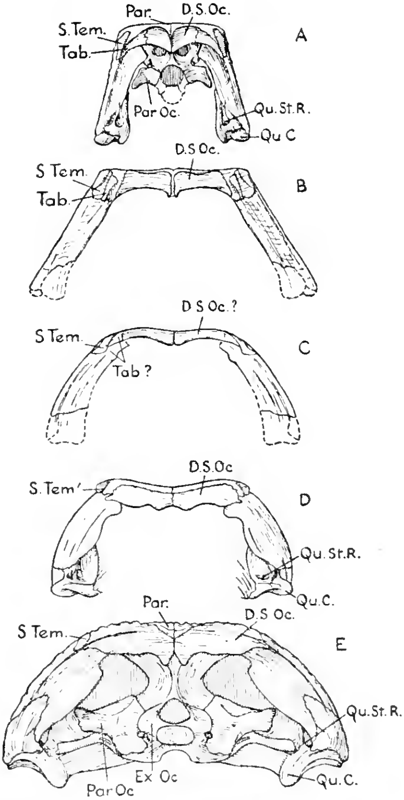

Fig. 9. Occipital aspect of the series of Captorhinid skulls shewn in Figures 7 and 7a, same magnification. *D.S.Oc.*, dermosupraoccipital; *D.S.Oc.?*, facet for dermosupraoccipital; *Ex.Oc.*, exoccipital; *Par.*, parietal; *Par.Oc.* paroccipital; *Qu.C.*, quadrate condyle; *Qu.St.R.*, quadrate stapedial recess; *S.Tem.*, supratemporal; *S.Tem′.* notch for supratemporal; *Tab.*, tabular; *Tab.?* facet for attachment of tabular.

side of the ridge, so separating a powerful lateral process which rises straight up from the supraoccipital to support the lateral margin of the dermosupraoccipital at its suture with the tabular.

Below the process which partly roofs it, lies the posttemporal fossa bounded laterally by the squamosal.

The paroccipital is a short bone whose admedian end is a surface for contact with the exoccipital, whilst the outer surface is apparently flattened and a little concave antero-posteriorly, and lies in contact (or nearly so) with the inner margin of the inturned hinder flange of the squamosal. The upper border of the paroccipital forms the lower margin of the small posttemporal fossa, and the lower part of the whole sweeps forward so that as much as can be seen of the lower surface is rounded.

The whole arrangement allows of a comparison with the braincase of *Captorhinus* as described by Price, although it is very different indeed in proportion and in general shape. The resemblance lies largely in the existence of the three dorsal processes of the supraoccipital, which serve to attach it to the dermosupraoccipital and the tabular. In *Protorothyris* the shape and directions of these processes are clearly determined by the shape of the occiput as a whole. Their nature in *Captorhinus* will be dealt with later.

The only other cartilage bone of the skull of which any description can be given is the quadrate, which is well shewn from behind and within in one of the specimens. The bone is in some ways like that of *Captorhinus*, the difference being due to the special functional adaptation of the bone in *Captorhinus*.

In *Protorothyris* the quadrate has a condyle whose lateral exposure is a small circular area which fits accurately a corresponding notch in the articular. This condyle is a little overhung by a small quite definite circumscribed process on the posterior surface of the quadrate which lies just mesial of the overlapped surface for the quadratojugal, a bone whose relations can be judged quite adequately from the figures. The inner condyle of the quadrate is somewhat longer anteroposteriorly than the outer one, from which it is separated by a shallow groove crossing the articular surface obliquely, and thus obscurely separating inner and outer condyles. The inner condyle is quite markedly produced in posterior view, and the whole posterior surface of the quadrate is crossed by a transverse ridge which thickens out towards the outer surface of the skull to form the small protuberance above referred to. Above this transverse ridge the bone extends dorsally perhaps to the region of the lower surface of the paroccipital, and at this point it is of considerable anteroposterior extent. The inner surface, which is of course overlapped in part by the pterygoid, is excavated by a rather sudden depression, the stapedial recess. This is overhung and bounded posteriorly by a strong ridge, extending upwards from the posterior surface of the quadrate. This surface is narrow, notched at one point for a quadratojugal foramen, and is otherwise in contact with the quadratojugal for an unknown distance.

It may be noted here that in the Captorhinid *Melanothyris morani* Romer, from the Dunkard near Blacksville, West Virginia, I was able to prepare an almost complete stapes which agrees in principle with that of *Captorhinus*, but in effect shews a modification in shape analogous to that found in the immensely larger stapes of *Ophiacodon*. The quadrate of this reptile, which I also prepared, is extremely similar to that of *Protorothyris*, and it is evident that the stapes rests in the stapedial recess in a way exactly similar to the stapes of *Captorhinus* itself.

This then affords very useful evidence of the existence of the pelycosaur-like arrangement of the ear region in a very primitive Cotylosaur.

The skull of *Protorothyris* is remarkable for the sharp distinction between a table essentially flat and lying on the upper surface and the cheeks, which are themselves again very nearly flat and stand nearly vertically on the side of the head, attached loosely to the table. The table is made for the greater part of its area by a pair of large parietals. The hinder edges of these bones appear to be down turned, are cut into by very definite rounded depressions, and support directly a pair of dermo-supraoccipitals and a pair of tabulars. These bones rest on the supraoccipital and serve to connect it with the skull table. The postero-lateral corner of the parietal is carried backward and outward for some distance as a plate whose upper surface is deeply notched for the attachment of a supratemporal. The free upper surface of the parietal is indeed extended into a long and rather slender point clasped between the admedian edge of the supratemporal and the upper part of the tabular, these two bones coming into contact behind it. On the flat upper surface of the parietal there is a pineal foramen a little in front of the emargination on the hinder border of the bone. Laterally to this the parietal extends directly outward as a flat sheet ending in a border directly continued by the lateral surface of the supratemporal, and not suturally attached to anything throughout at any rate the greater portion of its length. Anteriorly the parietal has a firm sutural attachment with the postfrontal and the frontal, but its lateral border is still without any direct sutural attachment to other bones.

The structure of the face is obvious from the Figures 7, 8 and 9 and need not be seriously discussed here, but the nature and mode of attachment of the cheek is of great importance.

The maxilla is in contact throughout the whole of its upper border with the lachrymal and jugal, the exact line of suture between these two bones being uncertain. The rather large circular orbit is bounded below largely by the jugal; the hinder part of its border is made by the postfrontal which extends downwards as a definite process for almost half the height of the opening, and by the postorbital which is attached by a long suture to the jugal and posteriorly has a suture with the squamosal.

The squamosal is a large bone with a somewhat rounded upper margin of the lateral surface, forming the greater part of the hinder border of the cheek, joining the quadratojugal below. Behind its apparent hinder border the bone is inturned onto the occipital surface, where it passes inwards covering the hinder surface of the quadratojugal and of the quadrate above the quadratojugal foramen for an unknown distance. This inturning continues to the margin of the pointed hinder end of the table formed by the tabular and supratemporal, when it turns forward and so runs for a considerable distance in contact with the under surface of the tabular, supratemporal and parietal.

In *Melanothyris*, whose structure in this region is identical, I have seen in a fragment accidentally removed in preparation that the upper surface of the squamosal and the lower surface of the tabular-supratemporal process completely lack any signs of sutural attachment to one another. They are perfectly smooth, connected in life only by soft tissue.

Anteriorly the squamosal in *Protorothyris* is attached to the postorbital and jugal, the exact line of sutural attachment being uncertain. The upper border of the squamosal and postorbital bones is in contact with the parietal, which rests upon them shewing in side view a thin strip of bone which is in effect a free lateral surface extending almost up to the attachment of the postfrontal to the parietal.

In other words there is a free "table" in the *Protorothyris* skull similar to that found in anthracosaurine Labyrinthodonts, remarkable in its non-sutural attachment to the postorbital and squamosal. To this point I shall return later in the paper. The postfrontal is attached by suture both to the parietal and the postorbital, the two bones remaining in articulation even in the two skulls in which the hinder parts of the cheek are pressed inwards.

The dentition of *Protorothyris* is interesting. There are two large somewhat backwardly directed teeth in the premaxilla. The sub-narial part of the maxilla and the part immediately behind has a row of small pointed recurved teeth. Then there are two large canines, followed by a rather uniform row of about twenty-two small teeth.

M.C.Z. 1963

A contemporary of *Protorothyris,* which is of somewhat more advanced structure, is represented by a skull, No. 1963, of the Museum of Comparative Zoology. This specimen is somewhat larger than *Protorothyris* but resembles it in having a flat "table" to which the cheeks are attached in such a way that the hinder part of the squamosal can be pushed inward below the table. There is somewhat unreliable evidence that the sides of the temporal region sloped outward at a greater angle than they do in *Protorothyris,* the quadrates being thus more widely separated. The hinder border of the table is emarginated on each side of the centre line, where a point passes down to the supraoccipital. The admedian part of each depression on the parietal is coated by dermosupraoccipital, the lateral areas by very small tabulars which do not meet the lateral borders of the dermosupraoccipitals.

The squamosal lies mainly on the lateral side of the cheek, but its upper margin turns inward below the "table", the flat surface so formed curving gently until it passes into the occipital surface. The lamina of bone which forms this surface passes downward to overlap the hinder surface of the quadrate and quadratojugal. It is bowed backward at about the middle of its height. That part of the squamosal which underlies the table is smooth, and the process made by the supratemporal and tabular rests directly on it.

The outer condyle of the quadrate resembles that of *Protorothyris.*

There is a septomaxilla lying within the nostril and forming a partial roof and hind wall to the olfactory chamber.

The dentition of this form comprises a graded series of four teeth in the premaxilla which are directed backward, the border of the bone being turned down in front. These are followed by three or four small teeth in the maxilla, behind which are an enlarged canine and a space for one anterior to it. Then follows a graded series, some shed teeth being represented by gaps, of about 19 or 20 small teeth becoming very small at the end of the maxilla.

Romeria

The next stage in the series is the type of *Romeria*, which comes from a higher horizon, the Putnam formation of the Archer City bone bed. This skull (M.C.Z. 1980) is essentially uncrushed and well preserved but lacks the occiput. In it the table is still obvious, and posteriorly at least is not attached by suture to the squamosal.

The supratemporal is a small bone which has, however, a little free lateral surface posteriorly but lies largely in a recess in the parietal. There is a facet on the hinder edge of the parietal which may be for a tabular, and mesial to this the hinder edge of the parietal, somewhat emarginated, is turned down at an angle, and was during life certainly covered by a dermosupraoccipital.

The posterior border of the outer part of the squamosal stands nearly vertically, and lies on a backwardly projecting ridge which borders a flat inwardly directed sheet of squamosal standing nearly vertically which must have overlapped part of the quadratojugal and the upper part of the quadrate. It is characteristic of the genus that the lateral surface of the squamosal is rounded and passes smoothly into the flat upper surface of the table. The quadratojugal and quadrate are both missing.

The dentition has an enlarged, rather blunt and somewhat backwardly directed tooth at the anterior end, behind which is a series of five smaller and progressively shorter teeth in the hinder part of the premaxilla. The anterior part of the maxilla has a series of four well spaced, small, but rather thick and blunt-pointed teeth, then two canines, the posterior with a recurved tip, and then a series of some fourteen teeth getting progressively smaller to the hinder end of the maxilla.

There is a septomaxilla of considerable dorsal extension whose floor plate presumably rests on the palatal processes of the premaxilla. It has a rounded depression in the hinder border leading backward, and a foramen anteriorly through the inner wall.

Romeria thus differs a little from the earlier form, M.C.Z. 1963, in the somewhat lesser emargination of the parietals, in the character of the supratemporal, and in the fact that the outer surface as seen in an occipital view is smoothly rounded.

M.C.Z. 1478

The next stage is represented by a single well preserved skull from Rattlesnake Canyon in the Admiral formation. In this skull the table is not distinguishable from the rest of the outer surface of the skull except posteriorly, where a small part of the extreme hinder end of the lateral border of the parietal is turned a little downwards, and borders a deep notch in which a very small supratemporal was fixed, the two forming a definite projection backward on the top of the squamosal. The hinder border of the two parietals forms a curve so slight that it is very nearly straight. It is continued by the hinder borders of the squamosal and quadratojugal. To this downturned flange is attached a pair of dermosupraoccipitals which pass downward and a little backward onto the occipital surface, where it is evident they are attached to the supraoccipital. They extend laterally almost, but not quite, to the notch for the supratemporal, where each is produced into a small free-standing process directed laterally.

There is no trace of a tabular, indeed there is little place for one. The mid-line of the parietal is a little depressed but otherwise the lateral parts of the bone pass down smoothly into the squamosal as they do in *Romeria*. There is an internal flange on the hinder part of the squamosal which bears a ridge flush with the outer surface, and this occipital part of the squamosal overlaps the quadratojugal and the upper part of the quadrate.

The quadrate still has an outer condyle which is cylindroid and little produced antero-posteriorly. The inner condyle, separated by a low oblique ridge, seems to be a good deal longer. A deep well marked stapedial recess, which ends in a definite pit, lies some little distance above the inner condyle to the vertical admesial side of which the pterygoid is attached, passing forward and inward in the normal manner.

The dentition of this animal consists of a graded series of four teeth in the premaxilla, all directed backward and the most anterior the largest. There are then four teeth in the anterior part of the maxilla, cylindroid with rather blunt points. Then there is rather suddenly a blunt pointed elongated canine tooth, behind which is a series of some fourteen teeth (including some lost ones) mostly short compared with the breadth, blunt, and getting smaller as they are followed backward.

This form is a good morphological ancestor (and perhaps an actual one) to *Captorhinus* itself.

Captorhinus

Captorhinus differs from the last form primarily in that the backward growth of the parietal has now proceeded so far that it has almost completely overridden the dorsal edge of the dermosupraoccipital, which however is visible as a very narrow strip of the upper surface of the skull. The supratemporal itself survives as a minute bone wedged in between the squamosal, dermosupraoccipital and parietal, with its posterior border continuous with those of the squamosal and dermosupraoccipital. The upper surface of the skull is rounded, the squamosal passing into the parietal without any break, though the hinder lateral extremity of the parietal (in some specimens at any rate) still forms a sharp outstanding point as in the Rattlesnake animal. The pineal foramen is bigger, and the general pattern remains as it was, but the outer condyle of the quadrate is elongated antero-posteriorly and is no longer cylindroid, the inner condyle is considerably lengthened, and the whole structure is one which slides rather than one which turns on a hinge.

The dentition still retains four backwardly directed teeth in the premaxilla of which the anterior is much the largest. The marginal teeth in the maxilla are all small and blunt pointed, though the fourth and fifth are enlarged "canines". They are followed by about a dozen small teeth. Mesial of this row two other rows of teeth occur, neatly spaced, with rounded and worn summits, forming a crushing mechanism. This is an individual peculiarity of *Captorhinus*.

It follows from all this that the earlier members of the Captorhinidae, especially *Protorothyris,* differ very greatly in structure from its late member *Captorhinus*, especially in the larger post-temporal and tabular bones of the skull table, in the loose attachment of the table to the bones of the cheek in *Protorothyris* in contrast to their firm attachment by suture in the latest form, and especially by the very extensive emargination of the hinder border of the parietals in *Protorothyris*, where these bones are connected to the supraoccipital by dermosupraoccipital and tabular bones, plunging down posteriorly deeply below neck muscles so that they rest on processes of the supraoccipital below. These attachments are three in number, one posteriorly where the extreme tip of the dermosupraoccipital rests on the most posterior point of the median ridge on the supraoccipital, and a lateral attachment somewhat further forward where the hinder borders of the dermosupraoccipital and tabular rest on a lateral process of the supraoccipital on the occiput. These three processes are separated from the dermal bones by passages which may only be very deep pits.

In the transition from *Protorothyris* to *Captorhinus* it is evident that one important part of the process is the steady obliteration of the emargination in the hinder part of the table by the growth backward, flush with the main surface of the table, of the effective posterior border of the parietal. This bone comes to override the upper border of the dermosupraoccipital, which itself extends out laterally to the disadvantage of the tabular, the process continuing until in *Captorhinus* the dermosupraoccipital stands nearly vertically on the occiput, has a broad upper surface on which rests the hinder border of the parietal, and actually sends upward a process which lies in contact with the posterior border of the parietal, and is visible on the upper surface of the skull roof.

As a result of these changes the three processes of the upper surface of the supraoccipital change their direction, though they retain their old contacts with the dermosupraoccipital, and thus attain the very remarkable shape seen in *Captorhinus* as figured by Price.

The significance of these changes and their nature may perhaps be better understood by an account of another form (a skull in my own collection, D.M.S.W., R 9) whose horizon and locality (other than that it came from Texas) are unfortunately unknown.

Paracaptorhinus neglectus gen. et sp. nov.

This skull with its articulated lower jaw was contained in a very hard, deep red nodule. Long weathering had removed a lamina from the top of the head, leaving, over most of the area, little above the lower table of the dermal bones. Similar fractures laterally display the sides of the face and series of teeth in section. On the left side the squamosal and quadratojugal have been entirely removed by weathering, though they are present, badly preserved, on the right. The occipital surface has been

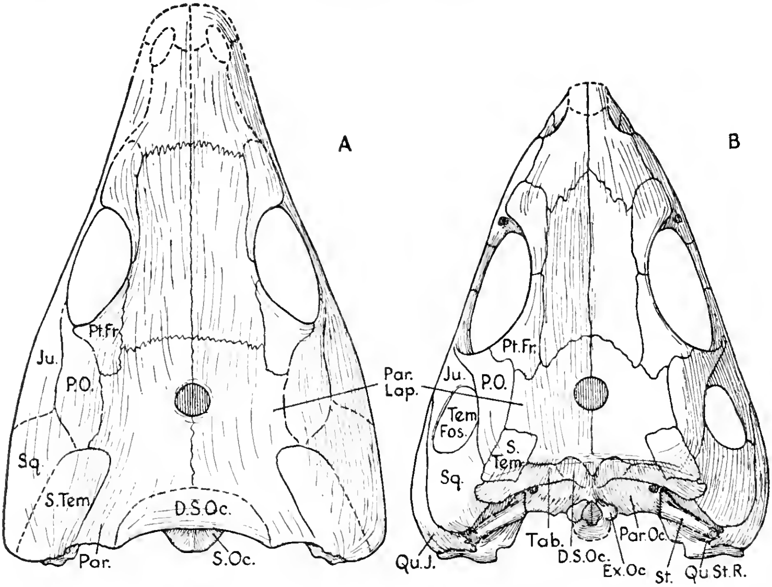

Fig. 10. Dorsal aspect of skulls. *A*, *Paracaptorhinus neglectus*, gen. et sp. nov., (type specimen D.M.S.W. R.9); *B*, *Eothyris parkeyi* Romer (type specimen M.C.Z. 1161); *D.S.Oc.*, dermosupraoccipital; *Ex.Oc.*, exoccipital; *Ju.*, jugal; *P.O.*, postorbital; *Par.*, parietal, *Par.Lap.*, parietal lappet; *Par.Oc.*, paroccipital; *Pt.Fr.*, postfrontal; *Qu.J.*, quadratojugal; *Qu.St.R.*, quadrate stapedial recess; *S.Oc.*, supraoccipital; *S.Tem.*, supratemporal; *Sq.*, squamosal; *St.*, stapes; *Tab.*, tabular; *Tem.Fos.*, temporal fossa. x 1.

prepared out and is well preserved, but it lacks opisthotics, exoccipitals, and a basioccipital. The outer side of the lower jaw is fairly well shewn and its hinder end is well preserved. So many features — such as a small conical retroarticular process and the square-cut occiput — resemble those of *Captorhinus* that for many years I regarded it as that animal. But re-examination and some preparation shews that it is really of very different structure.

The upper surface, which is continuous, is nearly flat, the lateral margin of the skull table being pushed up by the vertical squamosal on the right side and flattened on the left where the squamosal lay rather obliquely. Between the orbits it is transversely hollowed and the premaxillae are absent. Weathered fragments of the nodule retain excellent impressions of the outer surfaces of the maxillae and their teeth, and of the dentaries and some of the more anterior lower jaw teeth. On the whole the structure is very well shewn; the sutures (seen, it will be realized, as if from within the head) are in general confirmed by a comparison of the two sides. The structure will be better understood from the figures than from a lengthy description.

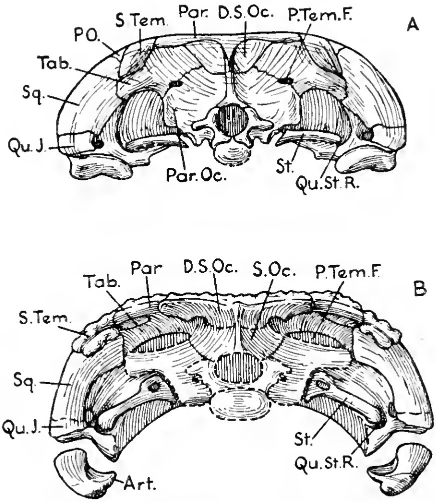

Fig. 11. Occiputs of *A*, *Eothyris*; *B*, *Paracaptorhinus*, x 1. Reference letters as in Figure 10 with: *Art.*, articular; *P.Tem. F.*, posttemporal fossa.

There is a large flat parietal which appears to reach the hinder extremity of the skull laterally to its attachment to the dermo-supraoccipital. This bone has a very considerable excavation of its lateral border, extending for nearly half its total length, which receives the upper border of the supratemporal. Anteriorly to this the lateral border, visible on the left side, is rounded and seems rather to have rested in a groove in the postorbital than to have been suturally attached to it. Anteriorly there is a square-cut notch in which the hinder end of the postfrontal lies, which is best seen on the left side of the specimen but can be traced on the right.

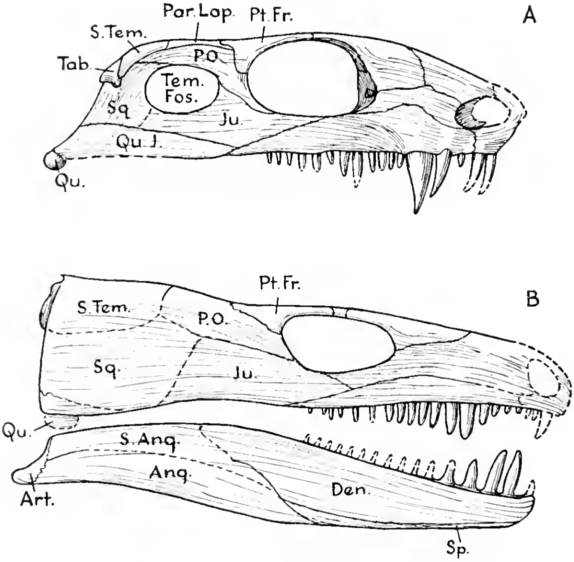

Fig. 12. Right lateral aspect of the skull of *A*, *Eothyris*; *B*, *Paracaptorhinus*. x 1. Reference letters as in Figures 10 and 11, with: *Ang.*, angular; *Den.*, dentary; *Qu.*, quadrate; *S.Ang.*, surangular; *Sp.*, splenial.

The frontal, also essentially flat, just enters the orbital margin between the pre- and postfrontals, which are attached to all the rest of its lateral margin. Anteriorly the bone ends in a suture with the nasal, which is imperfectly preserved.

The side of the face which stands nearly vertically (its widest part being in fact across the bosses of prefrontal in front of the eye) has a prefrontal extending about halfway from the orbit to the preserved portion of the nostril, below which there is an extensive lachrymal forming a good deal of the orbital margin and extending forward presumably to the nostril. The maxilla is an exceedingly shallow bone united to the lachrymal along most of its border, though posteriorly it is attached to the anterior end of the jugal.

The dentition is composed of comparatively large teeth apparently circular in section, or nearly so, there being in the maxilla some four teeth steadily increasing in size from the anterior end backward. These are followed by two enlarged canine teeth, and then by fourteen or fifteen teeth and tooth spaces which extend to the extreme end of the bone.

The position of the premaxilla is fixed by comparison with the lower jaw, whose perfectly preserved anterior end is present on each side, the two rami having been a little separated. One premaxillary tooth is preserved on the right side of the animal. It is a large tooth fitted to bite against the low anterior mandibular tooth in front of the anterior lower canine.

Something of the palate is seen in a natural transverse section a little behind the orbit. This cuts down through a large pterygoidal flange which descends nearly to the lower border of the lower jaw, whilst a few millimeters further forward in the region of the ectopterygoid the bone becomes thin. There is a thin sheet of bone which clearly represents the parasphenoid.

There being no otic notch, the borders of the occiput are in a wide sense continuous. The supraoccipital, whose posterior face is the only part visible, has a median ridge, narrow and deep. From this ridge the lateral surfaces pass outward, and in the middle of the height much forward so that a deep horizontal groove with a rounded floor plunges laterally into the posttemporal fossa. The expanded upper end of the bone is covered by the dermosupraoccipitals which turn backward so as to form an overhanging roof to the occiput. The dermosupraoccipitals form a small flat area behind the parietals on the upper surface, the hinder border being shallowly concave, ending laterally at a low rounded point crossed by the suture with the parietal.

The parietal is a large bone, which with its fellow surrounds a large, anteriorly placed pineal foramen. Its anterior border is attached to the frontal and laterally is notched for the postfrontal. The lateral border, behind the notch, has a long apparently not sutural attachment to the postorbital, and is then cut into by the long suture with the supratemporal. Finally the parietal forms part of the occipital border, lateral to the dermosupraoccipital.

The supratemporal, a very large bone, turns over from the upper to the lateral surface of the skull where its lower border (whose position can only be determined approximately) must overlap onto the outer face of the squamosal, a bone whose upper edge is represented only by the imprint it has made on the matrix on the left side of the skull. The hinder end of the supratemporal, which forms part of the hinder border of the skull, is carried out into a process which rests on a somewhat more protuberant structure perhaps made by the tabular. The supratemporal part of the process is carried out into three small knobs, but what is apparently the tabular bears two somewhat larger processes lying entirely behind the posterior border of the more lateral parts of the supratemporal, where it turns down onto the outer surface.

What is apparently the remainder of the tabular is a small delicate sheet of bone whose upper edge is at any rate very nearly in continuation with the occipital surface of the parietal which extends inwards towards, but much anterior to, the dermosupraoccipital. The supratemporal and its adherent tabular (if indeed the bone be separate) thus rests on the hinder surface of the inturned part of the squamosal, which is well shewn on the right hand side as a thin sheet coating the posterior surface of the upper part of the quadrate, passing inward below the tabular and the distal end of the upper process of the supraoccipital to end abruptly in a more or less vertical margin. This internally directed flange of squamosal continues vertically down on the occiput, overlapping the upper part of the quadratojugal above the notch which is part of the quadratojugal foramen and probably resting on the posterior surface of the quadrate near its summit.

The quadrate, seen comparatively well from behind and within on the right side of the specimen, has a vertically placed posterior face from which the bone stretches forward and inward, the lower border being drawn out into the inner condyle, which is directed outwards and a little downwards. The outer condyle, which is concealed by the quadratojugal and the attached lower jaw in the specimen, clearly extends laterally for some distance, being indeed a large structure not at all dissimilar to that of *Captorhinus* if we may judge its shape by the articular bone which moves upon it.

The other bones of the braincase are not intelligibly preserved but the right stapes is present, a little damaged in preparation but perfectly understandable. It has a comparatively slender shaft which rises from a large footplate of almost typical captorhinid pattern; that is, it extends vertically for a very considerable distance below the level of the shaft of the bone. There is a large foramen, above which a definite dorsal process rises abruptly from the base of the shaft and presumably just outside the upper part of the footplate.

Between the thickened posterior border of the quadrate and its almost vertical attachment to the pterygoid the bone is very markedly channelled by a very wide groove which ends in a well rounded cup, the stapedial recess.

As the supraoccipital is in position and apparently complete and the stapes known there is no real difficulty in making an approximate drawing of the braincase as a whole; such a drawing has of course no independent validity; it is merely an attempt to draw a structure which meets the rather rigid requirements of those features which are known.

The structure of the lower jaw is partially shewn and will readily be understood from Figure 12. It is noticeable that there is a small retroarticular process exceedingly similar to that of *Captorhinus,* and the whole structure of the jaw is like that of *Captorhinus*, which differs from that of the early forms such as *Protorothyris.*

PARACAPTORHINUS COMPARED WITH CAPTORHINUS

That *Paracaptorhinus* is related to *Captorhinus* is, I think, self evident. The general shape and appearance of the skull, the rather characteristic dentition with its two enlarged canine teeth, the shape of the supraoccipital, the character of the quadrate and stapes, and of the lower jaw are sufficient evidence.

But the nearly straight occipital border, superficially so much recalling that of *Captorhinus*, differs in the very considerable appearance of the dermosupraoccipital on the flat upper surface, in the very large size of the supratemporal, and in the backward projection from its posterior surface.

The very large size and character of the supratemporal is perhaps the governing consideration. Even in *Protorothyris*, the beginning of the series which leads up to *Captorhinus*, the supratemporal is very small and it appears to undergo a steady reduction throughout the series until in *Labidosaurus*, which is later in date of first appearance than *Captorhinus*, it vanishes altogether. As it is most unlikely that this trend of reduction should be reversed it would seem that *Paracaptorhinus* has followed a line of descent differing from *Captorhinus* and starting from a stage more primitive than *Protorothyris*.

But in many other features *Paracaptorhinus* is much more advanced than *Protorothyris* and advanced in the same ways as *Captorhinus*, the postorbital part of the skull for instance has already achieved the rounded external surface which occurs first in *Romeria* in the captorhinid series. In *Paracaptorhinus* this is made by a disruption of the original lateral border of the table of the skull, so that the supratemporal apart from its rigid attachment to the parietal overlaps, probably quite deeply, the upper part of the squamosal; and similarly the postorbital is a wide bone obviously firmly attached to the skull roof by underlying the parietal. It also has a considerable exposure in a lateral view.

Another feature in which *Paracaptorhinus* is advanced is in its development of a small backwardly projecting retroarticular process identical with that found in *Captorhinus*, but which does not occur in *Protorothyris*, nor in the similar West Virginian form *Melanothyris*.

We have, therefore, evidence of the existence amongst Cotylosaurs of a line of descent parallel to that which leads to *Captorhinus*.

Captorhinids Compared with Pelycosaurs

Protorothyris Compared

It is interesting to compare these two lines, so far as we know their skull structure, with the Pelycosaurs.

Price, when he first described *Protorothyris*, compared it with the primitive Pelycosaur *Eothyris*, and recognized that the two forms may well have arisen from a common stock not very far before. My new description of this animal renders the pelycosaur relationship even more obvious. The comparison is apparently best with a form like *Varanosaurus* rather than with *Eothyris*. In *Varanosaurus* it seems reasonably certain that the parietals extend outwards so that they completely overlap the admedian border of the postorbital, which is attached to their lower surface. In *Ophiacodon*, which is structurally very similar to *Varanosaurus*, the postorbital is visible in dorsal view as a bone which extends so far backward that it does underlie and come into contact with the lateral margin of the supratemporal, though for a considerable distance a special very narrow process of the parietal separates the two bones. In each case there is a tabular separated from the supratemporal anteriorly by another slender process from the parietal, so that the upper end of the supratemporal is received in a notch in the postero-lateral corner of the parietal exactly as it is in *Protorothyris*. In *Ophiacodon* the free margin of the parietal does not exist because the postorbital extends up far enough to meet the parietal and be visible from above.

None the less in both these Pelycosaurs there is a special process of the parietal which separates the postfrontal from the supratemporal. In other words the structure, especially in the case of *Varanosaurus*, is exceedingly like that which exists in *Protorothyris:* there is a similar insertion, as it were, of the front end of the supratemporal into a notch in the parietal[1] and a postfrontal whose suture with the parietal, rather transversely placed, leaves a lappet of parietal separating postfrontal and supratemporal bones, with its free margin underlaid by the postorbital which extends back toward the supratemporal. The fact that in *Proto-*

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[1] In my 1914 paper on *Varanosaurus* I regarded the supratemporal as part of the squamosal, and the bone labelled supratemporal is in all probability part of the tabular.

rothyris the postorbital does not extend sufficiently far back to come into contact with the supratemporal seems to me of very little importance.

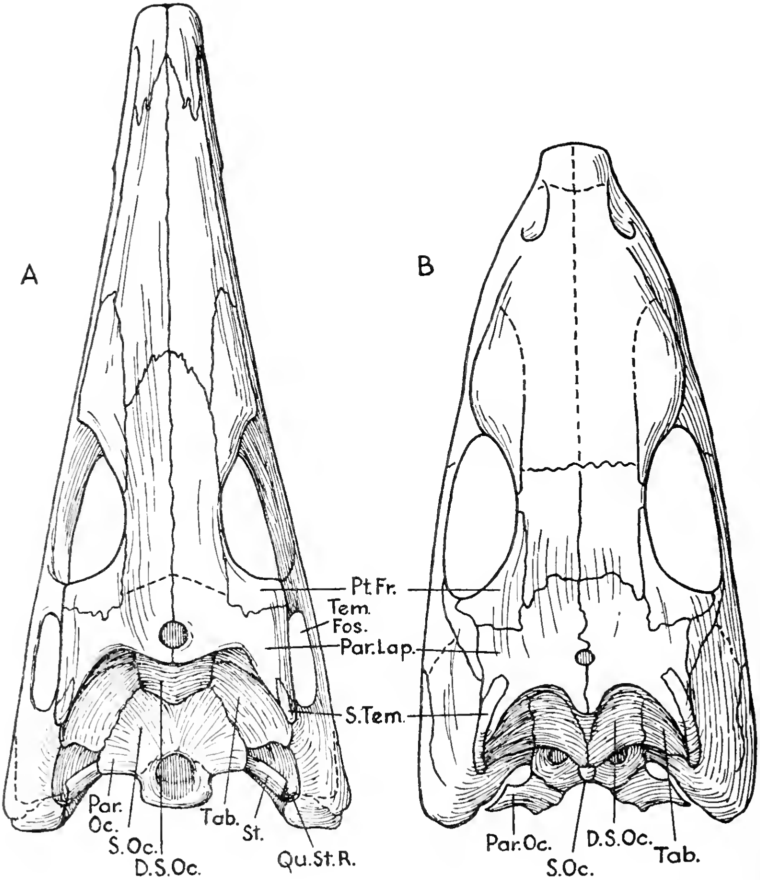

Fig. 13. Dorsal view of the skulls of *A, Varanosaurus acutirostris* and *B, Protorothyris,* reduced to the same width. Reference letters: *D.S.Oc.,* dermosupraoccipital; *Par.Lap.,* parietal lappet; *Par.Oc.,* paroccipital; *Pt.Fr.,* postfrontal; *Qu.St.R.,* quadrate stapedial recess; *S.Oc.,* supraoccipital; *S.Tem.,* supratemporal; *St.,* stapes; *Tab.,* tabular; *Tem.Fos.,* temporal fossa.

This resemblance in the structure of the upper part of the skull extends to the face, including the dentition, for in *Varanosaurus* the premaxilla is a little deflected so that the anterior teeth point backward, and there are two canines, preceded by six or seven smaller teeth, exactly as in *Protorothyris*.

In the temporal region the only real difference is in the development of the temporal fossa in the Pelycosaurs.

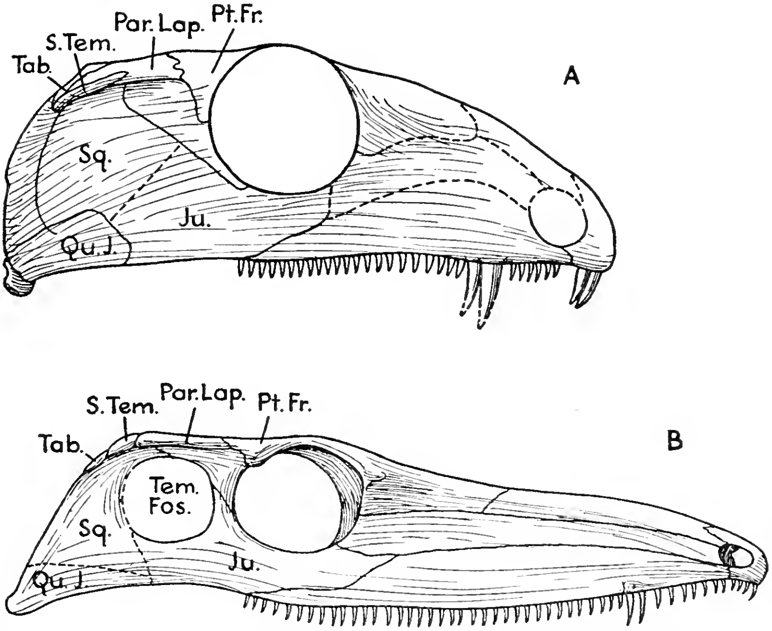

Fig. 14. Right lateral view of *A*, *Protorothyris* and *B*, *Varanosaurus*, reduced to the same width. Reference letters as in Figure 13 with: *Ju.*, jugal; *Qu.J.*, quadratojugal; *Sq.*, squamosal.

The occiput differs in a characteristic manner. In *Protorothyris* the flat upper surface of the parietal extends very considerably posterior to the pineal foramen as a point isolated by the two depressed areas, formerly covered with muscle, which are floored by the dermosupraoccipital and tabular on each side, these bones resting on downturned flanges of the parietals. The hinder border of the dermosupraoccipital and tabular on each side is markedly bowed forward, the result being that the supraoccipital articulates with the skull roof essentially by three processes of which the median lies much posterior to the lateral pair. The processes appear to be separated by fossae, but the preparation is not sufficiently complete to shew whether or not these are merely deep pits, the processes being connected far forward by bone.

In contrast, the supraoccipital of *Varanosaurus*, or of any Ophiacodont, is a wide flat sheet of bone, articulating laterally with the tabular, whilst its upper border is overlapped by the dermosupraoccipital, or interparietal.

The difference as observed is great, but may well depend entirely on the adaptation of the supraoccipital for attachment to the very different hinder border of the skull table found in the two groups.

One other very important point of resemblance between *Protorothyris* and Pelycosaurs such as *Varanosaurus* and *Ophiacodon* is the short paroccipital process extending out towards, but not into contact with the squamosal. It was obviously continued by cartilage in both cases.

The true posttemporal fossa occupies much the same position in *Ophiacodon* or in *Varanosaurus* as it does in *Protorothyris*. Furthermore the quadrate of *Protorothyris*, with its well defined stapedial recess, and the fact that its articulation with the lower jaw is cylindroid, the outer condyle not being antero-posteriorly elongated, is a further resemblance as, indeed, is the great relative depth of the suspensory region below the occipital condyle, whose position is obvious. Finally the stapes of *Melanothyris* very greatly resembles that of *Ophiacodon*.

There is thus every reason to suppose that the Captorhinids and the Pelycosaurs had a not very remote common ancestor, presumably somewhere in Pennsylvanian time.

Paracaptorhinus Compared

But the parallel I have so far drawn between *Protorothyris* and the Pelycosaurs *Ophiacodon* and *Varanosaurus* is not found in quite the same form if one compares my new *Paracaptorhinus* with these forms.

In *Paracaptorhinus*, instead of the small narrow supratemporal, wedged into a notch at the postero-lateral corner of the parietal, found in *Varanosaurus* and *Protorothyris*, there is a large supratemporal attached to a wide recess in the outer border of the parietal. Furthermore, whilst in *Varanosaurus* and *Protorothyris* the lateral borders of the parietal and supratemporal form a continuous margin which is freely exposed in side view above the confluent postorbital and squamosal, in *Paracaptorhinus* the "free" parietal margin is short, and the supratemporal extends much lateral to it to overlap the outer surface of the squamosal over a considerable area.

Paracaptorhinus no more resembles the Pelycosaurs in its occiput than does *Captorhinus*. But a comparison of *Paracaptorhinus* with *Eothyris* is illuminating.

The very remarkable Pelycosaur which Romer described as *Eothyris* is placed, rightly I think if attention be given to definitions, amongst the Ophiacodonts and differs from *Varanosaurus*, and even from *Ophiacodon*, almost exactly as *Paracaptorhinus* differs from *Protorothyris*. (cf. Figs. 10, 11, pp. 344, 345.)

In general skull shape *Protorothyris* and *Varanosaurus* are square cut in occipital view, and deeper than they are wide. *Paracaptorhinus* and *Eothyris* have depressed skulls, much wider than they are high, and with a rounded outline in occipital aspect. This difference evidently reflects differing habits. In *Eothyris* the supratemporal is a large bone meeting the postorbital by its lateral margin, and extending rather far forward, so that the piece of parietal lying between the supratemporal and the postfrontal, which extends out to the postorbital, has a square cut appearance in contrast to its anteroposterior elongation and narrowness in *Protorothyris*. Furthermore in both *Eothyris* and *Paracaptorhinus* the supratemporal and tabular form an irregular knob lying behind the squamosal at the side of and above the occiput proper. But they differ in the single wide excavation of the occiput in *Eothyris*, and the complete concealment of the originally double excavation there in *Paracaptorhinus* by a back growth of the table.

In *Eothyris* the paroccipital and supraoccipital are fused, the posttemporal fossa is exceedingly small, and the paroccipital, though it has a contact with the tabular has none with the squamosal, ending abruptly at a face which appears to be nearly flat, the occipital surface of the paroccipital ending at a backwardly turned ridge at this place. The exoccipitals are in position round the foramen magnum, below which they meet in the mid-line, their swollen bases forming part of the occipital condyle. The upper ends are swollen, presumably for contact with a pro-atlas, and there are lateral projections in contact with the paroccipital above the foramen for the Xth nerve.

The lower part of the paroccipital is carried down below the lateral extension of the exoccipital as a process obliquely truncated at its end, which lies very far from the mid-line, just below the level of the lower border of the paroccipital process. With the lateral border of this face the stapes articulates. It is present in position on one side of the type skull as a relatively powerful bone a little dorso-ventrally compressed, perforated vertically by a foramen and apparently with a dorsal process rising immediately anterior to the foramen. Its distal end is not present, but a stapedial recess in the quadrate is very well developed, being in fact underlain by a much produced horizontal sheet, apparently largely quadrate, but no doubt including some contribution of the pterygoid. The condylar part of the quadrate shews only a shallow groove separating an outer from an inner condyle. The outer condyle forms a large part of a circle in section.

The dorsal surface of the occiput is rounded in contour, the supratemporal passing down onto the lateral surface of the squamosal without any break in the surface of the temporal region. The face is in general structure similar to that of Captorhinids, but the lower border of the premaxilla is not downturned, and the outer surface of the internarial processes slopes upward and forward so as to shew that the nostrils were enlarged, as in *Casea.* Indeed it is not inconceivable that *Eothyris* may be an ancestor of the Caseids, whose earliest known occurrence is in the "Cacops Bone Bed" rather above the summit of the ordinary Arroyo formation of the Clear Fork. But this would imply that the group of Edaphosaurids is unreal.

The foregoing comparison shews that the Pelycosaur *Eothyris* differs from *Varanosaurus* in a series of ways which are the same as those which distinguish *Paracaptorhinus* from the *Captorhinus* ancestor *Protorothyris.*

The important differences are that the supratemporal is an exceedingly narrow bone in *Protorothyris* and in *Varanosaurus,* wedged into a notch in the postero-lateral corner of the parietal, one point of which separates the tabular from the supratemporal whilst the other passes backward along the lateral surface of that bone.

In *Protorothyris* and *Varanosaurus* the anterior end of the supratemporal is separated from the nearly transverse suture at the posterior border of the postfrontal by a lateral extension of the parietal, which has a smooth edge standing up dorsal to the upper border of the postorbital, that bone extending backward for a distance which may enable it to underlie the supratemporal or not, but which, for the whole of its length, lies below the parietal and supratemporal and is not connected to them by suture, so that it was easily displaced after death.

In *Eothyris* and in *Paracaptorhinus* the supratemporal, though still received in a notch in the lateral border of the parietal, and still in contact behind with the tabular, extends outwards so that it overlaps onto the outer surface of the squamosal and is attached to that bone (and in *Eothyris* also to the postorbital) by suture, the margin of that parietal process which stretches out to a lateral border between the supratemporal and the postfrontal having in these forms a firm attachment to the postorbital.

It is evident that in these matters *Eothyris* and *Paracaptorhinus* have advanced above the structure found in *Varanosaurus* and *Protorothyris*. On the other hand, the very small size of the supratemporal in *Protorothyris* and in *Varanosaurus* has presumably arisen by reduction from a larger bone more like that of the other two; and it therefore seems probable that the ancestors of all these forms must have possessed a skull table which was essentially flat, made up of large parietals extending outwards to a free lateral margin continued posteriorly along a relatively large supratemporal, and ending in a contact with a tabular bone of such a nature that a posterior pointed process made by these two bones passed a little outward and backward. The anterior border of that process of the parietal which has a free lateral border, the parietal lappet, is attached by suture to the inner part of the hinder border of the postfrontal, which continues beyond it to form much of the hinder border of the orbit. This part of the bone overlaps the outer surface of the postorbital, being firmly attached to it, so that the cheek does not depend entirely for support on its weak attachment to the lateral part of the table.

Another feature common to the two — or rather to the four — lines of descent is the nature of the dentition. The premaxilla bears large teeth, usually directed a little backward, whilst the maxilla, after an anterior series of a few small teeth, carries two markedly enlarged canines followed by a long series of small ones.

Nature of the Quadrate

The Captorhinids and Pelycosaurs have in common a remarkable and characteristic quadrate.

This bone has an articular surface for the lower jaw which varies greatly in shape in accordance with adaptive needs, but always shews some division into inner and outer condyles by an oblique depression passing across it. The outer condyle is the lower surface of a shallow process from the bone, whose upper surface, often horizontal and always nearly so, is a sutural surface for attachment of the quadratojugal. The inner condyle lies below the body of the bone which is a vertical sheet whose outer surface, in contact with the temporal muscles, is essentially flat; though a thickening of the nearly straight and vertical posterior border of the bone may make a local, linear concavity. The admesial surface of this body begins at the edge of the articular surface of the inner condyle and continues upward and forward, in a general direction nearly parallel to the outer surface. But this surface is considerably diversified. Above the inner condyle begins a scar of attachment of the quadrate ramus to the pterygoid, which becomes increasingly deep until ultimately it reaches that scar to which the squamosal is applied. Thus there remains visible in the articulated skull an area of the inner surface of the quadrate varying a good deal in size. This inner surface ends at the posterior surface of the bone, which in early forms is flat, whilst in *Dimetrodon* it is ridged and grooved for attachment to the quadratojugal and squamosal. Below this attachment the hinder surface is always notched and rounded to form the anterior border of the quadratojugal foramen. The triangular area on the admesial surface left visible in front of the posterior border and between the pterygoid and squamosal is crossed from above and in front to a point a little above the inner condyle by a groove, bounded below by a ridge which marks the pterygoid border. This groove usually ends in a hemispherical pit lying above the hinder end of the inner condyle. This groove and pit are the "stapedial recess".

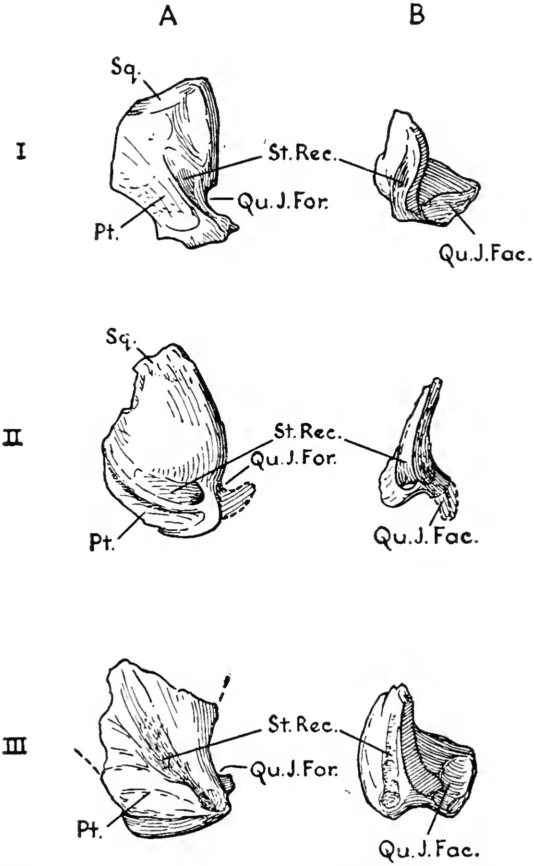

Fig. 15. Right quadrates of three Theropsids viewed from their mesial aspect in *A*, and from above in *B*. I, *Captorhinus*, approx. x 2 (D.M.S.W. R.410); II, *Dimetrodon*, x ⅔ (D.M.S.W. R.32); III, *? Secodontosaurus*, x ⅔ (D.M.S.W., R.71, Craddock bone bed). Reference letters: *Pt.*, facet for attachment of pterygoid; *Qu.J.Fac.*, facet for attachment of quadratojugal; *Qu.J.For.*, notch forming part of the quadratojugal foramen; *Sq.*, facet for squamosal; *St.Rec.*, stapedial recess.

In *Ophiacodon* the stapedial recess is enormously enlarged by an inward shelf, made by the pterygoid and that part of the quadrate which is attached to it, so that it forms a deep cup opening upward; the end of the stapes lies in it.

Stapes

The structure of the quadrate of Captorhinids and Pelycosaurs is related to the nature of the ear, and especially to that of the stapes, of the members of these two groups. In general morphology their stapes agree, but differences of skull shape, which means of habits, make those found within each group at first sight appear very varied.

The stapes of *Captorhinus* has been admirably figured by Price as it lies in position in the fenestra ovalis. It is a relatively enormous bone with an immense footplate covering a fenestra whose lower border is the most ventral part of the braincase. From the footplate the body of the bone passes outward and backward, becoming more slender until it ends abruptly at a cartilaginous continuation. The bone is perforated dorso-ventrally by a large foramen, and immediately lateral to this rises a slender process which articulates by an immovable attachment with the lower border of the lateral process of the proötic, so as to continue ventrally the front face of that bone. The distal part of the stapes lies in the stapedial recess of the quadrate, and the ventral surface of its shaft bears a scar for a ligamentous sheet tying it down to the quadrate ramus of the pterygoid.

The stapes of *Labidosaurus* is a slender version of that of *Captorhinus;* that of *Paracaptorhinus* differs in having its footplate ventrally prolonged and in the proximal position of the dorsal process which rises in front of the upper opening of the foramen. The *Melanothyris* stapes has a very extensive footplate and a proximally placed short dorsal process so directed as to shew that the stapes as a whole passed down ventrally.

In *Ophiacodon* the stapes is an immensely massive structure, a flattened rod, standing nearly vertically in the head, with a gently concave lateral and convex admedian border. The upper end is the dorsal process, which articulates with the under surface of the paroccipital process. The lower end had a cap of cartilage, and lay within the deep cup which is the end of the stapedial recess. The large head, which fits the cartilaginous lips of the fenestra ovalis, projects inward, cut off from the dorsal process by a deep notch, and from the lower part of the shaft by a step, the neck so formed being perforated "vertically" by a foramen. In *Dimetrodon* the articular head is offset from the shaft, its neck being perforated by a large foramen. The dorsal process, very long and narrow, rises so that its antero-lateral surface is continuous with that of the shaft of the bone, and has a very long articulation with a ridge on the undersurface of the proötic. The shaft lies in the stapedial recess in the quadrate, and its lower surface bears a scar for ligamentous attachment to the quadrate ramus of the pterygoid. *Edaphosaurus* has a little known stapes similar to that of *Dimetrodon; Eothyris* a straight rod with a dorsal process, proximally placed and directed forward.

BOLOSAURUS COMPARED WITH CAPTORHINIDS

Bolosaurus, whose structure, so far as it is known, is described earlier in this paper, is an animal of very different character, and discussion of its structure in comparison with that of the ancestral Captorhinid and Pelycosaur ancestor may be expected to throw light on the former existence of a common Captorhinomorph group. It may perhaps be recorded that the restored figures of the *Bolosaurus* skull published in this paper were completed before I had examined any Captorhinid, other than *Captorhinus* itself, and they are thus completely unbiased.

The first matter, then, is a comparison of the general structure of the skull in the two groups. In general shape *Bolosaurus* is very much unlike *Protorothyris* or *Varanosaurus*. In contrast to the flat table in these latter the corresponding region in *Bolosaurus* forms an almost hemispherical structure, the parietal surface passing ventrally, laterally and posteriorly from the borders of the pineal foramen. The parietal has a long lateral extension, the parietal lappet, which passes outward between the postfrontal and the supratemporal, its lateral border having an attachment to the postorbital, as in early Captorhinids and Pelycosaurs. The squamosal has, as in Captorhinids and many other forms, a considerable internally directed sheet which lies behind the back of the quadrate, and mesially comes into contact with a very large tabular which extends very much ventral to the supratemporal.

In all this there is little sign of any real resemblance to Captorhinids. The occiput, with an apparent wide extension of the supraoccipital and paroccipital, may really recall the Pelycosaur occiput, but the nature of the stapes is unknown, and indeed the position of the fenestra ovalis is in doubt. The quadrate in *Bolosaurus* bears no real resemblance to that of the Captorhinids. Its lower border is a transversely placed condyle, relatively short antero-posteriorly in comparison with its width, with an inner condyle projecting downward almost as a step below the outer condyle, and with a posterior surface rounded from side to side. The quadratojugal foramen lies exceedingly laterally, above the outer condyle, and the lower part of the quadratojugal is applied to a flat, nearly vertical lateral surface of the quadrate. The pterygoid is attached to the inner surface of the quadrate which sent out a pterygoid ramus in contact with it. The whole structure is thus antero-posteriorly short throughout the whole of its height and differs completely from that of Captorhinids and Pelycosaurs. It has no signs of a stapedial recess.

The dentition of *Bolosaurus* is again quite different from that of either Pelycosaurs or Captorhinids. The two premaxillary teeth are directed forwards, have a prehensile anterior cusp, and are narrow from side to side. The maxillary teeth, eleven in number, are individually far more complicated than those of any Captorhinid or Pelycosaur, and there is no sign whatsoever of any canine in upper or lower jaw.

It seems therefore to follow that *Bolosaurus* is a thing apart, an independent branch of the Cotylosaurs with a temporal fossa called into existence by the mechanical needs of its peculiar dentition and jaw musculature. It could be placed in the Captorhinomorphs only because it shews no sign whatsoever of any otic notch, nor indeed of any accommodation for a tympanic membrane.

Limnoscelis Compared with Captorhinids and Anthracosaurs

The only animal, other than the Captorhinids, which has ever been referred to the Captorhinomorph division of the Cotylosaurs is *Limnoscelis*, and this must therefore be discussed.

I have on several occasions examined the single known skull in Yale but have never been able to satisfy myself completely as to its structure. However Professor A. S. Romer in 1946 published a new account, which I have compared with the specimen directly, and which has every appearance of being correct, at any rate in all essentials. If this interpretation be true we have in *Limnoscelis* a very large Permian reptile retaining a skull table which posteriorly at any rate (that is for the supratemporal and tabular) is not connected by suture to the squamosal, but rests upon it, so that the two bones may readily be displaced with regard to one another. The postfrontal is notched into the parietal, very much as is that of a Captorhinomorph or early Pelycosaur, but the very considerable space between the postfrontal and supratemporal is filled by a special process of the parietal, a parietal lappet, for only a small part of its width, the remainder being occupied by a dorsal part of the postorbital, whose outer surface lies on the top of the skull at right angles to that part of the bone which passes downward behind the orbit. This arrangement is partially paralleled in *Paracaptorhinus.* It involves, however, a peculiar structure of the postorbital which may of course have occurred co-incidentally with a lateral widening of the supratemporal for an amount measured by the extent of the suture between the postorbital and supratemporal.[1]

The general structure of the cheek and face of *Limnoscelis* corresponds well enough (if the very large size of the animal be kept in mind) with that of a Captorhinid, even the dentition being similar in the fact that the most anterior premaxillary tooth is the largest and is a little backwardly directed. Although the third, fourth and fifth maxillary teeth seem to be larger than those either in front or behind, the definite double canines of Captorhinids and Pelycosaurs are not recognizable.

The nature of the quadrate is very difficult to determine because of the condition of the skull, but it does not strikingly recall a Captorhinid/Pelycosaur structure. The quadratojugal seems to have a somewhat different relationship from that found in the Captorhinomorphs, and, particularly if Dr. Romer's explanation of the strange vertical crack in the squamosal and quadratojugal, lying in front of and parallel to the posterior outer border of these bones (that it is the result of pressure over the edge of the

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[1] It is however conceivable that that part of the postorbital on the upper surface of the skull is really an intertemporal and that a suture might exist between it and the underlying postorbital.

quadrate) be true, then it is certain that the quadrate is entirely unlike that of a Captorhinid, though it may more nearly resemble the conditions in *Bolosaurus*.

The occiput is exceedingly difficult to interpret. There is no doubt that the occipital condyle was flat, that there are small exoccipitals round the sides of the foramen magnum, and that there is a paroccipital process projecting out laterally; this process ultimately comes into contact with a bone on the posterior surface of the skull, which is unlikely to be part of the squamosal, but may reasonably be interpreted as a tabular. The supraoccipital is evidently very wide, and there are definite though small temporal vacuities. Finally, lateral to the exoccipitals and placed rather far out, there is a descending process from the paroccipital, whose oblique lateral border lies anterior to the posterior surface of the paroccipital process.

It is, I think, evident that the fenestra ovalis lay at the outer end of this process. The position of the tympanic cavity seems to be fixed by the wide, horizontal, internally directed shelf from the lower border of the quadrate ramus of the pterygoid. But there is no position where a tympanic membrane can reasonably be expected to have existed, the stapes is missing, and there is no evident stapedial recess on the quadrate. But in both Professor Williston's and Professor Romer's figures there is visible a very curious process passing downward below the general level of the under surface of the paroccipital process and near to its anterior face, an elongated ridge extending outward from the neighbourhood of the basisphenoid tuber towards the upper part of the quadrate at the point where the tabular rests on it. This ridge seems evidence of the former existence of a dorsal process on the stapes homologous with that found in Pelycosaurs and is indeed not unlike the similar ridge on the proötic of *Dimetrodon*.

In general, I feel that Professor Romer's interpretation of *Limnoscelis* is justified. The existence of the flat table of the skull and the retention of a non-sutural connection between the posterior lateral corner of the table and the hinder part of the squamosal, which seemed to me evident, do suggest, as Professor Romer has shewn, a descent from such an anthracosaur labyrinthodont as *Palaeogyrinus*.

But in those forms the upper border of the postorbital is not visible in a dorsal view of the skull, and the fact that it is so visible in *Limnoscelis*, firmly wedged in between the postfrontal and the supratemporal in the skull table, is pretty clearly an indication that *Limnoscelis* is not quite so close to an amphibian ancestor as Professor Romer seems to have suspected.

Thus *Limnoscelis* presents itself as an animal retaining many primitive features, together with a number which are considerably advanced. One primitive quality is the wide appearance of the dermosupraoccipital and tabular bones on the roof of the skull. They turn down towards the occiput, it is true, but there is nothing analogous to the sharply marked emargination associated with the attachment of neck muscles found in different detailed form in *Protorothyris* and in a primitive Pelycosaur, for instance *Varanosaurus*.

To this extent *Limnoscelis* is more primitive than any Captorhinid or Pelycosaur. It resembles *Paracaptorhinus* and *Ophiacodon* in that the postorbital appears on the upper surface of the table of the skull between the postfrontal and the supratemporal and thus has a long sutural edge to edge attachment to the parietal, unlike the primitive condition found in *Protorothyris* and *Varanosaurus*. The supratemporal is no longer than it is in *Paracaptorhinus*, is indeed no longer than it is in *Protorothyris*, but it is much wider than in that animal. It seems in fact as if in the whole of the arrangements of the lateral margin of the table, *Limnoscelis* is a little advanced, parallel to *Paracaptorhinus*.

The rest of the skull shews nothing very characteristic. The very wide contact of the prefrontal and postfrontal above the orbit presumably depends on the very large size of the skull, which implies a relatively small orbit. It is a condition found in some of the other large forms, for instance *Diadectes*.

In Anthracosaurs some contact between the pre- and postfrontal is usual, but in none do the two bones extend far out above the orbit as they do in *Limnoscelis*. Here the difference is significant, for the majority of Anthracosaurs are of the same order of size as the reptiles.

The most primitive character in the whole skull of *Limnoscelis* is the fact that the paroccipitals, extending directly outward, seem to lie rather above the floor of the braincase and are ultimately attached apparently to the tabular very much as they are in such an amphibian as *Eryops*, altered only by a downward migration of the outer ends in a way which must certainly have occurred in the ancestors of the Pelycosaurs.

It is, in fact, easy by a comparison of *Limnoscelis* with *Protorothyris* or *Varanosaurus* to imagine the nature of a *Limnoscelis* ancestor, and such an animal is drawn, quite hypothetically, in Figure 16. If this figure be compared with that of *Palaeogyrinus* which is placed alongside it, it will be seen that the two animals agree in the existence of a table connected by suture with the postfrontal and resting upon the upper surfaces of the postorbital and squamosal without any interdigitated suture. The table ends posteriorly in a transverse row of dermosupraoccipitals and tabulars, whose posterior parts are forced down onto the occiput by being overridden by superficial cervical muscles. The cheeks, chiefly squamosal with ventrally a quadratojugal, attached to the skull by the postorbital and jugal, and having inwardly directed sheets of bone on the occipital surface which rest upon and support the hinder surface of the quadrate, are similar in both *Palaeogyrinus* and a modified *Limnoscelis*.

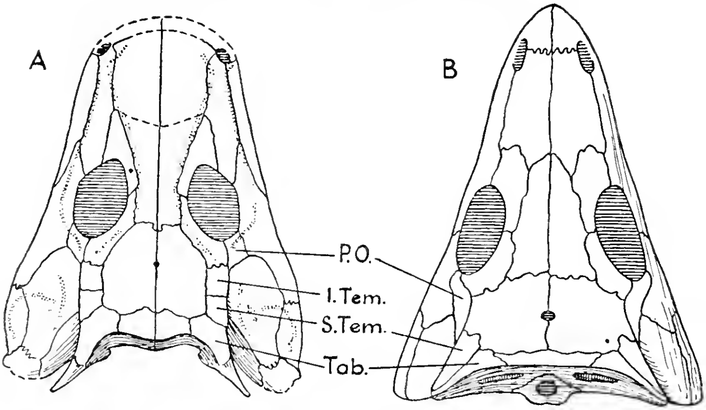

Fig. 16. Dorsal surface of the skull of *A*, the Anthracosaur *Palaeogyrinus* and *B*, a hypothetical ancestor of *Limnoscelis*, made by so reducing the width of the table that its lateral margin lies on that of the parietal lappet; the supratemporal, postorbital and postfrontal are thus narrowed and the width across the temporal region reduced. Reference letters: *I.Tem.*, intertemporal; *P.O.*, postorbital; *S.Tem.*, supratemporal; *Tab.*, tabular.

The differences lie mainly in the character of the braincase, which in the amphibian is narrow and directly attached to the dermal roof by the whole of the upper surface of the supraoccipital and the paroccipital and proötic, whereas in the reptile there is clearly a passage passing forward above the paroccipital process.

This parallel between the table of an Anthracosaur and that of *Limnoscelis* depends on the presence in both forms of a dermal bone separating the nearly transverse suture at the posterior end of the postfrontal from the similar suture at the anterior end of the supratemporal. In the amphibian this bone is an intertemporal, in the reptile it is a process of the parietal, the parietal lappet, which exactly fills the place left vacant, as it were, by the disappearance of the intertemporal.

Nevertheless, the general resemblance is so close that it cannot be matched by any comparison of the reconstructed primitive reptile with any other group of amphibia. In particular the whole picture is entirely unlike that presented by the so-called Microsaurs, which present a superficial resemblance to the skull of the advanced Captorhinus.

Romer, in an admirable paper (1950), has already pointed out that this assumed resemblance is not in fact genuine and that the whole suggestion of an origin of Captorhinomorphs from these amphibia rests on a basis which is patently unsound.

The most striking difference between an early Captorhinid such as *Protorothyris* and the Anthracosaur in the skull is the complete disappearance of a real otic notch from that of the reptile. This disappearance has quite evidently resulted from a pushing backward of the squamosal posteriorly and dorsally, so that the original last point of contact with the skull table which was the anterior end of the tympanic notch comes to move to the posterior end of the process formed by the supratemporal and tabular, which formerly extended freely backward apparently as a place of attachment to muscles connected to the shoulder girdle. This movement backward and the condition which results from it are associated with the production of an inwardly directed flange from the squamosal which underlies the hindermost portion of the skull roof. We do not, unfortunately, know exactly how far forward this inturned shelf extends, and it will be most interesting to discover its amount in *Protorothyris,* which is not now accessible to me.

But the flange in question is after all represented in the Anthracosaurs (if indeed the condition has arisen from a migration backward of the otic notch) by the upper part of the internal flange which, as in other Labyrinthodonts, underlies the otic region, eventually coming into contact with the upper border of the parotic flange of the pterygoid.

This flange is a new structure in Amphibia; it does not occur in fishes, except in so far as it is foreshadowed by a ridge on the inner surface of the preoperculum of *Osteolepis,* and it is associated with the need to support a quadrate whose condyle is transversely widened and which extends forward as bone and as cartilage for an unknown distance towards the otic notch.

The group of Captorhinomorphs thus contains the Captorhinids, including the ancestors of the Pelycosaurs, and *Limnoscelis.* Nothing in the structure of these animals really recalls that of *Bolosaurus* except the existence of a lappet of the parietal which comes out between the postfrontal and the supratemporal to have a contact with the postorbital. Any reference of *Bolosaurus* to the Captorhinomorphs is thus perfectly formal, a recognition of the actual absence of an otic notch; but an otic notch may be lost, and it is therefore necessary to compare *Bolosaurus* with diadectomorph Cotylosaurs before its systematic position may be held to be established.

DIADECTES

History of Material

The genus *Diadectes* was established by Cope in 1878, fragments of jaws with their eminently characteristic cheek teeth having been amongst the first recognizable materials found in Texas by Boll; indeed *Diadectes sideropelicus* is the first name given to any Texan Permian reptile. Cope described many species and even genera on such fragmentary jaws, but he soon got skulls of which he gave a short description in 1880. From these skulls the basioccipital bones had fallen out and Cope believed that the skull articulated with the atlas by the facets on the under surface of the supraoccipital to which the exoccipitals had, in fact, been attached.

In his last paper on the matter (1896) he describes the Cotylosaurs — the major group established on *Diadectes* and its allies — as follows: "Quadrate bone united by suture with the adjacent elements. Temporal fossa overroofed by the following elements: Postfrontal, postorbital, jugal, supramastoid [squamosal], supratemporal [prosquamosal], quadratojugal. Tabular bone present." This statement was presumably founded primarily on the skulls of *Diadectes* then in Cope's possession. Cope ultimately published some woodcut representations of a *Diadectes* skull which, however, shew extremely little of its structure. These were copied from lithographic plates which remained unknown until W. D. Matthew published them in 1915.

It was therefore an important advance when in 1905 E. C. Case published a most useful description founded essentially on a skeleton he had himself collected, together with other fragments including a nearly perfect palate. Unfortunately the skull of the principal specimen, although uncrushed and shewing the general shape admirably, is preserved in a matrix from which it was almost impossible to clean it.

Thus the detailed structure of the skull remained entirely unknown until 1910, when Robert Broom published a very short account, illustrated by a figure of the lateral and palatal surfaces, of the structure based entirely on a single skull in the American Museum of Natural History (A.M.N.H. 4839).

A little later (1911) Case, who had in fact discussed the original skull with Broom, published a much more extended account of the structure of the skull based on a considerable number of specimens. Case's restoration, founded in the main on the skull which Broom had examined, but with much additional material, led him to interpret the structure of *Diadectes* in a very different manner.

The next contribution, in 1911, was the description by Williston of *Nothodon lentus* Marsh, from New Mexico material in Yale University. This included the upper parts of two skulls of which the individual bones had been separated before burial, and were rearticulated by Williston, so that the structure of the top of the skull was shewn beyond dispute. Unfortunately the best of these two skull roofs is extremely arched from back to front and Williston's photographic figure of it is not easy to understand, whilst his drawing has flattened the whole out into a plane, so that many of the characteristic shapes of the bones have become lost.

In 1913 Case and Williston having collected new materials gave a further account, mainly of the palate, of *Diadectes lentus* and of another form which also came from New Mexico. Curiously enough in this paper Williston, who had already given a perfectly accurate account of the temporal region, goes out of his way to say that there is no evidence to draw the structure of the temporal region as Broom had done.

Subsequently (1913), von Huene examined the American Museum skulls of *Diadectes* and gave a series of figures representing individual specimens, without any attempt to make a restoration. Unfortunately von Huene's figures agree neither with Broom's restoration nor with Case's figures.

Finally in 1914 Broom responded to criticisms by a more detailed treatment of several different skulls of *Diadectes* in New York and gave a revised restoration of the side view which is, I think, essentially accurate (Broom 1914a, fig. 3).

It follows from all this that a new description of the skull of *Diadectes* was desirable, and Professor E. C. Olson produced one in 1947, based on an examination of a now large series of skulls in many museums in the United States. He also produced a complete series of restored views of the skull. These, however, did not gain wide acceptance and in 1950 Olson published a further account, especially of the temporal region, based on fifteen skulls which are represented in detail. The most interesting result of his new investigation was the interpretation of the temporal region as containing an independent intertemporal bone lying laterally to the parietal and between the supratemporal and postfrontal. The possible importance of this interpretation led me to examine further the structure of *Diadectes* with the results which follow.

The Museum of Comparative Zoology contains much of a *Diadectes* skull (M.C.Z. 1743) in absolutely perfect preservation. Quadrates with the pterygoids attached, palatines, maxillae, premaxillae, all in articulation, shew these parts in complete perfection, but there is practically nothing of the roof of the skull, and the braincase is missing. However M.C.Z. 1282 is a braincase associated with a quadrate which I prepared by softening the very hard matrix with acetic acid and then removing it mechanically.

The specimen A.M.N.H. 4843 is a good braincase whose cavity I described in 1916. The para-basisphenoid complex is well represented by a well preserved fragment found in Godwin Creek which is in the Museum of Comparative Zoology. From this material it is easy to get everything except the structure of the upper surface of the skull, which is given with complete certainty by the Yale type of *Nothodon* put together from its isolated bones by Williston. Furthermore, the admirable specimen A.M.N.H. 4378, which consists of a skull roof shewing anteriorly the deep rabbets in which lay the frontals and postfrontals, shews all the other sutures quite perfectly, as Broom has already pointed out, and confirms exactly the structure found in the New Mexico specimen.

There is thus no real difficulty in making a reconstruction of the skull although there are minor differences of proportion, including for instance the thickness of the dermal bones, which lead to necessary compromises.

The very discordant results which have thus been reached by capable palaeontologists who have studied the structure of the *Diadectes* skull suggest that reasons must exist which make it more difficult to understand than those of most of its contemporaries.

These difficulties are indeed genuine. The first and most obvious is the rough external surface, where not only are there very curious deep grooves but the whole surface is pitted in an irregular manner analogous to but on a much smaller scale than the ornament of a labyrinthodont dermal bone. But these difficulties do not fully explain the discrepancies in interpretation, for the inner surface of the dermal bones of the skull roof is smooth and should shew sutures quite readily. But in fact in most cases it does not. That separate bones are present is abundantly clear from the existence of partially or almost completely disarticulated skull roofs, but fusion between neighbouring bones takes place probably fairly early and certainly so completely that no visible traces of suture generally remain. I am inclined to relate this closure to the remarkable histological structure of the dermal bone. Each roofing bone is entirely cancellous, the external and internal surfaces, though generally continuous, being coated only with an excessively thin layer, the only trace of the inner and outer tables which would normally be expected to occur.

In the skull fragments (D.M.S.W. R 399) which are at present before me the anterior end of the tabular has a thickness of some 7.5 mm. The inner table seems seldom to be so much as .25 mm. in thickness and the outer table, whose surface is quite irregular, is of similar thickness. This condition contrasts very markedly with that in a labyrinthodont jugal 4.5 mm. thick, with an inner table nearly 1 mm. in thickness and an outer table varying from 2 mm. to a little less, the cancellar bone in the middle being only a couple of millimeters in thickness. Such a structure is what one commonly finds in both labyrinthodont and reptile dermal bones. These dermal bones of *Diadectes* thus fuse completely, presumably at a time when growth has ceased, and this fact renders it impossible to determine with safety the actual sutural pattern on most skulls, and thus arise the discrepancies in the accounts of them.

But the trouble goes even further. The pterygoid, squamosal and quadratojugal, which articulate with the quadrate, fuse with that bone so completely that the sutures which separate them may be lost, indeed may be invisible even in section. But even more remarkable is the fact that it is quite impossible in broken section to distinguish the supraoccipital from the dermosupraoccipital which overlies it. The two bones have fused completely over the greater part of their extent even in the Yale type of *Nothodon,* in which all the other skull bones are separate.

It is therefore worth while to give a complete account of the structure of the skull, or at any rate of such parts of it as have a disputed structure.

Description of Structure

Braincase

The basioccipital possesses a condyle which is essentially flat, with edges scarcely at all chamfered and usually with a very small representation of a notochordal pit. As seen in different specimens the condyle varies a good deal in shape; it always projects strongly behind the plane of the occiput as a cylindrical plug. The condyle may be circular, or almost circular, apart from an excavation of the upper surface below the foramen magnum.

In many specimens, however, it is depressed being sometimes no more than half as deep as its width. I am inclined to believe that this difference is to a considerable extent, or even entirely, the result of crushing. The bone is extremely spongy and in one case at least, not only it but the whole of the ear region of the braincase is squashed completely flat in a skull the general shape of whose occiput is not grossly distorted. The basioccipital is in all cases completely fused with the exoccipitals and nothing can be said of the contributions of these bones to the condyle. They do not completely surround the foramen magnum but are separated by a small amount of supraoccipital, which lies free between the great flat surfaces by which that bone articulates with the upper surface of the exoccipitals. The exoccipitals are carried backward by special processes so as to form a side wall to the brain. These are shewn not only in A.M.N.H. 4843, but in Professor Olson's

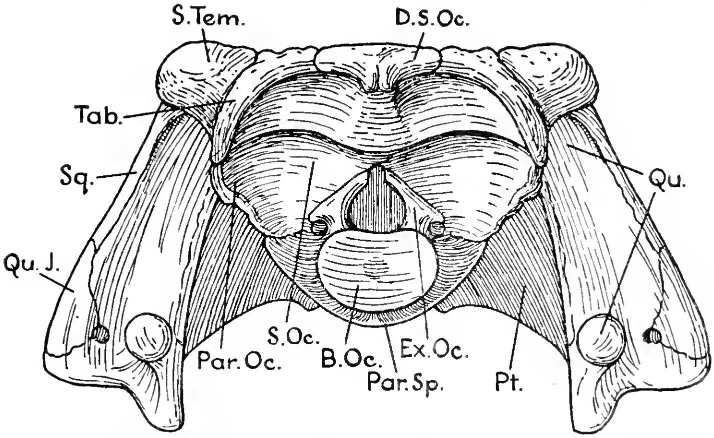

Fig. 17. *Diadectes*, occipital aspect of skull, x ⅔. This is a composite drawing, which agrees in size and shape with Figures 18, 22, and 23, from more than six individuals. It is thus necessarily a compromise between skulls which differ in size and shape, but it does no injustice to any morphological quality so far as I am able to judge this matter. Reference letters: *B.Oc.*, basioccipital; *D.S.Oc.*, dermosupraoccipital; *Ex.Oc.*, exoccipital; *Par.Oc.* paroccipital; *Par.Sp.*, parasphenoid; *Pt.*, pterygoid; *Qu.*, quadrate; *Qu.J.*, quadratojugal; *S.Oc.*, supraoccipital; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Tab.*, tabular.

figures drawn from reconstructed sections. Anteriorly the exoccipital ends at the great canal for the Xth nerve, and the basioccipital extends sufficiently far forward to come into contact with the lower end of the paroccipital just behind and below the great opening — the internal auditory meatus — into the cavity for the inner ear. The basisphenoid and the indistinguishably fused parasphenoid form an immensely more complicated bone. (This complex of two bones I shall call basisphenoid in the rest of this paper.) The most visible part of it when seen from below is a huge sheet of bone which ends posteriorly in a free margin lying considerably below the ventral surface of the basioccipital condyle and extending out to the fenestra ovalis. The whole surface may be continuous or it may be divided by a median groove into two well separated swellings. These lie below great excavations into which the anterior ends of the recti capitis muscles no doubt extended, the two spaces being apparently usually separated by a median septum anteriorly. Dorsal to these spaces lies the body of the bone, which fuses with the proötic in old individuals

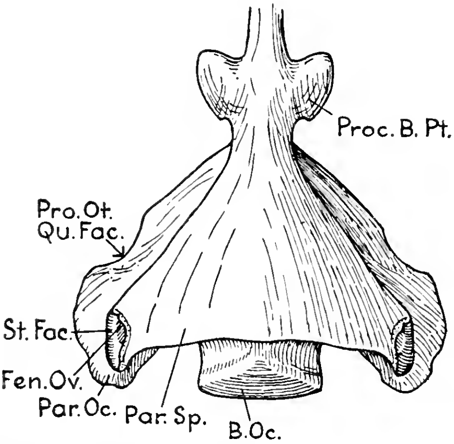

Fig. 18. *Diadectes,* isolated braincase seen from below. Composite (see Fig. 17) x ⅔. Reference letters as before with: *Fen.Ov.,* fenestra ovalis; *Pro.Ot.Qu.Fac.,* facet for articulation of the quadrate with the proötic; *Proc.B.Pt.,* basipterygoid process of the basisphenoid; *St.Fac.,* facet for the footplate of the stapes.

though it is separate from it in most. In all probability the dorsum sellae turcica is entirely proötic but the lower part of the wide, long and much overhung pituitary fossa is certainly basisphenoid. This bone therefore forms part of the posterior surface of the fossa extending outward lateral to it to form the core, at any rate, of the short, massive basipterygoid process, which is rounded from back to front on its lower surface and extends somewhat upwards laterally to the fossa. The floor of the pituitary fossa has a low median ridge and ends at a transverse line,

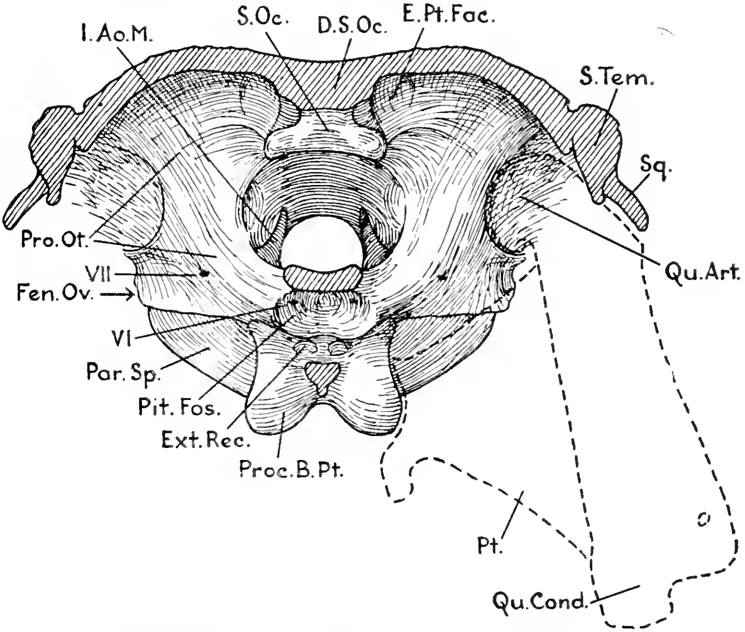

Fig. 19. *Diadectes*, the braincase seen from in front, the roof of the skull, parasphenoid and dorsum sellae cut through transversely. Composite and a different reconstruction from Figures 17, 18, etc. About natural size. Reference letters as before with: *E.Pt.Fac.*, facet for articulation of the upper end of the epipterygoid with the skull roof; *Ext.Rec.*, attachment of the external rectus muscle to the basisphenoid; *I.Ao.M.*, internal auditory meatus; *Pit.Fos.*, pituitary fossa; *Pro.Ot.*, proötic; *Qu.Art.*, articular head of the quadrate in pit on the proötic; *Qu.Cond.;* quadrate condyle; VI and VII, cranial nerve foramina.

below which a vertical, or nearly vertical face bears a pair of rather shallow anteriorly directed pits, presumably for the attachment of the external rectus muscles. Below these the single largely parasphenoidal rostrum extends forward. The extreme length of the pituitary fossa is remarkable but is shewn quite well in A.M.N.H. 4843. The detailed structure of the basisphenoid is best shewn in an unnumbered specimen from Godwin creek in the Museum of Comparative Zoology.

In all known specimens the proötics, opisthotics, supraoccipital, dermosupraoccipital and tabular bones are completely and indistinguishably fused for the greater part of their extent, but anteriorly the front end of the supraoccipital is usually cut off abruptly where its cartilaginous continuation still lies on the ventral surface of the dermosupraoccipital. In D.M.S.W. R 399 the line of separation is continued backward for almost three millimeters where the bones are in actual contact but not yet fused. The proötics extend forward in front of the ampulla of the anterior vertical semicircular canal for some distance, passing inwards below the brain mesial of a rounded margin which posteriorly is variously embayed to form the notch for exit of the Vth cranial nerve from the brain cavity. The floor so formed below the brain is perforated some distance mesial of the free border by a foramen for the VIth nerve, which passes through the roof of the pituitary cavity, emerging on its hind wall rather high up. The nerve must have passed out laterally through the open notch in the side wall of the pituitary space. The VIIth nerve lies somewhat posteriorly to the VIth but its foramen passes out through the proötic very far forward, almost immediately below that free upper border of the bone which passes upward and backward until at some unknown point it passes onto the supraoccipital.

The lateral face of the proötic behind its anterior margin, which is a marked ridge no doubt continued by a membrane, has a low swelling extending backward and upward; this covers the front part of the anterior vertical semicircular canal. Below the canal the outer surface of the proötic becomes nearly vertical and passes outward until it forms the front border of the quadrate facet. This structure varies a good deal in the emphasis of its separation; in some cases (M.C.Z. 1282) it lies very sharply separated from the rest of the proötic, almost carried out on a process in fact; in others (D.M.S.W. R 25) it is only very little marked off by slight changes in surface character of the bone; in still others (D.M.S.W. R 399) the limits are sharply defined, but more by shape and structure than by a definite ridge. In any case there seems no doubt that the facet lies on the proötic, the paroccipital not playing any part in its surface. Below this quadrate facet the proötic continues downwards until it terminates at a perfectly straight border. This border if followed back usually ends on a process which lies at the anterior end of a very well marked groove which receives the footplate of the stapes. This ventral border of the proötic has a definite structure. It is part of a strip of bone, perhaps of the order of four millimeters wide, which when viewed directly from its end is seen to possess an upstanding outer surface, mesial of which lies a groove in which the cancellous bone is displayed, and on the inner side of the groove there is another ridge, also proötic, which has a thin layer of continuous bone on its admesial side but is otherwise composed of cancellous bone.

Examination of complete skulls shews without doubt that this outer ridge of the proötic lay during life in contact with the lateral border of the immensely widened hinder part of the parasphenoid. Thus the groove within this ridge was occupied by an unossified extension of the proötic, whose outer surface must have been overlapped by the lateral border of the parasphenoid. The inner ridge, with its surface of hard bone, is actually part of a canal which ends posteriorly and laterally at the fenestra ovalis. The canal of which the groove is the upper half widens somewhat as it passes inward and then opens into the cavity for the labyrinth, the whole canal being apparently oval in section and considerably deeper from top to bottom than from side to side.

It is never possible to see any line of separation between the supraoccipital, proötic and paroccipital bones, but the known position of the upper parts of the vertical semicircular canals suggests that the great facet with which the exoccipital articulates is in part on the paroccipital. Thus that bone has a large smooth surface, anterior and lateral to the vagal foramen, which passes inward to the brain cavity, where it ends on the anterior border of the foramen and the posterior edge of that triangular area of braincase wall which lies between the tenth nerve and the wide opening into the space for the labyrinth. From here the bone extends outward and backward as a thin sheet, fused with the

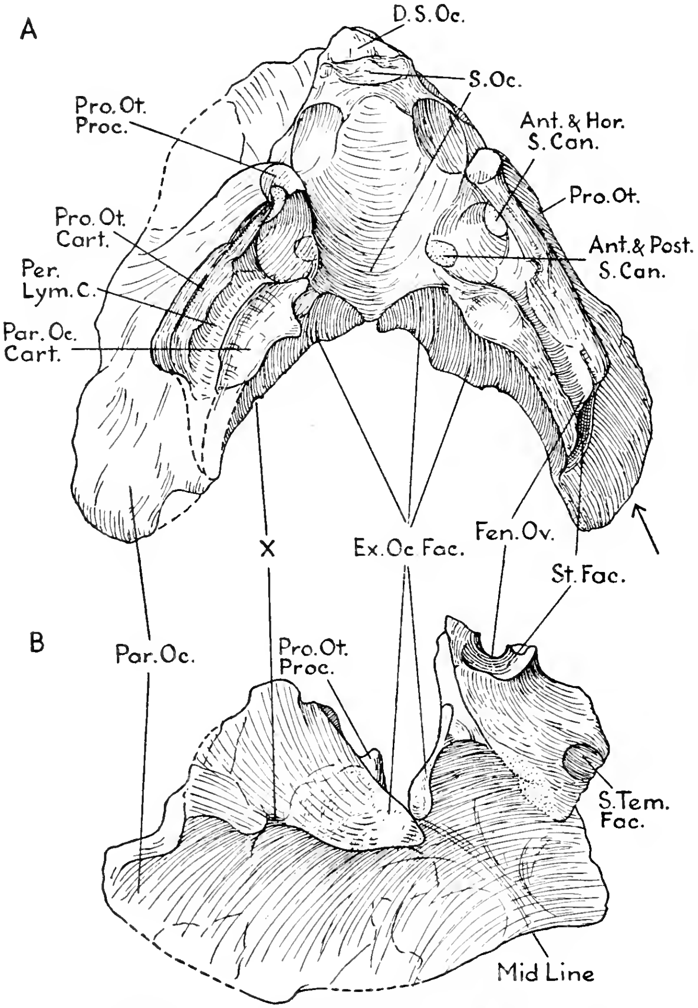

Fig. 20. *Diadectes*, disarticulated braincase (D.M.S.W., R 25) x 1. *A*, viewed directly from below; *B*, seen in the direction of the arrow along the canal of the left side which leads from the internal ear to the fenestra ovalis.

proötic along the roof of the canal leading to the fenestra ovalis. Here it bears part of the depression for the footplate of the stapes and then passes outward to form a rounded knob with whose upper surface the tabular is indistinguishably fused, the supratemporal perhaps reaching it in some individuals.

The canal which lies below the proötic and paroccipital was evidently completed by cartilaginous extension of these bones, which externally were concealed by the lateral extremity of the parasphenoid. The fenestra ovalis, which is the outer opening of this tube, lies nearly parallel to the principal plane of the

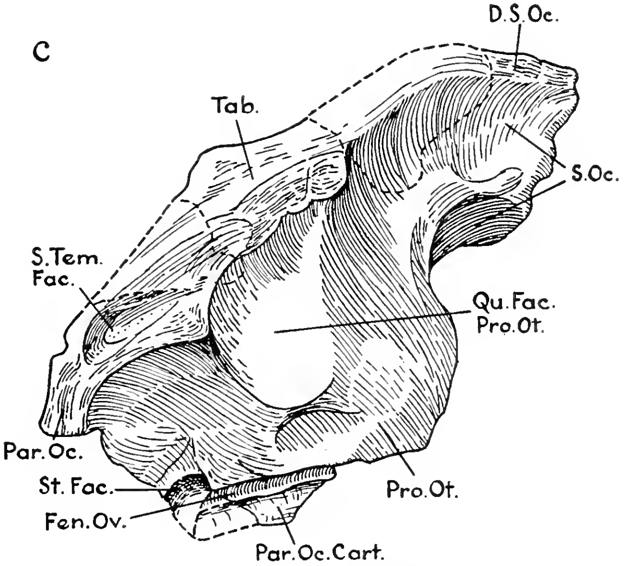

Fig. 21. The right side of braincase of *Diadectes* viewed at right angles to the principal plane. Reference letters for this and the previous figure as before, with: *Ant. & Hor. S. Can.*, anterior and horizontal semicircular canals; *Ant & Post. S. Can.*, anterior and posterior semicircular canals; *Ex. Oc. Fac.*, facet for exoccipital; *Par. Oc. Cart.*, face on the paroccipital continued by cartilage to surround the canal to the fenestra ovalis; *Per. Lym. C.*, perilymphatic canal; *Pro. Ot. Cart.*, groove occupied by cartilaginous extension of the proötic; *Pro. Ot. Proc.*, proötic process; *Qu. Fac. Pro. Ot.*, facet for articulation of the quadrate with the proötic; *S. Tem. Fac.*, facet on the tabular for attachment of the supratemporal; *St.Fac.*, facet for stapes.

skull, and cuts the canal obliquely. The upper part of the fenestra is surrounded by a sharply defined cartilage-covered ring-shaped depression, which must have been continued on the cartilage completion of the duct, and evidently received the foot-plate of the stapes. The interparietal (or dermosupraoccipital) is so completely fused with the supraoccipital that its limits on the occipital surface are unknown, but it extends onto the top of the head where it occupies a triangular area extending nearly as far forward as the pineal foramen.

Skull Roof

The next matter to be considered is the structure of the skull roof. This is shewn perfectly in the type of *Nothodon lentus.* In this specimen, as in all others I have seen, the dermosupraoccipital and the tabular are fused with the braincase. The front of the dermosupraoccipital is free, as I have already explained, though posteriorly it is completely fused with the supraoccipital. The tabulars are in all cases indistinguishably fused with the paroccipitals but their contacts with the supratemporal and parietal are obvious. The suture between the dermosupraoccipital and the tabular is perhaps doubtful, though it appears to be shewn satisfactorily in A.M.N.H. 4378. It is characteristic that the dermosupraoccipital has a triangular exposure on the flat upper surface of the skull, and that its external anterior point very nearly reaches the pineal foramen. This shape, shewn as a suture in A.M.N.H. 4378, by disarticulation in the type of *Nothodon lentus*, in the other skull roof of that species mentioned by Williston, in D.M.S.W. R 25, and in other isolated occipital regions, is important.

The parietal is a bone of very remarkable shape. Its admesial border is deeply excavated by the enormous pineal foramen, so that the median suture between the two bones is extremely short both in front of and behind this opening. Posteriorly the bone passes backward as a distinct corner, with edges almost at ninety degrees to one another, which has a suture with the tabular and with the supratemporal in a way which will be further described. Eventually, rather beyond its middle point, this border turns abruptly outward as an almost straight surface, not very deep but sutural, which completely covers the anterior end of the supratemporal. Lateral to this attachment the border of the parietal turns suddenly forward parallel to the middle line but is divided into two parts by a step, so that a short posterior region of comparatively thin bone has a suture by deeply prolonged interpenetrating processes with the anterior end of the squamosal. The anterior part of this border of the parietal is set in a little towards the middle line, is thin dorsoventrally and has an interlocked attachment to the upper border of the postorbital. From this point the border of the parietal turns abruptly inwards at right angles to the middle line as a straight face directed forwards to which the postfrontal is attached by suture, the attachment continuing over the whole of the anterior part of the lateral border of the parietal to its extremity, where the bone is overlapped by the frontal. Finally a very deep rabbet in the transverse and nearly straight anterior border of the parietal receives the hinder end of the frontal. It follows from this argument that the most striking feature of the *Diadectes* parietal is the existence of a square-cut outwardly directed process of the bone, the parietal lappet, whose lateral border is suturally attached to the postorbital and squamosal, the process separating the postfrontal from the supratemporal.

One other detail of the parietal remains to be discussed. This is that the lower part of the thickness of the parietal behind this process spreads outward for some distance as a sheet of bone so as to form a deep rabbet in which the supratemporal is placed. This arrangement is shewn in several specimens, though best in *Nothodon*. At first the supratemporal, though firmly held, is not fused. Subsequently, like all other bones in this part of the skull roof, it fuses completely.

The frontal is about the same length as the parietal with its lateral margin sometimes coming a little in towards the mid line as it is traced forward. Its hinder border, nearly transversely placed, lies in a deep rabbet in the anterior end of the parietal and its lateral border has a very deep sutural attachment for the pre- and postfrontals, which are connected to one another by suture a little in front of the mid point of the upper border of the orbit.

The nasal is attached to the frontal, whose general direction it continues. Its lateral surface is sutural, and for the whole of its length is in contact with the upper border of the lachrymal.

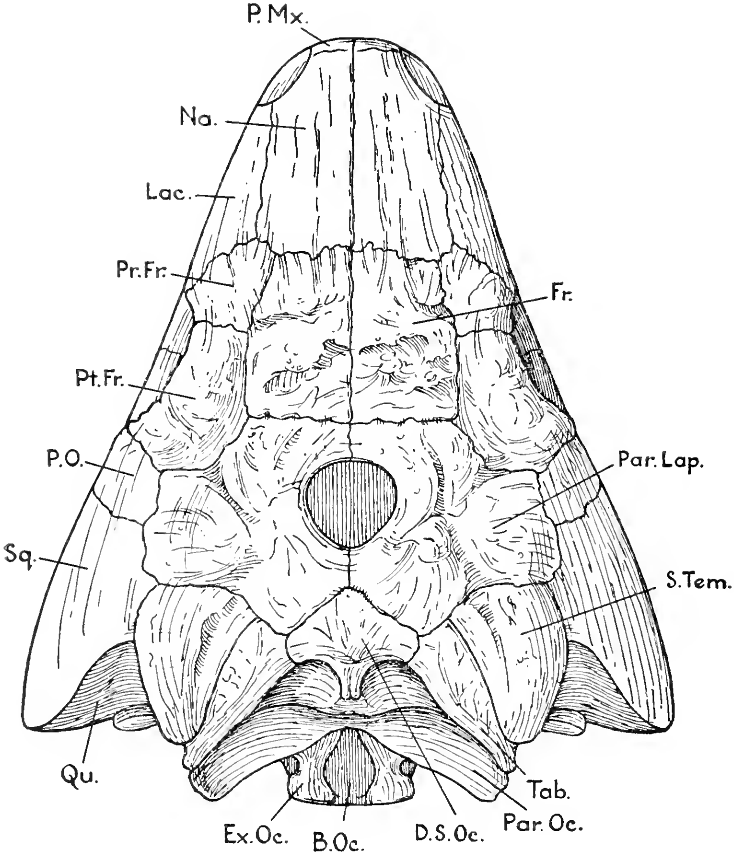

Fig. 22. *Diadectes*, dorsal view of skull. x ⅔. A composite drawing, part of the series reproduced in Figures 17, 18 and 23. The whole dorsal surface from the nasals to the tip of the paroccipital process is an accurate drawing of the type specimen of "*Nothodon lentus*, Marsh" No. 813 in the Yale Museum. The quadrate, parts of the cheek, jugal, maxilla and premaxilla are an accurate drawing of M.C.Z. 1743, no adjustment being necessary to make them fit either in shape or size. The occiput is largely from M.C.Z. 1282. Reference letters as in Figure 17, with: *Fr.*, frontal; *Lac.*, lachrymal; *Na.*, nasal; *P.Mx.*, premaxilla; *P.O.*, postorbital; *Par.Lap.*, parietal lappet; *Pr.Fr.*, prefrontal; *Pt.Fr.*, postfrontal.

Ultimately the nasal forms part of the border of the nostril and has a contact with the narrow internarial process of the premaxilla.

The orbit in actual specimens is generally a good deal shallower than its length but this seems to be due to crushing. At any rate the visibly undistorted and perfectly preserved pre- and postfrontals of *Nothodon* almost accurately surround a semicircle. The uncrushed and perfectly preserved maxilla, lachrymal and anterior part of the jugal of M.C.Z. 1743 also support a part of the circumference of a circular orbit, and A.M.N.H. 2443 — an obviously uncrushed fragment — again retains about one third of a circular orbit, and I have thus represented the orbit as circular in this paper.

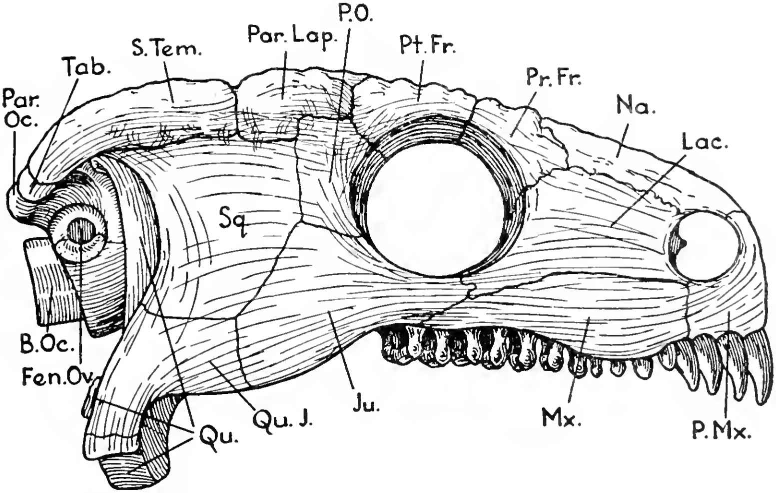

Fig. 23. *Diadectes*, right lateral aspect of skull, x ⅔. Drawn from the same materials as Figure 22. Reference letters as before with: *Fen.Ov.*, fenestra ovalis; *Ju.*, jugal; *Mx.*, maxilla.

The lachrymal extends as a quite deep bone from the orbit to the nostril. The maxilla is shallow, its outer surface standing vertically, and the jugal passes outward and backward to form a considerable part of the temporal region which must now be described.

Temporal Region

I have already explained that in young individuals the supratemporal lies in a rabbet on the lateral border of the parietal, but it extends back behind this bone until it is in contact with a great part of the lateral border of the tabular. Indeed, if the interpretation of D.M.S.W. R 25 given above be correct, the supratemporal is inserted into a groove in the tabular and may even reach the paroccipital. It is at any rate certain that tabular and supratemporal have a long contact on the upper surface of the skull.

The anterior end of the supratemporal rests against the hinder surface of that process of the parietal which separates it from the postfrontal, the parietal lappet, and the arrangements here vary a little. In some cases it seems quite certain that this part extends further laterally than the supratemporal, in others the reverse arrangement seems to obtain. But in any case there is no doubt that effectively the lateral border of the supratemporal continues the outer border of the parietal and does not extend appreciably lateral to that bone. This outer border of the supratemporal has a remarkable character; it is attached directly to the upper edge of the squamosal, but it is perfectly obvious that there is in many specimens no firm sutural attachment between the two bones. In a number of specimens (the *Nothodon* type, D.M.S.W. R 399 for instance) the lateral edge of the supratemporal, which is a thick bone, becomes extremely thin and may have a deep groove running along its outer surface, so that in what must have been a large skull the actual thickness of the lateral border of the skull here may be only about two millimeters. On the other hand, the anterior end of this border of the squamosal is firmly attached by suture to the parietal lappet and it is similarly attached to the hinder edge of the postorbital, a remarkably small, square, bone. The squamosal is a thin and rather delicate bone which projects far backward, but by an internally directed flange it soon comes into contact with the outer edge of the posterior surface of the quadrate, and the two bones fuse quite early in life. The squamosal is continued ventrally by a quadratojugal similarly attached to the quadrate, though separated from that bone by a quadratojugal foramen, and passing downward onto the outer condyle, and both squamosal and quadratojugal have a sutural attachment to the hinder end of the jugal. As a result of this arrangement there is an enormous and tortoise-like otic notch for the reception of the tympanic membrane.

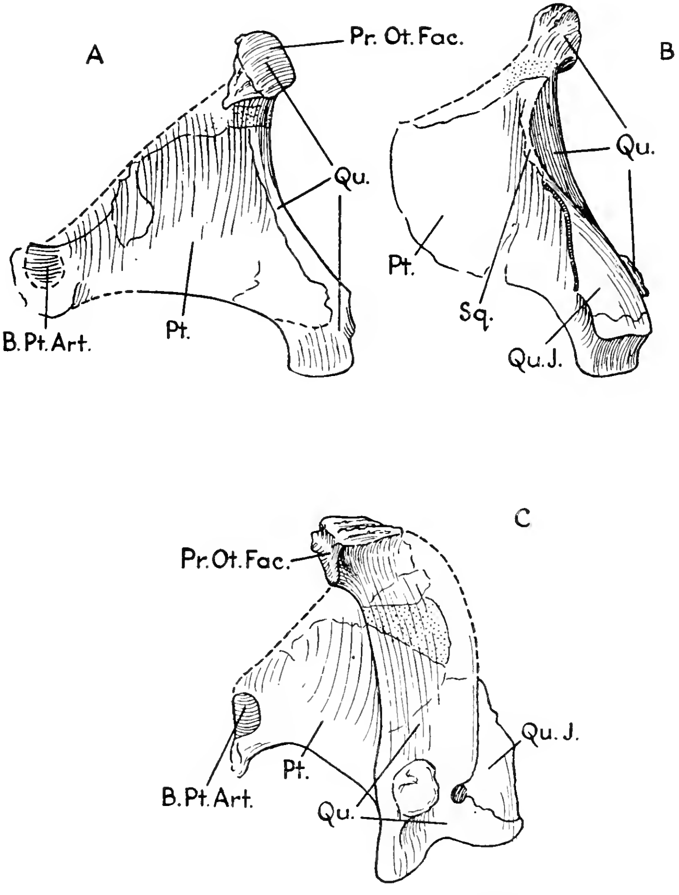

Fig. 24. *Diadectes, A* and *C,* right quadrate with attached quadrate ramus of the pterygoid and a strip of quadratojugal and squamosal; *B,* left quadrate, M.C.Z. 1743, x ⅔. *A,* from the admesian surface; *B,* external aspect; *C,* from behind. Reference letters: *B.Pt.Art.,* basipterygoid attachment on the pterygoid; *Pr.Ot.Fac.,* facet of quadrate for articulation with the proötic; *Pt.,* pterygoid; *Qu.,* quadrate; *Qu.J.,* quadratojugal; *Sq.,* squamosal.

Quadrate

The quadrate of *Diadectes* is beautifully shewn in M.C.Z. 1743, where the lower part of both bones, with the quadratojugal and pterygoid fused but still shewing the course of closed sutures, is completely free from matrix. The upper end of the right quadrate, again undamaged and entirely free from matrix over the whole structure, has lost its contact with the lower part of the bone, but the continuity of a white patch on the generally dark brown bone and the carrying on of the very elaborate and perfectly preserved surface enables one to restore it to its original position certainly, with a possible error of no more than one or two millimeters.

The quadrate is a bone of great height, considerable width, and very small antero-posterior extent. It is in essence a sheet of dense bone with very little cancellar tissue whose posterior surface bears a central vertical strip, perhaps slightly concave from side to side, whilst the margins of the bone round over as they pass to the sutures with the pterygoid, the quadratojugal and the squamosal. The anterior surface of the bone at about the middle of its height is concave, and the bone itself is unexpectedly thin, perhaps only three or four millimeters in a bone some twenty-five millimeters across. The posterior surface is a little concave dorso-ventrally and ends at the condyle. This gives the impression of being divided into two, an inner part lying some 8 mm. ventrally of the outer. Each was formerly covered by a pad of cartilage of presumably considerable thickness, and the antero-posterior extension of the whole structure is very small, perhaps of the order of 10 mm. The two parts of the condylar surface seem to lie accurately transversely. The posterior part of the quadrate ramus of the pterygoid is composed of thin bone 2 mm. or less in thickness, and this is applied to a straight inner border of the quadrate. The pterygoid runs forward and inward from this point for a very considerable distance. It is evident from the detached fragment of the right quadrate of M.C.Z. 1743 that it extended dorsally above the extreme upper part of the pterygoid, having there a free admesial surface, which is at its lower part directed almost entirely inward and stands nearly vertically. From this a process 6 or 7 mm. in length projects directly inward and is then truncated by a gently convex face with an irregular surface of continuous bone incised by a few irregular sharp edged grooves. This face is oval in shape and a little obliquely placed so that its main axis inclines a little forward at the top. It is quite evident from its whole character that this face articulated with the quadrate facet on the proötic; the two surfaces have identical qualities, the bone being continuous and overrun by canals, presumably for blood vessels.

The significance of this particular structure is that the material lying between the quadrate and proötic facets was not cartilage. It was presumably a modified perichondrium. The implication from this is that there did not exist an embryonic continuity of an otic process of the quadrate with the otic capsule, but that this contact is a secondary one, probably recently acquired.

The upper surface of the otic process has a triangular region, whose complete lateral extent is not shewn, in which the bone is deeply grooved and faintly recalls the character of the articular surface. In some older individuals this face fuses with the overlying skull roof, which in this region is likely to include the supratemporal and the parietal. But the articulation between the quadrate and the otic capsule may remain movable after the quadrate has fused with the membrane bones of the skull roof, and it is even a little doubtful whether fusion ever takes place in it. The outer surface of the quadrate is attached by a close suture to the quadratojugal and apparently to the squamosal even in M.C.Z. 1743; in older specimens the two bones are fused, the sutures completely disappearing.

The only other remaining structure is a flat surfaced, slightly pedunculate and large (10 mm. across) knob lying on the posterior surface above the inner condyle. The peduncle of this process has in some cases a wide shallow groove which passed forward and outward to become the inner wall of the quadratojugal foramen. This process is clearly a muscle or ligament insertion whereby the posterior part of the hyoid is attached to the skull.

The curious antero-posteriorly small though wide articular face of the quadrate has to be considered in connection with the structure of the lower jaw and the characteristic wear found on the maxillary and dentary teeth of *Diadectes*. It is evident that the character of the wear, which is discussed in a later section of this paper (p. 437), can only be explained by movements which involve an antero-posterior excursion of the lower jaw; possibly even lateral excursions are necessary. That such movements were possible is, I think, shewn by the fact that the perfectly sharply limited, cartilage-covered, articular surface of the lower jaw, which is divided into inner and outer parts by a median ridge, is much longer than the antero-posterior thickness of the quadrate condyle, even if allowance be made for a considerable swelling out of a cartilaginous extension bearing the actual articular surface of the quadrate.

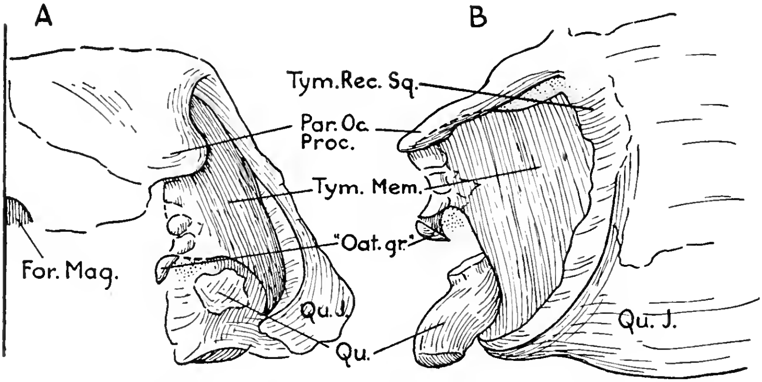

Fig. 25. *Diadectes.* Drawings of the right tympanic region of a distorted skull to shew the ossified tympanic membrane. Specimen in the M.C.Z. No. 2086, x ⅔. *A*, directly from behind; *B*, directly lateral. Reference letters as before with: *For.Mag.*, foramen magnum; "*Oat. gr.*", independent ossicle referred to in text; *Tym.Mem.*, tympanic membrane; *Tym.Rec.Sq.*, the internal flange of the squamosal which passes within the membrane to form the front wall of the outer part of the tympanic cavity.

Tympanic membrane

The conditions described above make it evident that there was a very large otic notch in *Diadectes,* reminiscent of that of a turtle. It remains to consider the nature of the membrane which spanned this notch, its position with regard to the external surface, and the sound transmitting apparatus whereby its vibrations were conveyed to the fenestra ovalis.

A partial preparation of a specimen of *Diadectes* in the Museum of Comparative Zoology shewed a series of small fragments of thin, smooth surfaced bone which tapered to a feather edge anteriorly, and lay pressed onto that smooth surface of the squamosal passing inward behind the ridge which forms its posterior border on the real outer surface. These fragments immediately suggested some ossification in a tympanic membrane, but were themselves inconclusive. However I subsequently found that the *Diadectes* skull in the Chicago Museum (C.N.H.M. U.R. 27) shews a complete, fully ossified tympanic membrane on each side, undistorted and in position. Somewhat later, by preparing a newly collected skull in the Museum of Comparative Zoology I saw another completely ossified tympanic membrane on each side of the head. The conditions here, where the preparation has been somewhat more complete than in the case of the Chicago skull, are as follows.

There is a flat membrane with a smooth outer surface which is essentially plane. This is placed within the otic notch, with its posterior border nearer the middle line than is the anterior part of the bone, and in a vertical sense it follows the slope of the outer surface of the squamosal and quadratojugal in the postorbital region. It is a little (3 or 4 mm.) depressed below the outer surface of the skull at its anterior border, but does not seem to come into contact with any underlying bone. The anterior border of the tympanic ossification follows accurately the ridge which marks the hinder border of the squamosal and quadratojugal on the outer surface of the head. Dorsally the bone lies parallel to, but not in contact with the lower border of the squamosal, supratemporal and tabular. Posteriorly the flat bone ends in a nearly straight border which turns a little backward ventrally, so that the bone ends in a narrow, back-turned point. The ventral two-thirds of this hinder border is a clean cut edge, but dorsally it is rolled inwards so that a rather narrow sheet of bone extends transversely inwards to the border. This part of the bone is broken up into small fragments by a series of cracks, but the individual fragments so isolated remain in what is obviously nearly their natural position, though their borders no longer fit tightly. This part of the bone ends at an almost vertical border, but the lower end of this structure turns a little backward and is projected down as a special outgrowth behind the hinder border of the lower part of the bone. This process, for such it seems to be, supports a very curious little bone of the general size and shape of an oatgrain. It is pointed at each end, roughly circular in transverse section and its lower end is directed a little inwards, but I am not quite certain that the bone is, in fact, separate. I naturally made further excavations to discover a stapes in position in the fenestra ovalis, but this specimen — in which the skull and lower jaw are in perfect articulation, and a series of vertebrae passes back from the occipital condyle — has suffered a local compression, such that although the skull as a whole is little distorted (the orbit being none the less about twice as long as it is high), the basicranial and otic regions are so completely broken up and condensed that their thickness has been reduced from something of the order of two and a half centimeters to two or three millimeters, and no intelligible preparation can be made of them.

The interpretation of this structure clearly calls for discussion. It shews beyond question that there did, in fact, exist in *Diadectes* a tympanic membrane in the place where one has always been assumed to occur. Whether the actual structure here preserved as bone is better regarded as the tympanic membrane itself, or as an ossification of an extra columella inserted in the membrane is disputable. No facts are known which allow a judgment to be made, nor do I think it very much matters, for it is at any rate obvious that the inwardly directed process from its hinder margin to which the possibly separate small bone is fastened is the point of attachment of the stapes to the structure. It lies, in fact, immediately opposite the place where the fenestra ovalis must be.

If we go further we may suggest that the inturned upper part of this bone, which lies immediately below the tabular corner of the skull, is effectively the dorsal process of the extra columella. The hyoid process might be anywhere; it might perhaps be represented by the isolated bone, or it may well have ceased to exist in an adult skull, the free upper end of the lower part of the hyoid arch being attached in the normal way by ligament to the boss on the hinder surface of the quadrate. That a stapes existed is made entirely certain by the presence of the cartilage-covered groove for its footplate which surrounds the upper part of the fenestra ovalis.

It may be emphasized that the existence of this membrane and its nature make it perfectly certain that the distal end of the stapes, although still unknown, cannot have articulated with the quadrate at all, and that there is no probability of an internal process having existed because there is nothing in the shape of an articulation on the posterior part of the surface of the quadrate to suggest its presence. It is also evident that in either of the two skulls in which a complete tympanic membrane is present a direct line between the inturned posterior border of the ossified tympanum and the fenestra ovalis passes a centimeter or more behind the posterior surface of the quadrate.

Thus *Diadectes* gives us the first evidence of the existence in Lower Permian times of an ear which agrees structurally with that found in all living reptiles, and contrasts very vividly with the sound conducting arrangements in the heads of the mammal-like reptiles — Pelycosaurs and Captorhinids — which are its contemporaries. These animals belong in fact to two groups, into one or other of which all reptiles fall, which may or may not have had a common ancestor, but have, at any rate, been separated for a long period before that of the Texan Permian deposits. It is evident that one group leads ultimately to mammals, the other to birds, and that we have already widely separated the two groups, the Theropsids and Sauropsids, which Goodrich distinguished in 1916 on the nature of the heart and aortic arches (see p. 427).

SAUROPSID QUALITIES

In contrast to the conditions in Theropsids the quadrate of a sauropsidan reptile has a posterior surface above its condyle which is very commonly visible, uncovered by other bones, for the whole height of the bone. It is customarily rounded from side to side and the pterygoid is attached to the inner surface of the bone, which is sometimes, but not always, produced into a definite pterygoid ramus. The quadratojugal foramen, if present, lies quite laterally and the quadratojugal and the squamosal which lies dorsal to it are attached to a lateral surface of the quadrate so that that bone in horizontal section appears U-shaped, a condition in the greatest contrast to the flat sheet of the theropsid quadrate.

It follows from these conditions that the hindmost part of the quadrate is commonly a ridge, rounded in section, which is freely visible from its lateral side in the complete skull. Furthermore the whole of this quadrate, with a few obviously secondary exceptions (e.g. a crocodile) lies anterior to the basioccipital condyle, and indeed leaves a good deal of the side wall of the otic capsule visible in a direct lateral view.

It is clear that *Diadectes* agrees completely with the sauropsid condition, and it is then necessary to consider how it is related to the most primitive members of the Theropsids, and this means from what amphibian stocks these two great groups of reptiles spring.

In the case of the Theropsids I have shewn that the most primitive members whose skulls are adequately known, *Protorothyris* and *Varanosaurus*, possess a skull table essentially flat, bounded posteriorly by postparietals and tabulars which in part (to a very small extent) lie on the upper surface but are largely represented by down turnings onto the occiput so as to provide for the attachment of neck muscles. In the pelycosaur group this downturning is continuous from side to side, in the Captorhinids it is broken by the preservation in the midline of a backward extension which separates two independent muscle masses. In both cases this depression for the nuchal muscles leaves unaffected backwardly projecting points of the tabulars, the outer surfaces of which are covered by similar very narrow supratemporals. The under surface of the whole of the corner so made is pressed down onto a rounded upper surface of the squamosal which lies above the top of the quadrate, and may in fact be moulded on a cartilaginous continuation of that bone.

On the upper surface the tabular and supratemporal form the corner of the table whose lateral border, very nearly straight, is carried on the supratemporal for a short distance, and then for a considerable extent on a lateral projection of the parietal, the parietal lappet, which separates the supratemporal from the postfrontal, the parietal process thus occupying exactly the space which in Anthracosaurs is held by the intertemporal. Only the anterior part of the lateral border of this table is suturally attached to the bones of the cheek, chiefly the postorbital but to a very small extent the anterior part of the squamosal. The squamosal for the greater part of its extent has an attachment to the table which is not by suture and was of such a character that the two parts could readily move with respect to one another after the death of the animal.

In *Diadectes* the table exists, but its nature is less easily appreciated because the downturned posterior flanges of the postparietal and tabulars have fused so completely with a widened supraoccipital and confluent paroccipital that the limits of the table posteriorly are not obvious. But it is none the less evident that were an open posttemporal fossa present the structure of the occipital border of the table would be quite comparable to that of the early Theropsids, especially perhaps to the form of the Captorhinids. For in *Diadectes*, exactly as in the early Theropsids, the lateral border of the tabular, which forms a posteriorly directed point, is in contact with the supratemporal. The supratemporal has a lateral border extending in a general sense anteriorly and posteriorly, which border is carried on — usually with a slight displacement — by the parietal lappet which, exactly as in the Theropsids, lies in the position of an intertemporal and separates the supratemporal from the postfrontal. In *Diadectes* the postorbital is attached by suture to the postfrontal and the anterior half of the lateral margin of the parietal lappet. The squamosal has a short suture with the hinder part of the parietal lappet border and then continues in contact with, but not united by suture to, the outer border of the supratemporal, to end ultimately in a point which may be received in a deep groove in the tabular. The whole of this hinder portion of the upper border of the squamosal is thus moveable in the sense that it is not rigidly attached to any other structure.

It is thus evident that in the structure of the table and in its relation to the squamosal, the earliest members of the Theropsida and Sauropsida agree. Such a table, with such a relationship to the squamosal and postorbital, is known only in Anthracosaurs. No other group of Palaeozoic amphibia affords a parallel.

Anthracosaur Jaw Articulation

When first I described the conditions in Anthracosaurs I was extremely puzzled to understand how animals which attained a skull length of some 38 cm., with a powerful dentition including teeth some 4 or 5 cm. high, could function with a quadrate which has to take so heavy a pull of the masticatory muscles and was so inadequately connected to the braincase, and hence to the backbone.

In my original account of the structure I refrained from any detailed discussion of the matter, merely saying that the ventral surface of the supratemporal bears a shallow but wide groove which ends posteriorly at an abrupt face of the tabular. This groove received the squamosal which was not originally attached by suture to any bone of the table. Laterally to the squamosal groove, the supratemporal bears a narrow smooth articular face which can only have been for the postorbital, which bone is attached by suture to a large pitted sutural face on the intertemporal. The upper edge of the squamosal which articulates with the supratemporal is thickened and concave so that there was during life a considerable mass of ligament between the two bones. With this statement I had thus to be content because I saw no other explanation of the nature of this highly peculiar articulation. But I have never been satisfied with it and now offer what may, I hope, be the true explanation.

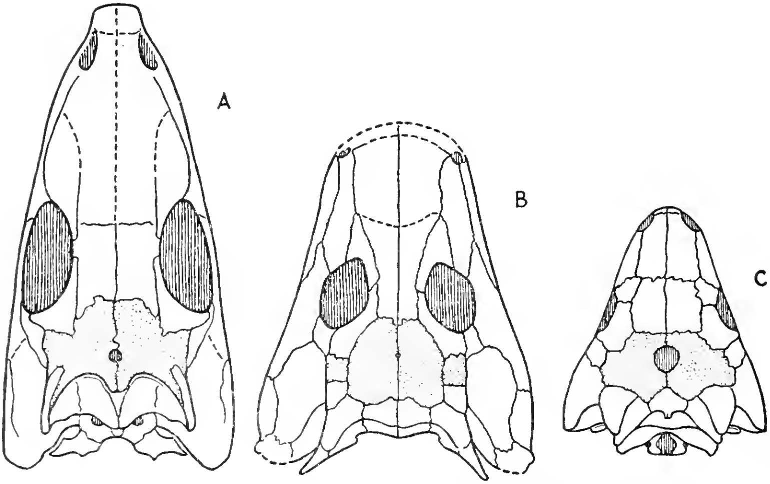

Fig. 26. Dorsal views of the skulls of *A*, *Protorothyris; B*, *Palaeogyrinus; C*, *Diadectes* reduced to the same width of table; the parietals and, in *B*, the intertemporal are stippled, to shew the fact that the reptilian "parietal lappet" occupies the position and has the attachments of the intertemporal.

In all Anthracosaurs with which I am acquainted the posterior border of the pterygoid meets that flange of the squamosal which is turned inwards below the otic notch and underlies part of the tympanic cavity, leaving visible posteriorly and ventrally, when their borders separate from one another, some part of the posterior surface of the quadrate. Although the quadrate of Anthracosaurs has never been very clearly seen from its anterior surface it is evident, as shewn for instance by the type of *Anthracosaurus russelli*, that it agreed structurally with that of Loxommids or of *Seymouria*. This implies that the bone extends forward with its posterior surface covered by the squamosal and pterygoid until it ends abruptly at a face which was formerly continued by cartilage for an unknown extent. In this cartilage at some stage of the animal's life history the epipterygoid arose. The only known epipterygoid of an Anthracosaur is that of *Palaeogyrinus;* and that is seen from its inner surface attached to the front border of the parotic plate of the pterygoid. It is a bone whose essentially horizontal dorsal border ends in a forwardly directed process, and bears two notches for V^2 and ^{3}. It is certain that at some time the whole posterior edge of this bone must have been connected with the upper end of the quadrate by a continuous sheet of cartilage whose inner surface was coated by pterygoid. Romer has shewn that such an arrangement occurred in the rather primitive rachitomous form *Edops*, and it is evident not only that it must have occurred at some stage of the life history but that it may well have persisted throughout life in Anthracosaurs. I shewed (1926) that in the Osteolepid fish *Megalichthys* the palatoquadrate cartilage survived into the adult as a structure spread out along the upper border of the parotic plate of the pterygoid from the basipterygoid process backwards, and that this cartilage was in *Megalichthys* ossified as a chain of bones whose individual existence was definitely proved by the displacement of so many of them as to make the arrangement clear. In the actual specimens this fringe of cartilage bones to the parotic part of the pterygoid is squashed completely flat, as are all cartilage bones in the material. Subsequently Stensiö shewed that in the much earlier *Eusthenopteron* the palatoquadrate cartilage might persist into the adult, being there completely filled by a single continuous ossification. Despite this difference, in both *Eusthenopteron* and *Megalichthys* the parotic part of the palatoquadrate cartilage formed as it were a border along the upper margin of the corresponding part of the pterygoid. It follows, therefore, that such development of the palatoquadrate cartilage must lie very near to the roof of the skull in these fishes.

Osteolepid Palatoquadrate

A series of specimens of *Osteolepis macrolepidotus* and other Osteolepids from Tynet Burn shews the arrangements very well.

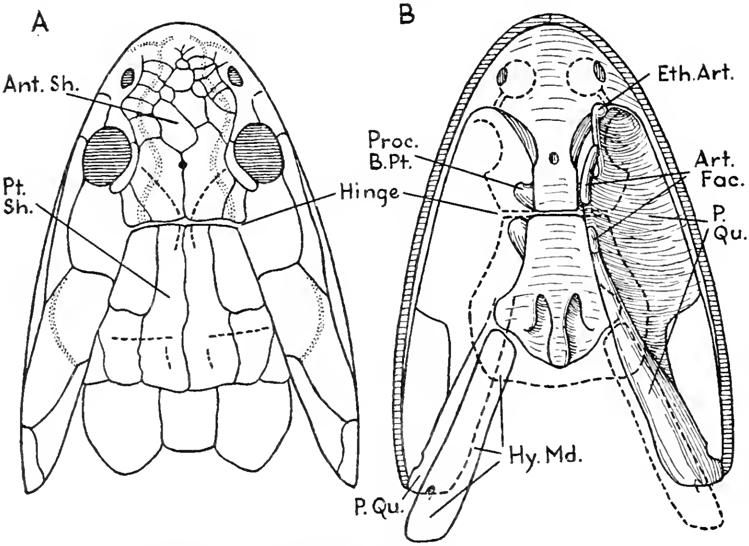

Fig. 27. *Osteolepis macrolepidotus*, x 2. Restorations of the skull from above. *A*, complete; *B*, with the dermal bones removed to shew the palate and braincase. Reference letters: *Ant.Sh.*, anterior shield; *Art.Fac.*, facets by which the palatoquadrate articulates with the skull roof; *Eth.Art.*, articulation of the palatoquadrate with the olfactory capsule; *Hinge*, between anterior and posterior dermal shields; *Hy.Md.*, hyomandibular; *P.Qu.*, palatoquadrate; *Proc.B.Pt.*, basipterygoid process; *Pt.Sh.*, posterior dermal shield.

O. macrolepidotus is shewn in the specimen C 90 (Dept. Zoology, University College, London) to possess a single great bone which clearly includes a completely ossified palatoquadrate cartilage together with a pterygoid. It seems impossible to differentiate between these two structures which in the material at hand appear to be entirely fused. That they are so fused seems to be confirmed by the fact that where, as in D.M.S.W. P 90, a part of the

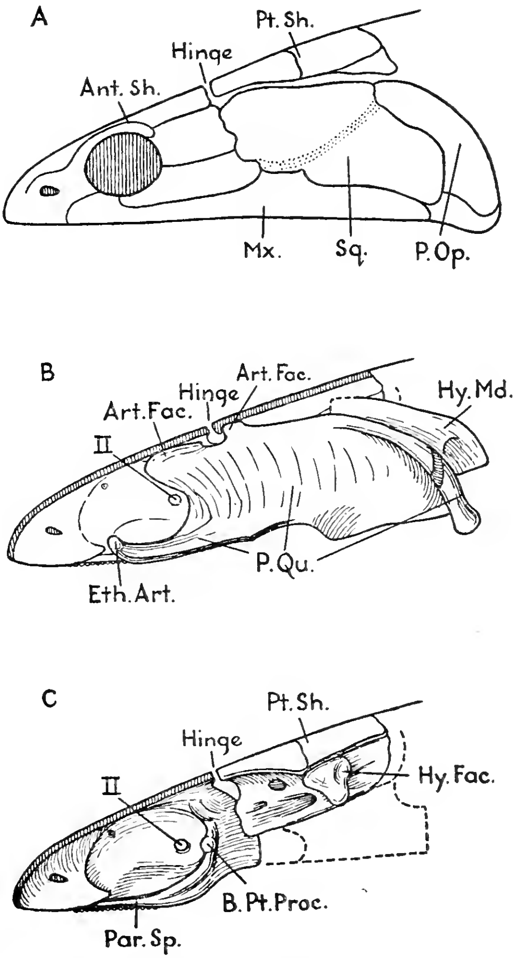

Fig. 28. *Osteolepis macrolepidotus*, x 2. Restorations of the skull from the left side. (These do not agree exactly with Figure 27, as they are founded on different specimens.) *A*, external view with dermal bones *in situ; B*, external view with dermal bones removed but the palatoquadrate and hyomandibular left *in situ; C*, the braincase, with the posterior dorsal shield in position. Reference letters as in Figure 27 with addition of: *B.Pt.Proc.*, basipterygoid process; *Hy.Fac.*, facet on the otic capsule for articulation of hyomandibular; *Mx.*, maxilla; *P.Op.*, preopercular; *Par.Sp.*, parasphenoid; *Sq.*, squamosal; *II*, the optic nerve foramen.

structure which lies in the position of an ectopterygoid is broken across, it is thick cancellar bone with only a very thin continuous table. It agrees indeed in structure exactly with the quadrate.

This bone very greatly resembles the palatoquadrate of an Elasmobranch, has a deep parotic part rounded above and cut off below at a point which lies a little above the level of the quadrate condyle. The whole of this posterior and upper border is everted, standing out transversely in the region of the quadrate and gradually becoming narrower when seen from above as it passes forward into the region of the epipterygoid. The outer surface at the quadrate end is covered with a continuous thin layer of bone for some distance above the quadrate condyle. This border is notched by a smooth floored groove which passes forward and downward exactly at a level with the lower opening of a canal for a blood vessel and nerve which passes through the hyomandibular, which bone lies immediately behind the quadrate. Above and below this groove the edge of the quadrate is not flat, although it is a "finished" surface. Anteriorly, as I have explained above, the upper border of this cartilage bone narrows until it ultimately ends in a forwardly projecting point which is quite thin from side to side. A little behind this point, and also behind the place where the palatoquadrate cartilage must meet the basis cranii, the upper border (here lying horizontally) is notched by a sharply defined transverse groove (with a small process posterior to it) through which the second and third divisions of the Vth nerve pass on their way from the braincase to their peripheral distribution. Below this forwardly directed point, which clearly occupies the position of the epipterygoid, the palatoquadrate cartilage border turns sharply downward and backward to form an anterior border of the epipterygoid. This part of the bone must bear at its lower end, on the admesial surface, some sort of a facet for attachment to the basipterygoid process. But no one of my specimens shews this structure, merely because they are seen from without.

As so seen, what is quite clearly the cartilage bone part of the structure in the epipterygoid region extends very considerably in advance of the border of the membrane bone, being comparatively thick from side to side, and having a very definite embayment for the first division of the Vth nerve. Ventrally the bone extends forward in the palate with its anterior margin upturned to form a cup below the eye and to articulate with the nasal capsule, as Jarvik has shewn it does in *Eusthenopteron*.

It seems evident that the outer surface of the palatoquadrate cartilage for some distance in front of the quadrate condyle must have had a contact with the preopercular bone of the cheek immediately lateral to the hyomandibular. In *Osteolepis* it is quite evident that the hyomandibular lay parallel to the posterior surface of the quadrate cartilage and was in fact in contact with it, or very nearly so. It retains this position in a number of specimens of different genera of Osteolepids from Tynet Burn. This bone (the hyomandibular) appears to be received in a groove on the upper and inner surface of the preopercular bone which lies behind a flange which appears to come into direct contact with the lateral surface of the quadrate part of the palatoquadrate. If this be so (as D.M.S.W. P 72 seems to make quite certain) then the contact between the cheek and the outer margin of the quadrate extends at least up to the summit of the preopercular, that is to a point approaching but not reaching the hinge on the top of the skull. In front of this point the upper border of the palatoquadrate lost contact with the cheek bones, passing admesial of the border of the table. The dorsal surface of the epipterygoid, anterior to the notch for nerve V^2 and V^3, comes into contact with the under surface of the skull lateral to the pineal foramen and on the inner side of the ridge, within which lies the supraorbital lateral-line canal. A scar for this attachment occurs in D.M.S.W. P 87 (front) on the right side. The process behind the notch for nerves V^2 and V^3 had a similar contact with the visceral surface of the hinder part of the skull roof, whose existence is shewn by attachment scars on the ridge enclosing the hinder part of the supraorbital canal, on the right side in D.M.S.W. P 72 and 87 (back) and both sides of D.M.S.W. P 92.

These two points separated by the hinge are, in Labyrinthodonts (according to Westoll's homologies), on the intertemporal and supratemporal. That is, the two attachment scars lie exactly where the smooth attachment groove exists in Anthracosaurs.

We may therefore hold that the palatoquadrate cartilage survived in Anthracosaurs complete from the quadrate to the epipterygoid, clasped on one side by the squamosal, on the other by the parotic plate of the pterygoid, and that this strip of cartilage (which was comparatively wide) was firmly attached to the under surface of the supratemporal lateral to the braincase. This arrangement provides an explanation of the structure in this region which is mechanically sound, and hence much easier to understand than is my original view that the squamosal was attached to the skull table by some strip of connective tissue of the general nature of a thick ligament.

This arrangement has certain sequels. It implies, for instance, that the jaw-closing musculature of Osteolepids and of Anthracosaurs lay entirely within the tube formed by the membrane bones of the cheek, the palatoquadrate cartilage, the pterygoid, and the cavity of the lower jaw, an arrangement analogous to that in all Elasmobranchs, paralleled amongst still living fishes most closely by *Polyodon*. It means that in tetrapods the normal attachment of masticatory muscles to the dermal bones of the skull roof, and ultimately to the braincase, is secondary and arose in the case of reptiles subsequent to their origin from Anthracosaurs.

It may here be pointed out that the occurrence of a strip of palatoquadrate cartilage anterior to the bony quadrate in Anthracosaurs provides the necessary material for making the articular head which in *Diadectes* brings the quadrate directly into contact with the proötic, and allows the masticatory muscles of that animal to gain their origin from the under surface of the dermal skull roof lateral to the point of attachment of the summit of the epipterygoid.[1]

It has now to be considered whether *Diadectes* came directly from an Anthracosaur, or whether its immediate ancestor was a Seymouriamorph — itself an Anthracosaur derivative.

Diadectes Compared with Seymouria

Broili, in his original description, said that *Seymouria* was a reptile, and in 1919 I set out in detail evidence in support of this view. Since that time *Seymouria* has been variously attributed to

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[1] The fact that in Osteolepids the homologues of the supra- and intertemporal bones rest directly on the palatoquadrate cartilage, that the same condition exists in Anthracosaurs, and survives to be shewn in *Seymouria* and ***Karpinskiosaurus*** where the epipterygoid is turned directly inward, may be brought into association with the absence of an intertemporal bone in reptiles. In *Diadectes* the epipterygoid is so placed as to shew that contact of the palatoquadrate cartilage with the skull roof ceases where the proötic process of the quadrate turns inward, a point which lies on the supratemporal.

the Amphibia and to the Reptilia and there are some real reasons — possible persistence of lateral line grooves on the skull for instance — which suggest that it is indeed an amphibian. Whether or not *Seymouria* possessed a larval stage, and was thus an amphibian, does not alter the true reptilian qualities which exist in its skeleton. The list which I set out in 1919 of the reptilian characters of *Seymouria* retains its validity, whatever be the technical position of the animal in a zoological classification.

Seymouria has recently been redescribed by Dr. T. E. White in an admirable paper which deals with the structure of a group of some nine individuals found together in West Coffee Creek, Texas. These specimens I had the opportunity of examining at leisure in 1952. It is perhaps useful to point out that the specimens, which must clearly belong to the same species and are with great probability members of one individual family, differ quite obviously, and presumably specifically, from many others. A straightforward comparison of the top of the skull in White's Figure 1 with Broili's Figure 1 will shew, I think, at once that the two animals differ. The occipital border is different, the shape and proportions of the otic notch differ, the shape and position of the articulation of parietal, postfrontal and supratemporals are all different. The specimen (B.M.N.H. R 5003) which I collected and described is again different, more greatly resembling Broili's type than White's; although known only fragmentarily it is evident that the arrangement of flanges of the tabular on the occipital surface differs from Dr. White's animal quite definitely, and may much more nearly resemble that of Professor Broili's individual; and so if one wishes one can go on. But these differences are of minor importance; they do not affect the general structure; and I call attention to them because different drawings of *Seymouria* reputedly of the same species differ so much *inter se* that it is natural to suppose some are incorrect.

That *Seymouria* is related to the Anthracosaurs is obvious. The two groups agree in practically all features of their skull other than the braincase, so that no one has yet disputed the close relationship. It is therefore necessary in any consideration of the possible derivation of *Diadectes* from *Seymouria*, or direct from an Anthracosaur, to consider those qualities found in *Seymouria*, which do not occur in the known Anthracosaurs, and which are (or may be) found in *Diadectes*.

The most obvious of such characters are in the postcranial skeleton. The *Diadectes* vertebra, of typical Cotylosaur pattern, is in principle extremely similar to that of *Seymouria,* and indeed only differs from it in the possession by *Seymouria* of two-headed ribs throughout the vertebral column, whilst *Diadectes* has single-headed ribs everywhere except quite anteriorly, and in the occurrence in the latter of accessory articular faces. The Anthracosaur possesses two-headed ribs apparently throughout the whole precaudal column.

The number of vertebrae in an embolomeran column is at present unknown, but it is likely to be of the order of thirty presacrals in *Eogyrinus.* In *Seymouria* there are twenty-three presacrals, in *Diadectes* twenty-two. The structure of the atlas of an Anthracosaur is not known except for a statement of Cope to the effect that a complete intercentrum of normal character articulates with the basiocciput. The *Seymouria* atlas, as I have shewn, agrees with the reptile condition. In *Eogyrinus,* an Anthracosaur, there are three rather unspecialised sacral vertebrae. *Seymouria* has one (or in Dr. White's specimen two) sacral vertebrae which carry normal reptilian sacral ribs, quite unlike those of *Eogyrinus.*

The shoulder-girdle of *Diadectes* has a scapula and apparently a single coracoid, though I have never myself seen a suture between them. *Seymouria* has a single coracoid, whereas the Anthracosaurs have only a single bone in the primary shoulder-girdle. We do not know the fore limb of an Anthracosaur, but that of *Eryops,* short, extraordinarily massive and powerful with the forearm carried at a right angle to the immensely widened distal part of the bone, agrees well enough with that of *Seymouria. Diadectes,* as determined by Romer, seems to have a digital formula of 2 : 3 : 4 : 5 : 3 in the pes, the phalangeal formula of the hand not being known. Similarly the digital formula of *Seymouria* seems to be 2 : 3 : 4 : ? 5 : ? 3 thus agreeing with *Diadectes.* The pes of no typical Anthracosaur is known, but in the anthracosaur skeleton which I described as *Diplovertebron* (which may, as Romer has suggested, be actually a Seymouriamorph) the digital formula in the hand appears to be 2 : 3 : 3 : 3 : 4. It might conceivably be however a normal reptilian number. The pelvis of *Seymouria* has an ilium with a backwardly directed blade recalling that of an Anthracosaur, the pubis and ischium both being completely ossified. The Diadectids have the same arrangement, retaining in fact a rather similar ilium, whilst the Anthracosaur ilium seems to have a long slender posterior projection with fully ossified pubis and ischium. There is therefore little in the postcranial region to shew whether the obvious similarities between *Diadectes* and *Seymouria* seen in it depend in each case on an origin from the Anthracosaurs, or on an affiliation through Seymouriamorphs to *Diadectes*. It must be remembered that the known material of *Seymouria* is later in date than the diadectid material with which this paper is concerned.

SKULL OF SEYMOURIA

The structure of *Seymouria*, as it has been excellently described by Dr. White, does raise certain problems of interpretation, and indeed the significance, of some structural detail. I have examined White's material carefully and am thoroughly satisfied that his account of the structure is reliable, but there are some details which call for further attention.

Firstly, with regard to the braincase itself. The very curious process arising from the proötic which is carried backwards to stand vertically above the inner end of the opisthotic is exceedingly remarkable. It is in fact separated from the body of the proötic by a fracture in the specimen that I examined, and its separation from the opisthotic is not perhaps quite certain. If so the proötic and opisthotic would both end within, so to say, their own region and the continuation of the cartilaginous supraoccipital would join them in a reasonable manner. Such an interpretation perhaps conforms rather more satisfactorily to the condition shewn in the small skull fragment belonging to the British Museum specimen which I described in 1919. In this specimen the admesial ends of the proötic and parotic with the facet on the paroccipital for the articulation of the exoccipitals are shewn, and an actual crack is in all probability the real articulation between them; an interpretation confirmed by the presence at its summit of the meeting of the two cartilage-continued upper surfaces of the proötic and paroccipital, at a sharp angle. From these surfaces a rather slender arch-shaped supraoccipital

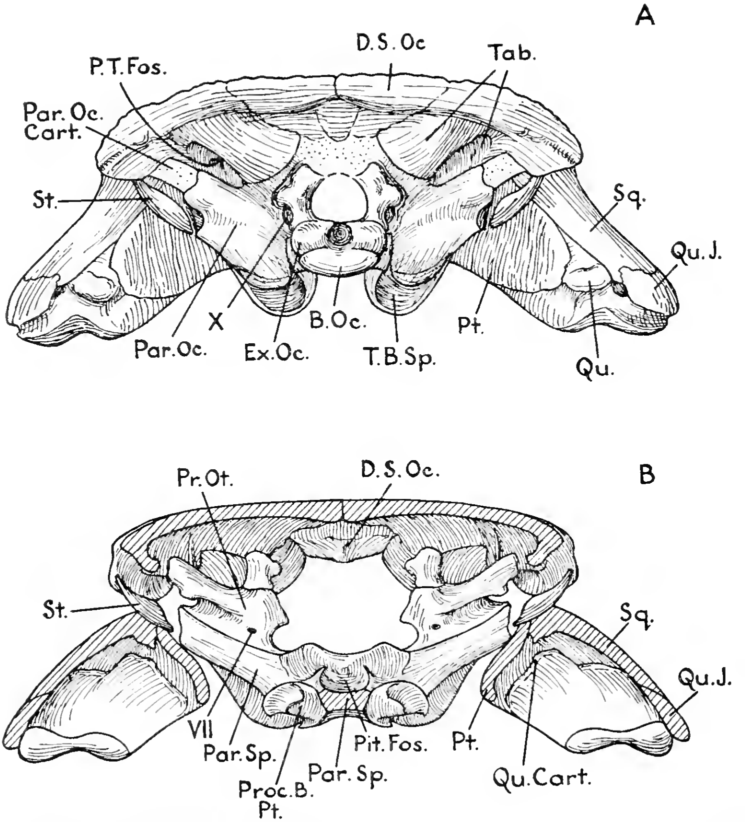

Fig. 29. *Seymouria* sp. Reconstructions of the skull from the material in M.C.Z., Nos. 1081, 1084, 1086, etc. used by T. E. White (1939). x 1. *A*, occipital aspect; *B*, the braincase seen from the front, the bones of the skull roof and suspensorium being cut behind the level of the pituitary fossa. Reference letters: *B.Oc.*, basioccipital; *D.S.Oc.*, dermosupraoccipital; *Ex.Oc.*, exoccipital; *P.T.Fos.*, posttemporal fossa; *Par.Oc.*, paroccipital; *Par.Oc.Cart.*, cartilaginous continuation of the paroccipital; *Par.Sp.*, parasphenoid; *Pit.Fos.*, pituitary fossa; *Pr.Ot.*, proötic, *Proc.B.Pt.*, basipterygoid process, *Pt.*, pterygoid; *P.T.Fos.*, posttemporal fossa; *Qu.*, quadrate; *Qu.Cart.*, the edge of the quadrate which is continued forward by cartilage; *Qu.J.*, quadratojugal; *Sq.*, squamosal; *St.*, stapes; *Tab.*, tabular; *T.B.Sp.*, tuber basi sphenoidalis; *VII*, foramen for the facial nerve; *X*, foramen for the vagus nerve.

cartilage would pass over to the corresponding bones of the other side of the head.

The shape of the otic capsule is very remarkable. As White's admirable figures shew, the parasphenoid is carried out laterally in contact with the proötic and opisthotic to reach the extremely laterally placed fenestra ovalis. This very characteristic arrangement is shewn also in the British Museum fragment, where there

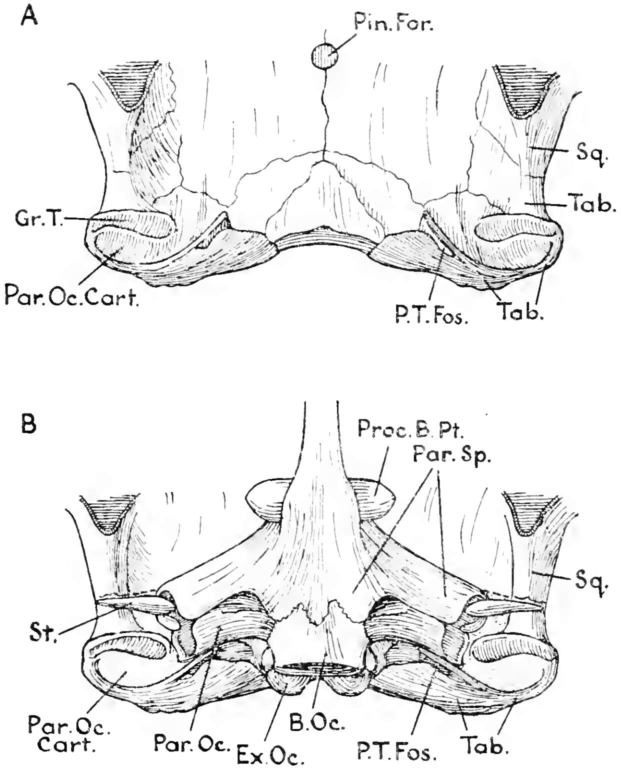

Fig. 30. *Seymouria* sp. Reconstruction of the skull as in Figure 29. *A*, the under surface of the skull table with part of the squamosal attached; *B*, the under surface of the braincase *in situ*. Reference letters as in Figure 29 with: *Gr.T.* deep groove on the lower surface of the tabular in front of that which receives a cartilaginous tip of the paroccipital; *Pin.For.*, pineal foramen.

is some reason to believe that the proötic and paroccipital were each continued ventrally by a cartilaginous extension, the two presumably meeting and the junction being covered by the parasphenoid process. In other words it would appear that the tube leading to the fenestra ovalis, which is obviously of considerable length, had a floor of a persisting strip of cartilage supported on its outer surface by parasphenoid. But no trace of any such structure is found in *Eogyrinus*, *Palaeogyrinus* or *Archeria* (*Cricotus*). It is therefore a new introduction in Seymouriamorphs.

Several examples of the stapes are preserved in the Harvard material; none of them seems to shew a stapedial foramen, the short bone having an expanded proximal end and a very slender tympanic part. There is a very uncertain suggestion of a pit for origin of a hyoid process on the lower surface. The structure of the basioccipital and basisphenoid is very satisfactorily shewn in the figures of Dr. White's paper, differing in obvious ways from the structure of the British Museum skull, and those in Munich.

The next matter to concern us is the structure of the squamosal and of the palatoquadrate, and the way in which the table of the skull is connected to the cheek. The general structure of the table has been known since the publication of Professor Broili's figures, and its lateral border — built up by postfrontal, intertemporal, supratemporal and tabular — has long been familiar. The supratemporal comes down towards the border of the table and the tabular forms part of the upper border of the otic notch. The intertemporal may have a pointed anterior margin wedged in between the postorbital and the postfrontal, the length of its contacts with these two bones being variable.

The squamosal articulates with the postorbital, intertemporal and supratemporal, the anterior border of the otic notch (as mapped out by the disappearance of the characteristic roughened ornamentation of the outer surface of the bone) lying variably between a position towards the anterior end of the intertemporal (in White's specimen) to one just at the point of junction of the intertemporal and supratemporal (in specimen B of Broili). In each form, however, a special process of the squamosal stretches backward above the anterior part of the long otic notch, separating it from the skull table. This process of the squamosal is hollow, the cavity it contains lying in a groove in the bone, which, as it is followed forward, turns downward in front of the notch and there continues backward until it rests upon the upper surface of the quadrate. Dr. White has already recognised the existence of this arrangement.

It is very easily seen that this arrangement is entirely consonant with the structure found in Anthracosaurs. It is a mere shape modification associated with a more deeply impressed otic notch or, what is essentially the same thing, a backward growth above a long otic notch.

KOTLASSIA AND KARPINSKIOSAURUS

The group of *Seymouria* relatives became larger with the addition to it by Amalitzsky, Sushkin and Bystrow of *Kotlassia*, of *Discosauriscus* from the Permian of Niederhässlich, and the recognition that the specimens from Czecho-Slovakia usually called *Melanerpeton* (now replaced — because it is founded on a species which belongs to a different group — by Romer's term *Phaiherpeton*) are Seymourids[1] These animals are indeed all similar to *Seymouria* in general structure though they differ a great deal in proportions, and it is desirable to consider them anew in connection with the present problem. In addition there is *Solenodonsaurus*, described by Broili and Pearson, which may well be a Seymouriamorph, and the possibility that the creature I described as *Diplovertebron* belongs to the same association deserves consideration.

It is convenient to begin with *Kotlassia*, of which the material is more satisfactory than most and includes the posterior half of a skull in my collection (D.M.S.W. B 100) which shews some features very well. The late Professor Amalitzsky in 1921 recognised that the great fauna of the Upper Permian of the Dwina contained the skeleton of what he then held to be a reptile, which was related to *Seymouria*. Of this material he gave a considerable account, accompanied by three very poor photographic plates, and he distinguished two species, *Kotlassia prima* represented by a complete skeleton, and *Kotlassia secunda* by a skull

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[1] In this paper I use "Seymourids" to include *Seymouria, Kotlassia, Karpinskiosaurus, Discosauriscus, Phaiherpeton, Letoverpeton* and *Waggoneria*. Seymouriid would imply a family in the technical systematic sense including *Seymouria. Gephyrostegus. Diplovertebron, Solenodonsaurus,* though Seymouriamorphs are not Seymourids, nor is *Lanthanosuchus*.

and two considerable fragments of the body now in Moscow. These were admirable materials.

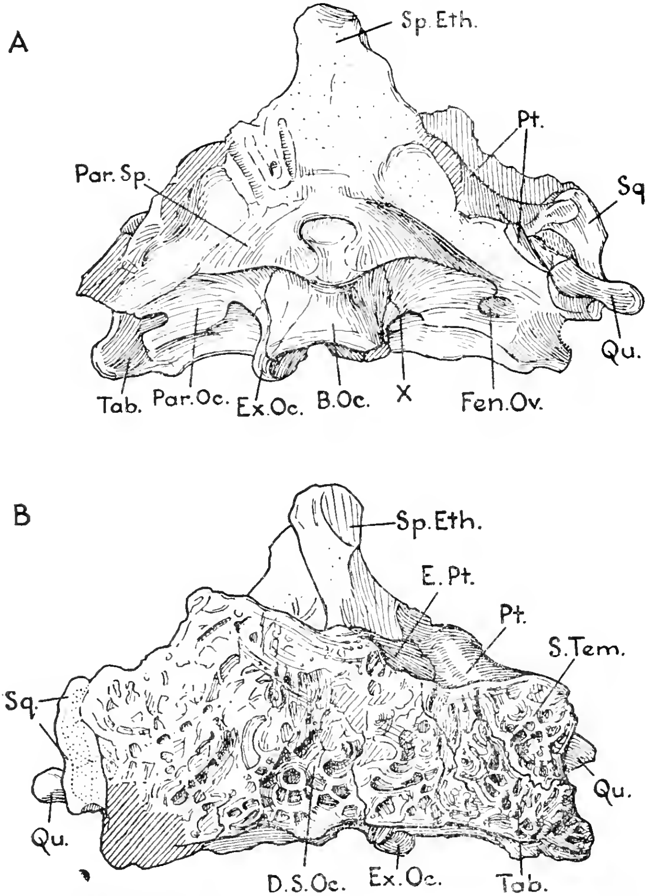

Fig. 31. *Karpinskiosaurus secundus* (Amal.). Drawings of the posterior part of a skull (D.M.S.W. B100). Nat. size. *A*, ventral view; *B*, dorsal view, dotted areas shew unremoved matrix; Reference letters: *B.Oc.*, basioccipital; *D.S.Oc.*, dermosupraoccipital; *E.Pt.*, epipterygoid; *Ex.Oc.*, exoccipital; *Fen. Ov.*, fenestra ovalis; *Par.Oc.*, paroccipital; *Par.Sp.*, parasphenoid; *Pt.*, pterygoid; *Qu.*, quadrate; *S.Tem.*, supratemporal; *Sp.Eth.*, sphenethmoid; *Sq.*, squamosal; *Tab.*, tabular; *X*, vagus.

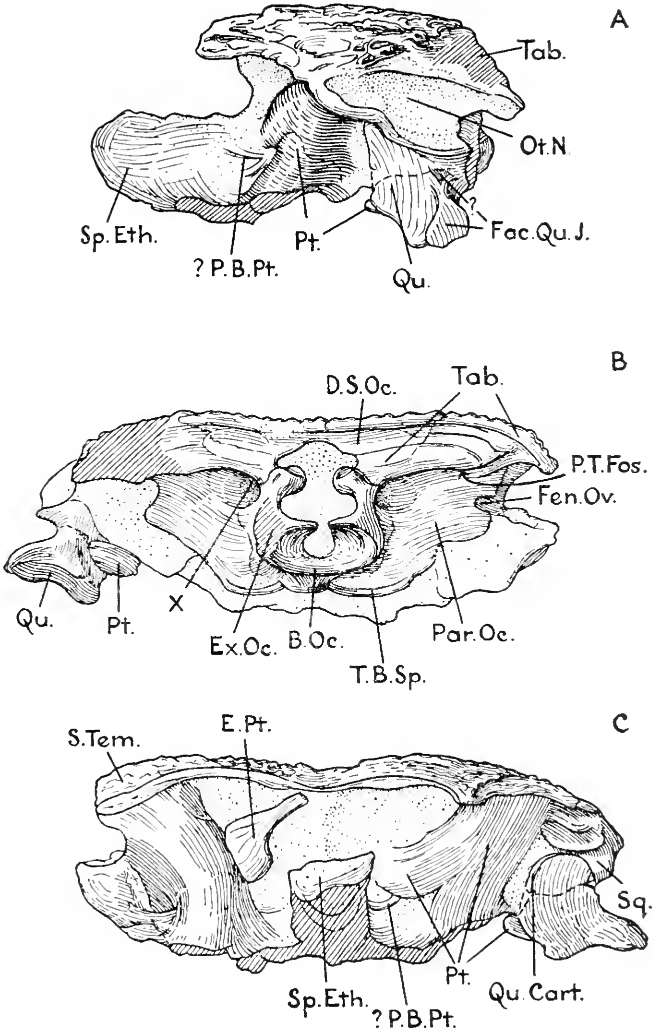

Fig. 32. *Karpinskiosaurus.* *A*, left lateral aspect; *B*, occipital view; *C*, anterior face of the specimen D.M.S.W. B 100. Reference letters as in Figure 31 with: *Fac.Qu.J.*, facet on quadrate for attachment of the quadratojugal; *Ot.N.*, otic notch; *? P.B.Pt.*, ?basipterygoid process; *P.T.Fos.*, posttemporal fossa; *Qu.Cart.*, the face to the cartilaginous continuation of the quadrate; *T.B.Sp.*, basisphenoidal tuber, parasphenoid.

In 1925 Professor Sushkin had re-examined this material and had also seen a good deal of the reptiles and amphibia of the Permian of Texas. He then wrote a series of three very important papers in which the material is referred to, and these contain admirable pen and ink drawings, fully labelled, which shew the structure of the otic region in a most intelligible form. The three papers appeared in 1925 and 1926. In this work Sushkin concluded that the two species represented by Amalitzsky's names existed, that they were generically different, and indeed represented not only different genera but different families. Although I have seen a good deal of the material I have never critically examined it, and have always taken for granted that the admirable account written by Bystrow made it evident that there was only one species involved, called *Kotlassia prima.* But examination of a specimen (D.M.S.W. B 100) which came from the Sokolki lens in the North Dwina, in comparison with Dr. Bystrow's figures, shewed some differences in the occipital region which were difficult to account for if the materials really represented one species. These differences cannot be explained on a basis of crushing, for my skull is essentially uncrushed and so are some of the originals of *K. prima,* and they are exactly those which, according to Sushkin, distinguished the genus *Karpinskiosaurus* (founded for Amalitzsky's *Kotlassia secunda*) from the original type.

The most noticeable difference is the disappearance when viewed from behind of the fenestra temporalis posterior, but the occiput is much wider compared with the width of the skull across the quadrates. Its fine reticulate ornament is different, and the upwardly directed paroccipitals differ a good deal in appearance. It is therefore justifiable to present an independent account of the skull as *Karpinskiosaurus.* It should be given for comparison with *Seymouria*, and with Dr. Bystrow's account of *Kotlassia prima.*

It is quite certain that generally speaking the figures and descriptions of Dr. Bystrow explain the anatomy of *Kotlassia* very accurately. In the occipital region my skull differs somewhat from his figures in that the occipital exposure of the dermosupraoccipital is small, there being a large excavation for the purely cartilaginous supraoccipital which comes down onto the upper and inner part of the exoccipital. Lateral to this place the occipital surface bears a deep transverse channel, along the middle of whose floor runs a suture separating the occipital flange of the dermosupraoccipital from a bone which lies ventral to it, and the suture turns upward onto the upper surface, where it can be seen as a separation between the tabular and the dermosupraoccipital. The tabular has a dorsal exposure at the corner of the skull exactly as is shewn in Bystrow's figure. It is rounded at its extremity but projects a good deal. It bears a considerable extension downward and inward on the occiput which is quite largely visible from above. It is bounded by the posterior border of the dermosupraoccipital and it passes inward toward the middle line for a very considerable distance. The lower edge of this part of the bone appears to be free and to form an upper margin of the posterior temporal fossa. But from a point further out on the occipital surface of the tabular another independent very thin strip of bone passes downward and inward separated by a space from the lateral part of that occipital flange of the tabular I have just described, and it is this more anterior flange of the table which comes into contact with the hinder surface of the paroccipital.

Thus the posttemporal fossa is scarcely visible from the back because its upper border lies on a deep flange of the tabular, the lower border being carried for its lateral part on another independent tabular process which lies, almost completely hidden, in front of the upper occipital flange. In other words the structure here differs from that in Bystrow's figure by a complete invisibility of the posttemporal fossa from behind, and it is very difficult indeed to attribute the differences to distortion.

The paroccipital is well shewn as a bone which passes outward from an attachment to the basis cranii (largely to the anterior end of the basioccipital) to a very distally placed termination at the fenestra ovalis, which in posterior view is separated by a very distinct notch from that upper part of the bone which lies essentially in contact with the skull roof, and ends abruptly in a face presumably completed by a small cap of cartilage. At its proximal end the paroccipital is very deeply notched so as to form, with the exoccipital, a relatively enormous foramen for the Xth nerve. Below this point it stretches downward in visible continuity of surface with the basioccipital, although the two bones are seen to be separated by a suture clearly visible on the right side of the specimen. The ventral border of the posterior surface of the paroccipital lies some distance above the free posterior margin of the parasphenoid, but it follows the same general course, the intervening space having no doubt been occupied by unossified cartilage. The main part of the proötic is hidden by the pterygoid, but such parts of it as are known resemble the corresponding bone in *Kotlassia* as figured by Bystrow, with the correction that much of the lower part of the anterior face is covered by a great lateral extension of the parasphenoid, whose tip lies less than five millimeters mesial of the fenestra ovalis, which lies in the floor of a notch passing horizontally through the paroccipital and proötic. The floor is narrow from front to back, the proötic flaring out above it to have the wide contact with the skull roof described above. No visible suture separates the proötic and paroccipital.

The specimen makes it evident that the structure of the basicranial region and the otic capsule is in all essentials that of *Seymouria*, where the parasphenoid is immensely widened, forming two wide ridges below the ventral margin of the paroccipitals which are the basisphenoidal tubera, and extending outward in contact with the front face of the proötic to, or very nearly to the fenestra ovalis.

The next point for consideration is the nature of the palatoquadrate cartilage and its connection to the pterygoid and squamosal. Some details of these matters are well shewn in my specimen. The quadrate is well shewn from in front and behind. Its articular margin, although wide from side to side, is singularly narrow from back to front, and above this the bone rises vertically in the skull, its posterior surface forming a rounded knob — the customary muscle or ligament insertion. The lateral border of the bone is cut in above the outer part of the condyle to form a step to which the quadratojugal was attached, the facet ending mesially at the smooth inner border of the quadratojugal foramen. The pterygoid ramus, which is of considerable length, continues forward, directed towards a point some distance in advance of the basipterygoid process, and the anterior surface of the bone forms a concavity rather abruptly truncated by a contact with the sub-tympanic part of the squamosal. Anteriorly the quadrate ends abruptly in a surface which was clearly continued by cartilage. The further continuation of the palatoquadrate cartilage can be inferred with very small possibility of error from the shape and character of the quadrate ramus of the pterygoid. The lower border of this bone is turned outward as a flange with a rounded lower surface which quite evidently sheathed the lower border of the palatoquadrate. That cartilage continued forward to a point where the summit of the quadrate ramus of the pterygoid meets the skull roof immediately in front of the tympanic notch. Here its surface swings round until it stands almost accurately transversely in the skull, and there is every reason to believe that the whole of this surface lay in contact with the palatoquadrate cartilage, at least as far as a well defined ridge on the pterygoid mesial to which that bone turns backward, presumably to end very shortly. The lower end of this ridge continues inwards to a place where the foot of an epipterygoid rests. This bone is nearly in position, its upper end reaching in to somewhere very near the middle line, and its lower end lying in contact with the lower part of the pterygoid, depressed a millimeter or so from the ridge referred to above. But the whole nature of the surface of the pterygoid, the size and position of the epipterygoid, and the pterygoid ramus of the quadrate, seem to make it quite clear that in *Karpinskiosaurus*, as in *Seymouria*, the palatoquadrate cartilage extended up to the skull roof. The pterygoid continues anteriorly flattening out onto the palate.

We have seen that the quadrate cartilage reaches the skull roof as it lies in contact with the pterygoid, and the place where it does so is related to the point where the anterior border of the squamosal reaches the table of the skull. This is shewn, though not quite perfectly, in my specimen where the smooth under surface of the sub-tympanic flange of the squamosal is continued laterally to come into contact with the skull roof, presumably with the supratemporal, whilst mesially of this there is a sudden abrupt transverse border to the squamosal above which is a cavity. This cavity has an irregular front wall made by a process from the ventral surface of what is apparently a supratemporal. It is not at all impossible that this cavity in the squamosal is homologous with that found in the squamosal of *Seymouria*, and that, as in *Seymouria*, an upward and backward process of the quadrate cartilage passed into it thus gaining an attachment to the lower surface of the skull roof essentially at the lateral edge of the table.

It thus appears that "*Seymouria*", which comes from the Lower Permian, and *Kotlassia* and *Karpinskiosaurus* from the very much later Upper Permian have skulls which are structurally very similar, though *Kotlassia* has a much flatter head than *Seymouria*. But in the details of the mode of attachment of the palatoquadrate cartilage to the pterygoid and squamosal, and of these structures to the skull roof, they agree very closely, and the arrangement here is capable of derivation from that in the Anthracosaurs. In both groups the most striking feature of the braincase is the very lateral position of the fenestra ovalis, and the very remarkable way in which an immensely widened hinder part of the parasphenoid underlies the otic region, covering a good deal of its anterior face and ending in a perfectly straight horizontal suture with the proötic. The proötic and the paroccipital are separated by a strip of persistent cartilage at the fenestra in *Seymouria*, whilst they apparently meet in *Karpinskiosaurus*.

Small Seymourids

The only other creatures clearly related to *Seymouria* are the small individuals found in Lower Permian deposits in Czecho-Slovakia and Germany which are referred to the genera *Discosauriscus* and "*Melanerpeton*" (now *Phaiherpeton*). The individuals referred to these genera, which are genuinely different, are all small; the skull is seldom more than about three centimeters in length and the specimens generally occur in large numbers together in fine bedded rocks which have every appearance of being pond deposits. In general the Czecho-Slovak specimens are found by themselves, but in the Niederhässlich materials the relatively rare individuals of *Discosauriscus* occur with immensely more abundant larval specimens of *Branchiosaurus*. A single specimen (D.M.S.W. B 141) certainly belonging to this group comes from the beds at Odernheim which have a fauna extremely like that of Niederhässlich. It has been pointed out that in these localities it seems certain that we are dealing with aquatic animals, and that *Discosauriscus* and *Phaiherpeton* are in fact aquatic animals, whether larval or not.

The specimen D.M.S.W. B 54 in my collection from Lhotka contains the remains of three individuals of *Phaiherpeton*. One of these, *Phaiherpeton falax*, is a skull viewed from below shewing the under surface of the bones of the cranial roof which are a little misplaced, a section of the maxilla and premaxilla with their teeth, a lower jaw in position, and a complete quadrate

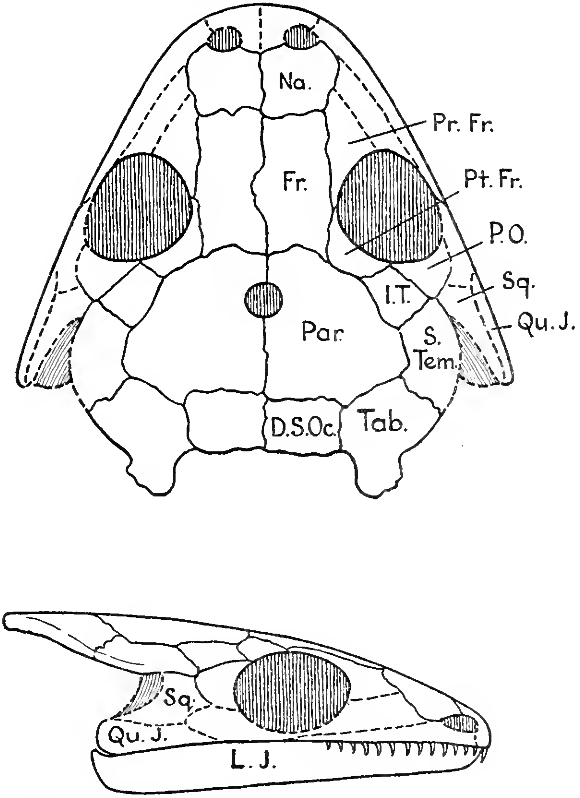

Fig. 33. *Phaiherpeton falax* (Fritsch). Reconstruction of a skull (D.M.S.W. B 54, back) x 2.66. The height of this skull is judged by the distance of the quadrate from the middle line, and the height of the parotic part of the pterygoid. Reference letters: *D.S.Oc.*, dermosupraoccipital; *Fr.*, frontal; *I.T.*, intertemporal; *L.J.*, lower jaw; *Na.*, nasal; *Par.*, parietal; *P.O.* postorbital; *Pr.Fr.*, prefrontal; *Pt.Fr.*, postfrontal; *Qu.J.*, quadratojugal; *S.Tem.*, supratemporal; *Sq.*, squamosal; *Tab.*, tabular.

ramus of the pterygoid of the left side, and part of that on the right. Tracings made from photographs of this specimen allow the individual bones to be fitted into place with respect to one another and shew the whole table, together with the frontals and nasals and the borders of the upper jaw. The fact that the left pterygoid is present in place determines within small limits the position of the quadrate condyle, and if this be given then projected drawings determine a minimum height of the skull at the occiput. The height so determined is confirmed by that of the parotic plate of the pterygoid of each side. The skull is, in fact, rather broad and low. The widely laterally projecting squamosals of most drawings of the skull of *Phaiherpeton* are shewn not to exist; they are the result of lateral displacement of bones in young skulls crushed between layers of mud.

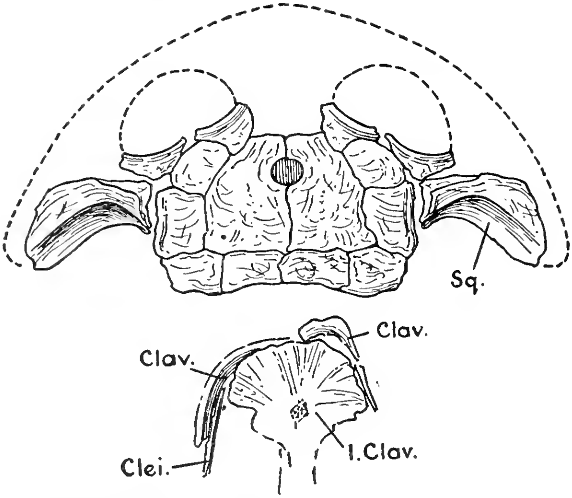

Fig. 34. *Phaiherpeton* sp. Dorsal view of skull, the left side copied from the right, the squamosal placed nearly in natural position but represented in the plane of the roof of the skull. The shoulder girdle is in the position with respect to the skull that it has in the specimen. D.M.S.W. B 124, x 1⅔. The small width across the clavicles should be noted. Reference letters: *Clav.*, clavicle; *Clei.*, cleithrum; *I.Clav.*, interclavicle; *Sq.*, squamosal.

Another *Phaiherpeton*, also from Lhotka, is D.M.S.W. B 124. This specimen shews exceedingly well, as an impression, half a table with a postorbital and disarticulated squamosal. It is represented in Figure 34 with the opposite side restored and the interclavicle, clavicle and cleithrum in the position that they actually occupy in the fossil. These bones give the width at the fore limbs with accuracy and seem to justify the shape given to the skull of *P. falax* in the reconstruction in Figure 33.

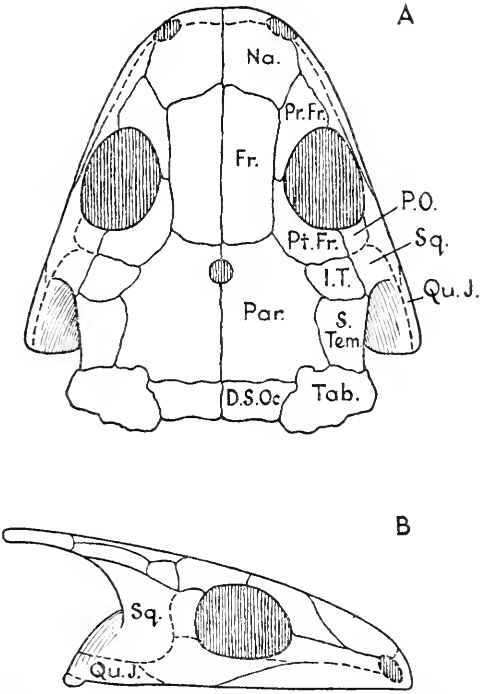

Fig. 35. "*Melanerpeton pulcherrimum*" from Neiderhässlich, restored from a squeeze made by Dr. Steen from the original of Credner, 1885, Pl. XXVII, fig. 1. x 2⅔. *A*, dorsal; *B*, lateral view; height of the skull dependent on comparison with Figure 33. Reference letters as in Figure 33.

Finally a series of squeezes which Dr. Steen made from one of Credner's specimens (1885, fig. 1, Pl. xxvii.) of *Phaiherpeton* in Leipzig have allowed me to draw the restorations in Figure 35 in which the position of the cheek depends on that in the two specimens whose reconstructions I have described above. For convenience I add a suggested restoration of the skull of *Discosauriscus* made from one of Credner's figures at the same magnification. This makes it reasonably clear that *Phaiherpeton* cannot be regarded as entirely composed of larval specimens of *Discosauriscus.*

Phaiherpeton has recently been dealt with by Dr. Špinar, who has added much to our knowledge, shewing that in *Phaiherpeton* the pterygoids are very wide bones, extending the whole length of the palate, and essentially in contact in the middle line. In other words the palate is completely closed, of *Seymouria* type, and in addition the parasphenoid forms a "broad ventral envelope of the braincase. Its long, orally elongated processus cultriformis stretches to the anterior part of the skull below the narrow sphenethmoidal part of the braincase. . . . In a caudal direction however the parasphenoid constantly enlarges, but the distinctness of its limits slowly declines, until it almost disappears in the places where it forms the base and the ventrolateral envelope of the braincase".

A specimen of *Phaiherpeton* from Lhotka in my own collection (D.M.S.W. B 54) shews the parasphenoid quite admirably (Pl. I). It is a bone with a narrow processus cultriformis which, behind the region of the basipterygoid processes, is triangular in general plan with laterally greatly produced pointed extremities, so that the whole structure is more than half as wide as is the skull table. It agrees in fact exactly with the parasphenoid of *Karpinskiosaurus* and *Seymouria.* In a recent work (1952) Dr. Spinar shews that the skeleton of *Phaiherpeton* has a single coracoid in addition to the scapula, and gives a further account of the structure of the animal. D.M.S.W. B 124 confirms the existence of a coracoid and shews very clearly the extraordinarily short squamosal, with a very definite border separating its ornamented outer surface from the tympanic flange which passes down above the quadrate. It shews also that the upper border of the ornamented outer surface of the squamosal is separated by a groove of some depth from that inner flange of the bone which is directed towards the under surface of the supratemporal, and is continuous with that which lies on the inner surface of the postorbital. It may also be noted that this particular individual shews the existence of a deep groove on the outer surface of the supratemporal parallel to the midline and only very little within its lateral border. This particular form is unusual in lacking any posterior projection of the tabular.

Thus it appears that something analogous to the dorsal part of the palatoquadrate cartilage, found in both *Seymouria* and

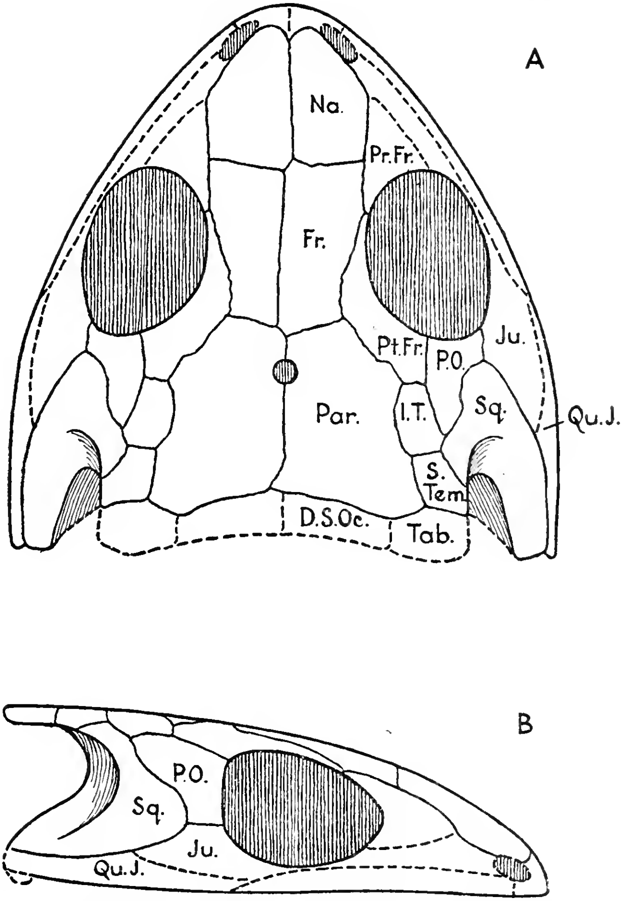

Fig. 36. *Discosauriscus permianus*, (Credner). Reconstruction of the skull from Credner's figure, 1890, Pl. XI, fig. 1. x 2⅔. *A*, dorsal; *B*, lateral view. Cheek placed as in *Seymouria*. Reference letters as in Figure 33, with *Ju.*, jugal.

Karpinskiosaurus, occurs in *Phaiherpeton.* In *Phaiherpeton* as a whole the limbs are quite exceptionally short and the body appears very long when comparison is made with *Seymouria.* But they agree much more closely with the condition found in *Kotlassia.*

Specimen D.M.S.W. B 141, which may well be *Discosauriscus,* shews that in some of them there is a distinct neck, the anterior end of the shoulder girdle lying about five vertebrae back from the skull, and the ribs lengthening at the next vertebra. In this individual all the ribs seem to be single headed, those in the middle of the back being slightly curved, the short ribs in front of the pelvis nearly straight, and long ribs being attached to the anterior part, at least, of the tail. Špinar has shewn that there are powerful reptile-like sacral ribs, and one such is shewn in this specimen. The ischia are always ossified; the pubes, though usually preserved as bone, are less bony than the ischia. Špinar has shewn that the hand and foot of *Phaiherpeton* have the normal reptile number of phalanges, as does *Seymouria.*

WAGGONERIA

Waggoneria is an interesting animal from the upper part of the Vale Formation of the Clear Fork in Texas. The known remains, in Chicago, are badly preserved but represent a "Seymourian" skull with a shallow otic notch not unlike that of *Discosauriscus.* It is shewn that the hinder end of the parasphenoid is very wide and therefore the fenestra ovalis laterally placed. The maxillae and dentaries carry several (four or five) rows of short conical teeth. Dr. Olson correctly places this animal in the neighbourhood of *Seymouria* and *Diadectes.*

LANTHANOSUCHUS

The extraordinary animal *Lanthanosuchus,* described with excellent figures by J. A. Efremov in 1946, comes from the Titanophoneus zone of Russia. The single specimen (which I have seen) is preserved with complete perfection, so that its structure, so far as it is bony, is certain. It is a large animal with a skull nearly 20 cm. long, but only 3 cm. high in the mid-line at the occiput. The dermal bones have a well developed "labyrinthodont'' ornament; the irregular orbits face entirely upward, and the temporal region is cut out into a large, irregular fossa.

The pattern of the skull roof is most unusual, no doubt on account of the great area and shallowness of the skull. Amongst other peculiarities the maxilla has a long contact with the nasal; the parietals form the hinder margin of the skull roof above the supraoccipital, and have a lateral projection to the postorbital. The quadratojugal and squamosal are safely determined by their relations to the quadrate and parotic plate of the pterygoid. But the upper border of the squamosal, though it has an attachment to the postorbital in the usual way, is separated from the parietal by two bones whose identity is not obvious. The inner of these bones, called dermosupraoccipital by Efremov, forms part of the occipital margin separated from its fellow by the parietals. It has a sutural attachment to the upper border of the posterior face of the paroccipital. The outer bone, which has a large area, much of it on a ledge hanging out over the occiput, does not meet the parietal, though it has a long suture with the postorbital. It is called tabular by Efremov, and has a powerful attachment to the upper surface of the outer end of the paroccipital. But further forward its lower surface is attached by suture to the upper edge of the parotic sheet of the pterygoid, a condition which would be unparalleled by tabulars, and suggests a supratemporal; but supratemporals do not at such an evolutionary stage articulate with the paroccipital. Anteriorly the bone has a long suture with the postorbital and admedially with the dermosupraoccipital.

Efremov's figures shew a large groove lying between the pterygoid and the paroccipital which appears to include the roof of the tympanic cavity. If so then a notch in the hinder border of the squamosal may mark the former site of the otic notch, but this is bounded by two knobs, in no way different from a great series found all round the hinder half of the skull. None the less it may well mark the direction of the stapes.

There is no trace of a proötic, or evidence of the fenestra ovalis. But this opening cannot easily be imagined at all far out, indeed it may very well have lain little outside the most lateral point of the parasphenoid, where it turns a little upward to the outer side of the basisphenoidal tuber.

Efremov apparently founded his interpretation of this animal as a Seymourian relative largely on the structure of the palate. The dorsoventrally flattened, concave, basioccipital condyle, with its contributions from the exoccipitals, is very Seymourid. The bony palate, interrupted only by narrow confluent interpterygoid vacuities and large nostrils, is of fundamentally anthracosaur pattern, and in the well marked descending flanges of the pterygoid + ectopterygoid is Seymourid.

It is evident that the animal is no normal labyrinthodont, or indeed other amphibian, for were it so the extreme flattening would be associated with large palatal vacuities and paired occipital condyles. Furthermore Seymourid vertebrae of appropriate size were found in the same excavation as the skull, and no other suitable skull, not even fragments of one, was found. Thus the Seymourid ancestry of *Lanthanosuchus* seems most probable. If this be true we have from it the very important fact that the fenestra ovalis has moved mesially, and the lateral projection of the hinder part of the parasphenoid below the proötic and paroccipital is very greatly reduced. The true homology of the bones called dermosupraoccipital and tabular is uncertain: the former might conceivably be a tabular, when the other would be supratemporal. But such uncertainty does not alter the probable systematic position or significance of the animal.

SUMMARY OF SEYMOURIAMORPHS

The survey of the known Seymourids, which range in time from *Seymouria* (of which poor fragments represent a species of Wichita age) in the Artinskian to *Kotlassia* in the Upper Permian, shews that the group as a whole is conservative — though *Lanthanosuchus* is a remarkable variant — and that many of its members were of aquatic habit. The general structure is obviously of immediate anthracosaur derivation, and the most striking change seen in the skull is the wide separation of the fenestrae ovales from the middle line, and the associated great widening of the hinder part of the parasphenoid below the otic capsules. This reduces the distance between the fenestra and the tympanic membrane, so that the stapes is both short, and light in weight. It lies in the usual labyrinthodont position, but seems to lack a foramen for the stapedial artery (though a notch occurs in

Kotlassia). There is some suggestion of the existence of a hyoid string, but there is no visible process attached to the ear capsule homologous with that of Labyrinthodonts, and the dorsal process of reptiles. Although a reduction in weight of the stapes is evidently desirable in a sound-transmitting element, it is attained at the expense of the introduction of a long tube full of perilymph interposed between the stapes and the labyrinth. It may thus have proved unsatisfactory and been abandoned in later descendants, e.g. *Lanthanosuchus*.

Whether the Seymourids were reptiles in the sense that a larval stage no longer occurred in their life history, the egg hatching into a miniature adult, is uncertain. It is evident that many Seymouriamorphs, *Kotlassia* for example, actually lived in water habitually, and *Lanthanosuchus* is obviously incapable of life on land. Phaiherpetons have every appearance of being aquatic, but no specimen shews any sign of gill arches comparable to those preserved in Branchiosaurs and in young *Archegosaurus*. Furthermore the skeletons of most individuals are well ossified, shewing no evidence of youth. In general, evidence of lateral line grooves is lacking, even in the obviously permanently aquatic *Lanthanosuchus*, where, had this system of sense organs existed in a larval stage, it could be expected to persist into adult life as it does generally in amphibia, even in cases like *Xenopus* whose ancestors at some time were land-living and without adult lateral line. It is thus possible to make a case for the reptilian nature of Seymourids.

It remains to discuss the Pennsylvanian *Diplovertebron* and *Solenodonsaurus*. *Solenodonsaurus* possesses reptilian vertebrae with small intercentra and large pleurocentra; the neural arches have horizontal articular faces, and the structure, though capable in principle of derivation from the embolomerous condition, is markedly cotylosaurian. Furthermore neither Broili's type skull, nor that described by Miss Pearson shews any trace of lateral line grooves. The otic notch, though represented only by a wide embayment of the hinder border of the squamosal, resembles that of *Phaiherpeton* and *Discosauriscus*, and Miss Pearson's specimen shews that the table was readily separated from the cheek. Thus the species may well be included in the Seymouriamorphs.

Diplovertebron was originally described by Fritsch from groups of scattered bones which included caudal vertebrae clearly embolomerous. To this genus I attributed a nearly complete skeleton of a young individual with unossified vertebrae, and, primarily on the basis of this specimen, suggested that Jaekel's type skull of *Gephyrostegus* might well belong to the same form. Jaekel's figure shews no sign of lateral line; my skeleton with its lizard-like build is that of a land-living animal. The shoulder girdle has the characteristic interclavicle which exists in *Phaiherpeton*, but the ilium still retains an anthracosaurine structure with a long backwardly directed dorsal process, and it appears to be connected with long ribs, and not to a thick short reptile-like sacral rib. It is evident that, if not actually a Seymourid, *Diplovertebron* might well be an immediate ancestor of *Seymouria*, or, as its contemporary *Solenodonsaurus* has already cotylosaurian vertebrae, it may well be a "surviving ancestor" of that form. Mrs. Brough (Dr. Steen) tells me that in *Solenodonsaurus* the hinder end of the parasphenoid is not widened, conforming in general to the anthracosaur pattern.

ORIGIN OF REPTILES

In an earlier section of this paper (p. 351) I pointed out that there existed in the skulls of the most primitive Captorhinid and the most primitive Pelycosaur (*Varanosaurus*) a "table" composed of a pair of parietals bordered by postparietals, supratemporals, tabulars and dermosupraoccipitals. That the parietal has a special lappet, projecting outward so as to separate the postfrontal from the supratemporal, having a sutural attachment to the postorbital. The lateral border of this table is sensibly straight and parallel to the middle line, and that part of it which lies on the supratemporal and tabular is visible in a side view of the skull, the squamosal, and sometimes part of the postorbital, being attached to its lower surface by some arrangement not involving a suture.

In a later section (p. 380) I shewed that what is in principle an identical arrangement is found in *Diadectes*. The only parallel to this arrangement (p. 394) is found in the anthracosaurian Embolomeri. Here we have a similar table, differing in that an intertemporal always exists in the place which in reptiles is occupied by the special lappet of the parietal. And this table is very commonly found detached, its attachment to the squamosal being not by suture but with a shallow groove on the lower surface of the supratemporal. Consideration of the position of the quadrate and epipterygoid in Anthracosaurs suggests that not the squamosal itself, but a persistent palatoquadrate cartilage (from quadrate to epipterygoid) which was attached to its inner surface actually lay in this groove and served effectively the mechanical need to attach the quadrate to the braincase and body. It is shewn that an identical arrangement exists in *Osteolepis* and other Osteolepids. It is probable that a similar arrangement existed in *Protorothyris* and *Varanosaurus* in front of the point to which the squamosal extends forward over the floor of the closed otic notch. In *Diadectes* the strip of palatoquadrate cartilage sends a process inward to impinge upon the proötic, without becoming continuous with that structure.

Thus the two groups of Cotylosaurs which I distinguished as Captorhinomorphs and Diadectomorphs in 1917 seem, on the evidence of the loose skull table and nature of the connection of the upper jaw with it, each to have arisen from the Anthracosauria.

There remains for consideration the Seymouriamorpha. It has never been doubted that this group is of labyrinthodont and specifically anthracosaur derivation, and everyone who has considered the matter is convinced that the skeleton of *Seymouria* is full of features which are characteristically reptilian. Whether it be amphibian or reptilian is almost by definition a matter of life history. This could only be determined in fossil material by the discovery, in a growth series of one species, of evidence of larval characters (associated with an aquatic life) which are lost or changed in the adult. Such growth series have been figured by Špinar (1952) for several of the small "Phaiherpetons" of Bohemia, which he refers to *Discosauriscus* and the new genus *Letoverpeton*. In these series the skull length in different species varies between 12 and 54 mm.; 10.5 and 34 mm.; 6.7 and 46 mm. In no case is there any noticeable alteration of proportions, still less any indication of a metamorphosis. In no case is there any indication of branchial arches analogous to those known in Branchiosaurs, *Archegosaurus*, etc. But Dr. Špinar (1952, p. 145) states that amongst the amphibian qualities of these animals is "1. The several times ascertained presence of outer, tree-like gills.'' Dr. Špinar has been good enough to send me two excellent photographs at a magnification of about 12 diameters which shew strange slender processes, sometimes seen in apparent transverse section, which it is difficult to explain otherwise than as external gills.

If this observation be confirmed it will be certain that the Seymouriamorphs are amphibia. But in any case the occurrence of very many individuals, representing so long a growth period in rocks certainly of pond origin, is much more suggestive of an amphibian than a reptilian life history.

For our immediate purpose it does not matter. If we compare a primitive Captorhinid, e.g. *Protorothyris,* with *Seymouria* we find no greater resemblance in the skull than we do with an Anthracosaur. Indeed we find less, for the wide separation of the fenestrae ovales in Seymouriamorphs together with the short, light stapes associated with this condition does not provide a starting point from which the very large stapes and the ventral position of the fenestra (which are characteristic of mammal-like reptiles) could be expected to have arisen. On the other hand, *Diadectes* agrees very closely with *Seymouria* in these matters, retaining the lateral position of the fenestra and its position high up in the skull in exactly the same form. And the immensely widened posterior part of the parasphenoid below the otic capsule, found in *Diadectes* alone amongst known reptiles, is shewn to occur in a wide range of Seymourids, and is no doubt present in all at an evolutionary stage above *Diplovertebron*, and perhaps above *Solenodonsaurus.*

These specific resemblances between *Diadectes* and Seymourids seem to me to imply a community of origin: that *Diadectes* (whose close relation *Desmatodon* comes from the Conemaugh, a high Coal Measure horizon little younger than the Nýrany Gas Coal from which comes *Solenodonsaurus*) arose from a Seymouriamorph of the general character of *Solenodonsaurus.*

If this conclusion be justified then it will follow that the separation of the Captorhinomorph stock from that of *Diadectes* may go back to a point where the last common ancestor was an amphibian — in each case an Anthracosaur. That the *Captorhinus* group is connected with the beginnings of the Pelycosaurs from which all later mammal-like reptiles sprang is, I think, now commonly accepted; now that I have shewn above that *Protorothyris* is essentially ancestral to *Captorhinus*, and is, as Romer recognised, very similar to *Varanosaurus*, it may, I think, be regarded as certain.

But Romer still (or at any rate recently) believes that *Captorhinus* was connected with the ancestry of lizards and two-arched reptiles generally. This view I regard as baseless. It rested on the nature of the supraoccipital of *Captorhinus* and its resemblance to that of lizards. I have shewn that this structure arises from a less developed condition in *Protorothyris*, which differs from that in *Varanosaurus* in ways evidently dependent on the existence of separate depressions on the occiput for superficial neck muscles in Captorhinids, whilst in Pelycosaurs this region shews only a single slightly divided area for their attachment. Apart from this one feature of the supraoccipital there are no resemblances between *Captorhinus* and the earliest certain "Diapsids", the Upper Permian "Eosuchids", other than that they are both Permian reptiles.

GOODRICH'S THEROPSIDA AND SAUROPSIDA

This separation from one another of the Captorhinomorpha and Diadectomorpha by their independent origins from the Anthracosaurs at once recalls Goodrich's division of all reptilia into Theropsida and Sauropsida. It is therefore necessary to consider the possibility that the two groups of Cotylosaurs are respectively the beginnings of Goodrich's two groups. His real evidence for the fundamental nature of his division came from the structure of the heart and base of the aorta. In all mammals, including the Monotremes, there is in postfoetal life a complete separation of the venous and arterial blood streams carried on through the auricles to the ventricles. All the venous blood from the right ventricle passes by a pair of pulmonary arteries to the lungs. But all the arterial blood from the left ventricle is forced into a single aorta. This divides into a right systemic arch, which is complete in the embryo, but in the adult passes to the right forelimb as a subclavian artery — there ending, whilst its homologue on the left side is greatly enlarged, passing round the thorax to supply the dorsal aorta. From this left systemic arch the left subclavian to the forelimb passes outward and from it, usually, the two

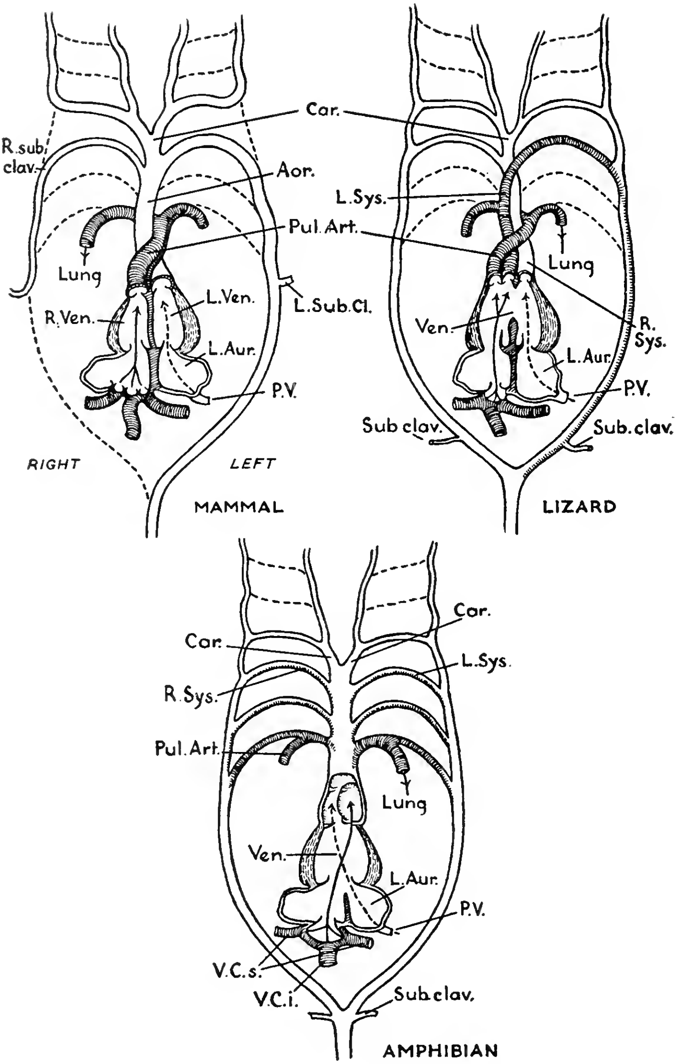

Fig. 37. Diagram of the heart and great vessels in a Mammal (Theropsid); Lizard (Sauropsid), and Amphibian. Modified from Goodrich, 1916 and 1930. The structures are seen from the ventral side so that the animal's right and left is the reverse of that of the reader. The heart is untwisted so as to be shewn in one plane. Vessels conveying venous blood are heavily shaded. The areas in broken line are the embryonic aortic arches; adult derivatives are represented by double lines as tubes. Arrows in the heart in broken line are arterial blood, in solid line venous blood. Reference letters: *Aor.*, the arch of the aorta; *Car.*, carotid artery; *L.Aur.*, left auricle; *L.Sub.Cl.*, left subclavian; *L.Sys.*, left systemic arch; *L.Ven.*, left ventricle; *P.V.*, pulmonary vein; *Pul.Art.*, pulmonary artery; *R.sub.clav.*, right subclavian; *R.Sys.*, right systemic arch; *R.Ven.*, right ventricle; *Sub.clav.*, subclavian artery; *V.C.i.*, inferior vena cava; *V.C.s.*, superior vena cava; *Ven.*, ventricle.

carotids arise. In development this condition arises by the appearance in the embryo of a horizontal septum in the bulbus cordis which cuts off a pulmonary from a ventral aortic division, followed by an enlargement of a left systemic arch at the expense of an obliteration of the right, presumably because the resistance to motion of a fluid is less in a single tube than in two smaller ones of the same cross sectional area. But the root of the aorta from which the systemics arise remains undivided.

In all living reptiles the conditions are entirely different. In addition to the horizontal septum which divides a pulmonary from a systemic trunk in the truncus, there is a further division following a spiral course, which divides a right from a left systemic down to its origin from the ventricle. In the less advanced living reptiles, all except the crocodiles in fact, there is an incompletely divided ventricle, so that only the right systemic trunk is certainly filled with arterial blood. It is from this right arch that the carotids arise. The subclavians are variously supplied, often by a clearly secondary device.

As Goodrich pointed out, these two conditions, which lead respectively to those of mammals and birds, are of such a nature, and are evident at so early a stage of embryonic development, as to imply a separation of two reptilian stocks back to a stage of heart development which is proper to the amphibia. Thus Goodrich's subdivision of the reptiles, based on this very early separation of the course of heart development in the phylogeny of the birds and mammals, is consistent with the view that the last common ancestor of the reptiles was an amphibian.

Goodrich, faced with the fact that the nature of the aortic arches can never be determined in extinct reptiles, felt it necessary for the practical purposes of the systematist to find some quality present in all living reptiles which was absent from mammals and from the mammal-like reptiles. He actually recognised such a character in the strange hook-shaped fifth metatarsal, which seems to owe its shape to the disappearance of the fifth distal tarsal and to some possibly functional divarication of the fifth toe. What the functional meaning of this condition may be Goodrich did not discuss: for his immediate purpose all that mattered was that it was a quality which can be traced far back into past time, and never occurred in any reptile which was demonstrably a member of the theropsid line. This statement is still true, but there are now known some reptiles, clearly not theropsid, which seem to lack the hook-shaped fifth metatarsal, and it is evidently very desirable to find some other condition, if possible widely recognisable, which may be used to distinguish Theropsids from Sauropsids.

Nature of Stapes and Quadrate as a Diagnostic Character

Although I am not prepared to state categorically that the character is to be recognised back to the point of separation of the two great stocks, I think that the nature of the stapes and its appendages, and of the quadrate, do afford easily recognisable conditions which will distinguish all except perhaps the very earliest members of the two fundamental divisions.

The rationale of the qualities is as follows: — both groups of reptiles arose from Anthracosaurs: Anthracosaurs possess an otic notch which (by analogy with Labyrinthodonts and Seymouriamorphs where complete stapes are known in place) must have been spanned by a tympanic membrane. This condition implies the formation (from the hyomandibular) of a stapes in order to transmit the vibrations induced in the tympanic membrane, by the impact of sound waves, to the perilymph surrounding the labyrinth.

In Sauropsida this condition is retained: the tympanic membrane was, and is, stretched across an otic notch cut into the tabular, supratemporal, squamosal and quadratojugal. The stapes[1] still stretches from the fenestra ovalis to the membrane, and its dorsal process of labyrinthodont derivation originally attached to the borders of the fenestra moves outwards along the paroccipital process. The original hyoidean string survives, at any rate during development. The existence of a relatively large tympanic membrane means a wider outer end to the tympanic cavity, which is air filled, and this cavity in turn must be supported above and below by some structures which will keep it open. In fact it rests upon the subotic flange of the squamosal, and lies against part, at any rate, of the posterior surface of the quadrate ramus of the pterygoid, its roof being the ventral

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[1] Stapes means columella + extracolumella and the homologue of these two jointly

surface of the paroccipital process. In Sauropsids the quadrate, which in the Anthracosaurs extends far back, its articular condyle often lying behind the occipital condyle, changes its position so that its hinder surface may stand nearly vertical, and the point of articulation of the lower jaw lies well in advance of the occipital condyle. The quadrate so placed has a wide transverse condyle, short from back to front, above which the hinder surface rises as a wide strip between the sutures by which the quadratojugal and squamosal are attached to its outer, and the pterygoid to its admedian edge, the attachment being usually strengthened by the development of a special pterygoid ramus directed forward from the inner border of the quadrate.

In contrast, the Theropsida have the following conditions. In the early Theropsids the anthracosaur tympanic membrane vanished, the stapes, homologous with the whole sound transmitting apparatus of the Sauropsids, remaining as a testimony of its former existence. Sound conduction must therefore have been carried on by the bones of the skull, perhaps from the earth through the fore limbs. The tympanic cavity evidently survived, but the relations of the cheek and the quadrate to the table of the skull are changed. The squamosal border below and in front of the former tympanic membrane is carried backwards (or perhaps, as Romer has suggested, carried backwards and upwards) into a contact with the under surface of the lateral border of the skull table made by the supratemporal and tabular. As a result of this arrangement the quadrate comes to stand vertically, about on the level of the occipital condyle. This arrangement increases the length of that space in the temporal region within which the masticatory muscles lie, whilst leaving the lower jaw at its original length. In consequence, what was originally the posterior surface of the quadrate comes in effect to face inwards, and its actual posterior edge is completely occupied by a quadratojugal foramen and the sutural attachment of the upper part of the quadratojugal and squamosal. With the disappearance of the tympanic membrane, the sound transmitting function of the stapes, if it does not pass into abeyance, changes its nature. It is no longer a vibration of a whole bone transmitting relatively large movements of a tympanic membrane to a membrane stretched across a fenestra ovalis, but a bony rod along which compression waves of infinitely small amplitude may pass. The bone as a whole does not vibrate: pressure waves pass through it.

Thus the stapes can become extremely heavy and massive and it is important that it should have a solid attachment to the bones on the outer side of the head on which sound waves fall. The theropsid stapes, therefore, has a large footplate in the fenestra ovalis, often so tightly held by cartilage and wide ligamentous attachments as to have been essentially immoveable. Its dorsal process becomes an extensive immobile attachment on the paroccipital process (chiefly on the proötic); its distal part, parallel to the quadrate ramus of the pterygoid, lies in a groove — the stapedial recess — ending in a rounded cup in the quadrate, and the stapes is tied down to the pterygoid and quadrate below the recess by a wide ligament.

Thus the conditions in this region differ completely in Theropsids and Sauropsids. They have been derived from the same ancestral state but through a series of intermediate stages in such widely divergent directions that no passage from one to the other is possible.

The position of the stapes in Theropsids differs greatly from that in Sauropsids in that in the former the "tympanic" end of the stapes in the stapedial recess lies only very little above the quadrate condyle, whilst in Sauropsids it is placed relatively high in the skull, always, so far as my knowledge goes, above the mid-point of the height of the quadrate which it crosses, usually without any contact. This difference of position is associated with a different placing of the fenestra ovalis. In Theropsids this opening lies, as always, between the proötic and the paroccipital, but so far ventrally that it is essentially lateral to the body of the basioccipital, which buttresses the sometimes cartilaginous process of the paroccipital forming its hinder half. In fact the uppermost point of the fenestra is, in nearly all cases known to me, ventral to the floor of the brain cavity in the occipital region. (Only in *Captorhinus*, which is a small animal, does the immense footplate of the stapes project a little — about one-third of its height — above the floor of the brain.) In all mammal-like reptiles from Pelycosaurs to mammals this statement is, so far as I know, literally true.

In contrast, in Sauropsid reptiles the fenestra ovalis lies relatively high in the skull, usually entirely above the floor of the braincase. The stapes is commonly slender, though in early forms it does not exhibit the "pin-like" thickness of all the living reptiles. The footplate is often enlarged, so that the columella arises abruptly from it, and there is usually no foramen for the stapedial artery. These differences in the position of the fenestra ovalis are associated with corresponding differences in the paroccipital process. In Anthracosaurs this process is so short that it is scarcely recognisable as such, but the lateral ends of the proötic and attached paroccipital slope upward to the skull table ending there, much mesial of its lateral border, at a powerful abutment of the paroccipital on a special face of the tabular. The lower surface forms the roof of the tympanic chamber. In *Limnoscelis,* which can reasonably be interpreted as an animal which has achieved certain advances from a very early Captorhinid stock (Watson 1917, 1919, Romer 1946), we have a reptile retaining what is essentially a labyrinthodont condition in which the lateral end of the paroccipital process articulates on the inner and lower border of the tabular, which, as in *Seymouria,* forms the whole upper border of the temporal fossa. As Romer has pointed out, the paroccipital process is directed horizontally, so that its extremity, if continued further outward, would meet and support the squamosal, or the quadrate which it sheaths, in a way leading on to that mode of supporting the suspensorial region found in and characteristic of the Theropsida. This downward movement of the paroccipital process drove the stapes before it, and we have evidence that the stapes was large in the existence of the ridge on the paroccipital process to which its dorsal process was attached, and in the characteristically ventral position of the fenestra ovalis. Thus the distal end of the stapes may well have lain not very far above the quadrate inner condyle, and may well have been tied to that bone, after the crushing out of existence of the ancestral tympanic membrane. In any case there is no difficulty in seeing how the *Limnoscelis* condition here leads on to that in Captorhinids and Pelycosaurs.

In *Diadectes,* as in all Sauropsids, the tympanic membrane persists, and the end of the paroccipital process lies posterior to it where it is attached to the end of the tabular and the supratemporal. It is thus separated completely from the quadrate by the upper part of the tympanic cavity, and cannot support the suspensorium however far it moves ventrally. Indeed the only obvious reason why it has been turned down so far from the original Labyrinthodont position is to increase the area available for the attachment of dorsal neck muscles. The stapes thus lies high up, its attachment to the tympanic membrane being at the level of the upper third of the quadrate, and passes behind that bone and not in contact with it. The ossification in the tympanic membrane of *Diadectes* in the region where it turns inward at right angles to the membrane surface is most reasonably interpreted as "extra columella", with dorsal, opercular and ?hyoidean processes. It is in fact characteristically Sauropsid.

Other Reptiles of the Low Permian

Thus in Basal Permian, and even before, in the upper part of Pennsylvanian time, these characteristic differences between Theropsids and Sauropsids are visible. They extend in fact back to the oldest known reptiles. But it does not necessarily follow that there may not have been other reptiles which do not fall into either group, and which have no living representatives. It is therefore necessary to survey all known early Permian reptiles.

Petrolacosaurus

It is convenient to begin with *Petrolacosaurus* because not only is it the oldest reptile (it is of Upper Conemaugh age) represented by more than fragments but it has been admirably described and reconstructed by Dr. F. E. Peabody. Dr. Peabody was so kind as to demonstrate the materials to me and enable me to examine them in detail. There is only one skull (of a young, lightly ossified individual which lost the whole of its roof before burial and is represented by the palate) which has been so skilfully prepared by Dr. Peabody that both its surfaces are visible. In another specimen there is part of a maxilla, and what is plausibly interpreted as a jugal shewing the existence of a lateral temporal fossa. It is evident that in general the palate conforms to a common pattern of early reptiles; that found in *Captorhinus, Palaeohatteria, Youngina, Broomia, Nyctiphruretus,* etc. The only feature (the existence of a suborbital fossa) of Sauropsid, indeed of Diapsid character recorded by Dr. Peabody does not seem to me safely determinable on the material. The quadrate is well shewn on the right side, where it is exposed from its outer surface as it lies in natural articulation with the pterygoid. And so shewn it is essentially a flat sheet of bone with a condylar surface a little widened at right angles to its lateral surface. It is in fact a typical Theropsid quadrate. The basioccipital and basisphenoid are very well shewn in their natural position with respect to the hinder part of the parasphenoid, and are separated by a great mass of cartilage. The exoccipitals are shewn, unexpectedly well ossified, but the otic capsule, though evidently present in place, is unrecognisable. But from the lower surface on each side a relatively large bone passes laterally and a very little backward to the quadrate from a position lateral to the basioccipital at the extreme posterio-lateral corner of the parasphenoid. There seems to be no doubt that it had a contact with the quadrate on its admesial surface little above its condylar end. This bone is, with considerable hesitation, regarded by Peabody as an opisthotic; it has a deep pit on its ventral surface which he seems to have interpreted as a fenestra ovalis. But in every respect — the position of the proximal end, the mode of its attachment to the quadrate, and the pit (if, as is possible, it was really a foramen) — the bone agrees with a Theropsid stapes. Indeed it would not make a practicable opisthotic for any reptile. Thus the reptile seems certainly Theropsid. Its most unexpected character is the lengthened cervical vertebrae, a quality it shares with the Wichita *Ophiodeirus* and Clear Fork *Araeoscelis*, related Theropsids.

Fragmentary and Incomplete Forms

The remaining Carboniferous and Lower Permian reptiles include the Pelycosaurs which have been completely examined by Romer and Price, and the Captorhinids adequately discussed in this paper. The Diadectids are wide spread and understandable. The only other reptiles are *Bolosaurus*, and a number of animals represented by such fragmentary and often exceedingly badly preserved remains (e.g. *Aphelosaurus*) that they are incapable of discussion.

Many other reptiles from low Permian horizons in Europe and North America have been recorded in the literature; most of them are represented by materials so incomplete, or more usually so badly preserved that their structure remains unknown in all important details. In Europe *Stereorachis, Neosaurus, Oxyodon, Pantelosaurus, Palaeohatteria* have been referred with justification to the Pelycosaurs. *Kadaliosaurus* is not unlike *Araeoscelis,* and may follow that animal into the Theropsida. *Haptodus* and *Callibrachion* and *Aphelosaurus* are slender reptiles at present quite undeterminable. *Stephanospondylus* is a Diadectid, *Datheosaurus* undeterminable. *Sphenosaurus* and *Phanerosaurus* are Cotylosaurs, presumably Diadectid. Texas and New Mexico have produced a number of small very imperfectly known tetrapods: *Pleuristion, Helodectes, Ectocynodon, Eosauravus* may be reptiles, but their structure and systematic position are effectively unknown. *Pariotichus* and *Pantylus* are amphibia.

It can, in fact, be said with some conviction that there is no early Permian reptile which is demonstrably neither a Theropsid nor a Sauropsid as these terms are used in this paper.

Consideration of Bolosaurus

It is thus convenient to return to the consideration of *Bolosaurus.* The account of this reptile early in this paper covers a good deal of its skeleton, but lacks much; the limbs and limb girdles are scarcely known and the skull shews very little of the braincase. At first sight the absence of an otic notch suggests a comparison with Captorhinomorphs, for the vertebral column is essentially Cotylosaurian and the temporal fossa a neomorph in relation to a unique dentition. The skull of *Bolosaurus* differs from all known Captorhinids in the hemispherical shape of the post-pineal part of its skull table. Not only is there no resemblance in this character to *Captorhinus* itself, but the primitive Captorhinid *Protorothyris* differs even more obviously; and the closely related primitive *Varanosaurus* is equally dissimilar. The parietal lappet which separates the postfrontal from the supratemporal and articulates with the postorbital is a reptile quality found in Diadectids as well as Captorhinids. Aberrant Captorhinids and Pelycosaurs, *Paracaptorhinus* and *Eothyris,* are almost equally dissimilar, though the large obliquely placed supratemporal is a point of resemblance. There is nothing characteristic about the orbit or preorbital region of the skull, nor is so much of the palate as is known helpful. The dentition of *Bolosaurus* is entirely unlike that of any contemporary Theropsid.

On the other hand, the rounded post-pineal upper surface has some resemblance to the rather rounded corresponding region in *Diadectes,* and many bones have comparable positions. The occiput of *Bolosaurus* has perhaps some slight resemblance to that of *Diadectes* in the absence of any visible posttemporal fossa, and in its continuously bony nature. But the complete absence of an otic notch, and presumably tympanic membrane, is a point of difference from *Diadectes* and, indeed, normal Sauropsids. It is not unparalleled: the snake has neither otic notch nor tympanic membrane, but it is a Sauropsid. We are thus driven to the nature of the stapes and quadrate. No stapes is visible, but the quadrate is well known. It is completely unlike that of a Theropsid. It has two rather separated transversely placed condyles, much wider from side to side than from front to back. The pterygoid process arises at 45° to 60° from the body of the bone. The quadratojugal foramen is very laterally placed, and the transverse posterior surface of the quadrate is widely exposed. There is no trace of a stapedial recess, nor of any attachment for the stapes.

Thus *Bolosaurus* is most readily interpreted as a primitive Sauropsid which has suppressed its tympanic membrane and otic notch. Some confirmation of this view is given by the anterior position of the quadrate compared with the basioccipital condyle. But a very striking difference from *Diadectes* is the narrow posterior expansion of the parasphenoid, and the probable proximal position of the fenestra ovalis. A further resemblance between *Bolosaurus* and *Diadectes* is in the nature of their dentition. In each there is a development of prehensile teeth forwardly directed at the anterior end of both upper and lower jaws. These differ in detail and in number, but in each case they are followed by a short transitional region of relatively small teeth to a succession of cheek teeth, worn by propalinal movements of the jaw, relatively few in number, rather wide set and laterally widened. An account of the dentition of *Bolosaurus* will be found on page 317 and it is necessary to give here a more detailed account of that of *Diadectes* than can be found in the literature.

Dentition of Diadectes

The general character of the dentition is known from the work of Cope, Case and Williston. In essence it is as follows. At a certain stage a complete dentition may be present, as it is in M.C.Z. 1743: here there are in the premaxilla four teeth set in a bone which fills a quadrant. Tooth one is inclined forward at about 45 degrees, its crown is unknown but is probably similar to that of the second tooth. This has a forwardly directed basal region, rounding off into a nearly vertical, slightly recurved hook with a rounded point. The third premaxillary tooth is similar but more upright. In skull M.C.Z. 2086 there are but three premaxillary teeth, in M.C.Z. 1743 there are four, all with damaged crowns, the root of the last completely overlapped by the maxilla. An early premaxillary tooth, the first or second (D.M.S.W. R 378), shews a wear facet on the posterior surface evidently made by a procumbent lower incisor. The maxilla holds eleven teeth in M.C.Z. 1743. The anterior three are round in section, with simple rounded crowns, and are well separated. Behind them, with no greater interval, lies the very small first widened tooth; all the members of the series of eight are much alike. All are transversely widened, with roots of flattened oval section, their long axes — at first placed at right angles to the mid line of the skull — gradually swinging round until the inner part of the last tooth lies so far behind its outer end that the long axis of the tooth is at little less than 45 degrees to a transverse line. The crown is very high, standing up for a centimeter above the lower surface of the maxilla. In horizontal section at the alveolus the tooth measures 3 or 4 mm. antero-posteriorly and sometimes as much as 14 mm. transversely. The enamel-covered crown appears swollen; the neck of the tooth is a little constricted by a shallow wide groove which runs round it. The root is deep, about a centimeter in a small specimen, flat and parallel sided, and vertically channelled. The pulp cavity survives, presumably holding a very thin pulp (*circa* 1 mm. thick by 8 mm. wide). The mature tooth is held in place by an ossification of the gum, which "fairs up" the tooth-bearing surface of the maxilla to the root of the tooth below the enamel. The exposed face of this new bone has a characteristic surface sculpture of short radial grooves. The crown, slightly bulbous, bears three low blunt cusps, the outer low and small, separated by a shallow concavity from the main cusp. This is often a short rounded antero-posterior ridge, separated rather widely from the inner cusp, low and rounded like the lateral one. Wear facets soon appear on these teeth, first on the inner side of the main and the summit of the inner cusps. These spread until they may join to form a single nearly flat surface, which may ultimately join a wear facet on the outer cusp. The joint surface so formed faces inwards and downwards.

The teeth of the lower jaw are naturally fitted to those with which they engage. The rounded symphysis bears three or four pairs of teeth, of which the first, or first and second, are narrow from side to side, project forward and fit within the corresponding premaxillary teeth. The next lateral tooth is more vertical, and the next forms a turning point in the dentition, being oval in section and set at about 45 degrees to the middle line. The first cheek tooth is nearly circular in section and the rest of the series agree exactly with those of the maxilla, but the labial side of a maxillary tooth agrees with the lingual side of one in the dentary, and the wear facets face upward and outward.

It is evident that the animals ate something which had to be torn off by the powerful anterior teeth, and then ground into fragments by the cheek teeth. The only suitable food, sufficiently widespread and abundant to meet the needs of large, very powerful land animals, is plant. *Diadectes* must have been vegetarian; it shares with *Edaphosaurus* the honour of introducing tetrapods to that mode of life.

Inspection of any large group of specimens of *Diadectes* will shew that tooth change took place even in very large individuals, and the nature of the process should be investigated. A right dentary (D.M.S.W. R 400), which was collected as a number of fragments only three or four millimeters cube, is well preserved and clean. The fragments fit well enough together to determine the order and relations of the teeth, and to shew the nature of the tooth roots and successional teeth in the jaw in a way a perfect specimen would not.

The process of tooth shedding and replacement conforms to the following series of stages.

A) The tooth is in wear, its crown stands well up, the neck below the enamel smooth and distinguishable from the ossified gum with its radiate ornament which cements it into its socket. The root is very deep, in bony continuity with the dentary throughout, but the pulp cavity remains.

B) A small spherical pit is eroded by osteoclasts into the dentine of the neck of the tooth and the surface of the ossified gum. This pit is on the lingual side of the tooth.

C) The erosion pit eats its way downward into the root of the tooth, and its deeper part cuts through to the pulp cavity whose walls are in turn eroded so that a very large crypt, bounded by the dentary, the dentine, and a surviving remnant of pulp is formed.

D) The crypt is then invaded by an enamel organ and a new dentine producing structure. A new tooth begins as a layer representing the upper surface of the crown, with sharp surface ridging unlike that on the fully developed tooth. This first formed layer is apparently dentine, for it may, even as a thin shell, be thicker than the enamel in the fully developed tooth. This partially formed tooth crown lies deep in the jaw below its predecessor which is still in place, firmly co-ossified with the dentary, but with the inner surface of its dentine eroded to form a smooth crypt wall.

E) The original tooth is now shed and the replacing tooth must move up into place, its root forming. During this period the last signs of the ossified gum surrounding the original tooth are removed, and a clean walled socket with a characteristic surface is formed. An empty clean finished socket in a fossil presumably implies the post-mortem loss of a new tooth before the ossification of its gum. The earlier stage, when the original tooth has been shed but some of the wall of the erosion cavity is still not made good, does exist and may be called stage E^1.

F) The newly erupted tooth is then fixed in place by ossification of its gums, the process beginning at the surface of the dentary, extending inward to the neck of the tooth and ultimately downward to the dentinal pulp. It is then in wear.

In the dentary on which the foregoing account is based, the anterior end of the specimen is the side of an alveolus from which a tooth had been lost; it is in stage E. This tooth is called 1) in the following account — it may be the first, but is possibly the second in the complete dentition.

2) An empty socket with some erosion cavity wall remaining — stage E^1.

3) A flattened and widened tooth with a complete longitudinally grooved root in situ, held in part at least by ossified gum — stage F.

4) An empty socket of circular section, trace of beginning of ossification of gum — stage F.

5) Tooth in situ with an erosion crypt — stage C.

6) Tooth in situ, beginning of erosion pit — stage B.

7) Empty socket, beginning ossification of gum — stage F.

8) Tooth in situ, large erosion crypt, new tooth forming — stage D.

9) Empty socket, beginning ossification of gum — stage F.

10) Tooth in situ, large erosion crypt, new tooth forming — stage D.

11) Empty socket, beginning ossification of gum — stage F.

12) Tooth in situ, large erosion crypt, new tooth forming — stage D.

13) Tooth in situ, beginning of erosion pit — stage B.

14) Empty socket, ? beginning of ossification of gum — stage F.

The general pattern of tooth change in the jaw is not evident, but it may be essentially an alternate replacement brought about by a wave of tooth shedding progressing along the jaw in some manner analogous to that found by Parrington in mammal-like reptiles.

Teeth Compared With Those of Bolosaurus

Comparison will shew that there is a real resemblance between the teeth of *Bolosaurus* and of *Diadectes*. There is in each a diversified dentition of a small number of individually characterised teeth. These teeth have elaborate crowns, somewhat transversely widened, cuspidate, worn by propalinal movements of the jaw so as to form flat wear facets facing downward and inward in the upper, upward and outward in the lower cheek teeth. The anterior teeth are prehensile, forwardly inclined and laterally compressed. The tooth crown is bulbous, the enamel ending so as to leave a high neck above the level of the tooth-bearing bone. There is a deep root vertically ribbed, which is secured in its socket by an ossified gum with radial canals in its substance and on its free surface. The tooth crown is formed buried in a large crypt in the tooth-bearing bone. No similar comparison can be made with the dentition of any other animal. One obvious difference is that the crown of the cheek tooth of *Bolosaurus* consists of a single swollen major cusp with only a single very small other cusp, not much more than a cingulum, whilst the crown of a *Diadectes* tooth has three cusps, one lying on the "inward" side of the crown. The tooth figured by Case (1911, pl. 1, fig. 4) as the type of *Diadectes biculminatus* Cope affords some approximation to the *Bolosaurus* condition. The interesting primitive Diadectid *Desmatodon* (Case 1911, pl. 8, fig. 2; Romer 1952, pl. 1, fig. 3) from the Pennsylvanian is perhaps still closer as it has only two definite cusps; whilst the Pennsylvanian specimen (Romer 1952, pl. 1, fig. 4) which is of the same order of size as *Bolosaurus* has a single sharp pointed bulbous cusp and worn surface like that of *Bolosaurus*, but recalls Diadectids in the transverse widening of its tooth crowns. In fact the series of teeth shewn by Case (1911, fig. 34, p. 89) may really express a true morphological series of intermediates between *Bolosaurus* and *Diadectes*.

Thus the original conclusion from the nature of the quadrate bone that *Bolosaurus* is a Sauropsid reptile is confirmed by an unexpected true resemblance of its dentition to that of Diadectids.

But *Diadectes* and the aberrant *Bolosaurus* are a very poor representation of that reptilian stock from which all living, nearly all Cretaceous, and an immense majority of all Jurassic reptiles belong. Neither is a possible ancestor to anything else; they are evidently highly specialised end forms. Thus the typical reptiles remain without an obvious ancestry. And their forerunners can only be discovered by working backward from the well known animals of the Upper Trias through the Lower Trias to those reptiles in the Upper Permian, predominantly the Cistiecephalus zone of South Africa, which, like *Youngina*, are well preserved and of unquestioned affinities. From there you can go back in time, hoping to interpret still earlier forms so as to get some assurance of their relationships. This I propose to do very shortly.

Much of the work on which this paper is based was carried out in the Museum of Comparative Zoology of Harvard University during a period in which I filled the office of Alexander Agassiz

Research Professor of Zoology. It was completed in the Department of Zoology of University College London.

It is a pleasure to express my thanks to the President and Corporation of Harvard College for the honour they did me in making this first appointment under the benefaction, and to Professor A. S. Romer, the Director, and the staff of the Museum not only for the use of its magnificent collections, but for assistance, criticism and kindness of every kind.

I owe to Professor Medawar many thanks for the hospitality of the Department of Zoology to Miss Townend and myself, and for much technical assistance.

To Miss Townend, and to the Royal Society which enabled her to work with me, I owe thanks for continuous help in the preparation of many drawings and the removal of many obliquities from the text.

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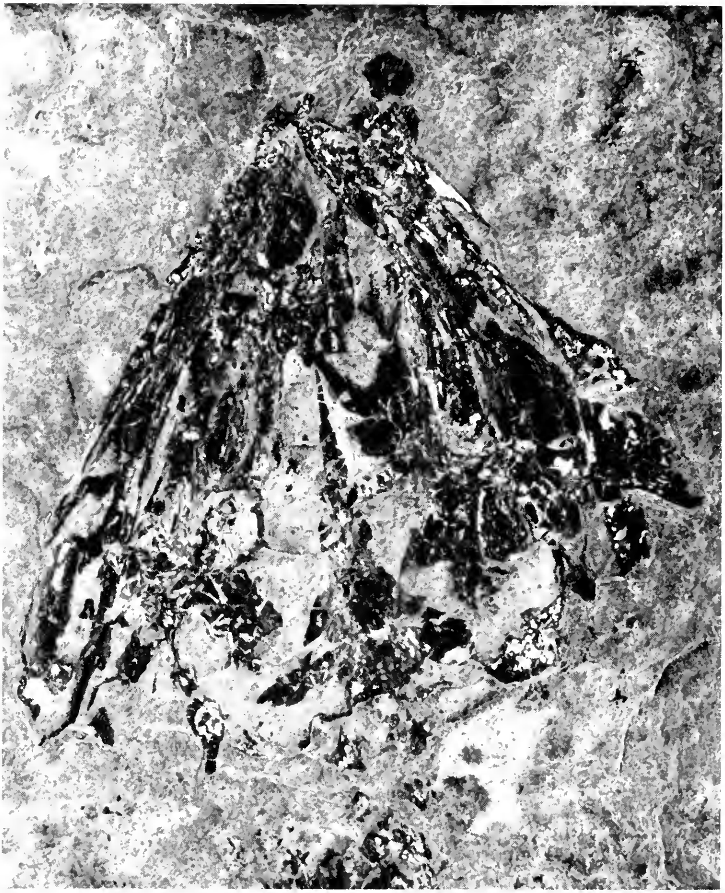

PLATE 1.

Phaiherpeton sp. x 2⅔. Photograph of specimen D.M.S.W. B 54, front. Shews the widened hinder end of the parasphenoid lying within the area of the table mapped out by pieces of cancellar bone with white masses of infilling. (This specimen from Lhotka is better preserved than most.)

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AT HARVARD COLLEGE
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DISTRIBUTION OF THE FORAMINIFERA IN THE NORTHEASTERN GULF OF MEXICO

By

Frances L. Parker

(With Thirteen Plates)

CAMBRIDGE, MASS., U.S.A.
PRINTED FOR THE MUSEUM
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No. 10 — *Distribution of the Foraminifera in the Northeastern Gulf of Mexico*

By

FRANCES L. PARKER

CONTENTS

ILLUSTRATIONS

INTRODUCTION

The distribution of the Foraminifera in the northeastern Gulf of Mexico has been studied to supplement the previous report by Phleger and Parker (1951) on the northwestern Gulf of Mexico. The area studied extends from the Mississippi River to Cedar Keys, Florida and southward from Cedar Keys excluding the continental shelf but extending westward from a depth of 100 m. in a series of zigzag traverses south to the Dry Tortugas. It includes roughly the region between N. Lat. 25-30° and W. Long. 83-90°.

In studying the foraminiferal distributions emphasis is given to establishing criteria by which the various environments may be recognized. In order to do this the death assemblages of planktonic and benthonic Foraminifera have been studied throughout the area and the living assemblages for a large part of it, excluding the continental shelf stations east of Mobile Bay, Alabama. Temperature and salinity data are given. The sediments are being studied by H. C. Stetson and no description of them is given at this time.

The samples were collected by H. C. Stetson using the Woods Hole Oceanographic Institution R/V ATLANTIS. Study of the Foraminifera has been supported by the Office of Naval Research (Project NR 081-050, Contract Nonr-233 Task 1). H. C. Stetson, F. B Phleger and W. R. Walton have read the manuscript and made valuable suggestions. Miss Ruth Todd and A. R. Loeblich of the U. S. National Museum have kindly compared specimens of several species with types deposited at the museum. Miss J. F. Peirson assisted with the laboratory work and drafting, and N. M. Curtis photographed the specimens for illustration.

LOCATION OF STATIONS

Figure 1 shows the locations of the stations, and Table 3 gives geographic position, depth in meters, and sampling gear used for each station. For convenience the samples have been divided into eleven traverses. *Traverse I* includes stations 201-211, from 51 m. to 430 m.; *traverse II*, stations 3-24, from 33 m. to 3017 m.; *traverse III*, stations 25-37, from 22 m. to 2388 m.; *traverse IV*, stations 212-225, from 20 m. (Mobile Bay) to 62 m.; *traverse V*, stations 74-97, 99-105, from 20 m. to 1417 m.; *traverse VI*, stations 38-73, 106, from 20 m. to 2697 m.; *traverse VII*, stations 174-191, 107, from 22 m. to 3017 m.; *traverse VIII*, stations 146, 148-172, from 12 m. to 3164 m.; *traverse IX*, stations 137-145, 108, from 183 m. to 3160 m.; *traverse X*, stations 126-136, from 950 m. to 3180 m.; *traverse XI*, stations 1, 2, 110-124, from 139 m. to 3283 m.

METHOD OF SAMPLING AND LABORATORY WORK

The samples were collected in 1951 during the months of February and March. Four types of sampling gear were used.

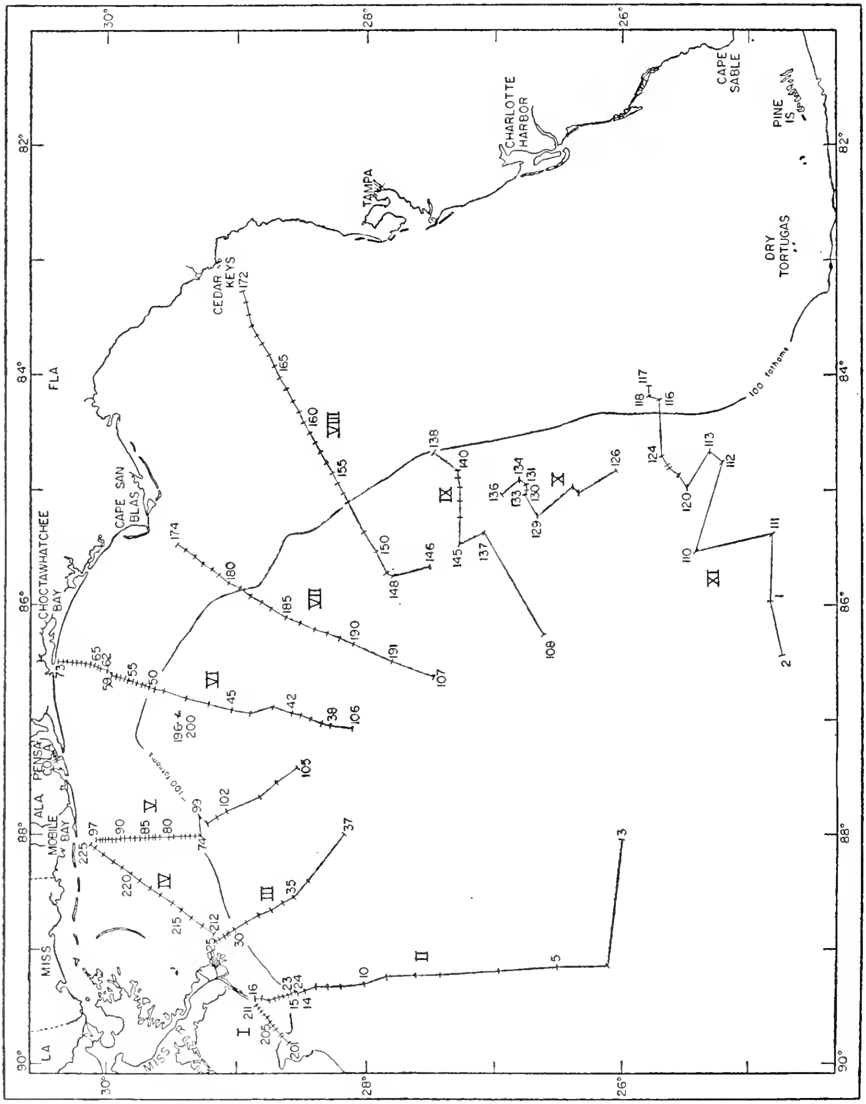

Fig. 1. Northeastern Gulf of Mexico showing station locations.

The Phleger sampler (Phleger, 1952, p. 321) was used where possible. On the continental shelf where the material is shelly and heterogeneous, samples were taken with the orange peel dredge (Phleger, 1952, p. 320) and the Stetson-Iselin sampler (Stetson, 1938, p. 7). In a few places the underway sampler designed by Ewing *et al* (1946, p. 925) was used.

When samples for the study of Foraminifera have been taken with such diverse types of gear, uniformity of results cannot be guaranteed. Such samples do not cover a uniform area and thickness of sediment. An attempt has been made, however, to use equal volume samples. In short cores taken with the Phleger sampler a section from the top of the core including half the surface area to a depth of approximately 2 cm. was taken, giving a sample of approximately 10 cc. volume. Total populations of Foraminifera in the samples taken with other tyes of gear were calculated for 10 cc. of dry material. This material was composed of sand and shells with little or no fine material and had approximately the same volume wet or dry. Samples containing shelly material cannot be measured accurately and for this reason the total populations given on Tables 4-24 should be regarded as representing approximations rather than exact numbers.

Neutralized formalin was added to the short cores at the time of collection so that the Foraminifera living at that time could be studied. After taking the samples from the cores additional formalin was added. It has been found necessary also to add a small amount of sodium carbonate to prevent the formalin from becoming acidic, especially if considerable time is to elapse before the samples are analyzed. Frequent checks of the pH of such samples should be made to insure that the basic character is maintained, a pH of 7-8 being the most satisfactory. Only a few samples exclusive of those taken with the Phleger sampler were preserved in formalin and counts of the living populations could not be made.

The samples were prepared by washing through a brass sieve having average openings of 0.074 mm. More accurate population counts of planktonic Foraminifera can be made using the residue left on a screen having larger openings of 0.114 mm., but this was not done in this case in order that the population counts would be comparable with those made in the study of the northwestern Gulf of Mexico area (Phleger, 1951). In counting the tests of planktonic forms from this fine material, however, small unidentifiable forms are of necessity omitted. Population counts of living Foraminifera were made using the rose bengal staining technique described by Walton (1952).

TEMPERATURE DISTRIBUTION

There is little available information on temperatures in the northeastern Gulf of Mexico. The temperatures found in the shoalest 130 m. of water depth have been taken from a compilation of data made by Adams and Sorgnit (1951). The data used were from all available bathythermograms for the winter months, January, February, and March, and the summer months, July, August, and September. The coverage of the area is not complete and there are almost no data for the region east of 87° W Long. and north of 29° N Lat. It is probable that bottom temperatures deeper than 130 m. are similar to those in the northwest Gulf of Mexico and these have been taken from Phleger's (1951) analysis of data obtained by the cruises of the MABEL TAYLOR in 1932 and the ATLANTIS in 1935 and 1947. Additional information may modify the situation as described below but it is believed to be a good approximation of the actual conditions.

In winter, isothermal water extends to depths of 15-100 m., in summer to depths of 12-15 m. The seasonal effect may disappear as shoal as 50 m. or may extend to a depth of 150 m. or more. Since present data are limited to the upper 130 m. of water, the exact depth of seasonal effect cannot be ascertained since it is still observable below this depth in many areas. In the northwestern Gulf of Mexico the maximum depth of the seasonal effect is 200 m. according to Phleger (1951, p. 15) and it is probable that it is similar in the northeastern area.

The following minimum and maximum bottom temperatures for the continental shelf shoaler than 50 m. have been deduced from data given by Adams and Sorgnit for the upper 50 m. of water in the various areas within the 100 fathom curve. These would represent average temperatures and would probably be exceeded in many seasons, especially close to shore. Minimum bottom temperatures from 0-50 m. are: 18°C. southeast of the

Mississippi Delta; 21°C. south of Mobile Bay; 18°C. just west of Cape San Blas; 21°C. near Cedar Keys and along the coast of Florida to the south. Maximum bottom temperatures from 0-50 m. are 31-32°C. southeast of the Mississippi Delta, 28°C. south of Mobile Bay, 28-31°C. along the west coast of Florida.

As nearly as can be ascertained from the available data, the temperature at the lower limit of seasonal effect varies from 18°C. to 21°C. Below this point it diminishes to the bottom of the permanent thermocline at 800-1000 m. to 5°C., and deeper than this shows no significant change.

Surface temperatures in the Gulf of Mexico according to Fuglister (1947) range from an average minimum of 20°C. in February to an average maximum of 29°C. in August.

SALINITY DISTRIBUTION

There are few salinity data for the area; the following information is taken from Parr (1935). Nearshore salinities in the upper 50 m. of water are <24 o/oo southwest of the Mississippi Delta (at the position of traverse 1), <35 o/oo south of Mobile Bay, and >36.25 o/oo on the continental shelf along the west coast of Florida. These figures might be lowered in the Mississippi Delta area and perhaps to a lesser extent south of Mobile Bay during times of exceptional runoff and mixing but normally there is a steep positive salinity gradient where fresh river water spreads over the surface. Parr gives no data for the shallow area between Cape San Blas and Cedar Keys but it is probable that the salinities are approximately 36 o/oo as they are farther south. At 200 m. the salinity is approximately 36 o/oo, and below this point it diminishes to about 35 o/oo at 400 m. with no significant change deeper.

DEPTH FACIES BASED ON BENTHONIC SPECIES

Introduction

Six depth facies based on benthonic species can be detected in the area. These have been given equal importance in discussion but some are more important than others. An example of this is the separation of facies 2 and 3; they perhaps should be combined to indicate a major facies change between 80 m. and 150 m. Benthonic facies boundaries are found at: 80-100 m., 130-150 m., 180-220 m., 350-600 m., 900-1000 m. There is a less distinct boundary at 30-50 m. which is considered here to represent a sub-facies boundary in facies 1, and a second one at 250 m. in facies 4. All boundaries are gradational and not sharply defined. Deeper than 1000 m. there are various gradual changes to the greatest depth sampled at 3283 m.; these are not concentrated at any particular depth and will be discussed under facies 6. There is little doubt that a close sampling grid in the shoal area between the shore and 100 m. would reveal more changes in the continental shelf faunas, but such fine gradations cannot be detected in the present reconnaissance sampling pattern. The facies changes indicated here should, therefore, be considered as gross changes. Foraminifera displaced from shoal areas are sometimes found in deep samples. This is especially true at the base of the escarpment parallel to the coast of Florida which is cut by traverses IX-XI. These displacements can be easily detected in analyzing Tables 4-23 which give the percentage distribution of the benthonic species. These tables list the benthonic species as percentages of total benthonic population and give the totals of planktonic Foraminifera found at each station.

In the following section each facies is discussed separately giving faunal characteristics and a detailed discussion of its appearance or non-appearance in each traverse. In this way lateral changes can be indicated for the various depth facies. These lateral changes also will be summarized in a later section. Figures 3-9 show generalized depth ranges of most of the species included in the population counts and the traverses in which they are found. All discussion of occurrence or non-occurrence of any species is based on its presence with a frequency of 0.1 per cent or more of the total population and it is, therefore, possible that the species may occur rarely under other conditions than those listed. Many species which appear only spasmodically in population counts are omitted as such and listed under "miscellaneous spp." in the tables. Table 1 gives a summary of temperature and salinity conditions in the various facies. These should be regarded as approximations.

Facies	Temperature	Salinity
1. 12 m. — 80-100 m. (Subfacies boundary at 30-50 m.)	(15 m.) 18-31°C.* (average) (50 m.) 20-26°C. (100 m.) 17-21°C.	Mississippi Delta 24 o/oo Mobile Bay 34 o/oo West Coast Florida 36 o/oo
2. 80-100 m.—130-150 m.	16-21°C.	36 o/oo
3. 130-150 m.—180-220 m.	(130 m.) 18-20°C. (200 m.) 13-15°C.	36 o/oo (or slightly higher)
4. 180-220 m.—350-600 m. (Subfacies boundary at 250 m.)	(200 m.) 13-15°C. (500 m.) 8-10°C.	35-36 o/oo
5. 350-600 m. — 900-1000 m.	(500 m.) 8-10°C. (1000 m.) 5°C.	35 o/oo
6. 900-1000 m. — ?	5°C.	35 o/oo

Table 1. Temperature and salinity in Facies 1-6 (These figures are approximations and refer in all cases to open-sea conditions).

Facies 1. 12 m. — 80-100 m.

The inner margin of this facies represents an open-ocean condition. In no case does a traverse extend into a bay at its inner end, although common bay forms such as "*Rotalia*" *beccarii* variants often are found in great abundance at the inner ends of various traverses.

The following species are found in facies 1 only:

Elphidium advenum	*N.* sp.
Globulina caribaea	*Quinqueloculina bicostata* (in most cases)
Guttulina australis	*Q. sabulosa*
Nouria polymorphinoides	

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* Minimum temperature near Mobile Bay and from Cedar Keys southward is 21°C. Maximum temperatures may be somewhat lower east of the Mississippi Delta.

The following species are found in fairly high concentration in this facies only:

Ammoscalaria pseudospiralis
  (also facies 2, in traverse I)
Asterigerina carinata
Bigenerina irregularis
B. textularioidea
Buliminella cf. *bassendorfensis*
Cibicidina strattoni
"Discorbis" bulbosa
Elphidium discoidale
E. gunteri
E. poeyanum
Epistominella vitrea
Eponides antillarum
Nodobaculariella cassis
Nonionella opima
Peneroplidae
Planulina exorna
Rosalina cf. *concinna*
R. floridana
"Rotalia" beccarii variants
Textularia earlandi
T. mayori
Virgulina punctata

The following species also may be found occurring in this facies including the shoalest stations:

Amphistegina spp.
Angulogerina bella
A. jamaicensis
Bolivina albatrossi
B. barbata
B. lowmani
B. striatula spinata
Buccella hannai
Bulimina marginata
Cancris oblonga (and *C. sagra*)
Cassidulina subglobosa
Cibicides deprimus
C. protuberans
Elphidium spp. (exclusive of
  named species)
Eponides repandus
E. turgidus
Gypsina vesicularis
Lagena spp. and related forms
Nonionella atlantica
Planorbulina mediterranensis
Pyrgo murrhina (rare)
P. cf. *nasutus*
Quinqueloculina compta
Q. horrida
Q. lamarckiana
Rectobolivina advena
Reussella atlantica
Robulus spp.
Rosalina parkerae
R. suezensis
Sigmoilina sp.
Spirillina vivipara
Spiroloculina cf. *grata*
S. soldanii
Stetsonia minuta
Textularia candeiana
T. conica
Triloculina cf. *brevidentata*
Uvigerina parvula
Virgulina complanata
V. pontoni
Wiesnerella auriculata

The following species have their shoalest occurrences between 35 and 50 m. and mark the boundary of what is considered here a subfacies:

- *Alveolophragmium* sp.
- *Bolivina fragilis*
- *B. subaenariensis mexicana*
- *B. subspinescens*
- *Bulimina aculeata*
- *Cassidulina carinata*
- *C. curvata*
- *C. laevigata*
- *Cibicides* aff. *floridanus*
- *C. io*
- *C. mollis*
- *C. umbonatus*
- *Conorbina orbicularis*
- *Gaudryina* cf. *aequa*
- *Goësella mississippiensis* (starts at 70 m.)
- *Lenticulina peregrina*
- *Loxostomum abruptum*
- *Marginulina marginulinoides*
- *Proteonina diffiugiformis*
- *Pseudoeponides umbonatus*
- *Reophax hispidulus*
- *R. irregularis*
- *Rosalina bertheloti*
- *R. floridensis*
- *Scabrookia earlandi*
- *Sigmoilina distorta*
- *Siphonina bradyana*
- *S. pulchra*
- *Spiroplectammina floridana*
- *Textulariella* spp.
- *Trifarina bradyi*
- *Valvulineria minuta*

There is considerable change laterally in facies 1. The following are species occurring in this facies, in one or more traverses, with a frequency of 10 per cent or more. They are not necessarily confined to this facies and may be found also in facies 1 at lower frequencies in other traverses.

	Traverse
Ammoscalaria pseudospiralis	I, IV
Amphistegina spp.	VI
Asterigerina carinata	VI-VIII
Buliminella cf. *bassendorfensis*	III
Cibicidina strattoni	IV-VII
Epistominella vitrea	III
Goësella mississippiensis	I
Miliolidae	VII
Nonionella atlantica	IV
N. opima	III, IV
Nouria sp.	I-III
Planulina exorna	V-VIII
Peneroplidae	VI, VIII
Rosalina cf. *concinna*	IV-VIII
‘‘*Rotalia*’’ *beccarii* variants	II, IV, VI
Textularia earlandi	I-III

It is probable that on the continental shelf along the Florida coast there is a further influx of West Indian forms such as are found in the Dry Tortugas. As can be seen from the above list, the fauna typical of calcareous areas is well established as far west as traverse VI, characterized by the abundance of *Amphistegina, Asterigerina carinata,* and the Peneroplidae. These forms are present, however, as far west as traverse IV.

Facies 1 is found in the various traverses as follows: traverse I, sta. 208-211 (51-73 m.); II, sta. 16-18 (33-88 m.); III, sta. 25-28 (22-106 m.); IV, all stations (20-62 m.); subfacies starts at sta. 221 (35 m.); V, sta. 77-97 (20-75 m.), subfacies starts at sta. 78 (71 m.); VI, sta. 59-73 (20-91 m.), subfacies starts at sta. 66 (39 m.); VII, sta. 174-177 (22-49 m.), subfacies starts at sta. 176 (46 m.); VIII, sta. 156-172 (12-62 m.), subfacies starts at sta. 161 (35 m.). The facies is not represented in traverses IX-XI.

Facies 2. 80-100 m. — 130-150 m.

The following species have their shoalest occurrence at 80-100 m.:

- *Ammobaculites* sp. A.
- *Bolivina ordinaria*
- *Cassidulina neocarinata*
- *Cibicides corpulentus* (starts at 120 m.)
- *Gaudryina (Pseudogaudryina) atlantica*
- *Globobulimina mississippiensis*
- *Haplophragmoides bradyi*
- *Höglundina elegans*
- *Liebusella* spp.
- *Nonion formosum*
- *Pseudoclavulina mexicana*
- *P.* aff. *novangliae*
- *Planulina foveolata*
- *Pullenia quinqueloba*
- *Robertina bradyi*
- "*Rotalia*" *translucens*
- *Rotamorphina laevigata*
- *Sphaeroidina bulloides*
- *Textularia foliacea occidentalis*
- *Trochammina quadriloba*
- *Uvigerina flintii*
- *U. laevis*
- *Virgulina mexicana*

The following species have their deepest occurrence at 130-150 m.:

- *Conorbina orbicularis* (160 m.)
- *Elphidium poeyanum*
- *Eponides antillarum*
- *Gaudryina* cf. *aequa*
- *Gypsina vesicularis*
- *Planorbulina mediterranensis* (mostly)
- *Quinqueloculina bicostata*
- *Q. compta*
- "*Rotalia*" *beccarii* variants

The following species occur only occasionally deeper than 150 m.:

Cassidulina laevigata
Cibicides io
C. mollis
Eponides repandus
Nodobaculariella cassis
Rosalina floridensis
Spiroloculina cf. *grata*
Textularia conica
T. mayori

The following species are not found with frequencies greater than 1 per cent deeper than 150 m.:

Nonionella atlantica
Planulina exorna
Quinqueloculina lamarckiana
Reussella atlantica

There is a marked lateral change in this facies also. The following species are found with frequencies higher than 10 per cent in the various traverses. They are not necessarily confined, however, to facies 2.

	Traverse
Alveolophragmium sp.	I
Ammoscalaria pseudospiralis	I
Amphistegina spp.	VII, VIII
Cassidulina subglobosa	VI
Cibicides protuberans	VIII
Goësella mississippiensis	I, II
Miliolidae	VI (1 sta.)
Nouria sp.	I
Proteonina difflugiformis	I
Rosalina cf. *concinna*	VI, VII
Trochammina quadriloba	I

As can be seen from the above list, many of the species also are found in high frequencies in facies 1. The species having a high frequency in the Mississippi Delta region form a discrete group as they did in facies 1. Facies 2 does not appear in enough of the traverses to give a complete analysis of its lateral development.

Facies 2 is found in the various traverses as follows: traverse I, sta. 204-207 (79-91 m.); traverse II, sta. 19-21 (106-142 m.); traverse V, sta. 76 (99 m.); traverse VI, sta. 54-57 (106-128 m.); traverse VII, sta. 178, 179 (86-146 m.); traverse VIII, sta. 154, 155 (79-117 m.). It is not represented in traverses III, IV, IX-XI. No species are found with high frequencies in this facies in traverse V. As can be seen, facies 2 is not represented at many stations and it might be more practical in many cases to combine it with facies 3. It seems advisable, however, to give its characteristics for what they might be worth for faunal analysis even though the results may not be statistically valid.

Facies 3. 130-150 m. — 180-220 m.

The shoaler limit of this facies is marked by the following species having their shoalest occurrence at 130-150 m.:

Bolivina goësii
B. translucens
Bulimina spicata
Cassidulina aff. *crassa*
Chilostomella oolina (125 m.)
Eggerella bradyi
Eponides regularis
Globobulimina affinis and variant
Glomospira charoides
G. cf. *gordialis*
Gyroidina orbicularis (165 m.)
Gyroidinoides soldanii altiformis
Karreriella bradyi
Planulina ariminensis
Pseudoglandulina comatula
Pullenia bulloides
Sigmoilina tenuis
Trochammina advena

The following species have their deepest occurrence at 180-220 m.:

Alveolophragmium sp.
Ammoscalaria pseudospiralis
Asterigerina carinata
Bigenerina irregularis
B. textularioidea
Buccella hannai
Cibicides io
C. mollis
"*Discorbis*" *bulbosa*
Elphidium discoidale
E. gunteri
Eponides repandus
Globobulimina mississippiensis
Goësella mississippiensis
(very occasionally deeper)
Quinqueloculina cf. *polygona*
Rectobolivina advena
Rosalina floridensis
Spirillina vivipara
Spiroplectammina floridensis
Wiesnerella auriculata

The following species do not occur deeper than 220 m. with a frequency greater than 1 per cent.

Bolivina striatula spinata
Reophax hispidulus
Rosalina cf. *concinna*
R. suezensis

Lateral changes are still marked in this facies. The following species occur with frequencies of more than 10 per cent. They are not necessarily limited to this facies.

	Traverse
Alveolophragmium sp.	I
Bolivina barbata	II, III
B. lowmani	VII
B. minima	VIII
B. subaenariensis mexicana	III, VI
Bulimina marginata	II
Cassidulina neocarinata	VI
Cibicides aff. *floridanus*	VII
C. protuberans	IX, XI
Eponides regularis	II
Goësella mississippiensis	I
Proteonina difflugiformis	I
Trochammina quadriloba	I, II
Uvigerina parvula	III, VII

The Mississippi Delta fauna is still prominent in this facies, to a greater extent in traverse I than in traverse II. High frequency occurrences appear to be rather spasmodic but this is probably emphasized by the choice of a definite frequency limit to indicate them.

Facies 3 is found in traverse I, sta. 202 (128 m.); traverse II, sta. 22 (168 m.); traverse III, sta. 29, 30 (155-205 m.); traverse V, sta. 75 (146 m.); traverse VI, sta. 50-53 (139-165 m.); traverse VII, sta. 180 (183 m.); traverse VIII, sta. 152, 153 (146-183 m.); traverse IX, sta. 138 (183 m.); traverse XI, sta. 116-118 (139-155 m.).

Facies 4. 180-220 m. — 350-600 m.

The deeper depth limit of this facies is not sharply defined, but between the depths of 350-600 m. very definite faunal differences occur, and the same is true to a much lesser extent at the shoaler depth limit. There is a less well-defined boundary at 250 m., also, so that the shoaler limit could be defined as 180-250 m. The faunal changes at 250 m. will be listed separately, however, as they appear to form a small but distinctive unit.

The following species have their shoalest occurrence at 180-220 m.:

Adercotryma glomeratum
Anomalinoides mexicana
Bulimina alazanensis
B. striata mexicana
Epistominella exigua
Gyroidina neosoldanii
Hormosina sp.
Laticarinina pauperata
Nodosaria hispida
Sigmoilina schlumbergeri
Trochammina cf. *japonica*
Uvigerina hispido-costata
U. peregrina

The following species have their shoalest occurrence at 250 m.:

Cassidulinoides tenuis
Cibicides robertsonianus
Epistominella rugosa
Loxostomum abruptum
Uvigerina auberiana

The following species have their deepest occurrence at 250 m. (exceptions noted):

Amphistegina spp.
Angulogerina bella
Bolivina fragilis
B. striatula spinata
Caneris oblonga
Cibicidina strattoni
Liebusella spp. (280 m.)
Nodobaculariella cassis
Pseudoglandulina comatula
Quinqueloculina lamarckiana (280 m.)
Reophax irregularis
Reussella atlantica
Sigmoilina sp.
Textularia conica (280 m.)
T. foliacea occidentalis
T. mayori
Triloculina cf. *brevidentata*

The following species have their deepest occurrence between 350 and 600 m.; a few having their deepest ranges shoaler or deeper also are noted:

Ammobaculites sp. A (390 m.)
Bolivina barbata (550 m.)
B. goësii (420 m.)
Bulimina marginata (550 m.)
Buliminella cf. *bassendorfensis* (370 m.)
Cassidulina laevigata (320 m.)
Marginulina marginulinoides (450 m.)
Nonionella atlantica (600 m.)
Planulina exorna (380 m.)
P. foveolata (550 m.)
Pseudoclavulina mexicana (450 m.)
P. aff. *novangliae* (350 m.)
Pyrgo cf. *nasutus* (550 m.)
Quinqueloculina horrida (370 m.)
Rosalina bertheloti (370 m.)
Sigmoilina distorta (550 m.)
Siphonina bradyana (650 m.)
S. pulchra (750 m.)
Spiroloculina cf. *grata* (650 m.)
S. soldanii (320 m.)
Textulariella spp. (320 m.)
Uvigerina flintii (420 m.)
Virgulina pontoni (500 m.)

The following species do not occur with a frequency greater than 1 per cent deeper than 600 m.:

Cassidulina aff. *crassa*
C. neocarinata
Eponides regularis
Planulina ariminensis
Uvigerina hispido-costata

The following species are found with frequencies greater than 10 per cent in the various traverses. Traverses I and II in the Mississippi Delta region still show differences from the more easterly ones:

	Traverse
Ammobaculites sp. A	I
Bolivina albatrossi	VI
B. minima	VIII
B. subaenariensis mexicana	V, VI
Bulimina marginata	II
B. striata mexicana	II
Cassidulina neocarinata	VII
C. subglobosa	IX
Epistominella rugosa	IX
Goësella mississippiensis	I, II
Proteonina difflugiformis	I, II
Reophax scorpiurus	II
''Rotalia'' translucens	VI-IX
Sphaeroidina bulloides	II
Textularia earlandi	I
Trochammina quadriloba	I, II
Uvigerina peregrina	II

Facies 4 is found in the various traverses as follows: traverse I, sta. 201, 203 (201-430 m.); traverse II, sta. 15, 23 (208-298 m.); traverse V, sta. 74, 99, 100 (204-530 m.); traverse VI, sta. 47-49 (183-446 m.); traverse VII, sta. 181-186 (186-347 m.); traverse VIII, sta. 151 (366 m.); traverse IX, sta. 140-142 (256-421 m.). The facies is not represented in traverses II, IV, X, XI.

Facies 5. 350-600 m. — 900-1000 m.

The deeper depth limit is well-defined, especially by the species having their shoalest occurrences at this point. These forms will be listed under facies 6. The species, with a few exceptions, having their shoalest occurrence between the depths of 350 m. and 600 m. are as follows:

Astrononion tumidum (320 m.)
Bolivina sp. (420 m.)
Cibicides kullenbergi (600 m.)
C. rugosa (600 m.)
C. wuellerstorfi (450 m.)
Cyclammina spp. (380 m.)
Eponides polius (600 m.)
Osangularia cultur (400 m.)
Plectina apicularis (550 m. mostly)
Quinqueloculina sp. (600 m.)
Rectobolivina dimorpha (350 m.)
Tolypammina schaudinni (550 m.)
Virgulina tessellata (360 m.)

The following species have their deepest occurrence at 900-1000 m.:

Rosalina floridana
R. suezensis
Textularia earlandi
Uvigerina hispido-costata
U. parvula

The following species do not occur with a frequency greater than 1 per cent deeper than 900-1000 m.:

Bolivina minima
E. ordinaria
Chilostomella oolina
Sphaeroidina bulloides
Trifarina bradyi

Traverse I did not penetrate this facies. The indications are, however, that there is more uniformity from east to west in this facies than in the shoaler ones. The following species have a frequency greater than 10 per cent in the various traverses in facies 5:

	Traverse
Bolivina albatrossi	II, III
B. ordinaria	II, III, VI
Bulimina aculeata	III, V
B. alazanensis	V, VI, IX
Cassidulina carinata	III
C. subglobosa	VI-VIII, XI
Epistominella exigua	II, VI, VII, IX
"Rotalia" translucens	VI-VIII
Sphaeroidina bulloides	II
Trochammina cf. *japonica*	II
T. tasmanica	II
Uvigerina laevis	II
U. peregrina	V, VI, VIII, IX

This facies is represented in the various traverses as follows: traverse II, sta. 12-14, 24 (314-732 m.); traverse III, sta. 31, 32 (373-400 m.); traverse V, sta. 101 (914 m.); traverse VI, sta. 40-46 (555-960 m.); traverse VII, sta. 187-190 (457-878 m.); traverse VIII, sta. 149, 150 (585-914 m.); traverse IX, sta. 144 (914 m.); traverse XI, sta. 124 (914 m.). The facies is not represented in traverses I, IV, X.

Facies 6. 900-1000 m. — ?

There is no marked facies boundary deeper than 900-1000 m. in this area. Several species appear or drop out deeper, however, before the greatest depth represented by these samples is reached at 3283 m.

The species having their shoalest occurrence at 900-1000 m. are as follows:

Alveolophragmium ringens (mostly)
Ammobaculites sp. B.
Ammoscalaria tenuimargo
Epistominella decorata
Gaudryina flintii
Pullenia sp.
Siphotextularia curta
S. rolshauseni
Tolypammina schaudinni (mostly)
Trochammina globulosa

Species having their shoalest occurrence deeper than the above are as follows:

Bolivina pusilla (1300 m., a few exceptions shoaler)
Nonion pompilioides (2250 m.)
Quinqueloculina venusta (1800 m.)
Reophax distans delicatulus (1200 m.)
Virgulina advena (1250 m.)

The following species have their deepest occurrence between 1000 m. and 3000 m.:

Alveolophragmium ringens (2400 m.)
A. wiesneri (1700 m.)
Angulogerina jamaicensis (1700 m.)
Anomalinoides mexicana (1700 m.)
Astrononion tumidum (2600 m.)
Bolivina ordinaria (2200 m.)
Chilostomella oolina (2900 m.)
Cibicides corpulentus (1700 m.)
C. deprimus (2500 m.)
C. aff. *floridanus* (1700 m.)
C. protuberans (1800 m.)
C. rugosa (2700 m.)
"Discorbis" bulbosa (2200 m.)
Epistominella vitrea (2300 m.)
Eponides regularis (1900 m. mostly)
Gaudryina flintii (2300 m.) (confined to facies 6)
Hormosina sp. (1900 m.)
Nonion formosum (1800 m.)
Nonionella opima (2300 m.)
Nummoloculina irregularis (2500 m.)
Planulina ariminensis (2500 m.)
Rectobolivina dimorpha (1400 m.)
Robertina bradyi (2600 m.)
Robulus spp. (2200 m.)
Sigmoilina tenuis (1700 m.)
Siphotextularia curta (2700 m.)
Virgulina punctata (2500 m.)
V. tessellata (2200 m.)

Facies 6 is fairly uniform throughout the area. The following species occur with a frequency of greater than 10 per cent in the various traverses:

	Traverse
Bolivina albatrossi	III (1 sta.)
Bulimina aculeata	II, III (not deeper than 1500 m.)
B. alazanensis	X (not deeper than 1100 m.)
B. spicata	X (not deeper than 1000 m.)
Cassidulina subglobosa	VI, VIII-XI
Cibicides wuellerstorfi	II, VII-XI (deeper than 2400 m.)
Epistominella decorata	II, III, V-VII, IX, X (deeper than 1400 m.)
Eponides turgidus	II, III, V, VI
Glomospira charoides	X (1 sta.)
Höglundina elegans	IX, X (1 sta. each)
Reophax distans delicatulus	III (1 sta.)
Uvigerina peregrina	II, V, VI (not deeper than 1500 m.)
Virgulina tessellata	III (not deeper than 1500 m.)

This facies is represented in the various traverses as follows: traverse II, sta. 3-11 (914-3017 m.); traverse III, sta. 33-37 (1024-2388 m.); traverse V, sta. 102-105 (1097-1417 m.); traverse VI, sta. 38, 39, 106 (1144-2697 m.); traverse VII, sta. 191, 107 (2999-3017 m.); traverse VIII, sta. 146, 148 (1730-3164 m.); traverse IX, sta. 108, 137, 145 (2268-3072 m.); traverse X, all stations (1051-2150 m.); traverse XI, sta. 1, 2, 110-113, 120-123 (1326-3283 m.). The facies is not represented in traverses I and IV.

LATERAL CHANGES IN FAUNAS

A study of the species forming the bulk of the faunas in the various facies in each traverse shows very clearly that there is a lateral change in faunas in this area. The traverses off the Mississippi Delta contain faunas which differ from those on both sides. Such species as *Goësella mississippiensis* n. sp. and *Textularia earlandi* are restricted to this region. This is probably due to the outflow of the Mississippi River which would affect the turbidity, light penetration, food supply and the chemistry of the water and sediments. The salinity is not affected very much except at the shoalest stations and probably is not a controlling factor.

Eastward from the Mississippi Delta there is an increase on the continental shelf and out to depths of 100-200 m. of West Indian species: *Asterigerina carinata*, various species of the Peneroplidae, *Amphistegina*, etc. These forms are well established as far west as traverse VI. They are not found in the northwestern Gulf of Mexico except on isloated reefs. A study of the Foraminifera in samples from the continental shelf east of the Mississippi Delta, which extends to a depth of about 75 m., shows that except for a few stations at the inner ends of the traverses the area is apparently non-depositional. The sediment is mostly gravel, sand, and shells and there is no material present which could produce turbid conditions. The sediment at the inner ends of traverses V-VIII usually is pure, coarse quartz sand. A large percentage of the Foraminifera in this non-depositional area is worn and discolored and many are filled with glauconite. The relative abundance, therefore, of such robust forms as *Amphistegina*, the Peneroplidae, Miliolidae, etc. may be due in part to their survival over long periods of time where other more delicate forms are not preserved. Short cores could not be obtained from this material and the samples were not treated with formalin to preserve the living forms. A study of these would give more definite information concerning the present-day fauna.

Although there are no samples from the continental shelf along the west coast of Florida, the few relatively shallow samples show a further increase of West Indian forms. Many of these occur so rarely that they have not been included in the population counts but a few of them are listed in a subsequent section.

It is interesting that although lateral differences in the shoaler facies are marked for the bulk of the population, the facies boundaries can be identified easily throughout the area, in many cases by the same species. In progressively deeper facies the lateral changes disappear to a great extent and deeper than 1000 m. the faunas are fairly uniform.

DISTRIBUTION OF LIVING BENTHONIC SPECIES

The living forms were studied in samples which were collected with the Phleger sampler (listed in Table 3). These extend over most of the area except that shoaler than 75 m. in traverses V-VIII and the few shoal stations in traverses X and XI. The absence of data for these stations makes it impossible to give a complete picture of the occurrence of living specimens in the area but the data obtained are given in Tables 25-28 so that they may be on file for study when additional work may supplement them. These tables list numbers of specimens of each species found in 10 cc. of sediment, the surface area covered being about 5 sq. cm., half the surface area sampled.

Population counts of living Foraminifera were made of all the samples in traverses I-IV and some interesting results were obtained. Phleger (1951, p. 65) has pointed out that relative rates of sedimentation may be estimated by comparing numbers of living forms present relative to the dead population. A decrease in the relative numbers of living specimens would indicate a decrease in the sedimentation rate since the dead population would not be so rapidly masked by sedimentation. Living populations expressed as percentages of total population (living and dead) for traverses I-IV are listed in Table 2. There is evidence in a few of the shoaler samples of decalcification of some of the specimens possibly due to the increasing acidity of the samples after collection. This is detected by the presence of casts composed of stained protoplasm. In such cases the percentages of living populations given are probably higher than they should be.

A study of Table 2 shows that in traverse I the living population in percentage of total population ranges from 68 at 51 m. to 7 at 430 m.; in traverse II it ranges from 100 per cent at 33 m. to 0 per cent at 3017 m. Living populations fall to 4 per cent at 314 m. and are very low, usually less than 1 per cent, deeper. The sample containing 100 per cent living specimens showed evidence of decalcification. In traverse III the percentage is 83 at 22 m., varies from 2-11 to a depth of 1719 m., and drops below 1 at 2388 m. In traverse IV, with all stations at depths shoaler than 62 m., the percentages are less than 1 at the Mobile Bay end (with the exception of sta. 217 which shows anomalous characteristics), remaining so southward to sta. 215 which has 3, sta. 214, 5, sta. 213, 40, and sta. 212, 18 per cent. These figures bear out the fact that in the vicinity of the Mississippi Delta sedimentation is more rapid than in the area to the northeast or at the deeper

Traverse I			Traverse II			Traverse III			Traverse IV		
Sta.	Depth in Meters	% Living	Sta.	Depth in Meters	% Living	Sta.	Depth in Meters	% Living	Sta.	Depth in Meters	% Living
211	51	68	16	33	100	25	22	83	225	20	0.4
210	86?	18	17	58	25	26	53	2	224	20	0.5
209	86?	6	18	88	8	27	77	2	222	33	0.1
208	73	15	19	106	0.4	28	106	11	221	35	0.2
207	82	17	20	113	3	29	155	8	220	37	0.5
206	79	8	21	142	10	30	205	8	219	38	1
205	82	7	22	168	3	31	373	2	218	42	0.3
204	91	11	23	208	5	32	400	2	217	40	24
202	128	12	15	298	0.4	33	1024	2	216	42	0.2
203	201	6	24	314	4	34	1262	6	215	47	3
201	430	7	14	471	0	35	1481	6	214	49	5
			13	631	2	36	1719	2	213	55	40
			12	732	0.2	37	2388	0.3	212	62	18
			11	914	2						
			10	1298	0.3						
			9	1372	0.5						
			8	1417	1						
			7	1875	0.6						
			6	2468	0.2						
			5	2788	2						
			4	2972	0						
			3	3017	0						

Table 2. Living benthonic population, in percentage of total benthonic population, in traverses I-IV.

stations to the south. There are insufficient data to draw any further conclusions, but the inference is clear that with sufficient data much could be learned about sedimentation rates by this means.

To a depth of 200 m. most of the species present in significant frequencies have living representatives; deeper than this the representation by living forms is spasmodic and they usually form less than 1 per cent of the total population. The various species of *Reophax* are an exception to the general rule. They are usually represented by a relatively large number of living specimens. This is especially true of *R. hispidulus*. The relatively large number of living specimens of these species and the low frequency of dead specimens suggests that these forms usually are destroyed soon after death. The tests of *R. hispidulus* are very fragile, the sand grains which form them being weakly cemented, so that once the supporting protoplasm is gone the specimens probably disintegrate rapidly. The same observation was made of such arenaceous species, in the shoal samples in the Mississippi Delta region, as *Goësella mississippiensis* n. sp., *Nouria polymorphinoides* and *Nouria* sp. Such fragile forms seldom appear in fossil assemblages and are probably not present in modern dead assemblages in the frequencies warranted by their actual rate of production.

DISTRIBUTION OF PLANKTONIC SPECIES (LIVING AND DEAD)

The relative distributions of the planktonic species are very similar throughout the area. Table 24 gives the percentage distributions in traverse VII and these may be taken, with some variation, as representative of the entire area. The total numbers of planktonic specimens in each sample are given in Tables 4-23. The species are not figured in the present report; the figures given by Phleger *et al* (1953) illustrate most of them and are accompanied by full taxonomic notes. The following species occur in the area:

Candeina nitida d'Orbigny
Globigerina bulloides d'Orbigny
G. digitata H. B. Brady
G. eggeri Rhumbler
G. inflata d'Orbigny
G. pachyderma (Ehrenberg)
G. sp.
Globigerinella aequilateralis (H. B. Brady)
Globigerinita glutinata (Egger)
Globigerinoides conglobata (H. B. Brady)
G. rubra (d'Orbigny)
G. sacculifera (H. B. Brady)
Globorotalia hirsuta (d'Orbigny) (4 occurrences)
G. menardii (d'Orbigny)
G. punctulata (d'Orbigny)
G. scitula (H. B. Brady)
G. truncatulinoides (d'Orbigny)
G. tumida (H. B. Brady)
Hastigerina pelagica (d'Orbigny)
Orbulina universa d'Orbigny
Pulleniatina obliquiloculata (Parker and Jones)
Sphaeroidinella dehiscens (Parker and Jones)

The species listed as *Globigerina* sp. is a small form with a maximum diameter of 0.25 mm. It is apparently identical to that referred by Rhumbler (1911, pl. 30, figs. 1-6) to *G. lamellosa*

Terquem. It is probably not this Eocene species which is later referred by Le Calvez (1949, p. 17) to "*Discorbis propinqua*" (Terquem). *Globigerina* sp. has a thin supplementary chamber extending from the dorsal side between the last-formed chamber and the first one in the last-formed whorl, to varying degrees over the umbilicus. There are supplementary apertures along the sides of this chamber which in many respects is similar to the supplementary chambers of *Globigerinita*. This chamber is apparently resorbed or destroyed when new regular chambers are added since there is no trace of previous ones. The species in other respects resembles a *Globigerina* of the *G. quinqueloba* Natland type. It is probable that it represents a new genus.

Globigerinita glutinata occurs in the area in some abundance. A re-examination of samples from the northwestern Gulf of Mexico shows that it is present there also although it is not reported by Phleger and Parker (1951).

The planktonic species appearing in the highest frequencies are (in order of abundance):

Globigerinoides rubra
Globigerina bulloides
G. eggeri
Globigerinoides sacculifera
Globorotalia truncatulinoides
G. menardii
Pulleniatina obliquiloculata
Globigerinita glutinata
Globigerinella aequilateralis

This assemblage of high-frequency species combines elements typical of both mid- and low-latitude faunas in the North Atlantic (Phleger *et al*, 1953). *Globigerina bulloides* and *Globorotalia truncatulinoides* are present in higher frequencies than they appeared in North Atlantic low latitudes although they are not quite so high as in the mid-latitudes. Conversely, *Globigerina eggeri*, *Globigerinoides sacculifera* and *Globorotalia menardii* are present in higher frequencies than they appeared in mid-latitudes but not so high as in the low. *Pulleniatina obliquiloculata* is present at frequencies characteristic of low latitudes. The remaining species are not diagnostic.

Of the rarer species, *Globigerina inflata* and *G. pachyderma* are diagnostic of mid-latitudes. *Globorotalia scitula* is present at mid-latitude frequencies. *G. tumida* is present at somewhat higher frequencies than are typical of mid-latitudes but less than those of low latitudes.

As stated previously, surface temperatures in the Gulf of Mexico range from an average minimum of 20°C. in February to an average maximum of 29°C. in August. The average maximum of 29°C. is higher than any found in the North Atlantic, except locally, even in the equatorial region. The minimum of 20°C. is comparable to that found between N Lat. 30° and 35° in the North Atlantic. There, the average maximum temperatures range from 26.5-27.5°C. In respect to temperature, then, the Gulf of Mexico combines the minimum of the North Atlantic mid-latitudes with a maximum in excess of that found in North Atlantic low latitudes. This may in part explain the anomalies of the planktonic assemblage found in the eastern Gulf of Mexico.

It is easy to explain the introduction of planktonic species which occur in low latitudes into the Gulf of Mexico by the surface current flowing north from the Caribbean Sea. The presence of *Globigerina inflata* and *G. pachyderma* (and possibly *Globorotalia hirsuta*, *G. punctulata* and *G. scitula*) are more difficult to explain since they apparently do not occur in the Caribbean nor are they found in the western part of the Gulf of Mexico. It is postulated that these species may be introduced from the Atlantic by a shallow coastal current flowing from east to west along the Florida coast. R. C. Reid (personal communication) says that it is very possible that such a current exists and that the conformation of the Florida Keys strongly suggests it. The circulation in the gulf itself being divided into two main eddies in the eastern and western parts probably would explain why *Globigerina inflata* and *G. pachyderma*, which are rare, appear only in the eastern Gulf of Mexico area.

The total number of planktonic specimens in the samples is very variable. In the Mississippi Delta region they do not occur in the sediments as shoal as in the rest of the area and are almost completely absent in traverse I to a depth of 430 m. In traverse II they occur at 88 m. but not significantly until considerably deeper and in traverses III-VIII in small numbers shoaler than 50 m. Their absence in the delta region is probably due to the outflow of the Mississippi River which causes water to flow out over the surface for long distances. Throughout the area samples taken at less than 100 m. usually contain planktonic specimens at less than 10 per cent of total population. Deeper than 1000 m.

they usually compose 90 per cent or more of the total population.

Deeper than about 150 m. the planktonic specimens at many stations show evidence of solution of the tests. This is shown especially by the large number of broken specimens. At some stations at least 50 per cent of the fauna appears to be affected. Since it is unknown how rapidly fresh tests are added, it is impossible to tell how rapidly solution takes place. The relatively small number of fresh specimens at some deep-water localities suggests that solution is fairly rapid.

Tables 29 and 30 list the number of living specimens of planktonic species found at the various stations. Since protoplasm is rapidly destroyed after death, probably not remaining in the test more than 12-14 hours, the specimens very likely represent actual living forms which for some reason have fallen to the bottom and survived. There are more living representatives of the abundant species than the rare ones. This implies that the living forms do not necessarily represent selected species which may have benthonic stages. Such rare species as *Globigerina inflata*, *Globigerinoides conglobata*, *Sphaeroidinella dehiscens*, etc. have no living representatives.

BENTHONIC SPECIES

Introduction

Two hundred and five benthonic species and thirteen generic or family groups have been used in compiling the data of the present report, including ten new species and one new genus. These constitute only a part of the fauna but are a large proportion of the total population. The remainder of the fauna is present in small quantities and for the most part the species have no distributional significance. Some of the species in this group which appear to have limited depth ranges are:

	Depth	Traverse
Buliminella elegantissima (d'Orbigny)	to 140 m.	IV-VIII
Cassidulina norcrossi australis Phleger & Parker	140-585 m.	VI-VIII
C. palmerae Bermudez and Acosta	135-255 m.	IX-XI
Cassidulinoides bradyi (Norman)	140-375 m.	scattered

	Depth	Traverse
Chrysalidinella sp.	to 155 m.	scattered
Cornuspira planorbis Schultze	to 185 m. (mostly)	scattered
Dorothia caribaea Cushman	140-155 m.	VI, VII, XI
Ehrenbergina undulata Parker	320-450 m. (mostly)	VI-X
Gaudryina antillana Bermudez and Acosta	85-180 m.	VI-IX
Patellina corrugata Williamson	to 240 m. (mostly) rare to 1300 m.	scattered
Siphotextularia subplana (Cushman)	115-255 m.	scattered
Stomatorbina concentrica (Parker and Jones)	55-185 m.	VI-IX, XI
Textularia mexicana Cushman	135-370 m.	VI-VIII
Uvigerina sp. (hirsute with undercut chambers)	deeper than 1550 m.	VI, IX-XI

There has been little previous work in this area. Flint (1899) and Cushman (1918-1931) report on samples collected by the U. S. Bureau of Fisheries ship ALBATROSS. Most of this material is from deep water stations. Lowman (1949, 1951) gives data on the distribution of genera off Pensacola and Choctawhatchee Bay, Florida.

About 75 per cent of the present fauna is reported by Phleger and Parker (1951) in the northwestern Gulf of Mexico. About 15 per cent of the species reported by them are not present or occur only rarely in the eastern area. There is an increase east of Mobile Bay in the number of species characteristic of the West Indian region, but many of the West Indian species found on the isolated reefs of the northwestern Gulf of Mexico are not present in the northeastern. It is possible that they may be found in shallow areas along the Florida coast not included in this report since many of them are reported from the Tortugas region by Cushman (1922). A few deep-water species characteristic of the North Atlantic, such as *Cibicides kullenbergi* and *Bolivina pusilla*, occur in the northeastern area but not in the northwestern.

Under each species details of depth and areal distribution are given. Cushman's classification is used for convenience although the writer is not in complete agreement with it. Figured specimens are deposited in the U. S. National Museum, Washington, D. C.

Discussion of Species

Family SACCAMMINIDAE

Under "Saccamminidae and related forms" in the population counts are included various single-chambered forms which could not be readily differentiated in counting. Probably included here are specimens of *Reophax* and *Hormosina* represented by single chambers. The group is included in the counts because in some cases it forms a large component of the fauna.

These forms have an overall depth range from 125 m. to 2700 m. In traverse II they occur with frequencies of 5-20 per cent from 140 m. to 170 m.; 1-5 per cent to a depth of 1400 m. In the remaining traverses the occurrence is scattered.

PROTEONINA ATLANTICA Cushman

(Plate 1, figure 1)

Proteonina atlantica Cushman, 1944, Spec. Publ. 12, Cushman Lab. Foram. Res., p. 5, pl. 1, fig. 4.

This species was combined with the following one by Phleger and Parker (1951). As I have previously pointed out (Parker, 1952, p. 393) the two species are very distinct.

P. atlantica has a scattered occurrence in traverses II, IV-VII, usually less than 1 per cent. In traverse IV it occurs with a frequency of 20 per cent and 48 per cent at two stations shoaler than 60 m. These two stations, however, showed a relatively small arenaceous fauna in which calcareous forms may have been destroyed by decalcification. Most occurrences are shoaler than 500 m. but there are a few between 1000 and 3000 m., mostly with frequencies between 1-5 per cent.

PROTEONINA DIFFLUGIFORMIS (H. B. Brady)

(Plate 1, figure 2)

Reophax difflugiformis H. B. Brady, 1879, Quart. Journ. Micr. Sci., vol. 19, p. 51, pl. 4, figs. 3a, b.

This species occurs in all traverses except IV. It is found at all depths. Frequencies of 6-10 per cent are found in traverse I from 70-200 m., and in traverse II from 1450-1700 m.; elsewhere they are less than 6 per cent.

Family REOPHACIDAE

Reophax bilocularis Flint

(Plate 1, figure 3)

Reophax bilocularis Flint, 1899, Rept. U. S. Nat. Mus., (1897), p. 273, pl. 17, fig. 2.

Three-chambered specimens occur frequently but the third chamber is relatively very small.

This species occurs in all traverses except I and IV, in most cases with a frequency of less than 1 per cent. In traverses II, III, V, it occurs deeper than 1000 m.; in VI-XI deeper than 320 m.

Reophax distans delicatulus Cushman

(Plate 1, figure 4)

Reophax distans H. B. Brady, var. *delicatulus* Cushman, 1920, Bull. U. S. Nat. Mus., vol. 104, pt. 2, p. 13, pl. 4, fig. 2.

Cushman's figured specimen has a length (exclusive of the connecting necks) of 0.33 mm. but the maximum length of specimens found in the present study is 0.65 mm. Due to the fragility of the necks only single chambers occur. It is possible that small specimens without necks have been included in the population counts under Saccamminidae, etc. so that the distribution given below may not show the complete occurrence of the species.

The species occurs in all traverses but I and IV deeper than 1200 m., at less than 6 per cent except at the outer ends of traverses II and III where it is 6 per cent and 12 per cent respectively.

Reophax gracilis (Kiaer)

Nodulina gracilis Kiaer, 1900, Rep't. Norwegian Fish Mar. Invest., vol. 1, no. 7, p. 24, text fig. 2 (1?).

This species occurs at 5 stations in traverses I, II, and IV between 47 m. and 430 m. Only living specimens were found. The fragility of the test makes survival in dried samples very unlikely.

REOPHAX GUTTIFERA H. B. Brady

(Plate 1, figure 5)

Reophax guttifera H. B. Brady, 1881, Quart. Journ. Micr. Sci., vol. 21, p. 49; 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 295, pl. 31, figs. 10-15.

This species has a scattered occurrence mostly at less than 1 per cent except in traverse II where it varies between 1 and 3 per cent from 300 m. to 914 m.

REOPHAX HISPIDULUS Cushman

(Plate 1, figures 6, 7)

Reophax hispidulus Cushman, 1920, Bull. U. S. Nat. Mus., vol. 104, pt. 2, p. 24, pl. 5, fig. 7.

The specimens appear to be identical with Cushman's species although they are less than 1 mm. in length whereas Cushman's exceed 3 mm. in length. Judging from the relatively large number of living specimens found, and the extreme fragility of the tests, it is probable that the figures shown in the total population counts are much lower than they should be. Very often living specimens are found when there are no empty tests in the dried samples.

The species occurs in all traverses but IV and IX, with frequencies ranging up to 3 per cent, at 45-3250 m.

REOPHAX IRREGULARIS n. sp.

(Plate 1, figures 9, 10)

Test medium in size; chambers not more than five in number, usually less, the initial one spherical, the remaining ones compressed with adjacent ones frequently set at an angle to each other, increasing in size as added; sutures depressed, often obscured by large fragments of wall material; wall rough, composed of sand grains, fragments of shell, etc. of varying sizes very irregularly cemented together. Maximum length of paratypes 1.7 mm.; width 0.6 mm. (not including projecting wall fragments).

Holotype from station 59, Lat. 29°58′ N, Long. 86°37′ W, at a depth of 91 m.

This species somewhat resembles *R. nothi* McFadyen but the wall of the test is much more irregular, the chambers do not increase so rapidly in size as added, and adjacent ones are often irregularly placed.

It occurs in traverses V-IX, XI, at depths of less than 185 m. except in IX where it is found to a depth of 255 m. Frequencies are below 6 per cent.

REOPHAX SCORPIURUS Montfort

(Plate 1, figure 11)

Reophax scorpiurus Montfort, 1808, Conch. Syst. Class. Meth. Coqu., p. 331, text fig. (p. 330).

This species occurs mostly in traverses I-III, with irregular occurrences elsewhere, to a depth of 400 m. Most deeper occurrences are at depths greater than 2600 m. Frequencies are less than 1 per cent except in traverses I and II where they range up to 5 per cent with one occurrence of 10 per cent at 208 m.

REOPHAX sp.

(Plate 1, figure 12)

This species is present in the form of isolated single chambers due apparently to weakness at the point of joining of the chambers. The maximum length of these chambers is 1.23 mm., width 0.2 mm. They are flask-shaped with the widest point below the middle.

Most occurrences are in traverse II from 315 m. to 735 m. Frequencies are below 6 per cent except for one occurrence of 10 per cent at 208 m.

HORMOSINA sp.

(Plate 1, figure 8)

This species occurs in traverses I-III, V-VII with frequencies of less than 1 per cent from 215-300 m. and 1750-1850 m. Frequencies are 1-5 per cent between 300 m. and 1750 m. There is one occurrence of 11 per cent in traverse I at 430 m.

Family AMMODISCIDAE

AMMODISCUS spp.

Species of this genus are grouped together owing to the lack of sufficient material for their proper analysis. Specimens occur in all traverses except IV usually with a frequency of less than 1 per cent, except in I where frequencies of 1-5 per cent are found at 128 m. and 201 m.

GLOMOSPIRA CHAROIDES (Jones and Parker)

(Plate 1, figure 14)

Trochammina squamata var. *charoides* Jones and Parker, 1860, Quart. Journ. Geol. Soc. London, vol. 16, p. 304.

This species occurs in all traverses but IV deeper than 130 m. at frequencies of less than 6 per cent in most cases. Higher frequencies up to 10 per cent occur in some areas deeper than 900 m.

GLOMOSPIRA cf. GORDIALIS (Jones and Parker)

(Plate 1, figure 13)

Trochammina squamata var. *gordialis* Jones and Parker, 1860, Quart. Journ. Geol. Soc. London, vol. 16, p. 304.

Trochammina gordialis Jones and Parker, Carpenter, Parker and Jones, 1862, Introd. Form. p. 141, pl. 11, fig. 4.

The specimens have a smooth, polished test and are questionably comparable to Jones and Parker's species.

The species has a scattered occurrence in the whole area deeper than 140 m. Frequencies are usually less than 1 per cent, occasionally higher.

TOLYPAMMINA SCHAUDINNI Rhumbler

(Plate 1, figure 15)

Tolypammina schaudinni Rhumbler, 1904, Archiv. Prot., vol. 3, pt. 1, p. 277, text fig. 126 (on p. 278).

Most occurrences are deeper than 914 m. with frequencies less than 6 per cent, in traverses II, III, VII-XI.

Family LITUOLIDAE

HAPLOPHRAGMOIDES BRADYI (Robertson)

(Plate 1, figure 16)

Trochammina robertsoni H. B. Brady, 1887 (not *T. robertsoni* H. B. Brady, 1876), Journ. Roy. Micr. Soc., p. 893.

Trochammina bradyi Robertson, 1891, Ann. Mag. Nat. Hist., ser. 6, vol. 7, p. 388.

This species is found in all traverses except IV, with two exceptions deeper than 165 m. Frequencies are less than 1 per cent in most of the area but may be as high as 5 per cent deeper than 630 m.

ADERCOTRYMA GLOMERATUM (H. B. Brady)

(Plate 1, figure 18)

Lituola glomerata H. B. Brady, 1878, Ann. Mag. Nat. Hist., ser. 5, vol. 1, p. 433, pl. 20, figs. 1a-c.

Most specimens are larger and composed of coarser sand grains than those from the Gulf of Maine and the Arctic; in other respects they seem identical.

The species occurs in all traverses except IV with a scattered occurrence from 200-1000 m., and a more consistent distribution deeper. Frequencies are less than 1 per cent to 1000 m. and 1-5 per cent, in most cases, deeper.

ALVEOLOPHRAGMIUM NITIDUM (Goës)

(Plate 1, figure 17)

Haplophragmium nitidum Goës, 1896, Bull. Mus. Comp. Zool., vol. 29, p. 30, pl. 3, figs. 8, 9.

The writer is following the opinion given by Loeblich and Tappan (1953, p. 28) in the use of the name *Alveolophragmium* for the genus having an interio-areal aperture which is undivided and forms a lineal slit. Many specimens of various species of this genus have been observed but in none of them has the aperture been subdivided. It would appear, therefore, that the divided aperture is restricted in its occurrence and is probably a true generic feature, giving separate status to the genus *Cribrostomoides*.

A. nitidum is found in all traverses but IV, in most cases deeper than 300 m. Frequencies are usually less than 1 per cent but occasionally 1-5 per cent.

ALVEOLOPHRAGMIUM RINGENS (H. B. Brady)
(Plate 1, figure 19)

Trochammina ringens H. B. Brady, 1879, Quart. Journ. Micr. Sci., n.s., vol. 19, p. 57, pl. 5, fig. 12

This species is more involute than others of this genus and the aperture is placed farther from the chamber margin, but in essentials it appears to be referable to *Alveolophragmium*.

Occurrences are scattered, mostly deeper than 1200 m., with frequencies of less than 1 per cent.

ALVEOLOPHRAGMIUM SCITULUM (H. B. Brady)

(Plate 1, figures 20, 21)

Haplophragmium scitulum H. B. Brady, 1881, Quart. Journ. Micr. Sci., vol. 21, p. 50; 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 308, pl. 34, figs. 11-13.

Gulf of Mexico specimens have an interio-areal aperture and this feature is also plainly visible in the section figured by Brady (fig. 13). Adult specimens are rare.

The species has a scattered distribution from 90-2950 m. usually at less than 1 per cent, occasionally higher.

ALVEOLOPHRAGMIUM SUBGLOBOSUM (G. O. Sars)

(Plate 2, figures 1, 2)

Lituola subglobosa M. Sars, 1868 (1869), Forh. Vid. Selsk. Christiania, p. 250 (nomen nudum); G. O. Sars, 1872, *ibid.*, p. 253.

Haplophragmium latidorsatum H. B. Brady, 1884 (not *Nonionina latidorsatum* Bornemann, 1885), Rept. Voy. CHALLENGER, Zool. vol. 9, p. 307, pl. 34, figs. 7, 8, 10, 14 (?) (not fig. 9).

Haplophragmoides subglobosum (G. O. Sars) Cushman, 1910, Bull. U. S. Nat. Mus., vol. 71, pt. 2, p. 105, text figs. 162-164.

Juvenile specimens are more irregularly coiled than are the adults. The species appears to be intermediate between *Recurvoides* and *Alveolophragmium* but is more closely allied to the latter in adult specimens.

The distribution is very scattered deeper than 300 m. with most occurrences deeper than 900 m. Frequencies are in most cases less than 1 per cent.

ALVEOLOPHRAGMIUM WIESNERI (Parr)

(Plate 1, figure 23)

Labrospira wiesneri Parr, 1950, B. A. N. Z., Antarctic Res. Exped., 1929-1931, Repts., ser. B, vol. 5, pt. 6, p. 272, pl. 4, figs. 25, 26.

Labrospira arctica Parker, 1952, Bull. Mus. Comp. Zool., vol. 106, no. 9, p. 399, pl. 2, figs. 7, 12.

This species has a very scattered distribution, in most cases 625-1750 m. Frequencies are less than 1 per cent except in traverses II deeper than 620 m. and III deeper than 1000 m. where they range from 1-6 per cent.

ALVEOLOPHRAGMIUM sp.

(Plate 1, figure 22)

This species is referred to *Labrospira* sp. by Phleger and Parker (1951, p. 3). It is possible that there are two species combined here as the distribution is divided. One group is found at less than 200 m. at frequencies of less than 1 per cent, except in traverse I where they range up to 14 per cent. A second group occurs deeper than 960 m. mostly at less than 1 per cent.

AMMOSCALARIA PSEUDOSPIRALIS (Williamson)

(Plate 2, figures 3, 4)

Proteonina pseudospirale Williamson, 1858, Rec. Foram. Great Britain, p. 2, pl. 1, figs. 2, 3.

Ammobaculites prostomum Hofker, 1932, Publ. Staz. Zool. Napoli, vol. 12, fasc. 1, p. 87, figs. 14, 15.

Two variant forms are included in this species. One appears to be identical to that figured by Williamson and perhaps more accurately by Brady (1884, pl. 33, figs. 1-4). The second form, found in the vicinity of the Mississippi Delta, is smaller, longer in relation to breadth, and more finely arenaceous. The two forms are sometimes found together, but the typical form is much more widespread. A detailed study of the distribution of the small form in the Mississippi Delta area would be needed to determine whether or not this is a variant form related to a specialized environment or whether it is a different species altogether. In most respects the forms are very similar.

The species occurs in traverses I-VIII from 20-210 m. Frequencies vary from less than 1 per cent to 30 per cent in traverses I, II, IV and are less than 1 per cent elsewhere.

AMMOSCALARIA TENUIMARGO (H. B. Brady)

(Plate 2, figure 5)

Haplophragmium tenuimargo H. B. Brady, 1882, Proc. Roy. Soc. Edinburgh, vol. 11, (1880-82), p. 715; 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 303, pl. 33, figs. 13-16.

The specimens are smaller than those described by Brady, being less than 1 mm. in length. The ratio of breadth to length is slightly larger.

The distribution is scattered in traverses II, V, VII-XI deeper than 950 m. Frequencies are less than 6 per cent.

AMMOBACULITES sp. A.

(Plate 2, figures 7, 8)

The specimens are very fragile, and very few are found in any one sample. It is probable that the tests are not preserved in the sediment very long after death. The species most closely resembles *A. americanus* Cushman and *A. rostratus* Heron-Allen and Earland but is not umbilicate.

A. sp. A occurs in traverses I-III, V at frequencies of less than 6 per cent except for one occurrence of 8 per cent in I at 201 m.

AMMOBACULITES sp. B.

(Plate 2, figure 6)

This species is apparently new but is not found at any one station in sufficient quantities to so describe it. It has a maximum length of 0.3 mm. and a maximum width in the coiled portion of 0.11 mm. The test is circular in cross section and has a smooth, polished, finely arenaceous wall.

It is found in all traverses except I and IV deeper than 820 m., with most occurrences deeper than 950 m. Frequencies are less than 6 per cent.

CYCLAMMINA spp.

This genus has a very scattered distribution deeper than 475 m. in most cases with frequencies of less than 1 per cent.

Family TEXTULARIIDAE

SPIROPLECTAMMINA FLORIDANA (Cushman)

(Plate 2, figure 9)

Textularia floridana Cushman, 1922, Publ. 311, Carnegie Instit. Washington, vol. 17, p. 24, pl. 1, fig. 7.

This is believed to be a valid species for the reasons given by Phleger and Parker (1951, p. 4).

It is found in traverses V-IX, XI at frequencies of less than 1 per cent, occasionally as high as 2 per cent in VI and VIII.

TEXTULARIA CANDEIANA d'Orbigny

(Plate 2, figures 16, 17)

Textularia candeiana d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 143, pl. 1, figs. 25-27.

Associated with typical *T. candeiana* are smaller specimens in which the chambers do not increase so rapidly in size as added. The two forms appear to grade into one another and are considered to belong to the same species.

There is one occurrence in traverse IV; consistent distribution is in traverses V-IX, XI to a depth of 345 m. Frequencies are less than 5 per cent.

TEXTULARIA CONICA d'Orbigny

(Plate 2, figure 13)

Textularia conica d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 143, pl. 1, figs. 19, 20.

Specimens of this species vary greatly in the amount of compression of the tests so that some in apertural view are almost completely circular while others are relatively narrow. All variations between the two extremes are observed.

The species occurs in traverses V-IX, XI down to a depth of 280 m. with frequencies of 2 per cent or less.

TEXTULARIA EARLANDI Parker

(Plate 2, figure 12)

Textularia elegans Lacroix, 1932 (not *Plecanium elegans* Hantken, 1868), Bull. Instit. Ocean. Monaco, no. 591, p. 8, text figs. 4, 6.

Textularia tenuissima Earland, 1933 (not Hausler, 1881), DISCOVERY Repts., vol. 7, p. 95, pl. 3, figs. 21-30.

Textularia earlandi Parker, 1952, Bull. Mus. Comp. Zool., vol. 106, no. 10, p. 458 (footnote).

This species occurs in traverses I-V, to a depth of 1000 m. Frequencies are variable with a maximum of 79 per cent in I at station 210 and in IV at station 212. Frequencies higher than 30 per cent only occur shoaler than 80 m.

TEXTULARIA FOLIACEA OCCIDENTALIS Cushman

(Plate 2, figure 10)

Textularia foliacea Heron-Allen and Earland var. *occidentalis* Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104,, pt. 3, p. 16, pl. 2, figs. 13.

It is possible that Cushman's variety should be raised to specific rank, but this cannot be done without a study of type material. It is here given subspecific rank since the two forms are so widely separated geographically. A related form occurs rarely in this area which varies in being much less compressed. It sometimes occurs with the typical form and sometimes elsewhere. It is omitted from the population counts due to its rarity, but is found in traverses IX and XI, to a depth of 520 m.

T. foliacea occidentalis occurs in traverses V-IX, XI from 65 m. to 255 m. at frequencies of usually less than 1 per cent, occasionally slightly higher.

TEXTULARIA MAYORI Cushman

(Plate 2, figure 11)

Textularia mayori Cushman, 1922, Publ 311, Carnegie Instit. Washington, vol. 17, p. 23, pl. 2, fig. 3.

This species occurs in traverses IV-IX, XI to a depth of 150 m. with some deeper occurrences in VI and IX to a depth of 255 m. Frequencies up to 6 per cent occur shoaler than 70 m.; deeper, they are less than 1 per cent.

SIPHOTEXTULARIA CURTA (Cushman)

(Plate 2, figure 15)

Textularia flintii var. *curta* Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 14, pl. 2, figs. 2, 3.

This species occurs in traverses III, V, VI, VIII-XI from 900 m. to 2650 m. with frequencies of less than 1 per cent.

SIPHOTEXTULARIA ROLSHAUSENI Phleger and Parker
(Plate 2, figure 14)

Siphotextularia rolshauseni Phleger and Parker, 1951, Mem. 46, Geol. Soc. America, pt. 2, p. 4, pl. 1, figs. 23, 24a, b.

This is a deep-water species occurring in traverses II, V-VIII, X, XI deeper than 2100 m. In most cases frequencies are less than 1 per cent.

BIGENERINA IRREGULARIS Phleger and Parker
(Plate 3, figures 1, 2, 3)

Bigenerina irregularis Phleger and Parker, 1951, Mem. 46, Geol. Soc. America, pt. 2, p. 4, pl. 1, figs. 16-21.

This species differs from the following one in its less compressed biserial portion and smaller size. The test may be formed of calcareous fragments or sand grains depending on the materials available. Associated with this species in traverses VI-VIII is a variant form which is very slender and has a very small, more compressed biserial portion. This variant may be mistaken for a *Reophax* on superficial examination. It has a maximum length of 1.5 mm.

B. irregularis occurs in traverses IV-IX to a depth of 185 m. At less than 100 m. depth frequencies up to 5 per cent are found; deeper they are less than 1 per cent.

BIGENERINA TEXTULARIOIDEA (Goës)
(Plate 3, figures 4, 5)

Clavulina textularioidea Goës, 1894, Kongl. Svensk. Vet.-Akad. Handl., vol. 25, no. 9, p. 41, pl. 8, figs. 387-399.

This species is not reported in the northwestern Gulf of Mexico. Like the previous one the test may be formed of any material available.

It occurs in traverses V-IX, XI to a depth of 190 m. Frequencies may be as high as 6 per cent except in traverse VIII where they reach a maximum of 9 per cent.

Family VERNEUILINIDAE

GAUDRYINA cf. AEQUA Cushman
(Plate 3, figure 12)

Gaudryina aequa Cushman, 1947, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 87, pl. 18, figs. 18-21.

This species occurs in traverses V-VIII, XI to a depth of 150 m. at frequencies of less than 1 per cent.

GAUDRYINA (PSEUDOGAUDRYINA) ATLANTICA (Bailey)

(Plate 3, figure 7)

Textularia atlantica Bailey, 1851, Smithsonian Contr., vol. 2, art. 3, p. 12, pl., figs. 38-43.

This species occurs in traverses II (once), VI-IX, XI from 85 m. to 320 m. with frequencies of less than 1 per cent.

GAUDRYINA FLINTII Cushman

(Plate 3, figure 6)

Gaudryina subrotundata Flint, 1899 (not Schwager, 1866), Ann. Rept. U. S. Nat. Mus., (1897), p. 287, pl. 33, fig. 1.

Gaudryina flintii Cushman, 1911, Bull. U. S. Nat. Mus., vol. 71, pt. 2, p. 63, text fig. 102.

Specimens have a maximum length of 2 mm. and most have a shorter biserial stage than those figured by Cushman and Flint.

This species occurs in traverses VI-XI from 900 m. to 2250 m. Frequencies are not over 1 per cent.

GAUDRYINA cf. MINUTA Earland

(Plate 3, figures 15, 16)

Gaudryina minuta Earland, 1939, DISCOVERY Repts., vol. 10, p. 121, pl. 5, figs. 45, 46.

The specimens are larger and more elongate than *G. exilis* Cushman and Bronnimann and in some cases reach a greater length than that given by Earland for his species. The maximum length is 0.4 mm.

The distribution is scattered in traverses II-VIII to a depth of 1800 m. Frequencies are less than 1 per cent except in II where they reach a maximum of 8 per cent.

PSEUDOCLAVULINA MEXICANA (Cushman)

(Plate 3, figure 8)

Clavulina humilis H. B. Brady var. *mexicana* Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 83, pl. 16, figs. 1-3.

This species has a scattered distribution in all traverses but I-IV from 80 m. to 455 m., with frequencies of less than 1 per cent.

PSEUDOCLAVULINA aff. NOVANGLIAE Cushman
(Plate 3, figures 9, 10)

Clavulina nodosaria d'Orbigny var. *novangliae* Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 82, pl. 15, figs. 3-5.

This is probably a new subspecies of Cushman's species but there is insufficient material from any one locality to make a statistical analysis. The Gulf of Mexico form has a maximum length of 2 mm. and width of 0.4 mm. It appears to be a somewhat smaller form, relatively more slender, the initial triserial portion being smaller in relation to the remainder of the test. In other respects the two are similar.

This form occurs in traverses VI-IX, from 115 m. to 370 m. Frequencies are less than 1 per cent.

Family VALVULINIDAE

EGGERELLA BRADYI (Cushman)
(Plate 3, figure 17)

Verneuilina pygmaea H. B. Brady 1884 (not *Bulimina pygmaea* Egger 1857), Rept. Voy. CHALLENGER, Zool., vol. 9, p. 385, pl. 47, figs. 4-7.

Verneuilina bradyi Cushman, 1911, Bull. U. S. Nat. Mus., vol. 71, pt. 2, p. 54, text figs. 87a, b.

As pointed out by Phleger *et al* (1953, p. 27) this species sometimes develops a biserial stage. Such specimens occur very rarely in this area.

The species occurs in all traverses but I and IV, deeper than 150 m. in a few cases but chiefly deeper than 420 m. Frequencies are less than 1 per cent shoaler than 915 m.; deeper they may be as high as 5 per cent.

TEXTULARIELLA spp.

Many of the specimens are probably referable to *T. barrettii* (Jones and Parker). Whether or not the low-spired, rapidly accelerated specimens which are found should be referred also to this species is open to question. Since the various forms have similar distributions, no attempt has been made to separate them in the population counts.

The group occurs in traverses V-IX, XI to a depth of 180 m. except in IX where they continue to 320 m. Frequencies are variable with a maximum of 3 per cent.

PLECTINA APICULARIS (Cushman)
(Plate 3, figure 18)

Gaudryina apicularis Cushman, 1911, Bull. U. S. Nat. Mus., vol. 71, pt. 2, p. 69, text figs. 110a, b.

This species occurs in all traverses but I and IV. There is a very scattered occurrence of less than 1 per cent frequency between 230 m. and 915 m.; deeper, the occurrences are more consistent and frequencies are often 1-5 per cent.

GOËSELLA MISSISSIPPIENSIS n. sp.
(Plate 3, figures 13, 14, 19)

Test of medium size, the greatest width at the apex of the triserial portion of the test which with the multiserial portion composes about five-eighths of the adult test, all stages of development being greatly accelerated, with the uniserial portion in the adult usually only consisting of a single chamber; chambers distinct, inflated; sutures slightly depressed; wall smooth, composed of rather small sand grains of varying size; aperture round or elliptical. Maximum length 0.72 mm., width 0.32 mm.

Holotype from station 28, Lat. 29°24.5′ N; Long. 88°52′ W at a depth of 106 m.

This species is smaller than *G. flintii* Cushman, has a much smoother wall composed of fine arenaceous material. The general shape of the test in the two species is very similar except that I have never seen *G. mississippiensis* with more than one uniserial chamber. Many of the specimens are juvenile, having reached only the triserial stage.

The species occurs in traverses I-IV, V (once) in most cases shoaler than 210 m. Frequencies are very high: up to 44 per cent in I, 92 per cent in II, and somewhat lower in the remaining traverses.

KARRERIELLA BRADYI (Cushman)
(Plate 3, figure 11)

Gaudryina bradyi Cushman, 1911, Bull. U. S. Nat. Mus., vol. 71, pt. 2, p. 67, text figs. 107a-c.

This species occurs chiefly in traverses VI-XI deeper than 135 m. In traverses II, III, V there are a few occurrences deeper than 900 m. All frequencies are less than 1 per cent.

LIEBUSELLA spp.

There is not sufficient material to make a study of the various species. They occur in traverse V (once), VI-IX, XI from 70 m. to 275 m. with frequencies of less than 1 per cent.

Family MILIOLIDAE

Under Miliolidae in the population counts are grouped various species which are not sufficiently common to be considered separately. Taken together they form a large group which occurs chiefly in traverses IV-XI with the majority of occurrences shoaler than 500 m. Some or all occurrences deeper than 1300 m. probably represent displaced specimens. The highest frequencies are found shoaler than 150 m., ranging in a few cases as high as 42 per cent, most frequently between 5 and 20 per cent. The frequencies decrease to less than 1 per cent at 250 m. A few occurrences deeper than 1300 m. exceed 1 per cent.

QUINQUELOCULINA BICOSTATA d'Orbigny

(Plate 4, figures 1, 2)

Quinqueloculina bicostata d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 195, pl. 12, figs. 8-10.

Gulf of Mexico specimens are larger than d'Orbigny's, reaching a maximum length of 0.9 mm.

The species occurs in traverses IV-VIII to a depth of 100 m. except in VIII where it goes to 145 m. Most frequencies are less than 1 per cent; a few shoaler than 50 m. reach a maximum of 3 per cent.

QUINQUELOCULINA COMPTA Cushman

(Plate 3, figures 20, 21)

Quinqueloculina compta Cushman, 1947, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 87, pl. 19, fig. 2.

The distribution is in traverses IV-VIII, XI (once), to a depth of 155 m. Frequencies up to 3 per cent occur shoaler than 50 m.; deeper, they are less than 1 per cent.

QUINQUELOCULINA HORRIDA Cushman
(Plate 4, figures 3, 4)

Quinqueloculina horrida Cushman, 1947, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 88, pl. 19, fig. 1.

The species occurs in traverses IV-IX to a depth of 370 m. With a few exceptions all frequencies are less than 1 per cent, never greater than 3 per cent.

QUINQUELOCULINA LAMARCKIANA d'Orbigny
(Plate 4, figures 5, 6)

Quinqueloculina lamarckiana d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 189, pl. 11, figs. 14, 15.

This species, as I have defined it in this area, may represent a "species group" rather than a discrete species. There is great variation in the acuteness of the chamber angles and the extent to which they project. There is also variation in the length of the apertural neck.

The distribution is in traverses IV-XI to a depth of 275 m.; scattered deeper than 180 m. Frequencies are 1-5 per cent at the shoaler ends of the traverses extending to various depths but never deeper than 150 m. There are a few specimens, probably displaced, found deeper than 1500 m. in traverses II and X.

QUINQUELOCULINA cf. POLYGONA d'Orbigny
(Plate 4, figures 7, 8)

Quinqueloculina polygona d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 198, pl. 12, figs. 21-23.

This species is very similar to d'Orbigny's figured specimen but is relatively broader, has a more elongate aperture and a shorter neck.

Specimens occur in traverses IV-IX, XI, consistently to a depth of 100 m.; scattered to 185 m. All frequencies are less than 1 per cent.

QUINQUELOCULINA SABULOSA Cushman
(Plate 4, figures 9, 10)

Quinqueloculina sabulosa Cushman, 1947, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 87, pl. 18, fig. 22.

This species occurs in traverses IV-VIII to a depth of 100 m. All frequencies are less than 1 per cent.

QUINQUELOCULINA VENUSTA Karrer
(Plate 4, figures 13, 14)

Quinqueloculina venusta Karrer, 1868, Sitz. K. Akad. Wiss. Wien, vol. 58, Abt. 1, p. 147, pl. 2, fig. 6.

This species occurs in traverse VI (once), VIII (once), IX-XI, deeper than 1700 m. Frequencies are less than 1 per cent except for one occurrence of 2 per cent at 3164 m. in VIII.

QUINQUELOCULINA sp.
(Plate 4, figures 11, 12)

This species is similar to the form referred by Phleger *et al* (1953, p. 28) to *Q.* cf. *weaveri* Rau, except that it has a small, simple tooth. The species is not sufficiently common to describe adequately. The maximum length is 0.6 mm.

It occurs in traverses II, III, V-XI, but chiefly in VI-XI deeper than 915 m., except in VII where it occurs deeper than 585 m. Frequencies are less than 1 per cent except occasionally in IX-XI where the maximum is 3 per cent.

SPIROLOCULINA cf. GRATA Terquem
(Plate 4, figure 15)

Spiroloculină grata Terquem, 1878, Mém. Soc. Géol. France, ser. 3, vol. 1, p. 55, pl. 5 (10), figs. 14, 15.

This species is referred by Phleger and Parker (1951, p. 8) to *S. antillarum* d'Orbigny. I sent specimens to Miss Ruth Todd for study and she agrees that they closely resemble *S. grata.* The test of *S. antillarum* has a polished surface, *S. grata* a dull, slightly roughened one.

S. cf. *grata* occurs in traverses IV-VIII to a depth of 145 m. except in VIII where it extends to 585 m. Frequencies are mostly less than 1 per cent; 1 per cent occasionally.

SPIROLOCULINA SOLDANII Fornasini
(Plate 4, figure 16)

Frumentaria sextae speciei Soldani, 1780, Saggio Orittografico, p. 111, pl. 9, figs. 52t, T, V.

Spiroloculina soldanii Fornasini, 1886, Boll. Soc. Geol. Ital., vol. 5, p. 25.

There is some question whether or not this may be a gradational form of *S. depressa* d'Orbigny. Miss Ruth Todd reports (personal communication) that the two species grade into one another. A careful study of type and topotype material should be made to determine this. I am referring the Gulf of Mexico species to *S. soldanii* since it resembles this form more closely.

It occurs in traverses IV-IX, XI to a depth of 320 m. Most frequencies are less than 1 per cent.

SIGMOILINA DISTORTA Phleger and Parker
(Plate 4, figures 17, 21)

Sigmoilina distorta Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 8, pl. 4, figs. 3-5.

This species occurs chiefly in traverses IV-VIII, with rare occurrences in IX-XI. Most occurrences are shoaler than 500 m. but there are a few deeper ones, possibly displaced, in X and XI. Frequencies are variable with a maximum of 3 per cent.

SIGMOILINA SCHLUMBERGERI A. Silvestri
(Plate 4, figure 18)

Sigmoilina schlumbergeri A. Silvestri, 1904, Mem. Pont. Accad. Nuovi Lincei, vol. 22, p. 267.

This species is widely distributed in all traverses but I and IV, deeper than 175 m. The most consistent occurrence is deeper than 585 m. All occurrences shoaler than 915 m. have a frequency of less than 1 per cent; slightly higher ones occur occasionally in deeper water.

SIGMOILINA TENUIS (Czjzek)
(Plate 4, figure 19)

Quinqueloculina tenuis Czjzek, 1848, Haidinger's Nat. Abhandl. vol. 2, p. 149, pl. 13, figs. 31-34.

This species occurs in traverses III (once), V (twice), VI-XI, deeper than 140 m. All frequencies are less than 1 per cent except at the inner ends of IX and XI where frequencies of 1 per cent occur.

SIGMOILINA sp.
(Plate 5, figure 1, Text figure 2)

This species may be referable to "*Spiroloculina arenaria*" H. B. Brady. Sectioning shows that the Gulf of Mexico form is a *Sigmoilina* and since it would be preferable to section Brady's specimens before transferring his species to *Sigmoilina* I have not given the Gulf of Mexico species a name at this time.

The species occurs in traverses V (once), VI-IX, XI to a depth of 255 m. Frequencies are less than 1 per cent except in VII where they are 1 and 3 per cent at 86 m. and 146 m. respectively.

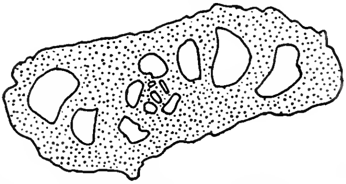

Fig. 2. *Sigmoilina* sp. Transverse section. X 55. Sta. 59.

NUMMOLOCULINA IRREGULARIS (d'Orbigny)

(Plate 4, figure 20)

Biloculina irregularis d'Orbigny, 1839, Voy. Amer. Mérid., vol. 5, pt. 5, "Foraminifères," p. 67, pl. 8, figs. 20, 21.

The distribution of this species is very scattered. It occurs in traverse IX from 320 m. to 425 m., in traverses II (once), III (once), X, XI deeper than 914 m. Frequencies are less than 1 per cent except in X (once) and XI where they reach a maximum of 5 per cent.

TRILOCULINA cf. BREVIDENTATA Cushman

(Plate 5, figures 2, 3)

Triloculina brevidentata Cushman, 1944, Spec. Publ. 12, Cushman Lab. Foram. Res., p. 16, pl. 2, figs. 25a, b.

Gulf of Mexico specimens are relatively broader than those of Cushman's species and the chambers are slightly more inflated.

This species occurs in traverses IV-IX, XI to a depth of 255 m. Frequencies are less than 1 per cent except in V where there is a maximum of 2 per cent at the inner end and VII with a maximum of 1 per cent at the inner end.

TRILOCULINA TRICARINATA d'Orbigny

(Plate 4, figure 22)

Triloculina tricarinata d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 299, no. 7; Modèles, no. 94.

The distribution is scattered in all traverses but I and IV. The most consistent occurrence is deeper than 1000 m. but the species is found deeper than 55 m. Frequencies are usually less than 1 per cent, never more than 1 per cent.

PYRGO MURRHINA (Schwager)
(Plate 5, figure 7)

Biloculina murrhina Schwager, 1866, Novara Exped., Geol. Theil., vol. 2, p. 203, pl. 4, figs. 15 a-c.

There is a good deal of variation in the sinus at the base of the test. It is sometimes curved with two sharp points at either end and may be straight with no projecting points.

This species is widely distributed in all traverses except I and IV but most occurrences are in VI-XI. It is found at all depths but is more abundant deeper than 900 m. where frequencies as high as 4 per cent occur in IX-XI. Elsewhere frequencies are less than 1 per cent.

PYRGO cf. NASUTUS Cushman
(Plate 5, figure 4)

Pyrgo nasutus Cushman, 1935, Smithsonian Misc. Coll., vol. 91, no. 21, p. 7, pl. 3, figs. 1-4.

Gulf of Mexico specimens have a less serrate periphery than the form described by Cushman.

The species occurs in traverses III-IX, XI to a depth of 530 m. Frequencies are usually less than 1 per cent; occasionally slightly higher.

Family OPHTHALMIDIIDAE

NODOBACULARIELLA CASSIS (d'Orbigny)
(Plate 5, figure 8)

Vertebralina cassis d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, ''Foraminifères,'' p. 51, pl. 7, figs. 14, 15.

N. atlantica Cushman and Hanzawa may be included in the population counts under this species. The specimens are often much worn and specific identification difficult.

N. cassis occurs in traverses IV-VIII, IX (once), XI. Most occurrences are shoaler than 150 m., a few extending to 240 m. At less than 100 m. frequencies up to 5 per cent occur, with one occurrence in VIII of 11 per cent. Deeper than 100 m. frequencies are less than 1 per cent.

WIESNERELLA AURICULATA (Egger)
(Plate 5, figure 13)

Planispirina auriculata Egger, 1893, Abhandl. k. bay. Akad. Wiss. München, vol. 18, pt. 2, p. 245, pl. 3, figs. 13-15.

This species occurs chiefly in traverses V-VIII, with single occurrences in I and III, and two in IV. All but two occurrences are shoaler than 185 m. Frequencies are less than 1 per cent.

Family TROCHAMMINIDAE

TROCHAMMINA ADVENA Cushman

(Plate 5, figures 5, 6)

Trochammina advena Cushman, 1922, Publ. 311, Carnegie Instit. Washington, p. 20, pl. 1, figs. 2-4.

This species occurs at frequencies of 1-5 per cent in traverse I from 128 m. to 430 m. Other occurrences are scattered in traverses II, III, V, VI at various depths to 1100 m., at frequencies of less than 1 per cent (except for one occurrence of 4 per cent in II at 314 m.).

TROCHAMMINA GLOBULOSA Cushman

(Plate 5, figures 11, 12)

Trochammina globulosa Cushman, 1920, Bull. U. S. Nat. Mus., vol. 104, pt. 2, p. 77, pl. 16, figs. 3, 4.

There is some variation in the texture of the test walls, some being smoother and more fine grained than others. The specimens were not as big as Cushman's, having a maximum diameter of 0.62 mm.

The species occurs in all traverses but I and IV deeper than 1000 m., except in II where it occurs deeper than 915 m., with frequencies up to 6 per cent.

TROCHAMMINA cf. JAPONICA Ishiwada

(Plate 5, figures 9, 10)

Trochammina japonica Ishiwada, 1950, Japan Geol. Surv. Bull., Kawasaki, Japan, vol. 1, no. 4, p. 190, pl., figs. 2a-c.

Northeastern Gulf of Mexico specimens are the same as *Trochammina* sp. Phleger and Parker (1951, p. 9).

The occurrence is most consistent in traverses I-III from 200 m. to 1750 m. at frequencies from 1 to 13 per cent. In traverses V-VII, X, XI the species has a scattered distribution at all depths deeper than 130 m. with frequencies less than 1 per cent.

TROCHAMMINA QUADRILOBA Höglund
(Plate 5, figures 14, 15)

Trochammina pusilla Höglund, 1947, (not *Serpula pusilla* Geinitz, 1848), Zool. Bidrag Uppsala, vol. 26, p. 201, pl. 17, figs. 4a-c, text figs. 183, 184.

Trochammina quadriloba Höglund, 1948, Contr. Cushman Lab. Foram. Res., vol. 24, pt. 2, p. 46.

This species has a very scattered distribution at various depths except in traverses I-III where it occurs between 70 m. and 430 m. Frequencies are as high as 22 per cent in I and 17 per cent, shoaler than 210 m., in II. Elsewhere frequencies are less than 1 per cent except for one occurrence of 6 per cent in II at 914 m.

TROCHAMMINA SQUAMATA Jones and Parker and related spp.

Trochammina squamata Jones and Parker, 1860, Quart. Journ. Geol. Soc. London, vol. 16, p. 304; Parker and Jones, 1865, Philos. Trans. Roy. Soc. London, vol. 155, p. 407, pl. 15, figs. 30, 30a-c.

Representatives of this group occur in all traverses but II and IX usually shallower than 100 m. Frequencies are mostly less than 1 per cent although they are occasionally as high as 5 per cent.

TROCHAMMINA cf. TASMANICA Parr
(Plate 5, figures 16, 17)

Trochammina tasmanica Parr. 1950, B. A. N. Z. Antarctic Res. Exped. 1929-31, ser. B, vol. 5, pt. 6, p. 279, pl. 5, fig. 18.

Gulf of Mexico forms are similar to Parr's but are smaller, with a maximum diameter of 0.26 mm., and appear to have a slightly higher spire.

This species has a very scattered occurrence throughout the area with frequencies in traverses I-III, where it occurs most consistently, up to 5 per cent (once 18 per cent). Other frequencies are less than 1 per cent.

NOURIA POLYMORPHINOIDES Heron-Allen and Earland
(Plate 5, figure 19)

Nouria polymorphinoides Heron-Allen and Earland, 1914, Trans. Zool. Soc. London, vol. 20, pt. 12, p. 376, pl. 37, figs. 1-15.

Proteonina comprima Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 2, pl. 1, figs. 1-3.

The distribution is in traverses IV, V, VII, VIII to a depth of 75 m. Frequencies are less than 1 per cent except for one occurrence of 9 per cent in IV at 40 m.

NOURIA sp.

(Plate 5, figure 20)

This species is smaller than *N. polymorphinoides* with a more regular oval shape and more finely arenaceous wall. The wall is constructed of sand grains of irregular size, some being much larger than others, and is very thin and fragile. It may be new.

It occurs in traverses I-IV to a depth of 130 m. Frequencies are high with maxima of 59 per cent in I, 81 per cent in II, 11 per cent in III and 22 per cent in IV.

Family LAGENIDAE

ROBULUS spp.

All species of this genus are combined in the population counts. They occur in all traverses, except I, at all depths. Occurrences are scattered in traverses II-IV. Frequencies of 1-5 per cent occur to a depth of 450 m. in VI-IX, XI; elsewhere they are less than 1 per cent.

LENTICULINA PEREGRINA (Schwager)

(Plate 5, figure 18)

Cristellaria peregrina Schwager, 1866, Novara Exped., Geol. Theil., vol. 2, p. 245, pl. 7, fig. 89.

This species has a wide distribution in all traverses except I and IV. Most occurrences are deeper than 145 m. Frequencies are less than 1 per cent.

MARGINULINA MARGINULINOIDES (Goës)

(Plate 5, figure 21)

Cristellaria aculeata var. *marginulinoides* Goës, 1896, Bull. Mus. Comp. Zool., vol. 29, p. 56, pl. 5, figs. 15, 16.

No keeled specimens are found but in other respects this form closely resembles Goës' species. Other species of *Marginulina* are found in the area but occur only rarely, being confined to a depth of less than 500 m.

The distribution is scattered with single occurrences in traverses II, V, VIII and more consistent occurrences in VI and VII. The depth range is 50 m. to 450 m. All frequencies are less than 1 per cent.

DENTALINA spp., NODOSARIA spp.

These genera have a scattered distribution at all depths, usually deeper than 100 m. Frequencies are low.

NODOSARIA HISPIDA d'Orbigny

(Plate 6, figure 1)

Nodosaria hispida d'Orbigny, 1846, Foram. Foss. bass. tert. Vienne, p. 35, pl. 1, figs. 24, 25.

Specimens which may be referred to var. *sublineata* H. B. Brady are included here though most of them are hirsute in character.

Single occurrences are found in traverses V, IX, XI; more consistent ones in VI-VIII. They occur deeper than 145 m. and, with one exception, no deeper than 715 m. Frequencies are less than 1 per cent.

PSEUDOGLANDULINA COMATULA (Cushman)

(Plate 5, figure 22)

Nodosaria comatula Cushman, 1923, Bull. U. S. Nat. Mus., vol. 104, pt. 4, p. 83, pl. 14, fig. 5.

There is a scattered distribution in traverses VI-XI, mostly between 135 and 255 m. Frequencies are less than 1 per cent.

LAGENA spp. and related forms

The species included in this group usually have a scattered or rare occurrence but the group taken as a whole is an important part of the fauna, occurring in all traverses but I at all depths. Frequenices are usually less than 1 per cent to a depth of 140 m., 1-5 per cent elsewhere except in traverses II (once), X, and XI where they may be as high as 10 per cent.

Family POLYMORPHINIDAE

GUTTULINA AUSTRALIS (d'Orbigny)
(Plate 6, figure 2)

Globulina australis d'Orbigny, 1839, Voy. Amer. Mérid., vol. 5, pt. 5, "Foraminifères," p. 60, pl. 1, figs. 1-4.

This species occurs in traverses IV-VIII to a depth of 85 m. Frequencies are usually less than 1 per cent but reach a maximum of 2 per cent at the inner end of IV.

GLOBULINA CARIBAEA d'Orbigny
(Plate 5, figure 23)

Globulina caribaea d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 135, pl. 2, figs. 7, 8.

Occurrences are in traverses IV-VIII to a depth of 58 m. Frequencies are less than 1 per cent.

Family NONIONIDAE

NONION FORMOSUM (Seguenza)
(Plate 6, figure 3)

Nonionina formosa Seguenza, 1880, Atti R. Accad. Lincei, ser. 3, vol. 6, p. 63, pl. 7, figs. 6, 6a.

Nonion barleeanum (Williamson) var. *inflatum* van Voorthuysen, 1950 (not *Nonionina inflata* Alth, 1850), Meded. Geol. Sticht., n. s., no. 4, p. 41, text fig. 7, pl. 3, figs. 6a, b.

Anomalinoides barleeanum (Williamson) var. *zaandamae* (van Voorthuysen) van Voorthuysen, 1952, Journ. Pal., vol. 26, no. 4, p. 681.

Comparison with specimens sent by van Voorthuysen and of these with topotype material of *N. formosum* at the U. S. National Museum by A. R. Loeblich appears to confirm this identification. Similar specimens were so referred by Phleger *et al* (1953, p. 30).

This species occurs in traverses V-IX, XI from 60 m. to 1750 m. Most frequencies are less than 1 per cent.

NONION POMPILIOIDES (Fichtel and Moll)
(Plate 6, figure 4)

Nautilus pompilioides Fichtel and Moll, 1798, Test. Micr., p. 31, pl. 2, figs. a-c.

There are single occurrences in traverses III, VI, VIII and X and there is a more consistent distribution in traverses II, VII, IX, XI. All occurrences are deeper than 2200 m. Frequencies are usually 1-4 per cent except at the outer end of XI where they are as high as 8 per cent.

ASTRONONION TUMIDUM Cushman and Edwards
(Plate 6, figure 5)

Nonionina stelligera H. B. Brady (pt.), 1884 (not d'Orbigny 1839), Rept. Voy. CHALLENGER, Zool., vol. 9, p. 728, pl. 109, fig. 5 (not figs. 3, 4).

Astrononion tumidum Cushman and Edwards, 1937, Contr. Cushman Lab. Foram. Res., vol. 13, pt. 1, p. 33, pl. 3, fig. 17.

The only reported occurrence of this species is that of Brady's figured specimen from CHALLENGER station 344, in 240 fms. off Ascension Island, south Atlantic.

There are single occurrences in traverses V, VI, IX, and XI, consistent ones in VII, VIII, X. The depth range is 320 m. to 1400 m., with one occurrence at 2550 m. All frequencies are less than 1 per cent.

NONIONELLA ATLANTICA Cushman
(Plate 6, figures 6, 7)

Nonionella atlantica Cushman, 1947, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 90, pl. 20, figs. 4, 5.

Combined in the population counts with this species are specimens of a more compressed form (Pl. 6, figs. 8, 9) and a small form which resembles *N. sloanii* (d'Orbigny).

N. atlantica occurs in traverses II-VIII, XI (once). The most consistent occurrence is shoaler than 500 m. with frequencies up to 10 per cent shoaler than 140 m., less than 1 per cent deeper than 140 m. A few single occurrences are at great depths and probably represent displaced specimens.

NONIONELLA OPIMA Cushman
(Plate 6, figures 10, 11, 12)

Nonionella opima Cushman, 1947, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 90, pl. 20, figs. 1-3.

This species occurs in traverses I-VII, XI. Consistent occurrences are found shoaler than 400 m. and scattered ones deeper. Frequencies up to 20 per cent may occur shoaler than 100 m., up to 5 per cent deeper. There is one occurrence of 31 per cent in III at 53 m.

ELPHIDIUM ADVENUM (Cushman)
(Plate 6, figure 14)

Polystomella advena Cushman, 1922, Publ. 311, Carnegie Instit. Washington, p. 56, pl. 9, figs. 11, 12.

The specimens in this area have a larger umbo than those described by Cushman. In other respects they appear similar.

All occurrences are shoaler than 115 m. in traverses IV-VIII. Frequencies are in most cases less than 1 per cent.

ELPHIDIUM DISCOIDALE (d'Orbigny)
(Plate 6, figure 15)

Polystomella discoidalis d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 56, pl. 6, figs. 23, 24.

This species occurs in traverses IV-VIII shoaler than 185 m. Frequencies are up to 5 per cent to a depth of 100 m., less than 1 per cent deeper.

ELPHIDIUM GUNTERI Cole
(Plate 6, figure 16)

Elphidium gunteri Cole, 1931, Florida State Geol. Surv. Bull. 6, p. 34, pl. 4, figs. 9, 10.

Elphidium gunteri Cole var. *galvestonensis* Kornfeld, 1951, (part), Contr. Dept. Geol. Stanford Univ., vol. 1, no. 3, p. 87, pl. 15, figs. 2a, b, 3a, b (not figs. 1a, b).

?*Elphidium littorale* Le Calvez and Le Calvez, 1951, Vie et Milieu, vol. 2, no. 2, p. 251, text figs. 5a, b.

E. littorale is placed in the synonymy questionably because the types have not been seen. It appears from the description and figures, however, to be synonymous. The only apparent difference is that it is described as having 10-12 chambers in the last-formed whorl whereas Cole's species may have as many as 14. As stated by Parker *et al* (1953, p. 8) part of Kornfeld's form *E. gunteri* var. *galvestonensis* is referable to *E. gunteri* as shown by a study of his types.

E. gunteri occurs in traverses III (once), IV-VIII to a depth of 80 m. except in VIII where it occurs to a depth of 185 m. Frequencies up to 5 per cent occur shoaler than 55 m., less than 1 per cent deeper. There are two occurrences of 9 per cent at the inner ends of IV and V.

ELPHIDIUM POEYANUM (d'Orbigny)
(Plate 6, figure 17)

Polystomella poeyana d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 55, pl. 6, figs. 25, 26.

The species occurs in traverses IV-VIII shoaler than 145 m. Frequencies up to 2 per cent occur at the inner end of various traverses; elsewhere they are less than 1 per cent.

ELPHIDIUM spp.

This group includes various species which have very low frequency distributions when considered separately. It occurs mostly in traverses III-VIII with some occurrences in I, II, IX, XI. Frequencies up to 5 per cent occur to a depth of 150 m., less than 1 per cent deeper. Occurrences are consistent to 185 m. and extend deeper in V and XI.

Family PENEROPLIDAE

This family has been considered as a group owing to the impossibility of identifying a relatively high proportion of the specimens. Many are badly weathered and there is usually a profusion of juvenile forms present.

The distribution is shoaler than 145 m. in traverses IV-VIII, with a single occurrence in XI. There is one occurrence in II at 375 m. Frequencies up to 16 per cent shoaler than 60 m., up to 5 per cent shoaler than 90 m. and less than 1 per cent elsewhere.

Family BULIMINIDAE

BULIMINELLA cf. BASSENDORFENSIS Cushman and Parker
(Plate 6, figure 13)

Buliminella bassendorfensis Cushman and Parker, 1937, Contr. Cushman Lab. Foram. Res., vol. 13, pt. 1, p. 40, pl. 4, figs. 13a, b.

This species occurs in traverses I-VI to a depth of 80 m. except in III where it extends to 370 m. at a frequency of less than 1 per cent. There are two occurrences deeper than 1700 m. Frequencies are variable but reach a maximum of 35 per cent at 77 m. in III.

ROBERTINA BRADYI Cushman and Parker
(Plate 6, figure 18)

Robertina bradyi Cushman and Parker, 1936, Contr. Cushman Lab. Foram. Res., vol. 12, p. 99, pl. 16, figs. 9a, b.

This species has a scattered occurrence in traverses VI-VIII and a more consistent one in IX-XI. The depth range is 105 m. to 2600 m. Frequencies are less than 1 per cent except in X and XI where they reach a maximum of 2 per cent deeper than 1300 m.

BULIMINA ACULEATA d'Orbigny
(Plate 6, figure 19)

Bulimina aculeata d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 269, no. 7.

This species is widely distributed in all traverses except I and IV deeper than 220 m., except for a shallow occurrence in III. Between 370 m. and 1850 m. frequencies up to 16 per cent occur; elsewhere they are usually less than 1 per cent.

BULIMINA ALAZANENSIS Cushman
(Plate 6, figure 21)

Bulimina alazanensis Cushman, 1927, Journ. Pal., vol. 1, p. 161, pl. 25, fig. 4.

This is a widely distributed species in all traverses but I and IV, deeper than 220 m. Frequencies are usually 1-5 per cent but may be as high as 15 per cent.

BULIMINA MARGINATA d'Orbigny
(Plate 6, figure 20)

Bulimina marginata d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 269, no. 4, pl. 12, figs. 10-12.

As in the northwestern Gulf of Mexico, specimens are smaller than typical, more spinose, and have more undercut chambers.

This species occurs in traverses II-VII to a depth of 530 m. It does not occur shoaler than 75 m. except in IV. Frequencies are very variable, reaching a maximum of 33 per cent in II at 168 m. Deeper than 320 m. frequencies are less than 1 per cent.

BULIMINA SPICATA Phleger and Parker
(Plate 6, figures 22, 23)

Bulimina spicata Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 16, pl. 7, figs. 25a-c, 30, 31.

This is a widely distributed species in all but traverses I and IV deeper than 70 m. Frequencies vary up to a maximum of 5 per cent.

BULIMINA STRIATA MEXICANA Cushman
(Plate 6, figure 24)

Bulimina striata d'Orbigny var. *mexicana* Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 95, pl. 21, fig. 2.

This species occurs in all traverses but I and IV deeper than 170 m. Frequencies seldom exceed 5 per cent.

GLOBOBULIMINA AFFINIS (d'Orbigny) and variant
(Plate 6, figure 25; Plate 7, figures 1, 2)

Bulimina affinis d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 105, pl. 2, figs. 25, 26.

Occurring with, or independently of, the typical form are specimens which are relatively much more narrow. These forms appear to have a somewhat deeper range, although there are exceptions. It is often difficult to separate the two forms, and for this reason they have been combined in the population counts.

The distribution is rather scattered in all traverses except I and IV, deeper than 165 m. Frequencies up to 5 per cent occur.

GLOBOBULIMINA MISSISSIPPIENSIS n. sp.
(Plate 7, figures 3, 4, 10)

Test of medium size, ovate, with the greatest width usually below or near the middle, sometimes almost as long as broad; initial end rounded in the megalospheric form, slightly pointed in microspheric; chambers slightly inflated, the last-formed whorl making up 1/8 to 1/7th of the test; sutures very slightly depressed; wall thin, translucent, finely perforate; aperture with a thickened border, the tongue extending from the test, curved, with a regular, non-toothed border. Maximum length 0.51 mm.; width 0.36 mm.

Holotype from station 29, Lat. 29°04.5′ N; Long. 88°52′ W at 155 m.

This species differs from *G. ovula* (d'Orbigny) in the non-depressed suture and non-inflated area of the last-formed chamber leading down from the aperture; the remaining chambers also are less inflated so that the outline of *G. mississippiensis* is much more regular. The species from the Caribbean discussed by Höglund (1947, p. 244) as *G.* sp. A is much larger, has fewer chambers, a deeply depressed portion of the suture near the aperture, and the last-formed whorl makes up a greater portion of the test.

There are single occurrences in traverses I and II and consistent ones in III from 105-205 m. Frequencies in III are 2-3 per cent.

VIRGULINA ADVENA Cushman

(Plate 7, figure 5)

Virgulina (?) *advena* Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 120, pl. 25, figs. 1-3.

As pointed out by Phleger *et al* (1953, p. 34) this appears to be a true *Virgulina.*

It has a scattered occurrence in all traverses but I and IV, deeper than 1250 m. Most frequencies are less than 1 per cent but they reach a maximum of 2 per cent at 2697m. in VI.

VIRGULINA COMPLANATA Egger

(Plate 7, figure 6)

Virgulina schreibersiana Czjzek var. *complanata* Egger, 1893, Abhandl. k. bay. Akad. Wiss. München, vol. 18, pt. 2, p. 292, pl. 8, figs. 91, 92.

This is a widely distributed species in all traverses but I and at all depths. Frequencies are less than 1 per cent.

VIRGULINA MEXICANA Cushman

(Plate 7, figures 7, 8)

Virgulina mexicana Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 120, pl. 23, fig. 8.

This species is widely distributed but does not occur consistently. It occurs in all traverses but I and IV deeper than 110 m. Frequencies are less than 1 per cent.

VIRGULINA PONTONI Cushman
(Plate 7, figure 9)

Virgulina pontoni Cushman, 1932, Contr. Cushman Lab. Foram. Res., vol. 8, pt. 1, p. 17, pl. 3, fig. 7.

This species has a scattered occurrence in all traverses but IX-X. Most occurrences are shoaler than 205 m. but some go to 530 m., with two deep occurrences in XI. Frequencies may be as high as 4 per cent, shoaler than 105 m.; deeper they are less than 1 per cent in most cases.

VIRGULINA PUNCTATA d'Orbigny
(Plate 7, figure 11)

Virgulina punctata d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, ''Foraminifères,'' p. 139, pl. 1, figs. 35, 36.

This species occurs in traverses III-VIII, X, XI. The most concentrated occurrence is shoaler than 150 m. but in V, X, XI specimens occur to a depth of 2550 m. Shoaler than 130 m. frequencies may be as high as 5 per cent; deeper they are less than 1 per cent.

VIRGULINA TESSELLATA Phleger and Parker
(Plate 7, figure 12)

Virgulina tessellata Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 19, pl. 9, figs. 15a, b, 16a, b.

This species occurs in traverses II, III, V-VIII, XI (once) from 375-2200 m. Shoaler than 1000 m. frequencies are usually less than 1 per cent but may be as high as 2 per cent; deeper than 1000 m. they reach a maximum of 15 per cent at 1262 m. in III.

BOLIVINA ALBATROSSI Cushman
(Plate 7, figure 13)

Bolivina albatrossi Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 31, pl. 6, fig. 4.

This species has a wide distribution, most commonly from 145 m. to 1900 m. but with scattered occurrences elsewhere. Frequencies may be as high as 10 per cent between 180 m. and 1300 m.

BOLIVINA BARBATA Phleger and Parker
(Plate 7, figure 14)

Bolivina barbata Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 13, pl. 6, figs. 12a, b, 13.

This species has a scattered occurrence in traverses I-III, V-VII. Most occurrences are shoaler than 205 m. but extend, mostly in V, to 530 m. Frequencies are variable reaching a maximum of 26 per cent in III at 155 m. In most cases deeper than 205 m. they are less than 1 per cent.

BOLIVINA FRAGILIS Phleger and Parker
(Plate 7, figure 15)

Bolivina fragilis Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 13, pl. 6, figs. 14, 23, 24a, b.

This species occurs in traverses V-IX, XI shoaler than 255 m. (3 exceptions). Frequencies from 1-5 per cent occur from 100-255 m. with one occurrence of 7 per cent in V at 146 m.

BOLIVINA GOËSII Cushman
(Plate 7, figure 16)

Bolivina goësii Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 34, pl. 6, fig. 5.

This species occurs in traverses VI-XI from 135 m. to 320 m. with a few scattered low-frequency occurrences deeper. Frequencies vary up to a maximum of 7 per cent in IX at 256 m.

BOLIVINA LANCEOLATA n. sp.
(Plate 7, figures 17, 18, 19, 20)

Test regularly tapered, initial end sometimes with a very short spine, compressed, periphery acute, sometimes with a very narrow keel, especially on the last-formed chambers; chambers uninflated, narrow, increasing gradually in height as added; sutures very slightly limbate, straight, at an angle of forty-five degrees with the horizontal; wall with medium-sized perforations except on clear areas on the inner and upper portion of the earlier chambers, sometimes with a few fine costae extending two-thirds of the way up the test; aperture narrow, keeled. Maximum length 0.6 mm.; width 0.14 mm.

Holotype from station 180, Lat. 29°04′ N, Long. 85°49′ W, at a depth of 183 m.

This species differs from *B. acerosa* Cushman in having a larger test, a higher ratio of breadth to length, and in having clear areas on the inner portions of the chambers. The initial portion of the test is less closely costate, but the costae when present extend farther up the test. It differs from *B. punctata* d'Orbigny in having costae, in being keeled on the later portion of the test rather than the earlier portion, and in the less curved sutures.

This species is widely distributed in traverses V-XI, deeper than 45 m. Frequencies are usually low but may be as high as 4 per cent.

BOLIVINA LOWMANI Phleger and Parker
(Plate 7, figure 21)

Bolivina lowmani Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 13, pl. 6, figs. 20a, b, 21.

This is a very common, widely distributed species in all traverses but I, at all depths. Frequencies are usually 1-5 per cent but reach a maximum of 8 per cent in VIII at 1730 m.

BOLIVINA MINIMA Phleger and Parker
(Plate 7, figures 22, 23)

Bolivina minima Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 14, pl. 6. figs. 22a, b, 25; pl. 7, figs. 1, 2.

This species is a very common one in traverses V-XI deeper than 110 m. with a single occurrence in IV at 55 m. Frequencies to a depth of 530 m. vary from 1-14 per cent; they do not exceed 5 per cent between 530 m. and 915 m. Deeper than this they are less than 1 per cent.

BOLIVINA ORDINARIA Phleger and Parker
(Plate 7, figure 24)

Bolivina simplex Phleger and Parker, 1951 (not *B. interjuncta* Cushman var. *simplex* Cushman and Renz, 1941), Mem. Geol. Soc. America, vol. 46, pt. 2, p. 14, pl. 7, figs. 4-6.

Bolivina ordinaria Phleger and Parker, 1952, Contr. Cushman Found. Foram. Res., vol. 3, pt. 1, p. 14.

This species is widely distributed in all traverses but I and IV deeper than 115 m. (one exception). The most consistent distribution is not deeper than 1800 m. but there are scattered occurrences deeper. Frequences are variable reaching a maximum of 19 per cent in III at 205 m.

BOLIVINA PAULA Cushman and Cahill
(Plate 7, figure 26)

Bolivina paula Cushman and Cahill, 1932, in Cushman and Ponton, Bull. Florida State Geol. Surv. vol. 9, p. 84, pl. 12, figs. 6a, b.

This species is reported from the Recent in the North Atlantic (Phleger, *et al*, 1953, p. 35) in displaced faunas from shallower water. Other reports are from the Miocene of the eastern United States.

It has a scattered occurrence at all depths in traverses II, V-XI. Frequencies are less than 1 per cent.

BOLIVINA PULCHELLA PRIMITIVA Cushman
(Plate 7, figure 36)

Bolivina pulchella (d'Orbigny) var. *primitiva* Cushman, 1930, Bull. Florida State Geol. Surv., vol. 4, p. 47, pl. 8, figs. 12a, b.

No specimens of typical *B. pulchella* occur in this area.

Occurrences are in traverses II, IV-XI at all depths. Frequencies are less than 1 per cent in most cases.

BOLIVINA PUSILLA Schwager
(Plate 7, figure 31)

Bolivina pusilla Schwager, 1866, Novara-Exped. Geol. Theil., vol. 2, p. 254, pl. 7, fig. 101.

Specimens are the same size as those described by Schwager (0.35 mm. in length) but smaller than those observed in the North Atlantic by Phleger *et al* (1953, p. 36) which have a maximum length of 0.54 mm.

There are three shallow occurrences at less than 250 m. but the species usually occurs deeper than 1300 m. in traverses II, III, V, VI, VII-XI. Frequencies are less than 1 per cent except in V where they reach a maximum of 2 per cent.

BOLIVINA STRIATULA SPINATA Cushman
(Plate 7, figure 29)

Bolivina striatula Cushman var. *spinata* Cushman, 1936, Spec. Publ. no. 6, Cushman Lab. Foram. Res., p. 59, pl. 8, figs. 9a, b.

The types of *B. striatula* have not been studied but a comparison with specimens of that species from shallow water of the San Antonio Bay region off Texas show that the spinate form should perhaps be given specific rank. It is less compressed, more striate and has an initial spine. Included here with typical specimens are some that are narrower and less strongly striated. Typical specimens seem to grade into this variant especially in the region to the east of traverse V.

With two exceptions the distribution is shoaler than 240 m. in traverses I, III-VIII. Frequencies vary up to a maximum of 5 per cent.

BOLIVINA SUBAENARIENSIS MEXICANA Cushman

(Plate 7, figure 33)

Bolivina subaenariensis Cushman var. *mexicana* Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 47, pl. 8, fig. 1.

The chief distribution is in traverses III, V-IX from 100 m. to 370 m. but there are scattered occurrences to 35 m. shoaler and 3250 m. deeper; traverses II, IV, X, XI have scattered occurrences. The highest frequencies are between 100 m. and 270 m. reaching a maximum of 32 per cent in III at 155 m.

BOLIVINA SUBSPINESCENS Cushman

(Plate 7, figures 30, 35)

Bolivina subspinescens Cushman, 1922, Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 48, pl. 7, fig. 5.

This species varies, as it does in the northwestern Gulf of Mexico, in the number of spines ornamenting the test and in the amount of undercutting of the chambers.

It is widely distributed in all traverses except I at all depths. Frequencies do not exceed 5 per cent.

BOLIVINA TRANSLUCENS Phleger and Parker

(Plate 7, figure 34)

Bolivina translucens Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 15, pl. 7, figs. 13, 14a, b.

This species occurs in traverses II, III, V-XI deeper than 145 m. The distribution is rather scattered and does not exceed 1 per cent in frequency.

BOLIVINA sp.

(Plate 7, figure 25)

This species although fairly widely distributed in the area never is very common. It is smaller, with less coarse perforations than *B. seminuda* Cushman, but in other respects is quite similar to that species.

It occurs in traverses VI-XI deeper than 420 m. Frequencies are less than 1 per cent.

LOXOSTOMUM ABRUPTUM Phleger and Parker

(Plate 7, figure 32)

Loxostomum truncatum Phleger and Parker, 1951 (not Finlay, 1947), Mem. Geol. Soc. America, vol. 46, pt. 2, p. 17, pl. 7, figs. 15-19.

Loxostomum abruptum Phleger and Parker, 1952, Contr. Cushman Found. Foram. Res., vol. 3, pt. 1, p. 14.

The resemblance of this species to *Bolivina minuta* Natland has been pointed out by Phleger *et al* (1953, p. 35). A study of additional specimens from the California coast shows that Natland's species is more regular with less highly raised sutures. The thicker, more twisted specimens mentioned by Phleger and Parker (1951) do not appear in the California material. The specimens from the Atlantic deep-sea cores are of this type.

The species occurs in all traverses but I and IV but most consistently in VI-XI. Most occurrences are deeper than 445 m. though there are scattered occurrences deeper than 100 m. Deeper than 580 m. frequencies may reach a maximum of 3 per cent; shoaler they are less than 1 per cent.

RECTOBOLIVINA ADVENA (Cushman)

(Plate 7, figure 27)

Siphogenerina advena Cushman, 1922, Carnegie Instit. Washington, Publ. 311, p. 35, pl. 5, fig. 2.

In referring this and the following species to the genus *Rectobolivina,* rather than to *Siphogenerina* as has been done by many authors, I am following the analyses of the two genera given by Hofker (1951 b, pp. 116, 232). The differences in internal structure seem to be borne out by differences in the external characters of the tests: *Rectobolivina* being compressed at least in the early portion of the test and usually throughout, *Siphogenerina* being often cylindrical, almost invariably non-compressed and costate. It seems probable that further analysis of the internal structure and chamber arrangement of the various species assigned to these genera will establish these external characters.

R. advena occurs in traverses IV-VIII, IX (once), XI (once) to a depth of 185 m. There are 3 deeper occurrences. Frequencies are usually less than 1 per cent.

RECTOBOLIVINA DIMORPHA (Parker and Jones)
(Plate 7, figure 37)

Uvigerina (*Sagrina*) *dimorpha* Parker and Jones, 1865, Philos. Trans. Roy. Soc. London, vol. 155, p. 364, pl. 18, fig. 18.

The reasons for referring this species to *Rectobolivina* are given under the previous species.

It occurs in traverses VI-VIII with single occurrences in IX and XI. The depth range is 345 m. to 1400 m. Frequencies are less than 1 per cent.

REUSSELLA ATLANTICA Cushman
(Plate 7, figure 28)

Reussella spinulosa (Reuss) var. *atlantica* Cushman, 1947, Contr. Cushman Lab. Foram. Res., vol. 23, pt. 4, p. 91, pl. 20, figs. 6, 7.

This species occurs in traverses IV-IX, XI to a depth of 235 m. There are two probably displaced occurrences deeper than 900 m. Frequencies reach a maximum of 8 per cent in V at 71 m.

UVIGERINA AUBERIANA d'Orbigny
(Plate 7, figure 38; Plate 8, figure 1)

Uvigerina auberiana d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 106, pl. 2, figs. 23, 24.

This and the following species are retained in the genus *Uvigerina*. There is some question in my mind of the necessity or practicality of the genera set up by Hofker (1951b) subdividing this genus. His genus *Alluvigerina* should be placed in the synonymy under *Uvigerina* since the two have the same genotype: *U. pigmea* d'Orbigny. Those interested in the subdivisions into which the Gulf of Mexico forms should be placed according to the Hofker classification will probably find this information in his forthcoming paper on the West Indian fauna.

As pointed out by Phleger *et al* (1953, p. 37), *U. auberiana* shows great variation in size. The species was described as 0.33 mm. in length by d'Orbigny. Gulf of Mexico specimens range from 0.30 mm.-1.0 mm.

This species occurs in traverses II, V-XI deeper than 250 m. Frequencies are usually less than 1 per cent. There is one occurrence of 9 per cent, and several between 1 and 3 per cent in traverses IX-XI.

UVIGERINA FLINTII Cushman
(Plate 8, figure 2)

Uvigerina flintii Cushman, 1923, Bull. U. S. Nat. Mus., vol.104, pt. 4, p. 165, pl. 42, fig. 13.

This species occurs in traverses VI-IX, XI from 85 m. to 420 m. Frequencies are never higher than 5 per cent.

UVIGERINA HISPIDO-COSTATA Cushman and Todd
(Plate 8, figure 3)

Uvigerina hispido-costata Cushman and Todd, 1945, Spec. Publ. no. 15, Cushman Lab. Foram. Res., p. 51, pl. 7, figs. 27, 31.

This species occurs in traverses VI-X from 220 m. to 1000 m. Frequencies vary up to 13 per cent.

UVIGERINA LAEVIS Goës
(Plate 8, figure 4)

Uvigerina auberiana Goës, 1882 (not d'Orbigny, 1839), Kongl. Svensk. Vet. Akad. Handl., vol. 19, no. 4, p. 60, pl. 4, figs. 71-74.

Uvigerina auberiana d'Orbigny var. *laevis* Goës, 1896, Bull. Mus. Comp. Zool., vol. 29, p. 51.

This species has been raised to specific rank as there seems to be no close relationship to *U. auberiana*. The wall of the test is much less rugose, the chambers less inflated and more elongate in shape, and the whole test relatively more elongate. Gulf of Mexico specimens have a maximum length of 0.6 mm. The maximum length given by Goës is 1.0 mm.

The distribution is in traverses V-XI with a single occurrence in IV. With a single exception occurrences are deeper than 80 m. The highest frequencies are between 160 and 275 m. reaching a maximum of 9 per cent. Shoaler than 90 m. and deeper than 915 m., frequencies are less than 1 per cent.

UVIGERINA PARVULA Cushman
(Plate 8, figure 6)

Uvigerina peregrina Cushman var. *parvula* Cushman, 1923, Bull. U. S. Nat. Mus., vol. 104, pt. 4, p. 168, pl. 42, fig. 11.

It is possible that more than one form has been included here in the population counts. There is considerable variation in the character of the costae which are much more numerous and finer in some specimens than in others. All these forms, however, are distinct from *U. peregrina* which usually is much larger, with higher plate-like costae, frequenly broken up into spines in the upper part of the test.

This species occurs in traverses III-IX, XI to a depth of 445 m. except in V where it extends to a depth of 914 m. Shoaler than 290 m. the frequencies are highest with a maximum of 9 per cent; deeper, they are usually less than 1 per cent.

UVIGERINA PEREGRINA Cushman
(Plate 8, figure 5)

Uvigerina peregrina Cushman, 1923, Bull. U. S. Nat. Mus., vol. 104, pt. 4, p. 166, pl. 42, figs. 7-10.

The Gulf of Mexico specimens are identical to topotypes from the northeastern coast of the United States.

This is a widely distributed species in all traverses but I and IV deeper than 200 m. (2 exceptions). Frequencies are relatively high to a depth of 1600 m. reaching a maximum of 25 per cent at 1144 m. in VI, although they are usually less than 20 per cent.

ANGULOGERINA BELLA Phleger and Parker
(Plate 8, figure 7)

Angulogerina bella Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 12, pl. 6, figs. 7, 8.

This species occurs in traverses III-V, VII, VIII to a depth of 235 m. In X and XI there are 3 occurrences deeper than 940 m. probably representing displaced specimens. Most frequencies are less than 1 per cent.

ANGULOGERINA JAMAICENSIS Cushman and Todd
(Plate 8, figure 8)

Angulogerina jamaicensis Cushman and Todd, 1945, Spec. Publ. no. 15, Cushman Lab. Foram. Res., p. 53, pl. 8, fig. 3.

Specimens were compared with the types by Miss Ruth Todd and found to be identical. The species has not been reported hitherto from Recent sediments.

It occurs in traverses I, IV-IX, XI with the chief occurrence in V-VII. The greatest abundance is shoaler than 150 m. but there are occurrences to a depth of 1750 m. Most frequencies are less than 1 per cent but a maximum of 4 per cent is reached shoaler than 150 m.

TRIFARINA BRADYI Cushman

(Plate 8, figure 9)

Trifarina bradyi Cushman, 1923, Bull. U. S. Nat. Mus., vol. 104, pt. 4, p. 99, pl. 22, figs. 3-9.

This species has a wide distribution in traverses V-XI at all depths. The most consistent occurrence is from 140 to 2150 m. Frequencies are variable reaching a maximum in IX of 8 per cent. Shoaler than 255 m. and deeper than 1900 m. they are always less than 1 per cent.

Family ROTALIIDAE

SPIRILLINA VIVIPARA Ehrenberg

(Plate 8, figures 15, 16)

Spirillina vivipara Ehrenberg, 1843 (1841), Abhandl. k. Akad. Wiss. Berlin, Theil. 1, pp. 323, 422, pl. 3, sec. 7, fig. 41.

This species occurs in traverses VI-VIII, XI to a depth of 285 m. There are three single occurrences, probably of displaced specimens, deeper than 914 m. in III, IX and X. All frequencies are less than 1 per cent.

CONORBINA ORBICULARIS (Terquem)

(Plate 8, figures 13, 14)

Rosalina orbicularis Terquem, 1876, Ess. Anim. Plage Dunkerque, pt. 2, p. 75, pl. 9, figs. 4a, b.

This species has a scattered occurrence in traverses VI-VIII, XI to a depth of 160 m., except for one occurrence at 225 m. Frequencies are less than 1 per cent.

"DISCORBIS" BULBOSA n. sp.

(Plate 8, figures 10, 11, 12)

Test small, globose, with a low spire, ventrally concave with an open umbilicus; chambers 8-12, 4 in the last-formed whorl, inflated; sutures curved, depressed; wall thin, often translucent, with coarse perforations; aperture simple, a high arch at the base of the last-formed chamber from the edge of the previous chamber to the periphery. Maximum diameter 0.25 mm.; thickness 0.18 mm.

Holotype from station 220, Lat. 29°49′ N, Long. 88°21′ W, at a depth of 37 m.

This species is referred to *Discorbis* pending further investigation of that genus and related ones. It is apparently not referable to any described genus as presently understood. It differs from *"D." subglobosa* Cushman in having 4 chambers in the last-formed whorl instead of 5, and in the higher spire.

"D." bulbosa occurs in traverses IV-VIII, XI to a depth of 205 m. Shoaler than 100 m. frequencies may be as high as 2 per cent; deeper, they are less than 1 per cent.

ROSALINA BERTHELOTI d'Orbigny

(Plate 8, figures 22, 23)

Rosalina bertheloti d'Orbigny, 1839, in Barker-Webb and Berthelot, Hist. Nat. Îles Canaries, vol. 2, pt. 2, "Foraminifères," p. 135, pl. 1, figs. 28-30 (*R. berthelotiana* in expl. of plate).

Hofker (1951a) has made this species the genotype of his genus *Discopulvinulina.* Since he later (Hofker, 1951b) includes in this genus *Rosalina globularis* d'Orbigny, designated as the genotype of *Rosalina* by Galloway and Wissler (1927, p. 62), *Discopulvinulina* becomes a synonym of *Rosalina* d'Orbigny, 1826.[1] *Rosalina* has been made a synonym of the genus *Discorbis* by many authors. As pointed out by Galloway and Wissler and later by Brotzen (1942, p. 15), the character of *Discorbis vesicularis* (Lamarck), the genotype of the genus, is very uncertain.

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[1] This presupposes that Hofker is correct in placing *R. bertheloti* and *R. globularis* in the same genus. This question is discussed by Hornibrook and Vella (1954, The Micropaleontologist, vol. 8, no. 1, p. 26).

This in itself is not sufficient to discard the name *Discorbis* as they maintain, but the figures of *D. vesicularis* obviously do not represent a form similar to the majority of species placed in that genus. Hence an entirely wrong concept of the genus *Discorbis* has been erected on a very shaky structure. It seems best not to speculate further on the real character of *D. vesicularis* and its place in the classification until the type is studied. The recent definition of *Discorbis* given by Bermudez (1952, p. 32) is not borne out by the figures of *D. vesicularis*. *Rosalina* appears to be closely related to *Cibicidina* Bandy and *Hanzawaia* Asano.

R. bertheloti occurs in traverses IV-VI, VIII-XI chiefly between the depths of 100 m. and 265 m. There are a few shoaler occurrences, and two deeper than 900 m. probably representing displaced specimens. Frequencies are usually less than 1 per cent occasionally as high as 3 per cent.

ROSALINA cf. CONCINNA (H. B. Brady)
(Plate 8, figures 17, 18)

Discorbina concinna H. B. Brady, 1884, Rept. Voy. CHALLENGER, Zool. vol. 9, p. 646, pl. 90, figs. 7, 8.

The specimens are very similar to Brady's figured ones and may be identical. They appear, however, to be bigger and more finely perforate, having a maximum diameter of 0.36 mm. Brady reports a diameter of 0.25 mm. The species differs from *R. columbiensis* (Cushman) in being less coarsely perforate, and having a more sharply angled periphery.

This species occurs chiefly in traverses IV-VIII, X, XI with a few occurrences in II, III, IX. It is abundant to a depth of 180 m. but has a scattered occurrence deeper. To a depth of 30 m. frequencies may be as high as 26 per cent, then decreasing until deeper than 235 m. where they are less than 1 per cent.

ROSALINA FLORIDANA (Cushman)
(Plate 8, figures 19, 20)

Discorbis floridanus Cushman, 1922, Publ. no. 311, Carnegie Instit. Washington, p. 39, pl. 5, figs. 11, 12.

This species occurs in traverses IV-VIII, IX (once), XI to a depth of 285 m. except in V where it extends to 915 m. A maximum frequency of 15 per cent occurs at the inner end of VI but in most cases frequencies do not exceed 5 per cent to a depth of 110 m.; deeper they are less than 1 per cent.

ROSALINA FLORIDENSIS (Cushman)

(Plate 8, figures 28, 29)

Discorbis bertheloti (d'Orbigny) var. *floridensis* Cushman, 1930, *in* Cushman and Jarvis, Journ. Pal., vol. 4, no. 4, p. 364, pl. 33, figs. 13a-c; 1931, Bull. U. S. Nat. Mus., vol. 104, pt. 8, p. 17, pl. 3, figs. 3-5.

Cushman's figured specimens (1931) are apparently identical with ours. The figures of the fossil species (1930) appear more finely perforate but the type has not been examined.

The distribution is scattered in traverses V-IX, XI from 40 to 180 m. with frequencies mostly less than 1 per cent.

ROSALINA PARKERAE (Natland)

(Plate 8, figures 24, 25)

Discorbis parkeri Natland, 1950, Mem. Geol. Soc. America, vol. 43, pt. 4, p. 27, pl. 6, figs. 11a-c.

Doubt is expressed by Phleger *et al* (1953, p. 40) of the validity of this species because suites of *R. williamsoni* (Parr) from the North Atlantic include specimens of this type. In the Gulf of Mexico, however, the specimens are all similar to Natland's species and do not range into the typical form of *R. williamsoni.*

R. parkerae occurs in all traverses but I-III at all depths. Frequencies are usually less than 1 per cent.

ROSALINA SUEZENSIS (Said)

(Plate 8, figures 21, 26, 27)

Discorbis suezensis Said, 1949, Spec. Publ. 26, Cushman Lab. Foram. Res., p. 36, pl. 3, fig. 34.

This species is similar to *R. candeiana* d'Orbigny but is much more finely perforate. Gulf of Mexico specimens resemble topotypes of *R. suezensis* from the Gulf of Suez. The specimens referred by Phleger and Parker (1951, p. 20) to *Discorbis candeiana* should be referred to Said's species.

R. suezensis occurs in traverses III-IX, XI (once). The most concentrated distribution is to 320 m. but there is scattered occurrence mostly in IX to 914 m. There are two occurrences deeper than 2300 m. Frequencies between 1 and 6 per cent occur to 200 m.; deeper, they are usually less than 1 per cent.

VALVULINERIA HUMILIS (H. B. Brady)

Truncatulina humilis H. B. Brady, 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 665, pl. 94, figs. 7a-c.

This species is omitted from the population counts due to its small size and superficial resemblance to juvenile planktonic specimens. It is present at many deep-water stations in the area.

VALVULINERIA MEXICANA n. sp.

(Plate 9, figures 1, 2, 3)

Valvulineria cf. *araucana* (d'Orbigny), Phleger and Parker, 1951 (not *Rosalina araucana* d'Orbigny, 1839), Mem. Geol. Soc. America, vol. 46, pt. 2, p. 25, pl. 13, figs. 7a, b, 8a, b.

Test medium in size, biconvex but more so on the ventral side, periphery rounded; chambers 6-7 in the last-formed whorl of the adult, usually 13 in all excluding the proloculus, increasing fairly rapidly in size as added, later ones slightly inflated on the dorsal side, very much so on the ventral especially toward the umbilicus where they often have a bulbous protuberance, the last-formed chamber with a large flap extending over the umbilical area, the flap of the next-to-last chamber often visible below and to one side of it, the flaps of earlier chambers occasionally visible; sutures narrow but broader in the early portion, curved on the dorsal side, somewhat less so on the ventral, later ones slightly depressed on the dorsal side, more so on the ventral especially toward the umbilicus; wall thin, rather coarsely perforate, the perforations much less closely spaced on the early chambers and often only on the outer part of the chambers of the ventral side; aperture below the extended flap of the chamber. Maximum diameter 0.4 mm.

Holotype from station 31, Lat. 28°56′ N, Long. 88°46′ W, at a depth of 373 m.

This species resembles *V. nipponica* Ishizaki but differs in the non-keeled periphery of the early portion of the last-formed whorl and in the sutures of the early portion not being raised.

It is smaller than *V. palmerae* Cushman and Todd, with a less broadly rounded periphery, less inflated chambers, and less closely spaced perforations. The species referred by Phleger *et al* (1953, p. 40) to *V.* cf. *araucana* is not referable to *V. mexicana.*

This species has a very scattered distribution in traverses II, III, VII-IX, XI deeper than 75 m. Frequencies are usually less than 5 per cent but reach a maximum of 11 per cent in III at 400 m.

VALVULINERIA MINUTA n. sp.
(Plate 9, figures 4, 5, 6)

Test small, concavo-convex with a rounded periphery and a deep umbilicus on the ventral side; chambers 7 in the last-formed whorl, 11-13 in all excluding the proloculus, increasing gradually in size as added, slightly inflated, somewhat more so on the ventral side; the last-formed chamber with a small, narrow flap extending a short way into the umbilicus; sutures narrow, very slightly curved, later ones slightly depressed on the dorsal side, somewhat more so on the ventral; wall thin, finely perforate, aperture extending from the periphery, partially concealed by the chamber-flap. Maximum diameter 0.3 mm.

Holotype from station 184, Lat. 28°45′ N, Long. 86°02.5′ W, at a depth of 274 m.

This species differs from *V. araucana* (d'Orbigny) in its somewhat less convex dorsal side, deeper umbilicus, fewer chambers with less curving sutures on the dorsal side, and finer perforations.

V. minuta occurs in traverses V-XI at all depths deeper than 75 m. and in II and IV at a few scattered localities. All frequencies are less than 1 per cent.

GYROIDINOIDES SOLDANII ALTIFORMIS (R. E. and K. C. Stewart)
(Plate 9, figures 7,8)

Gyroidina soldanii d'Orbigny var. *altiformis* R. E. and K. C. Stewart, 1930, Journ. Pal., vol. 4, no. 3, p. 67, pl. 9, fig. 2.

This species occurs chiefly in traverses V-XI with single occurrences in II and III. With one exception all occurrences are deeper than 150 m. Frequencies are less than 1 per cent.

GYROIDINA NEOSOLDANII Brotzen
(Plate 9, figures 9, 10)

Rotalia soldanii H. B. Brady, 1884 (not *Gyroidina soldanii* d'Orbigny, 1826), Rept. Voy. CHALLENGER, Zool., vol. 9, p. 706, pl. 107, figs. 6, 7.

Gyroidina neosoldanii Brotzen, 1936, Sver. Geol. Unders., ser. C, no. 396, p. 158.

This species resembles *Gyroidinoides* in having its aperture extend into the umbilicus. In other respects it conforms more closely to *Gyroidina*. Specimens referred by Phleger *et al* (1953, p. 41) to *G. soldanii* var. are referable to *Gyroidinoides neosoldanii.*

The distribution is scattered in traverses III, VI, VIII-XI chiefly in IX-XI. All occurrences are deeper than 185 m. Frequencies are less than 1 per cent.

GYROIDINA ORBICULARIS d'Orbigny
(Plate 9, figures 13, 18)

Gyroidina orbicularis d'Orbigny, 1826, Ann. Sci. Nat., ser. 1, vol. 7, p. 278; Modèles, no. 13.

This is a widely distributed species in all traverses but I and IV, deeper than 165 m. Frequencies are less than 1 per cent to 585 m.; deeper, they are usually 1-5 per cent.

EPONIDES ANTILLARUM (d'Orbigny)
(Plate 9, figures 14, 15)

Rotalina antillarum d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 75, pl. 5, figs. 4-6.

This species has "sutural" foramina which according to Hofker (1951b) would place it in the genus *Gyroidina.* It is retained in *Eponides* for the reasons given under *E. repandus* (Fichtel and Moll).

E. antillarum occurs in traverses IV-VIII to a depth of 145 m. Frequencies are variable with a maximum of 9 per cent in V at 44 m.

EPONIDES POLIUS Phleger and Parker
(Plate 9, figures 11, 12)

Eponides polius Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 21, pl. 11, figs. 1a, b, 2a, b.

This species has "sutural" foramina which according to Hofker (1951b) would place it in *Gyroidina* (*vide E. repandus*).

It occurs in all traverses but I and IV deeper than 585 m. Frequencies vary to a maximum of 5 per cent except in II where they reach a maximum of 8 per cent at 2788 m.

EPONIDES REGULARIS Phleger and Parker
(Plate 9, figures 16, 17)

Eponides regularis Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 21, pl. 11, figs. 3a, b, 4a-c.

This species has "sutural" foramina which according to Hofker (1951b) would place it in the genus *Gyroidina* (*vide E. repandus*).

It occurs in traverses II, III, V-VII from 145 m. to 3000 m. Most frequencies are from 1-5 per cent but in III a maximum of 21 per cent occurs at 205 m.

EPONIDES REPANDUS (Fichtel and Moll)
(Plate 9, figures 27, 28)

Nautilus repandus Fichtel and Moll, 1803, Test. Micr., p. 35, pl. 3, figs. a-d.

Examination of specimens from the Mediterranean and Gulf of Mexico show that the foramina are "sutural" rather than "areal" as shown by Hofker (1951b, p. 332) for specimens from Siboga material. "Sutural" foramina according to Hofker are a characteristic of the genus *Gyroidina* as contrasted to *Eponides* whose foramina are "areal." Since *Eponides repandus* is the genotype of *Eponides*, Hofker's classification is not used here pending further study.

E. repandus occurs in traverses V-IX, XI, to a depth of 185 m. Most frequencies are less than 1 per cent, occasionally higher.

EPONIDES TUMIDULUS (H. B. Brady)
(Plate 9, figures 19, 24)

Truncatulina tumidula H. B. Brady, 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 666, pl. 95, figs. 8a-d.

This species occurs chiefly in traverses II, IX-XI with scattered occurrences in III, V, VI. Frequencies vary up to 5 per cent.

EPONIDES TURGIDUS Phleger and Parker
(Plate 9, figures 22, 23)

Eponides turgidus Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 22, pl. 11, figs. 9a, b.

This species has "sutural" foramina which according to Hofker's (1951b) classification would place it in the genus *Gyroidina* (*vide E. repandus*).

It is widely distributed in all traverses but I and IV at all depths. Frequencies shoaler than 175 m. are less than 1 per cent; 1-5 per cent mostly to 1500 m.; deeper than 1500 m. a maximum of 22 per cent is reached in III at 2388 m. and frequencies are often 5-20 per cent.

PSEUDOEPONIDES UMBONATUS (Reuss)
(Plate 9, figures 20, 21)

Rotalina umbonata Reuss, 1851, Zeitschr. deutsch. Geol. Ges., vol. 3, p. 75, pl. 5, figs. 35a-c.

Supplementary apertures are frequently observed on the dorsal side of the specimens but the ventral ones described by Uchio (1953, p. 157) are obscure. Small specimens possibly referable to *Eponides tenera* (H. B. Brady) are included with this species in the population counts. Supplementary apertures were not observed in these specimens.

These forms are widely distributed in all traverses but I and IV. Frequencies are less than 1 per cent to a depth of 875 m.; deeper they are often 1-5 per cent.

BUCCELLA HANNAI (Phleger and Parker)
(Plate 9, figures 25, 26)

Eponides hannai Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 21, pl. 10, figs. 11a, b, 12a, b, 13a, b, 14a, b.

This species occurs in traverses IV-VIII to a depth of 185 m. Frequencies to 40 m. are usually 1-2 per cent; deeper they are less than 1 per cent.

OSANGULARIA CULTUR (Parker and Jones)
(Plate 9, figures 29, 30)

Planorbulina cultur Parker and Jones, 1865, Philos. Trans. Roy. Soc. London, vol. 155, p. 421, pl. 19, fig. 1.

This species occurs in all traverses but I and IV deeper than 400 m. Frequencies are 1-5 per cent to a depth of 2000 m.; deeper they are usually less than 1 per cent.

"Rotalia" beccarii (Linné) variants

(Plate 10, figures 1, 2, 5, 6)

Nautilus beccarii Linné, 1758, Syst. Nat. ed. 10, p. 710.

The variants of this species are lumped together here as they are all confined to very shallow water in the area and do not show any individual distributions in the open-ocean environment represented here. A finer grid of sampling might reveal a more variable distribution.

The distribution is in traverses I-VIII shoaler than 125 m. At the inner ends of the traverses frequencies may be as high as 34 per cent but quickly reduce to 1-5 per cent, and in most cases deeper than 70 m. are less than 1 per cent.

"Rotalia" translucens Phleger and Parker

(Plate 10, figures 3, 7)

"Rotalia" translucens Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 24, pl. 12, figs. 11a, b, 12a, b.

This is a widely distributed species in all traverses but I. It usually occurs deeper than 220 m. but there are occurrences as shoal as 60 m. Frequencies from 220 to 735 m. are often 5-20 per cent with a maximum of 27 per cent. Deeper than 735 m. they do not exceed 5 per cent and decrease until deeper than 1700 m. where they are usually less than 1 per cent.

Höglundina elegans (d'Orbigny)

(Plate 10, figures 4, 8)

Rotalia (Turbulina) elegans d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 276, no. 54.

This is a widely distributed species in traverses II, V-XI deeper than 65 m. Frequencies are less than 1 per cent to a depth of 345 m.; 1-5 per cent deeper, with a few higher frequencies deeper than 1300 m. The maximum is 25 per cent in X at 2150 m.

SIPHONINA BRADYANA Cushman
(Plate 10, figures 9, 10)

Siphonina bradyana Cushman, 1927, Proc. U. S. Nat. Mus., vol. 72, art. 20, p. 11, pl. 1, figs. 4a-c.

This species occurs in traverses VI-XI from 45 m. to 650 m. The occurrence in X is a single one at 950 m. Most frequencies are less than 1 per cent.

SIPHONINA PULCHRA Cushman
(Plate 10, figures 11, 12)

Siphonina pulchra Cushman, 1919, Carnegie Instit. Washington, Publ. 291, p. 42, pl. 14, figs. 7a-c.

The distribution is chiefly in traverses V-IX, XI to a depth of 640 m. There is a single occurrence in II at 2000 m. probably representing displacement. Most frequencies are less than 1 per cent with a few as high as 2 per cent between 100 and 300 m.

CANCRIS OBLONGA (Williamson)
(Plate 10, figures 13, 14)

Rotalina oblonga Williamson, 1858, Rec. Foram. Great Britain, p. 51, pl. 4, figs. 98-100.

Included in the population counts with this species are specimens of *Cancris sagra* (d'Orbigny) (Plate 10, figures 15, 21). The two species appear to have the same overall distribution.

The distribution is in traverses I (once), IV-XI to a depth of 255 m. There are a few occurrences deeper than 915 m. in X and XI probably representing displaced specimens. Frequencies are less than 1 per cent except between 35 m. and 145 m. where they reach a maximum of 2 per cent.

Family AMPHISTEGENIDAE

ASTERIGERINA CARINATA d'Orbigny
(Plate 10, figures 16, 17)

Asterigerina carinata d'Orbigny, 1839, in De la Sagra, Hist. Phys. Pol. Nat. Cuba, "Foraminifères," p. 118, pl. 5, fig. 25; pl. 6, figs. 1, 2.

This species occurs in traverses IV-VIII, XI (once) to a depth of 185 m. Frequencies shoaler than 85 m. are high, reaching a maximum of 31 per cent although frequently much lower. Deeper than 100 m. they are usually less than 1 per cent.

AMPHISTEGINA spp.

It is probable that most, or all, of the specimens are referable to *A. lessonii* d'Orbigny but owing to the weathered condition of many of them it is impossible to be sure.

The distribution is in traverses IV-XI to a depth of 240 m. though the main occurrence is not deeper than 150 m. There are a few occurrences in XI deeper than 1700 m. probably representing displaced specimens. Frequencies shoaler than 200 m. vary to a maximum of 50 per cent although usually less than 20 per cent; deeper they are less than 1 per cent.

Family CASSIDULINIDAE

EPISTOMINELLA DECORATA (Phleger and Parker)
(Plate 10, figures 18, 19)

Pseudoparrella decorata Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 28, pl. 15, figs. 4a, b, 5a, b.

This is a deep-water species occurring in all traverses but I and IV usually deeper than 1000 m. though with a few occurrences as shoal as 820 m. and single occurrences at 155 m. and 600 m. Frequencies deeper than 1100 m. are high, usually over 5 per cent and reaching a maximum of 22 per cent.

EPISTOMINELLA EXIGUA (H. B. Brady)
(Plate 10, figures 22, 23)

Pulvinulina exigua H. B. Brady, 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 696, pl. 103, figs. 13, 14.

This is a widely distributed species in all traverses but I and IV deeper than 220 m. Frequencies are usually high especially between 550 m. and 960 m. where they reach a maximum of 16 per cent. Outside these limits they do not exceed 5 per cent and deeper than 1400 m. are often less than 1 per cent.

EPISTOMINELLA RUGOSA (Phleger and Parker)
(Plate 10, figures 24, 25)

Pseudoparrella rugosa Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 28, pl. 15, figs. 8a, b, 9a, b.

This species occurs chiefly in traverses V-XI, with single occurrences in II and III; deeper than 250 m. most frequencies are 1-4 per cent except in IX where they are 11 per cent at 320-421 m.

EPISTOMINELLA VITREA Parker
(Plate 10, figures 20, 26)

Epistominella vitrea Parker, *in* Parker, Phleger and Peirson, 1953, Spec. Publ. 2, Cushman Found. Foram. Res., p. 9, pl. 4, figs. 34-36, 40, 41.

Some of the specimens referred to *E. exigua* by Phleger and Parker (1951, p. 28) may be referable to *E. vitrea.*

This species is widely distributed in traverses III-XI with a single occurrence in II. It is found at all depths. Shoaler than 100 m. frequencies are variable reaching a maximum of 34 per cent; deeper, they are usually less than 1 per cent.

STETSONIA n. gen.

Genotype: *Stetsonia minuta* n. sp.

Test calcareous, perforate, slightly trochoid; almost completely involute; aperture elongate in the apertural face, in the plane of coiling, slightly ventral of the periphery.

This genus is closely related to *Epistominella* but differs in being almost completely involute. In the genotype one or two chambers of the second whorl are sometimes visible on the dorsal side. The genus is at present monotypic so that variations of the amount of test which may be evolute cannot be delimited here, except to say that the chambers are not all visible on the dorsal side, as in *Epistominella,* and probably that only a small amount of the second whorl might be visible. This genus is considered to have developed from *Epistominella* and is at present unknown as fossil.

STETSONIA MINUTA n. sp.
(Plate 10, figures 27, 28, 29)

Test small, compressed, with a narrowly rounded periphery; chambers 8 or 9 in the last-formed whorl, very slightly inflated; sutures slightly curved, slightly depressed; wall thin, somewhat translucent, finely perforate; aperture elongate, narrow, slightly ventral of the periphery, with a narrow lip. Maximum diameter: 0.18 mm.

Holotype from station 218, Lat. 29°40′ N, Long. 88°28.5′ W, at a depth of 42 m.

This species is usually completely involute, but occasionally one or two chambers of the second whorl are visible on the dorsal side. Its involute character differentiates it from species of the genus *Epistominella* to which it is most closely related.

This species occurs in all traverses but I at all depths. Frequencies are usually less than 1 per cent.

CASSIDULINA CARINATA Silvestri
(Plate 10, figure 30)

Cassidulina laevigata d'Orbigny var. *carinata* Silvestri, 1896, Accad. Pont. N. Lincei, Mem. 12, p. 104, pl. 2, fig. 10.

Gulf of Mexico specimens are very similar to those from the Pliocene of Siena, Italy, but have a larger clear area in the center. This is true also of specimens observed from the North Atlantic.

This species has a rather scattered occurrence in traverses III, V-X at all depths. Frequencies are variable up to a maximum of 17 per cent. They are usually much lower, not exceeding 5 per cent and often less than 1 per cent.

CASSIDULINA aff. CRASSA d'Orbigny
(Plate 10, figure 31)

Cassidulina crassa d'Orbigny, 1839, Voy. Amer. Mérid., vol. 5, pt. 5, "Foraminifères," p. 56, pl. 7, figs. 18-20.

The specimens found in this area are less compressed and more lobulate than that figured by Brady (1884, pl. 54, fig. 5). The species as it occurs in the northwestern Gulf of Mexico conforms more closely to Brady's interpretation of d'Orbigny's species.

The distribution is chiefly in traverses VI-XI, with a few occurrences in II, III, V, deeper than 135 m. Frequencies are usually less than 1 per cent, shoaler than 500 m. sometimes 1-4 per cent.

CASSIDULINA CURVATA Phleger and Parker
(Plate 11, figure 1)

Cassidulina curvata Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 26, pl. 14, figs. 5a, b.

This species occurs in traverses II (twice), V-XI, at all depths deeper than 60 m. except for one occurrence at 35 m. To a depth of 600 m. frequencies are usually 1-5 per cent; deeper, they are less than 1 per cent.

CASSIDULINA LAEVIGATA d'Orbigny
(Plate 11, figure 2)

Cassidulina laevigata d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 282, no. 1, pl. 15, figs. 4, 5; Modèles, no. 41.

This species has a scattered distribution in traverses V-VIII, X, XI. Frequencies are less than 1 per cent except for a few shoaler than 150 m. which reach a maximum of 6 per cent.

CASSIDULINA NEOCARINATA Thalmann
(Plate 11, figure 3)

Cassidulina laevigata d'Orbigny var. *carinata* Cushman, 1922, (not Silvestri, 1896), Bull. U. S. Nat. Mus., vol. 104, pt. 3, p. 124, pl. 25, figs. 6, 7.

Cassidulina neocarinata Thalmann, 1950, Contr. Cushman Found. Foram. Res., vol. 1, pts. 3, 4, p. 44.

This species occurs in traverses II, V-XI, deeper than 75 m. Between 120 and 600 m. frequencies are usually 1 per cent or more reaching a maximum of 11 per cent. Deeper than 600 m. they are usually less than 1 per cent. The occurrences deeper than 950 m. are very scattered.

CASSIDULINA SUBGLOBOSA H. B. Brady and variants
(Plate 11, figures 4, 5, 6, 7, 8, 9)

Cassidulina subglobosa H. B. Brady, 1881, Quart. Journ. Micr. Sci., n. s., vol. 21, p. 60; 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 430, pl. 54, figs. 17a-c.

There are several variants present in the area, as well as the typical form (Pl. 11, figs. 4, 5). A small compressed variant (Pl. 11, fig. 6) is similar to var. *depressa* Asano and Nakamura, and has a widespread distribution. A small globose form (Pl. 11, figs. 8, 9) with a sharply curved aperture in the juvenile specimens resembles var. *horizontalis* Cushman and Renz. This form and the large typical specimens seem to occur in deep water only. All these variants appear to merge into one another, and since in counting it was impossible to always differentiate them accurately it seemed best not to attempt to do so.

This is a very abundant, widely distributed group occurring in all traverses but I although chiefly in V-XI. Deeper than about 80 m. frequencies are usually between 5 and 20 per cent (maximum 23 per cent); deeper than about 2300 m. frequencies are often less than 5 per cent.

CASSIDULINOIDES TENUIS Phleger and Parker
(Plate 11, figure 14)

Cassidulinoides tenuis Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 27, pl. 14, figs. 14a, b, 15-17.

This species occurs in traverses II (twice), VI-XI, deeper than 255 m. Deeper than 1100 m. occurrences are very scattered. All frequencies are less than 1 per cent.

EHRENBERGINA SPINEA Cushman
(Plate 11, figure 12)

Ehrenbergina spinea Cushman, 1935, Smithsonian Misc. Coll., vol. 91, no. 21, p. 8, pl. 3, figs. 10, 11.

This species occurs only in traverses IX-XI. Four occurrences are between 135 m. and 255 m., and two are at 914 m. and 950 m. The occurrences between 139 m. and 155 m. have frequencies of 3-6 per cent, the others are less than 1 per cent. The deep occurrences probably represent displaced specimens.

Family CHILOSTOMELLIDAE

ROTAMORPHINA LAEVIGATA (Phleger and Parker)
(Plate 11, figures 10, 11)

Valvulineria laevigata Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 25, pl. 13, figs. 11a, b, 12a, b.

Eponides exigua Cushman, 1931 (not *Pulvinulina exigua* H. B. Brady, 1884), Bull. U. S. Nat. Mus., vol. 104, pt. 8, p. 44, pl. 10, figs. 1, 2.

Valvulineria sp. Parker, 1948, Bull. Mus. Comp. Zool., vol. 100, no. 2, p. 240, pl. 4, figs. 13a, b.

This species occurs in all traverses but I and IV, but chiefly in V-XI, deeper than 100 m. Frequencies are usually less than 1 per cent.

CHILOSTOMELLA OOLINA Schwager
(Plate 11, figure 15)

Chilostomella oolina Schwager, 1878, Boll. Com. Geol. Ital., vol. 9, p. 527, pl. 1, fig. 16.

This species occurs in traverses II, III, V-VIII, X (twice), XI (once), deeper than 125 m. Frequencies are usually less than 1 per cent but occasionally as high as 2 per cent.

SEABROOKIA EARLANDI Wright
(Plate 11, figure 13)

Seabrookia earlandi Wright, 1891, Proc. Roy. Irish Acad., ser. 3, vol. 1 (1889-91), no. 4, p. 477, pl. 20, figs. 6, 7.

This species occurs in traverses IV (once), V-XI at all depths but chiefly 100-2300 m. Frequencies are less than 1 per cent.

PULLENIA BULLOIDES (d'Orbigny)
(Plate 11, figure 17)

Nonionina bulloides d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 293; 1846, Foram. Bass. Tert. Vienne, p. 107, pl. 5, figs. 9, 10.

This is a widely distributed species in all traverses but I and IV, deeper than 145 m. Shoaler than 900 m. frequencies are less than 1 per cent; deeper, they may be as high as 2 per cent.

PULLENIA QUINQUELOBA (Reuss)
(Plate 11, figure 16)

Nonionina quinqueloba Reuss, 1851, Zeitschr. deutsch. Geol. Ges., vol. 3, p. 71, pl. 5, fig. 31.

This species occurs in all traverses but I and IV, deeper than 100 m. Shoaler than 530 m. all frequencies are less than 1 per cent; deeper, they may be as high as 2 per cent.

PULLENIA sp.
(Plate 11, figures 20, 24)

This is a small species with a maximum diameter of 0.3 mm. It is compressed with a narrowly rounded periphery and has seven chambers in the last-formed whorl. It most closely resembles *P. trinitatensis* Cushman and Stainforth but is smaller and more compressed, especially in the initial portion. It is probably a new species but there is not sufficient material to describe it adequately.

It occurs in traverses II, III (once), VI (once), VII (once), VIII-XI, deeper than 960 m. Frequencies are less than 1 per cent except in II where they are 2-3 per cent from 1900 m. to 2800 m.

SPHAEROIDINA BULLOIDES d'Orbigny
(Plate 11, figure 18)

Sphaeroidina bulloides d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 267, no. 1; Modèles, no. 65.

This is a widely distributed species in all traverses but I and IV, deeper than 100 m. Between 180 m. and 1000 m. frequencies are usually 1-5 per cent but reach a maximum of 9 per cent in II at 314 m. Outside these limits they are less than 1 per cent.

SPHAEROIDINA COMPACTA Cushman and Todd
(Plate 11, figure 19)

Sphaeroidina compacta Cushman and Todd, 1949, Contr. Cushman Lab. Foram. Res., vol. 25, pt. 1, p. 19, pl. 4, figs. 14a, b.

This species has a very scattered distribution from 120 m. to 3250 m. in traverses II, VI, VIII, X, XI. Frequencies are less than 1 per cent.

Family ANOMALINIDAE

ANOMALINOIDES MEXICANA n. sp.
(Plate 11, figures 21, 22, 23)

Test small, biconvex, involute, ratio of width to length 3: 4, periphery broadly rounded, non-lobulate in early portion, slightly lobulate in later portion of the test; chambers 7 or 8 in last-formed whorl, non-inflated in the early portion, last-formed one or two in the adult slightly inflated; sutures narrow, flush with the test except for the last ones in the adult which are slightly depressed, slightly curved; wall thin, somewhat translucent, finely but conspicuously perforate; aperture extending from the umbilicus to the periphery on the ventral side, with a distinct lip. Maximum diameter 0.4 mm.

Holotype from station 184, Lat. 28°45′ N, Long. 86°02.5′ W, at a depth of 274 m.

This species has fewer chambers than *A. plummerae* Brotzen, is more finely perforate, has non-elevated sutures in the early portion of the test, and is not round in outline.

A. mexicana occurs in traverses II (once), III (once), V-X, XI (once) deeper than 220 m. Frequencies are less than 1 per cent.

PLANULINA ARIMINENSIS d'Orbigny
(Plate 11, figure 27, 30)

Planulina ariminensis d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 280, no. 1, pl. 14, figs. 1-3 bis; Modèles, no. 49.

This species occurs in traverses V (once), VI-XI from 155 m. to 2550 m. Deeper than 740 m. the occurrence is very scattered. Frequencies are usually less than 1 per cent; the maximum frequency is 4 per cent.

PLANULINA EXORNA Phleger and Parker
(Plate 11, figures 28, 29)

Planulina exorna Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 32, pl. 18, figs. 5a, b, 6a, b, 7a, b, 8a, b.

This is a very abundant shallow-water species. It occurs in traverses II (once), IV-IX, XI (once) to a depth of 255 m., except in VIII where it extends to 365 m. At less than 100 m. frequencies are greatest reaching a maximum of 43 per cent, but usually less than 20 per cent. They decrease seaward until deeper than 150 m. where they are less than 1 per cent.

PLANULINA FOVEOLATA (H. B. Brady)
(Plate 11, figures 25, 26)

Anomalina foveolata H. B. Brady, 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 674, pl. 94, figs. 1a-c.

This species occurs in traverses II (once), V-IX, XI, from 75 m. to 345 m. except in V where it extends to 530 m. Frequencies from 120 m. to 270 m. may be as high as 5 per cent; elsewhere they are less than 1 per cent.

LATICARININA PAUPERATA (Parker and Jones)
(Plate 12, figure 3)

Pulvinulina repanda var. *menardii* subvar. *pauperata* Parker and Jones, 1865, Philos.Trans., Roy. Soc. London, vol. 155, p. 395, pl. 16, figs. 50, 51.

This species occurs in all traverses but I and IV, deeper than 255 m. Most frequencies are less than 1 per cent but deeper than 915 m. they may be as high as 2 per cent.

CIBICIDES CORPULENTUS Phleger and Parker

(Plate 12, figures 4, 8)

Cibicides robustus Phleger and Parker, 1951 (not Le Calvez, 1949), Mem. Geol. Soc. America, vol. 46, pt. 2, p. 31, pl. 17, figs. 1a, b, 2a, b, 3a, b, 4a, b.

Cibicides corpulentus Phleger and Parker, 1952, Contr. Cushman Found. Foram. Res., vol. 3, pt. 1, p. 14.

This species occurs in all traverses but I and IV, chiefly in V-XI, from 100 m. to 1800 m. There is a single occurrence at about 3000 m. Frequencies are less than 1 per cent.

CIBICIDES DEPRIMUS Phleger and Parker

(Plate 12, figures 1, 2)

Cibicides deprimus Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 29, pl. 15, figs. 16a, b, 17a, b.

This species occurs in traverses IV-XI to a depth of 915 m. with a few scattered occurrences to 2600 m. Shoaler than 150 m. frequencies are usually 1-5 per cent but reach a maximum of 19 per cent; deeper, they are less than 1 per cent.

CIBICIDES aff. FLORIDANUS (Cushman)

(Plate 12, figures 5, 9)

Truncatulina floridana Cushman, 1918, Bull. U. S. Geol. Surv., vol. 676, p. 62, pl. 19, fig. 2.

This species as defined here includes the same range of varying forms as occurs in the northwestern Gulf of Mexico. Included also are forms which were designated by Phleger and Parker (1951, p. 32, pl. 17, figs. 10, 11) as *Cibicides* sp. 1. The variant forms are not all figured here but may be found in Phleger and Parker (1951, pl. 16, figs. 1-4).

This is a widely distributed group in all traverses but I and IV from 35 m. to 1750 m. with a single occurrence at 2150 m. Frequencies are usually 1-5 per cent. Deeper than 1400 m. and shoaler than 60 m. they are less than 1 per cent.

Cibicides io Cushman
(Plate 12, figures 6, 7)

Cibicides pseudoungeriana (Cushman) var. *io* Cushman (part), 1931, Bull. U. S. Nat. Mus., vol. 104, pt. 8, p. 125, pl. 23, fig. 1 (not fig. 2).

As has been stated previously by Phleger and Parker (1951, p. 30), Cushman has figured two species under this name. Figure 2 in the above reference was erroneously labelled the holotype in the explanation of plates. Figure 1 represents the holotype as shown by its catalogue number and the designation given by Cushman in the text.

This species occurs in traverses V-VIII from 50 to 150 m. Frequencies are usually less than 1 per cent.

Cibicides kullenbergi Parker
(Plate 12, figures 10, 11)

Cibicides kullenbergi Parker, 1953, in Phleger, Parker and Peirson, Repts. Swedish Deep-Sea Exped., vol. 7, no. 1, p. 49, pl. 11, figs. 7, 8.

This species has scattered occurrences in traverses II, III, V and more consistent ones in VI-XI deeper than 580 m., with the greatest deeper than 1000 m. Frequencies are usually less than 1 per cent but may be as high as 2 per cent.

Cibicides mollis Phleger and Parker
(Plate 12, figures 12, 15)

Cibicides mollis Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 30, pl. 16, figs. 7a, b, 8a, b, 9a, b.

This species occurs in traverses V-VIII, XI from 50 to 185 m. There is a single occurrence at about 455 m. Frequencies are less than 1 per cent.

Cibicides protuberans n. sp.
(Plate 12, figures 13, 14, 16)

Test large, plano-convex, with 3-3½ whorls, lobulate in the adult and often very irregular in outline, regular in juvenile specimens, periphery keeled in the early chambers, later narrowly rounded, with a clear protuberant umbo; chambers 8-12 in the adult whorl; sutures slightly limbate in the early portion, later depressed, curved; wall thin, somewhat translucent, with large to medium perforations sometimes very closely spaced and sometimes irregularly scattered; aperture peripheral extending for a short distance on the evolute side. Maximum diameter 1.3 mm.

Holotype from station 116, Lat. 25°43′ N, Long. 84°13′ W, at a depth of 155 m.

This species most closely resembles *C. fletcheri* Galloway and Wissler but is larger, less convex on the involute side, and has a more protuberant umbo.

C. protuberans occurs in traverses IV-XI to a depth of 1850 m. The lower range is progressively deeper to the east: in IV, 42 m.; in V, 100 m.; in VI, 183 m.; in VII, 878 m.; in VIII, 585 m.; in IX, 420 m.; in X, 1317 m.; in XI, 1829 m. Deep occurrences in X and XI and possibly elsewhere probably represent displaced specimens. Shoaler than 200 m. frequencies are variable with a maximum of 21 per cent. They decrease deeper, and below 320 m. are less than 1 per cent.

CIBICIDES ROBERTSONIANUS (H. B. Brady)
(Plate 13, figures 2, 5)

Truncatulina robertsonianus H. B. Brady, 1881, Quart. Journ. Micr. Sci., vol. 21, p. 65; 1884, Rept. Voy. CHALLENGER, Zool., vol. 9, p. 664, pl. 95, figs. 4a-c.

In traverses II and III this species occurs deeper than 1200 m.; in V deeper than 914 m.; in VI-IX deeper than 275-585 m.; in X deeper than 950 m., and in XI deeper than 155 m. Deeper than 1000 m. frequencies are usually 1-5 per cent; shoaler they are usually less than 1 per cent.

CIBICIDES RUGOSA Phleger and Parker
(Plate 13, figures 1, 4)

Cibicides rugosa Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 31, pl. 17, figs. 5a, b, 6a, b.

This species occurs in traverses II (once), V-XI, from 575 m. to 2650 m. Frequencies are less than 1 per cent.

CIBICIDES UMBONATUS Phleger and Parker
(Plate 12, figure 17, 18)

Cibicides umbonatus Phleger and Parker, 1951, Mem. Geol. Soc. America, vol. 46, pt. 2, p. 31, pl. 17, figs. 7a, b, 8a, b, 9a, b.

This species occurs in traverses V-IX, from 35 m. to 600 m.

There is one occurrence in XI at 914 m. probably representing displacement. Frequencies shoaler than 150 m. and deeper than 550 m. are less than 1 per cent; between these limits they may be as high as 5 per cent.

CIBICIDES WUELLERSTORFI (Schwager)
(Plate 13, figure 3, 6)

Anomalina wuellerstorfi Schwager, 1866, Novara Exped., Geol. Theil., vol. 2, p. 258, pl. 7, figs. 105, 107.

I have previously referred this species to the genus *Planulina*. Since, however, it has an involute and an evolute side instead of being almost completely planispiral, it seems more logical to place it in *Cibicides*.

It occurs in all traverses but I and IV deeper than 800 m. except in traverses VII and VIII where it occurs deeper than 455 m. and 580 m. respectively. Deeper than 1000 m. frequencies are usually greater than 5 per cent and may be as high as 47 per cent; elsewhere they are usually 1-5 per cent but occasionally higher or lower.

CIBICIDINA STRATTONI (Applin)
(Plate 13, figures 8, 11)

Truncatulina americana Cushman var. *strattoni* Applin, 1925, *in* Applin, Ellisor and Kniker, Bull. Amer. Assoc. Petr. Geol., vol. 9, no. 1, p. 99, pl. 3, fig. 3.

C. concentrica (Cushman) (Plate 13, figures 7, 10) is often found occurring with this species but seldom in as great abundance. The two species appear to have the same distribution and have been combined in the population counts.

O. L. Bandy has pointed out to me (personal communication) that the genus *Cibicidina* is probably synonymous with *Hanzawaia* Asano. I have previously pointed out its resemblance also to *Rosalina* d'Orbigny.

The distribution is in traverses III (once), IV-VIII, IX (twice), XI (once) to a depth of 150 m. with a scattered occurrence to 235 m. There is a single occurrence at 914 m. in IX probably representing displacement. Frequencies at less than 100 m. are usually greater than 1 per cent, frequently greater than 5 per cent, and may be as high as 35 per cent. Deeper, frequencies decrease until at 150 m. they are less than 1 per cent.

Family PLANORBULINIDAE

PLANORBULINA MEDITERRANENSIS d'Orbigny
(Plate 13, figure 9)

Planorbulina mediterranensis d'Orbigny, 1826, Ann. Sci. Nat., vol. 7, p. 280, no. 2, pl. 14, figs. 4-6 bis.; Modèles, no. 79.

This species occurs in traverses IV (once), V-XI to a depth of 185 m. There are two occurrences in XI deeper than 1300 m. probably indicating displacement. Frequencies are usually less than 1 per cent.

GYPSINA VESICULARIS (Parker and Jones)
(Plate 13, figure 12)

Orbitolina vesicularis Parker and Jones, 1860, Ann. Mag. Nat. Hist., ser. 3, vol. 6, p. 31, no. 5.

This species occurs in traverses VI-VIII, XI to a depth of 155 m. Frequencies are less than 1 per cent.

CONCLUSIONS

1. Five faunal depth facies boundaries occur at: 80-100 m., 130-150 m., 180-220 m., 350-600 m., and 900-1000 m. There are less distinct boundaries at 30-50 m. and 250 m. Deeper than 1000 m. there are various changes which are not concentrated at particular depths. Salinity and temperature data show changing conditions with depth and may contribute to differentiation of facies.

2. Lateral changes from west to east are marked in facies 1-4. Factors affected by the outflow of the Mississippi River including turbidity, light penetration, food supply and the chemistry of the water and sediments are probably an important influence on faunas in traverses in that area. The increase to the east of the West Indian fauna is marked and the fauna of the continental shelf appears to be largely residual. In facies 5 and 6 lateral changes are less marked.

3. Displaced specimens from shallow stations occur at deep stations especially below the escarpment running north and south along the coast of Florida.

4. Most species present in significant frequencies are represented by living specimens at stations shoaler than 200 m.; at greater depths the presence of living specimens is irregular. There appears to be an analogy in the Mississippi Delta region between the percentage of total population found living and the rate of sedimentation.

5. Planktonic populations show similar distributions in the various traverses. They combine elements of North Atlantic mid- and low-latitude faunas. The extreme annual range of surface temperatures may partially explain this. To explain the presence of *Globigerina inflata* d'Orbigny and *G. pachyderma* (Ehrenberg), an east to west coastal current along the Florida coast is postulated. Other species may be introduced from the Caribbean.

6. Planktonic faunas compose less than 10 per cent of the total population shoaler than 100 m. and 90 per cent or more deeper than 1000 m. They do not appear in the shallow stations most affected by the outflow of the Mississippi River.

7. The tests of planktonic species often show the effect of solution of calcium carbonate. The high percentage of such tests at many stations suggests that solution is fairly rapid.

8. Living planktonic specimens occur at many of the deeper stations. They probably represent forms which have fallen to the bottom and survived rather than bottom-living stages.

9. Two hundred and five species and thirteen generic and family groups are used in the analysis of faunal distributions. One new genus *Stetsonia*, and ten new species: ***Anomalinoides mexicana*, *Bolivina lanceolata*, *Cibicides protuberans*, "*Discorbis*" *bulbosa*, *Globobulimina mississippiensis*, *Goësella mississippiensis*, *Reophax irregularis*, *Stetsonia minuta*, *Valvulineria mexicana*** and ***Valvulineria minuta*** are described.

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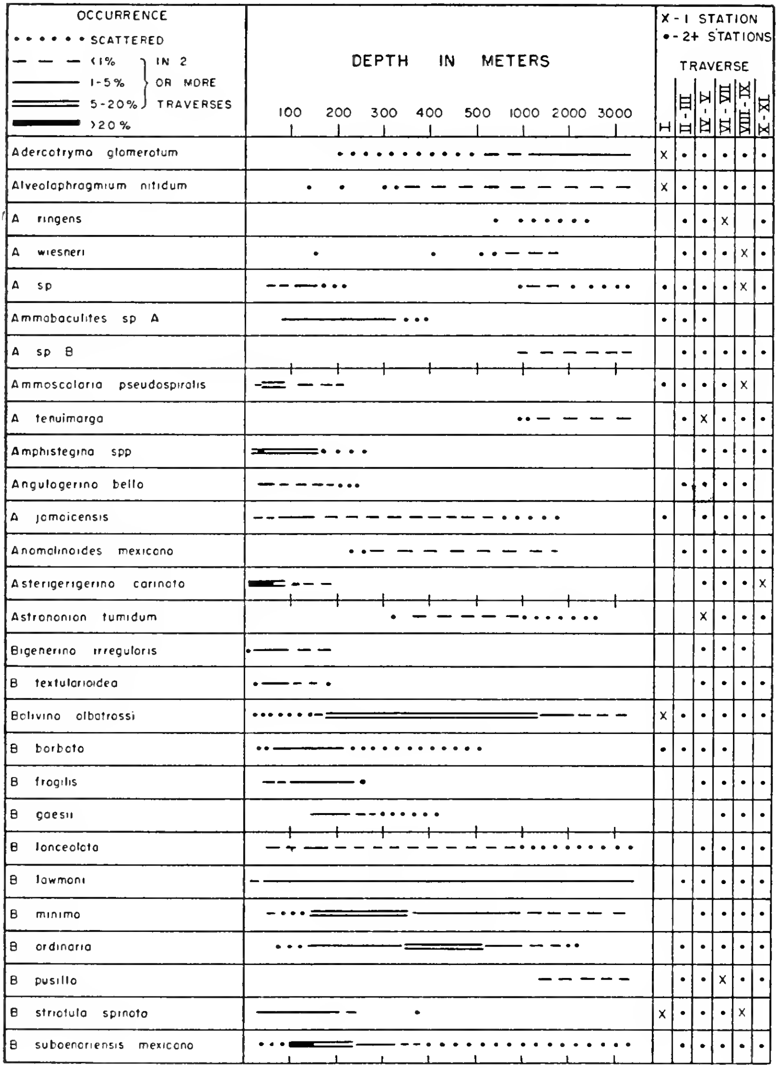

Fig. 3. Generalized distributions of benthonic Foraminifera by depth.

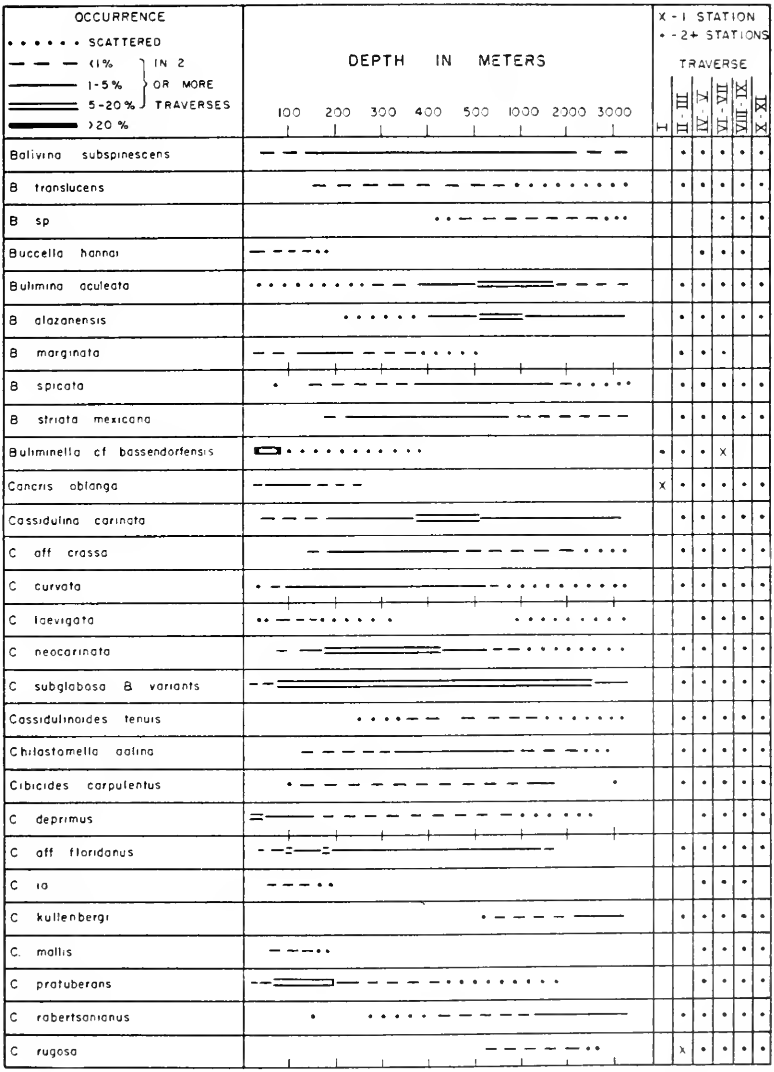

Fig. 4. Generalized distributions of benthonic Foraminifera by depth.

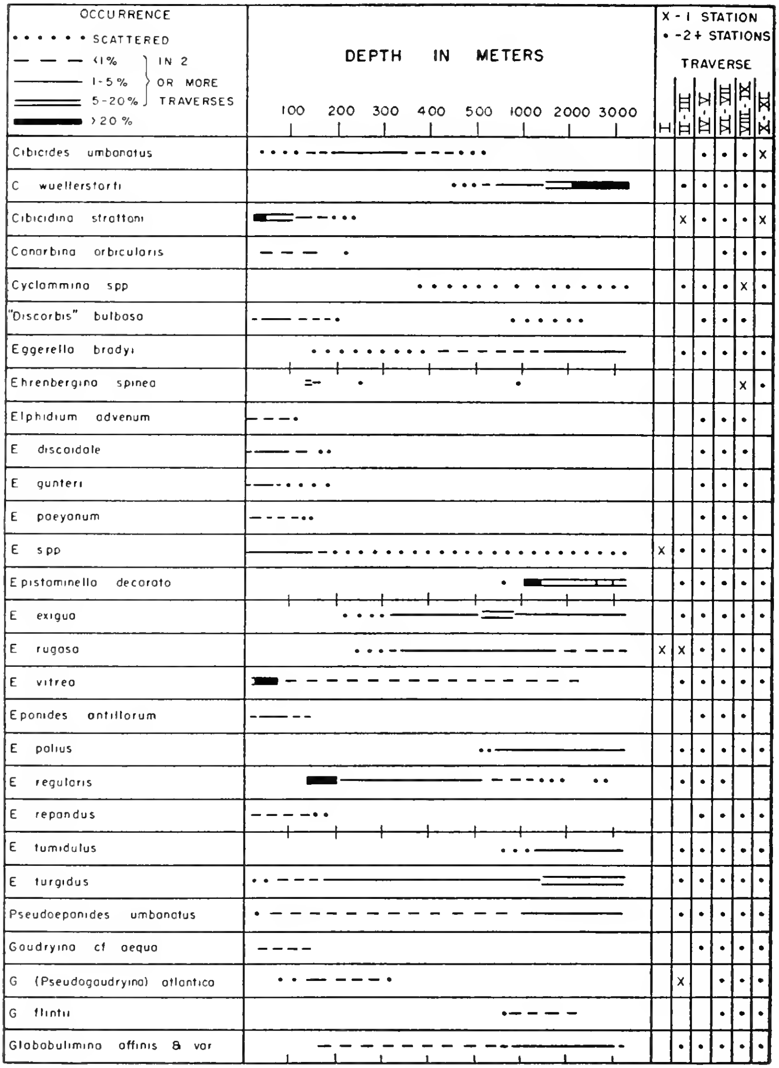

Fig. 5. Generalized distributions of benthonic Foraminifera by depth.

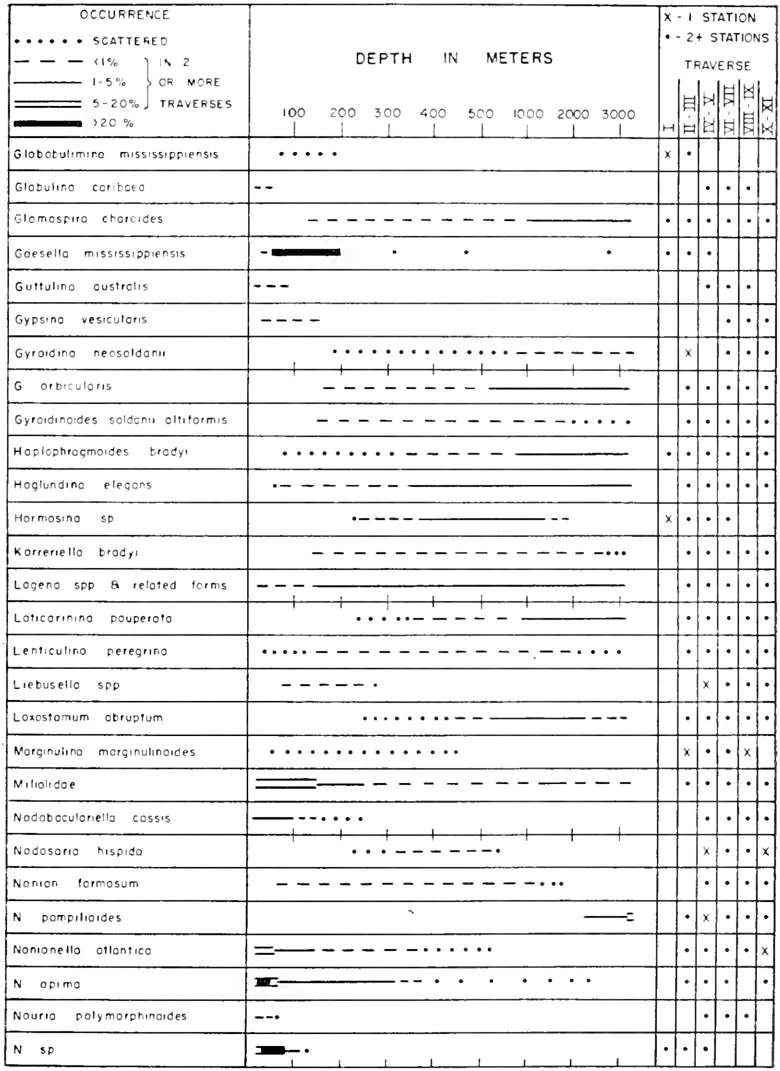

Fig. 6. Generalized distributions of benthonic Foraminifera by depth.

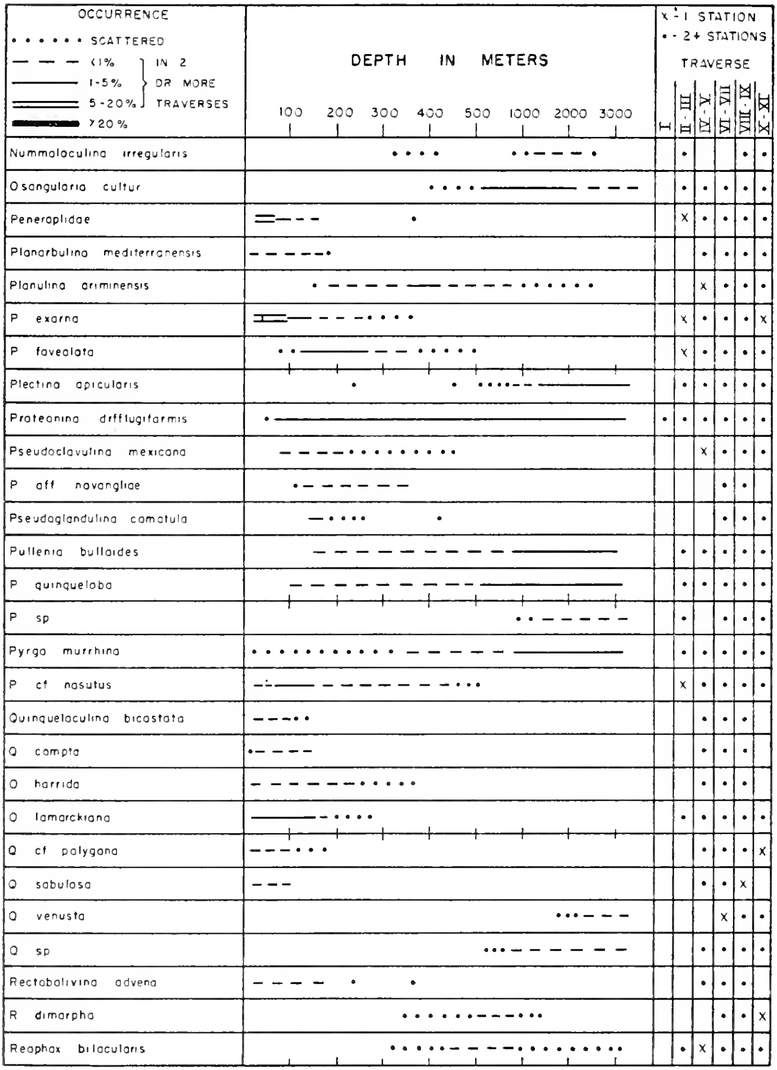

Fig. 7. Generalized distributions of benthonic Foraminifera by depth.

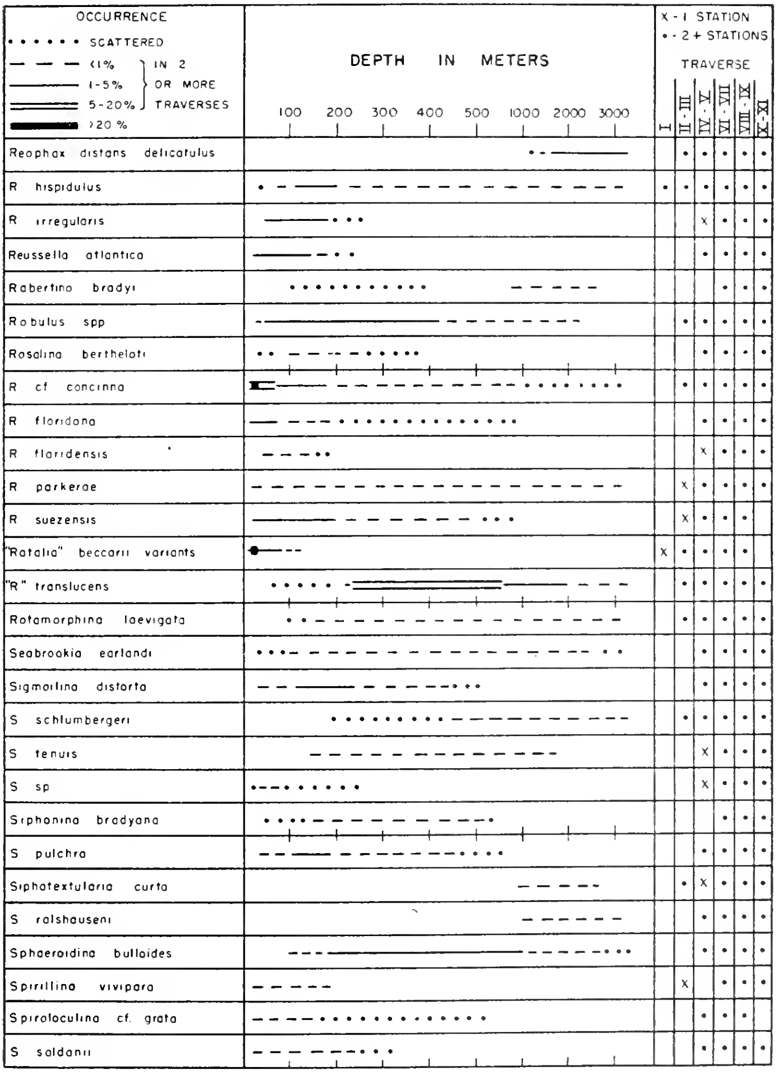

Fig. 8. Generalized distributions of benthonic Foraminifera by depth.

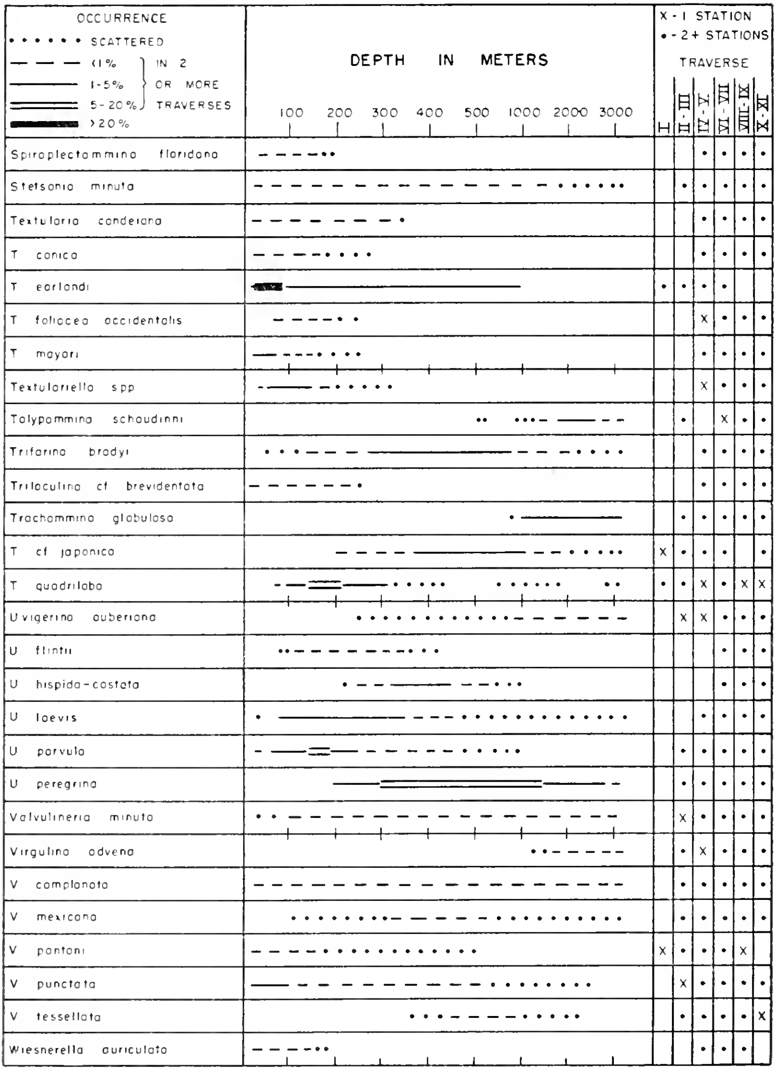

Fig. 9. Generalized distributions of benthonic Foraminifera by depth.

TABLE 3

Locations of stations giving depth and type of sampling gear used. (P — Phleger sampler, O — orange peel dredge, S — Stetson-Iselin sampler, U — underway sampler)

Station	*Sampler*	*N. Latitude*	*W. Longitude*	*Depth in Meters*
1	P	24°51′	85°58′	3237
2	P	24°45.5′	86°27′	3237
3	P	26°01′	88°03′	3017
4	P	26°07′	89°09′	2972
5	P	26°31′	89°09.5′	2788
6	P	26°58.5′	89°12′	2468
7	P	27°26′	89°14′	1875
8	P	27°37.5′	89°14.5′	1417
9	P	27°51′	89°15′	1372
10	P	28°01.5′	89°19′	1298
11	P	28°12′	89°20′	914
12	P	28°18′	89°20′	732
13	P	28°23.5′	89°20′	631
14	P	28°29′	89°22′	471
15	P	28°33.5′	89°22′	298
16	P	28°52′	89°26′	33
17	P	28°49′	89°26′	58
18	P	28°45.5′	89°27′	88
19	P	28°43′	89°26′	106
20	P	28°41′	89°25.5′	113
21	P	28°39′	89°25′	142
22	P	28°37′	89°24.5′	168
23	P	28°35′	89°24′	208
24	P	28°32.5′	89°24′	314
25	P	29°10′	88°56′	22
26	P	29°08.5′	88°55′	53
27	P	29°06′	88°53′	77
28	P	29°04.5′	88°52′	106
29	P	29°04.5′	88°52′	155
30	P	29°01′	88°49.5′	205
31	P	28°56′	88°46′	373
32	P	28°50.5′	88°42.5′	400
33	P	28°44.5′	88°39.5′	1024
34	P	28°39′	88°36′	1262
35	P	28°34′	88°33′	1481
36	P	28°27.5′	88°24.5′	1719

Station	*Sampler*	*N. Latitude*	*W. Longitude*	*Depth in Meters*
37	P	28°10.5′	88°00′	2388
38	P	28°17′	87°03.5′	1573
39	P	28°22′	87°02′	1144
40	P	28°26.5′	87°00′	960
41	P	28°31′	86°58′	860
42	P	28°35′	86°57′	823
43	P	28°44′	86°53.5′	677
44	P	28°54′	86°57′	650
45	P	29°03′	86°55′	631
46	P	29°13.5′	86°52′	555
47	P	29°24′	86°49′	446
48	P	29°34′	86°45′	223
49	P	29°38.5′	86°44′	183
50	P	29°40.5′	86°43′	165
51	P	29°42.5′	86°42.5′	155
52	P	29°44.5′	86°42′	146
53	P	29°46.5′	86°41′	139
54	P	29°48.5′	86°40.5′	128
55	P	29°50.5′	86°40′	119
56	P	29°52′	86°39′	113
57	P	29°54′	86°38.5′	106
58	P	29°56′	86°38′	—
59	P	29°58′	86°37′	91
62	O	30°00′	86°34.5′	64
63	O	30°02′	86°33.5′	55
64	O	30°04′	86°33′	49
65	O	30°06′	86°32′	43
66	O	30°08′	36°31.5′	39
67	O	30°10′	86°31′	24
68	O	30°12′	86°30.5′	27
69	O	30°14′	86°30.5′	29
70	O	30°16′	86°30.5′	24
71	O	30°18′	86°30′	24
72	O	30°20′	86°30′	22
73	O	30°22.5′	86°30′	20
74	P	29°16.5′	88°01′	204
75	P	29°19′	88°01′	146
76	P	29°21.5′	88°01′	99
77	O	29°24′	88°01′	75
78	P	29°26′	88°01′	71
80	O	29°31′	88°01.5′	42

Station	*Sampler*	*N. Latitude*	*W. Longitude*	*Depth in Meters*
81	O	29°38.5′	88°01.5′	44
82	O	29°35.5′	88°01.5′	36
84	O	29°40′	88°02′	36
85	U	29°42.5′	88°02′	36
86	U	29°45′	88°02′	36
87	U	29°47.5′	88°02′	40
88	U	29°50′	88°02′	40
89	U	29°52′	88°02′	36
90	U	29°53.5′	88°02′	35
91	U	29°55.5′	88°02.5′	31
92	O	29°57.5′	88°02.5′	33
93	O	29°59′	88°02.5′	36
95	U	30°01.5′	88°02.5′	36?
96	U	30°03′	88°03′	21
97	U	30°05′	88°03′	20
99	P	29°18′	87°50′	238
100	P	29°14′	87°54.5′	530
101	P	29°09.5′	87°51′	914
102	P	29°05′	87°48′	1097
103	P	28°50′	87°40.5′	1822
104	P	28°42′	87°33′	2213
105	P	28°32′	87°25′	1417
106	P	28°07′	87°05′	2697
107	P	27°29′	86°38′	3017
108	P	26°38′	86°16′	3072
110	P	25°27′	85°32′	3218
111	P	24°50′	85°23′	3251
112	P	25°13′	84°46′	3283
113	P	25°19′	84°40′	2280
116	U	25°43′	84°13′	155
117	U	25°48′	84°06′	139
118	U	25°48′	84°11′	146
120	P	25°30′	84°59′	3246
121	P	25°34′	84°52′	2560
122	P	25°38′	84°49′	1829
123	P	25°39′	84°47′	1326
124	P	25°42′	84°42′	914
126	P	26°03.5′	84°50.5′	1317
127	P	26°21′	85°01.5′	2150
128	P	26°23.5′	84°58′	1737
129	P	26°41′	85°14′	3180

Station	*Sampler*	*N. Latitude*	*W. Longitude*	*Depth in Meters*
130	P	26°45.5′	85°00′	3200
131	P	26°46′	84°58′	1920
133	P	26°46′	85°02.5′	—
134	P	26°49′	84°55′	950
136	P	26°57′	85°02.5′	1051
137	P	27°06′	85°22′	3160
138	S	27°29′	84°41′	183
140	P	27°18′	84°50′	256
141	P	27°17.5′	84°54.5′	320
142	P	27°17′	84°59′	421
144	P	27°17′	85°15′	914
145	P	27°16.5′	85°29′	2268
146	P	27°31′	85°40′	3164
148	P	27°47.5′	85°45′	1730
149	P	27°51′	85°44′	914
150	P	27°56′	85°32′	585
151	P	28°01.5′	85°22′	366
152	P	28°09′	85°07′	183
153	P	28°11.5′	85°02′	146
154	P	28°14′	84°57′	117
155	S	28°16.5′	84°52′	79
156	S	28°19′	84°46.5′	58
157	S	28°22′	84°41′	62
158	S	28°24.5′	84°36′	60
159	S	28°27′	84°31′	51
160	S	28°30′	84°25.5′	46
161	S	28°32′	84°20′	35
163	S	28°38′	84°08′	36
164	S	28°41′	84°02′	31
165	S	28°43.5′	83°56′	31
166	S	28°46′	83°50′	29
167	S	28°49′	83°44′	26
168	S	28°51.5′	83°39.5′	22
169	S	28°54′	83°34.5′	20
170	S	28°55′	83°28.5′	20
171	S	28°56.5′	83°22′	15
172	S	28°58′	83°16.5′	12?
174	S	29°28′	85°29′	22
175	S	29°24′	85°32′	31
176	S	29°20′	85°35.5′	46
177	S	29°16′	85°39′	49
178	S	29°12′	85°42′	86

Station	*Sampler*	*N. Latitude*	*W. Longitude*	*Depth in Meters*
179	P	29°08.5′	85°45′	146
180	S	29°04′	85°49′	183
181	P	28°59′	85°52′	186
182	P	28°54.5′	85°56′	237
183	P	28°49′	85°59′	274
184	P	28°45′	86°02.5′	274
185	P	28°38′	86°07′	320
186	P	28°31.5′	86°10′	347
187	P	28°24.5′	86°13′	457
188	P	28°18.5′	86°15.5′	585
189	P	28°13′	86°18′	732
190	P	28°06.5′	86°21′	878
191	P	27°48′	86°30′	2999
196	P	29°26.5′	86°59′	713
197	P	29°26.5′	86°57.5′	549
198	P	29°26.5′	86°57′	549
199	P	29°27′	86°58′	735
200	P	29°27.5′	86°58′	600
201	P	28°37′	89°49′	430
202	P	28°40.5′	89°45′	128
203	P	28°40′	89°45.5′	201
204	P	28°42.5′	89°42′	91
205	P	28°44′	89°40′	82
206	P	28°45.5′	89°38.5′	79
207	P	28°46.5′	89°36.5′	82
208	P	28°48′	89°34.5′	73
209	P	28°49′	89°33′	86?
210	P	28°50.5′	89°31′	86?
211	P	28°51.5′	89°29.5′	51
212	P	29°11′	88°52′	62
213	P	29°16′	88°48′	55
214	P	29°21′	88°44′	49
215	P	29°25.5′	88°40′	47
216	P	29°30′	88°36′	42
217	P	29°35.5′	88°32′	40
218	P	29°40′	88°28.5′	42
219	P	29°45′	88°24.5′	38
220	P	29°49′	88°21′	37
221	P	29°53′	88°17.5′	35
222	P	29°57.5′	88°14.5′	33
223	P	30°01.5′	88°11′	33
224	P	30°05.5′	88°07.5′	20
225	P	30°08′	88°05.5′	20

TRAVERSE	I											II																					
STATION	211	210	209	208	207	206	205	204	202	203	201	16	17	18	19	20	21	22	23	15	24	14	13	12	11	10	9	8	7	6	5	4	3
DEPTH IN METERS	51	?86	?86	73	82	79	82	91	128	201	430	33	58	88	106	113	142	168	208	298	314	471	631	732	914	1298	1372	1417	1875	2468	2788	2972	3017
TOTAL PLANKTONIC POPULATION	0	0	0	0	0	0	0	9	0	0	0	0	0	3	0	0	0	21	0	300	17	2	7	75	0	2000	5000	7000	100000	50000	10000	30000	60000
TOTAL BENTHONIC POPULATION	44	1200	225	650	175	125	250	175	175	150	125	31	450	250	275	175	125	650	100	800	550	36	250	425	175	325	375	425	175	550	700	500	1200
Adercotryma glomeratum										.7									2				.4			1	1	5		1		3	2
Alveolophragmium nitidum									.5											.5		3	.4		1	.3	.8	2					
A ringens																										.9	.3	.9					
A scitulum									2		4							.3	2	.2	.4	6			1			.5			.6	.4	
A subglobosum																				.2								2		.4		1	
A wiesneri																							1	.5	5	3	2						
A sp			.5	1	14	9	5	9	7	3					1	1	3										.8	2					
Ammobaculites sp A						3		2	3	8					.4	3	2	.8	3		1												
A sp B																									.6	.9	1					.8	
Ammodiscus spp						.7		.6	1	5							4				1	3	.4	.7	3	.9	.3			.4	.6		1
Ammoscalaria pseudospiralis			1	8	18	9	5	3	.5					.4			8	.3	.9														
A tenuimargo																										.3	.3	5	1	2		2	.3
Angulogerina jamaicensis									1		2																						
Anomalinoides mexicana																											.3						
Bolivina albatrossi																		.5		9	8		3	6	3	8	.8	3	4				
B barbata		.2		7														13		1													
B lowmani														.4						.7				1		2	1	.2			2	.4	4
B ordinaria																		3		3	4		11	7									
B paula																																.4	1
B pulchella primitiva																														.4	.6	.4	2
B pusilla																											.8		1		.6	.8	
B striatula spinata				4																													
B subaenariensis mexicana																				.7								.2		.4			
B subspinescens																				1			.4	1			.5			.4	1	1	1
B translucens																							.8	.2									
Bulimina aculeata																							14	2	4	11	13	2	7		.6		
B alazanensis																										5	1	2		.7		.4	.7
B marginata																		33		13	1												
B spicata																		.2		1	.2		4	.7		4	1	2	2				
B striata mexicana																		3		12	2		13	5		.6		.9	.6	1	.6		.3
Buliminella cf bassendorfensis				30								3																					.7
Cancris oblonga				.3																													
Cassidulina aff crassa																												.2				.4	
C curvata																				2			.4										
C neocarinata																				.5			.8	.2									.3
C subglobosa & variants																				.7				.2		2	4	4	11	6	4	3	2
Cassidulinoides tenuis																														.4			.3
Chilostomella oolina																					1		2	.7		.9					.6	.4	
Cibicides corpulentus																											.3						.3
C aff floridanus																				4			4	3	.6	4	3	4					
C kullenbergi																											.3					.4	
C robertsonianus																										2	.8	.2	5	4	3	6	.7
C rugosa																										.3							
C wuellerstorfi																										.9	.8	2	3	18	3	20	13
Cyclammina spp																						3	.8	.2	.6		1	.7					
Dentalina - Nodosaria																				.7	.2									.4	.6		
Eggerella bradyi																								.5		.9	.5	.5		1		1	.3
Elphidium spp									2							.6				.7													
Epistominella decorata																										.3	3	2	18	4	20	8	21
E exigua																							7	4		4	1	.5	3	.4	2		1
E rugosa																																	.3
E vitrea														.4																			
Eponides polius																				.5							.3			3	8	4	6
E regularis																		12		2	3		2								.6		
E tumidulus																											.3		2	.4	3	6	3
E turgidus																							4	.5		.6	6	.9	.6	4	12	4	6
Pseudoeponides umbonatus																										.3	.5		.6	3	1	.4	1
Gaudryina (Pseudogaud.) atlantica																				.2													
G cf minuta																			.9	.2	1	8	1	3	5	.3	.3						
Globobulimina affinis & variant																		.8		.2			.4	2	.6	3			2	5	1		
G mississippiensis				.3														.2															
Glomospira charoides									.5	3	4									.2	.7		.4	.7	2	6	6	1				1	
G cf gordialis											3						.9	.3	3		.5	6		.5						.4			
Goesella mississippiensis		.6	21	24	22	31	43	30	44	20				3	92	86	53	1	15		.5	3									.6		

Table 4. Percentage distribution of benthonic Foraminifera in traverses I and II (pt.).

TRAVERSE	I											II																					
STATION	211	210	209	208	207	206	205	204	202	203	201	16	17	18	19	20	21	22	23	15	24	14	13	12	11	10	9	8	7	6	5	4	3
DEPTH IN METERS	51	?286	?286	73	82	79	82	91	128	201	430	33	58	88	106	113	142	168	208	298	314	471	631	732	914	1298	1372	1417	1875	2468	2788	2972	3017
Gyroidina orbicularis																				.2				.7		2	2	4	5	3	1		
Gyroidinoides soldanii altiformis																										.3							
Haplophragmoides bradyi						.7				2								.3	4	.2	3		.4	3	7	1	.5	.9	3	3		2	2
Hoglundina elegans																													6	4	.6	2	3
Hormosina sp											11									.7	1		2	2	4	.6	3	4					
Karreriella bradyi																										.9							
Lagena spp & related forms																		.2		1			.4	1			3	.5	2	6	9	2	5
Laticarinina pauperata																										.9	1	.9	1	3	.6		.3
Lenticulina peregrina																										.3		.2	.6				.3
Liebusella spp																																.8	
Loxostomum abruptum																												.2					
Marginulina marginulinoides																				.7													
Miliolidae																										.3	.3			.4	.6	.4	.3
Nonion pompilioides																														2	.6	2	1
Nonionella atlantica																							.4						.6				.7
N opima	9				1															.2	2												
Nouria sp	59	16	16	6	10	4	7	2	.5			81	18	30	3						.2												
Nummoloculina irregularis																										.3							
Osangularia cultur																							.4	5	.6	2	.8	3	2			.4	
Planulina exorna																			.9														
P foveolata																				.2													
Plectina apicularis																									.6	.3	1	2	.6	.7		3	1
Proteonina atlantica																				.2									1	1	2		
P difflugiformis			.9	7	18	25	20	24	9	13	5			2	2	6	3	3	8	1	3	3	.8	2	3	.6	6	3			.6	3	
Pullenia bulloides																				.7	.2		.4			2	1	.7	1	2	1	.8	.3
P quinqueloba																									.6	2			.6	.4	.6	.8	.3
P sp																												.2	.6	3	2	.8	
Pyrgo murrhina																											.5						.3
P cf nasutus																										.3							
Quinqueloculina lamarckiana																			.9										.6				
Q sp																										.6	.3				.6		.7
Reophax bilocularis																										.3	2	.2				.4	
R distans delicatulus																												4	.6	1	.6	6	1
R guttifera																		.2	.9	1	1	3		2	2								
R hispidulus			.9		3			2	3	1				.4		.6	2	.3	2		.7		.8	2		.6		.2		.4			.3
R scorpiurus				1	3	2	5	4	3								2	.3	10	1	3											.4	
R. sp																			9		.7	3		1									
Robulus spp.																		.9		3						.3		.7	.6				
Rosalina cf concinna																		.2									.3						
R parkerae																																	1
"Rotalia" beccarii variants		3					.4					16	2																				
"R" translucens																				.2						.3	.3		.6			.8	.3
Rotamorphina laevigata																							.4	.2							.6		
Saccamminidae & related forms									2	.7	.9						7	5	2	.7	.9	3	.8	3	18	3	2						
Sigmoilina schlumbergeri																										.9	.3	.9		.4			1
Siphonina pulchra																																	.3
Siphotextularia rolshauseni																											.5	.2				1	1
Sphaeroidina bulloides																		3		8	9		8	8	1		.8	.5	.6				
S compacta																										.3							
Stetsonia minuta																										.3	4					.4	
Textularia earlandi	30	77	48	5			.4			15	35		79	61			.9				.9	11	2	9	3								
Tolypammina schaudinni																			.9						4	.6	1	1	.6			.4	
Triloculina tricarinata																													.6		1	.4	.7
Trochammina advena									1	2	5							.3			4												
T globulosa																									1	.9	2	2	1	2		.4	.7
T cf japonica											7								4	1	8	13	3	5	9	1	2	1					
T quadriloba				1	11	12	12	22	9	20	12				1	2	4	8	17	.5	5		.4		6								
T squamata & related spp	2																																
T cf tasmanica			3			3	2		2	5							3	3	5	2	18			.2	2	1	.5	.9					
Uvigerina auberiana																																.4	
U peregrina																		.6		16	5		6	12	1	6	6	15	5	4		1	
Valvulineria mexicana																		.8		4	5		2	.2				.7		2	2	.4	.7
V minuta																				.2							.3	.2					
Virgulina advena																															.6	.4	
V complanata																											.8			.4	.6	.4	1
V mexicana																							.4								.6		.7
V pontoni				2														.5			1												
V tessellata													.2										1	2		3							
Wiesnerella auriculata											.9																						
Miscellaneous spp		3	9	3				1	9	2	9		.8	2	.6	.8	7	5	8	3	4	32	2	4	11	4	5	9	5	5	9	4	6

Table 5. Percentage distribution of benthonic Foraminifera in traverses I and II (pt.).

TRAVERSE	III													IV												
STATION	25	26	27	28	29	30	31	32	33	34	35	36	37	225	224	222	221	220	219	218	217	216	215	214	213	212
DEPTH IN METERS	22	53	77	106	155	205	373	400	1024	1262	1481	1719	2388	20	20	33	35	37	38	42	40	42	47	49	55	62
TOTAL PLANKTONIC POPULATION	0	1	29	11	21	10	69	300	425	1400	700	1400	7800	4	175	550	800	850	725	1000	0	250	200	100	0	5
TOTAL BENTHONIC POPULATION	125	650	1 200	700	1 300	900	750	700	700	450	300	325	325	1 200	10 800	30 700	27 500	9 700	19 100	27 200	150	14 900	9 900	4 300	92	350
Adercotryma glomeratum								.1		.2	.7	2														
Alveolophragmium nitidum						.1				2	1															
A ringens												.6														
A. scitulum						.1	.4	.1					.6													
A subglobosum							.3					.6														
A wiesneri					.3			.4	2	3	6	.9														
A. sp										.9	2	2													1	.3
Ammobaculites sp A						.9	.4																			
A sp. B												.3														
Ammodiscus spp.						.1		.3	.9	.2	1	1	.3													
Ammoscalaria pseudospiralis				.3		.2								2	1	.2	1	.4	.7	.8	30	.3	4	2	22	.9
Amphistegina spp																.1		.1	.2			.2				
Angulogerina bella				.1											.1	.4	.9	1	2	2		2	6	4		
A jamaicensis															.3				.2					.2		
Anomalinoides mexicana											.3															
Asterigerina carinata														2	1	2	2	.7	.5	.6		.4	.7			
Bigenerina irregularis														5	2	2	3	3	5	3		2	4	2		
Bolivina albatrossi						.2	.8	10	5	8	2	1														
B barbata			.2	15	26	14			.6																	
B lowmani				.3			3	.6	1	.9	3	2	2	.3	.3		.7	.4	.3	.5		.4		1		1
B minima																									1	
B ordinaria						19	16	6	.6	.5	.3	.9														
B pulchella primitiva															.8	.8	.9	.5	.7	1		.6	1	1		
B pusilla												.6	.6													
B striatula spinata		.3	5	3		2											.2		.2	.2		.3	1	2		
B. subaenariensis mexicana				21	32	1	1				.3													.2		
B subspinescens							.3	.4			.3	2	1									.1	.3			
B translucens							2			.5																
Buccella hannai														2	1	1	1	.7	1	.5		.7	.3	.8		
Bulimina aculeata				.3			.8	10	16	10	16	7	.3													
B alazanensis								6	3	4	.7	.3														
B marginata				.3	14	13	.5								.1					.8		1	1	1		
B spicata						.1	.5	3	3	.2	2	1														
B striata mexicana							4	8				.9														
Buliminella cf bassendorfensis	6	27	35	7	.6		.3					1			.6	.2	.2	.1	.5	1	.6	4	5	5		
Cancris oblonga																.2	.2	.5	.5	.8		.3	1	.8		
Cassidulina carinata							13	17	.3	.5																
C. aff crassa					.3																					
C subglobosa & variants								.6		2	.3		.6	.1	.2	.6	2	.9	2	3	.6	2	1	2		
Chilostomella oolina								1	1	2		1														
Cibicides corpulentus										.2		.3														
C deprimus														1	5	6	5	4	2	2		2	.2	1		
C aff floridanus							1	1		1	.7	.9														
C kullenbergi													.3													
C protuberans														.1				.1		.1						
C robertsonianus										.5	.3	.9	6													
C. wuellerstorfi										.5	.7	2	.9													
Cibicidina strattoni					.2									20	9	15	15	17	16	16	2	9	12	5		
Cyclammina spp							.1	.4		.2		.9														
Dentalina - Nodosaria							.2											.1			.6	.1		.2		
"Discorbis" bulbosa															.1	.9	.6	1	1	2		1	.2			

Table 6. Percentage distribution of benthonic Foraminifera in traverses III and IV (pt.).

TRAVERSE	III													IV												
STATION	25	26	27	28	29	30	31	32	33	34	35	36	37	225	224	222	221	220	219	218	217	216	215	214	213	212
DEPTH IN METERS	22	53	77	106	155	205	373	400	1024	1262	1481	1719	2388	20	20	33	35	37	38	42	40	42	47	49	55	62
Eggerella bradyi									.3	.5	.3	1	2													
Elphidium advenum														.3	.1											
E. discoidale														2	.4	.7	2	2	5	2		2	.7	.4		
E gunteri			.2											9	1	3	.8	1	1		1	2	4	1		
E poeyanum														.3	.8	.3	.9	.2	.6	.6		.1	.8	.4		
E. spp.														5	4	4	3	3	3	3	1	2	2	2		
Epistominella decorata												1	14													
E. exigua					.3			3	2	2	1	.6														
E. rugosa										1																
E. vitrea		34	29	17	4					1				.2	.7	.1	.4	.7	2	3		8	5	14		
Eponides antillarum														.1		.2	.6	.7	.3	.1						
E polius												.3														
E. regularis					.6	21	6	.6	5	.2																
E tumidulus											.7	.3														
E. turgidus										1	1	5	22				.1									
Pseudoeponides umbonatus								.3				.3	.6													
Gaudryina cf minuta							.1			.2				.3	.4	.1								.2		
Globobulimina affinis & variant							.5	.6	3	6	3	.6	2													
G mississippiensis				2	3	3																				
Globulina caribaea														.2	.1		.1		.2							
Glomospira charoides						.2			3	.7	8	4	1													
G cf. gordialis						.2		.1					.3													
Goësella mississippiensis			2	9	1	6																		.2	22	12
Guttulina australis														2	1	.1	.3	.1	.2	.1	.6	.2	.7			
Gyroidina neosoldanii												.3														
G. orbicularis								.6	3	.9	2	5	2													
Gyroidinoides soldanii altiformis								.1																		
Haplophragmoides bradyi						.2		.6	.3		4	1	5													
Hormosina sp.						.1	.1	1	1	5	3	1														
Karreriella bradyi										.2	.3															
Lagena spp. & related forms			.2	.1	.2	.1	1	.1	2	.9	.7	1	2		.1		.1			.5		.2	.5	.6		
Laticarinina pauperata											.7	.3	.9													
Lenticulina peregrina						.4	.4	.1		.2	.3															
Loxostomum abruptum										.2	.3															
Miliolidae										.2				6	2	1	4	4	.7	.8		2				
Nodobaculariella cassis														.2	.3	.8	.2					.2				
Nonion pompilioides													.3													
Nonionella atlantica					.7	.2	.5							2	3	10	5	6	7	7	.6	6	10	9		
N opima	2	31	19	7	5	1	1		.6	2			1	2	9	1	1	2	5	7	2	11	15	20		
Nouria polymorphinoides														.3	.3				.2		9					
N. sp.	11	2	4	3																					22	5
Nummoloculina irregularis											.3															
Osangularia cultur								2	4	4	2	3	.6													
Peneroplidae							.1							1		.7	.2	.7	.2							
Planorbulina mediterranensis																			.2							
Planulina exorna														1	.1	4	4	7	6	3		2	1	1		
Plectina apicularis											.3	2	4													
Proteonina atlantica															.3	1	1	.7	1	1	48	.8	3	1	20	.3
P difflugiformis			.2	.1		.8	3	2	2	4	5	9	.3													
Pullenia bulloides							.7	.6	.9	.5	.3		.9													
P quinqueloba								.1	1	.9	.7	.9	.6													
P sp.													.3													
Pyrgo murrhina															.3											
P cf nasutus																.1	.4			.5		.8		.2		
Quinqueloculina bicostata														.1	.2	.1	.1		.2	.1		.1		.2		
Q compta														2	.4	1	1	2	2	.5		1		.6		
Q horrida																	.4		.3	.6			.2	.2		

Table 7. Percentage distribution of benthonic Foraminifera in traverses III and IV (pt.).

TRAVERSE	III													IV												
STATION	25	26	27	28	29	30	31	32	33	34	35	36	37	225	224	222	221	220	219	218	217	216	215	214	213	212
DEPTH IN METERS	22	53	77	106	155	205	373	400	1024	1262	1481	1719	2388	20	20	33	35	37	38	42	40	42	47	49	55	62
Quinqueloculina lamarckiana														1	.4	1	1	1	3	1		1		.4		
Q. cf. polygana																						.1				
Q. sabulosa														.3	.2	.5	.1	.5	.3							
Q. sp.										.2																
Rectobolivina advena																.2	.4	.5	.3	.8		.7	1	1		
Reophax bilocularis											.3															
R. distans delicatulus												5	12													
R. guttifera										.2																
R. hispidulus				.4	.3	.1		1	.3	2	1	.9	2													
R. scorpiurus						.8	.4	.1									.1									
R. sp.						.4			.3																	
Reussella atlantica															.7	1	.8	4	2	1		1	2	2		
Robulus spp.			.2	.8	.2	.1	.3	.3			.3					.1	.1	.5	1	.7	1	.8	.7	.6		
Rosalina bertheloti																	.2	.1								
R. cf. concinna					.2									11	21	24	23	18	11	16	.6	18	1	.2		
R. floridana														6	5	4	3	2	2	2		1	2	1		
R. parkerae																	.2		.2	.4			.2	.4		
R. suezensis													.3			.4	1	1	2	2		1	.3			
"Rotalia" beccarii variants	.2	.6	.3											14	20	4	3	3	2	2	.6	3	5	3		
"R" translucens							3	3		.7	.7	.6														.9
Rotamorphina laevigata								.1		.7	.3		.3													
Saccamminidae & related forms						.2	.3	.1			1	1														
Seabrookia earlandi																	.1									
Sigmoilina distorta																	.2		.5	1		.4	.7			
S. schlumbergeri											.3	.3														
S. tenuis													.3													
Siphonina pulchra																			.2				.2			
Siphotextularia curta										.2	.3	.3														
Sphaeroidina bulloides						.3	1	3	4	.5																
Spirillina vivipara											.3															
Spiroloculina cf. grata															.8	.8	.5	.4								
Stetsonia minuta										.2	.3				.3	.5	.8	.7	.8	2			1	2		
Textularia candeiana																.1	.1									
T. earlandi	21	5	.3	3	.6	5	.8	2	2																12	79
T. mayori															.2	.9	2	2	1	1		.6				
Tolypammina schaudinni											.3	.9	.3													
Triloculina cf. brevidentata														.1	1	.7	.4	.4		.4		.2		.4		
T. tricarinata								.1		.7																
Trochammina advena						.4	.1																			
T. globulosa									.6	1	5	4	3													
T. cf. japonica							.8	1	1	.5	.7	3														
T. quadriloba						.8	.4		.9			.3														
T. squamata & related spp.				.4										.2	.2			.1		.1						
T. cf. tasmanica						.1	.1				2	1	.3													
Uvigerina laevis																.1										
U. parvula			2	9	7												.2		.5	.9		1	1	3		
U. peregrina						2	12	7	16	7	5	.3	1	.1												
Valvulineria mexicana							11	.7																		
V. minuta																						.1				
Virgulina advena													1													
V. complanata							.1					.9	.6		.2		.2	.2	.5	.1		.2	.2			
V. mexicana							.5	3																		
V. pontoni		.2	1	1	.3	.1										.1	.2	.1	.3	.9		2	2	4		
V. punctata			.2												.8	1	2	2	.5	1		.2		.4		
V. tessellata							.1	.6	13	15	5	.9														
Wiesnerella auriculata												.9			.1							.2				
Miscellaneous spp.	59		1		3	6	11	1	.4	2	6	12	6	2	3	3	2	3	4	3	2	2	1	2		.6

Table 8. Percentage distribution of benthonic Foraminifera in traverses III and IV (pt.).

TRAVERSE	V																																
STATION	97	96	95	93	92	91	90	89	88	87	86	85	84	81	82	80	78	77	76	75	74	99	100	101	102	103	104	105	197	198	200	196	199
DEPTH IN METERS	20	21	?36	36	33	31	35	36	40	40	36	36	36	44	36	42	71	75	99	146	204	238	530	914	1 097	1 822	2 213	1 417	549	549	600	713	735
TOTAL PLANKTONIC POPULATION	64	24	10	600	475	80	24	96	400	275	44	52	150	4	650	125	5 000	1 600	5 800	950	650	900	1 400	2 600	900	3 600	1 900	22 400	4 600	4 800	34 900	17 500	35 300
TOTAL BENTHONIC POPULATION	5 600	4 900	2 100	15 100	22 400	7 300	2 300	3 000	8 000	7 400	1 900	2 200	4 000	1 100	7 000	1 400	22 000	4 400	12 800	5 000	3 100	3 200	2 900	1 300	550	650	650	1 900	1 100	2 500	3 200	4 100	5 800
Adercotryma glomeratum																									1	1	.3		.5	.5		.2	
Alveolophragmium nitidum																							.1		.7	1	.3			.3			
A. ringens																										.3		.4					
A scitulum																											.3						
A subglobosum																							.1		.7			.4		.3			
A wiesneri																									.7	6		.4	.2	.2			
A sp																									1	.6							
Ammobaculites sp A																			.2	.2													
A sp. B																										.3	1						
Ammodiscus spp.																									2	.3	.3		.7				
Ammoscalaria pseudospiralis	.3	.3	.3	.3		.4		.1			.6	.5	1																				
A tenuimarga																										.3							
Amphistegina spp.				.1		.8	3	2	.8	.6	3	1	.8				.3	5				.1											
Angulogerina bella		.2	.3	.1	.6	.2		.1	.8	.2	.2	.7	.2		.5		.9	.4	.8	.8	.5	.4											
A. jamaicensis								.1		.4	.2	.2			.5		1	1	2	4	.8	2	.3	.6	.4								
Anomalinoides mexicana																							.3	1		.6	.3	.4	.5	.3	.2		.7
Asterigerina carinata	2	5	4	2	2	2	3	1	1	2	.6	1	3	2	.7	.6	2	2	.8														
Astrononion tumidum																												.4	.4				
Bigenerina irregularis	1	1		1	2	3	1	2	5	2	2	3	3	4	4	3	5	1	2														
B textularioidea							.7		.2		.9	1	1	2	.9	5	.3	1	.5														
Bolivina albatrossi																				.2	1	3	2	7	3	.3		4	3	3	6	9	9
B. barbata																				2	1	.4	.1										
B fragilis										.2							.3		1	7	3	2	.3										
B lanceolata																			.5	.8	2	1	.4	.3									.3
B. lowmani				.2	.1	.4	.3		.2	.4	.2	.2					1		.2	4	3	3	7	2	3	3	4		1	3	2		1
B minima																				.5	6	4	8	.9						.2	1	.6	2
B ordinaria																							2	4	1	.3			7	9	8	1	6
B paula																							.1	.3									
B pulchella primitiva	.8	.5		.2	.1	.4		.1		.2	.2	.2							.2	.3	.6	.8	.1	.3									
B pusilla																	.3			.3						2	2						
B striatula spinata															.2			.7	1	.6	.5	.1		.3									
B subaenariensis mexicana																			1	4	8	10	1	.6							.8		.6
B subspinescens						.2										.3	.6	1	.5	2	3	4	3	.9		.9	.9		3	2	1		.4
B translucens																				.2	.3	.1	.7	.3	.7								
B sp																														.5			.8
Buccella hannai	1	2	2	.4	1	1		1	.4	3		.4	1		1		.6		.5	.2													
Bulimina aculeata																							3	10	8	2	3	10	4	1	6	3	4
B alazanensis																							1	9	4	.9		4	7	5	1	12	9
B marginata																		.4	.8	3	2	1	.6										.4
B spicata																	.3			1	1	1	.8	2	2	2	1	1	.2	.2		.4	.4
B striata mexicana																					.9	.5	2	2	.4		1	.8	2	2	3	5	5
Buliminella cf bassendorfensis				.1		.2					.2																						
Cancris oblonga	.3			.6	.1	.2			.6	.2	1	.4	.2		1	.9	1	2	2	1	.6	.1											
Cassidulina carinata																							6	1	.4			.4	.9	2	.5	.2	7
C aff crassa																						.3		.6						.3	.2	.2	.3
C curvata												.2					.6	.4	.8	1	2	3	.4						.2	.2	.8	1	
C laevigata																	1	.7	2			.1											
C neacarinata																			.5	3	2	3	4	1				.4	2	1	5	6	1
C subglobosa & variants				.2	1	.2		1	.4	2	6	1	.2	.4	2	.6	4	3	8	17	23	16	11	2	.7	.9	4	8	9	8	4	3	2
Cassidulinoides tenuis																													.5	.3	.2		.1
Chilostomella oolina																				.6	1	.8	1	2	.7		.3		2	1	1	.2	.6
Cibicides corpulentus																			.2	.2					.4				.2	.3	.5		
C deprimus	12	6	9	5	5	3	.7	2	.8	.9	.2	.2	.8	.4	.7		1	2	2	.5	.4	.6		.3									
C. aff floridanus																	2	4	6	5	2	.6	.6	3	1	.6		.4	3	4	5	4	1
C io																	.3	1	1	.2													
C. kullenbergi																										.3							
C. mollis																	.9		1	.3													
C protuberans								.4	.2		.2	.4	.4	.4	.2	1	5	10	2														
C. robertsonianus																								.3	.4	2	1	3		.2			
C rugosa																								.6	.4				.2				

Table 9. Percentage distribution of benthonic Foraminifera in traverse V (pt.).

TRAVERSE	V																																
STATION	97	96	95	93	92	91	90	89	88	87	86	85	84	81	82	80	78	77	76	75	74	99	100	101	102	103	104	105	197	198	200	196	199
DEPTH IN METERS	20	21	236	36	33	31	35	36	40	40	36	36	36	44	36	42	71	75	99	146	204	238	530	914	1097	1822	2213	1417	549	549	600	713	735
Cibicides umbonatus														.4								.4									.2		
C wuellerstorfi																								.6	1	.9	.9	1	.4				
Cibicidina strattoni	17	24	19	20	19	25	26	28	27	27	22	30	35	33	30		14	9	7	1	.5	.1											
Cyclammina spp																									.4			.8	.2	.2	.2		
Dentalina - Nodosaria																			.2	.8								.4	.2	.3	.9	.4	.6
"Discorbis" bulbosa			.3	.1	.6	.7	1	.7	1	2	2	.2	.4	.4	.5	.6	.6		1	.4		.3											
Eggerella bradyi																							.1	.3	.4	1		.4	.2				
Elphidium advenum		.3	2		.1	.2	.3	.3							.4	.3			.2														
E discoidale	.6	2	3	2	1	1	3	2	.6	2	2	2	2	2	2	.6	3	.7	2														
E gunteri	2	9	5	1		.7	.3							.4	.5																		
E poeyanum	2	.7	.8	1	.7	1	1	.3	.6		.2	.4	1	.4	.7	.6	.6			.3													
E spp	4	3	4	2	3	3		2	2	3	3	.7	1	.7		.6	.3	.4		.2	.3	.6	.3	.3									
Epistominella decorata																										4	9	17			.2		
E exigua																						.1	2	2	2	2	3	2	9	9	2	1	3
E rugosa																							1	.3			.3	2	.9	1	1	4	.8
E vitrea		.2			.1			.1			1	.2			.2		.9	.7	.5	.6	.4	.6	.4	.6		.3					.2		
Eponides antillarum				.1	.4	2	4	4	3	.6	2	4	6	9	4	8	1	6	2	.2													
E polius																										.3	.9	3		.2			
E regularis																				1	4	2	2	.6		.3							
E repandus							.7	.1				.2			.2	.3		.4															
E tumidulus																										.3		.4					
E turgidus																		.4		.2	.9	.4	2	1		6	19	8	3	3	.5	.6	2
Pseudoeponides umbonatus															2		.3		.2	.2	.1		.4	.3		1	2		.5	.2	.2	.4	.7
Gaudryina cf aequa													.2			.3	.3	.7	.5														
G cf minuta		.2	.3		.1		.7	.1		.2	.4	.2														.6				.5			
Globobulimina affinis & var																							1	.6	8	.6	1				.5	1	1
Globulina caribaea				.1		.2			.2			.2	.2																				
Glomospira charoides																								.3	.7	6	9	.8		.2		.2	
G cf gordialis																											.9						
Goesella mississippiensis																			.5														
Guttulina australis	.6	1		.7	.3	.7	.3	.5	.6	.4	.2		.4	1															.2				
Gyroidina neosoldanii																													.2		.8		
G orbicularis																						.1			3	2	4	4	.7	.5	.5	1	.3
Gyroidinoides soldanii altiformis																				.3	.5	.3	.1	.6		.3				.2		.6	.6
Haplophragmoides bradyi																					.1			.6	3	2	4	2	.4	2			
Hoglundina elegans																			1	.2			.3						.4	.5	2	.4	.1
Harmosina sp																						.1		.3	3	.3			.5	.5			
Karreriella bradyi																								.3	.4						.2		
Lagena spp & related forms				.3			.7		.6	.9	.6	.5			.5			.7	.2	1	1	.9	1	1	1	2	1	1	2	1	1	.8	2
Laticarinina pauperata																								.3		2		2	.2				.3
Lenticulina peregrina																				.2			.4	.3	.4	.3			.5	.2	1	.4	
Liebusella spp																		.7															
Loxostomum abruptum																							.1	2				.4	.9		.5		
Marginulina marginulinoides																			.5														
Miliolidae	11	5	5	5	4	4	6	3	3	4	6	5	3	3	3	6	10	4	5	1	.3	.1				.6	.3					.2	
Nodobaculariella cassis	.6	.8	.5	.4	.4	.4		.5	1	.4	.4	.2	.6				.9	2	1			.1											
Nodosaria hispida																				.2										.3	.2	.2	
Nonion formosum																		1	1	.2	.1	.1										.2	
Nonionella atlantica	5	2	4	10	6	3	3	4	4	5	5	1	2	.7	3	1	3	1	1	2	.2	1	.2							.2			
N opima	.3	.3		1	.8	.2			.6	.4	.6	.2			.7	.3	.6	.4	1	1	1	1	.7			.3							
Nouria polymorphinoides							.3					.2	.2			.6																	
Osangularia cultur																								5	4	9	5	3	.5	.2	.8	1	.6
Peneroplidae	1	2	4	1	2	4	4	3	4	3	1	6	5	11	3	3	2	1	1														
Planorbulina mediterranensis				.1	.1			.1	.6		.4	.2	.4		2	1		1	.4														
Planulina ariminensis																							.7						.4	.6	1	1	.6
P exarata	2	3	4	4	7	9	12	12	13	12	4	11	13	13	11	43	9	7	6	2	.8	.5											
P foveolata																					.5	.9	.3										
Plectina apicularis																										2	2	.8	.2		.5		
Proteonina atlantica											.2	.2	.8		.7		.6	.4	.2	.2	.3	.3	.3		.4								
P difflugiformis																							.1		3	6	2		.2	.2			
Pseudoclavulina mexicana																					.1												
P aff novangliae																															.5		
Pullenia bulloides																					.3	.5	.3	.3	.7	.3	2	2		.3	.5	.4	.4
P quinqueloba																			.2	.3	.5	.3	.1	1	2	.6	2	2	.6	.3	2	.2	1
Pyrgo murrhina																			.2		.6	.1					.3						
P cf nasutus				.5				.3			.2				.2		.6	1	1	2	.1	.9	.3										
Quinqueloculina bicostata			.3	.3	.4	2	3	2	.4	.9	2	3	.6	3	2	3		.4															
Q compta	2	1	2	.6	1	.4	1	2	2	2	2	3	3	1	2	3	.6	.4	.2														
Q horrida		.3		.2	.1	.7		.1	.2		.4							1	.5	.5	.1												

Table 10. Percentage distribution of benthonic Foraminifera in traverse V (pt.).

TRAVERSE	V																																
STATION	97	96	95	93	92	91	90	89	88	87	86	85	84	81	82	80	78	77	76	75	74	99	100	101	102	103	104	105	197	198	200	196	199
DEPTH IN METERS	20	21	236	36	33	31	35	36	40	40	36	36	36	44	36	42	71	75	99	146	204	238	530	914	1097	1822	2213	1417	549	549	600	713	735
Quinqueloculina lamarckiana	.8	.8	1	.7	1	2	3	2	1	1	2	3	2	3	2	3	3	3	.5	.2													
Q cf polygona		.5		.5	.3	.2		4	.2	.2		.2		.4	.7	3	.6		.2														
Q sabulosa	.8	.3		.6	.3	.4	1		.8		.2	.5		.4		.6	.6	4															
Q sp																	.3								.4			.4					
Rectobolivina advena					.1	.4		.1	.2	.4			2		2		.6		.8	.2													
R dimorpha																														.2	.5	.2	
Reophax bilocularis																											.3			.2		.2	
R distans delicatulus																										1	.3	.4		.5			
R guttifera																									.7				.2	.2			
R hispidulus																				.2	.4	.9					.9	.4	.2	.5			
R irregularis																.3																	
Reussella atlantica	6	2	.5	2	.9	3	2	4	5	3	2	1	1	.4	4	2	8	1	1	2	.4	.5											
Robulus spp					.3				.2	.4			.2			.3	1	3	2	.8	1	1	.8	.3	.4		.3		.4	3	1	4	.1
Rosalina bertheloti																			.2	.3	.1	.1											
R cf concinna	20	12	14	19	26	12	10	6	6	8	8	3	2	7	2	.6	2	3	4	4	3	5	.7	.6									
R floridana	5	8	5	5	3	2	1	.9	.2	1	.4	.4					.6	1		3	.1	.3		.3									
R floridensis																		7															
R parkerae				3	.1				2								.3		.2	.5	.8	6		.3		.6		.4					
R suezensis	1		.8	.9	1	2	1	1	2	1	2	9	1	.4	2	.6	1	2	2	1	2	.9	.3										
"Rotalia" beccarii variants	4	4	6	2	3	2	2	3	2	3	2	2	2	1	1	.4	5																
"R" translucens																					.1	2	14	3	4			2	15	19	8	5	7
Rotamorphina laevigata																				1	1	1	.4	.9	1	.9	.9		.5				.1
Saccamminidae & related forms																										2	.6		2	8			
Seabrookia earlandi																			.5	.5	.4	.5	.3	.6			.3	.4					
Sigmoilina distorta																	.3	.4	.8	1	.9	1	.6							.2			
S schlumbergeri																							.1		.4	.3					.2	.4	
S tenuis																							.3			.3				.3			
S sp																		.4															
Siphonina pulchra							.3						2		.2		.6	.4	2	.3	.4	.3	.1							.2	.8		.1
Siphotextularia curta																										.3							
S rolshauseni																										6	.3	.4					
Sphaeroidina bulloides																			.5	.3	.5	1	2	2	2	.9		8	3	2	6	4	3
S compacta																														6	.2	.2	
Spiroloculina cf grata				.3	.1		.7	.1				.2					.9	.7	.8	.2													
S saldanii				.2					.4			2	.2						2	.3		.1											
Spiroplectammina floridana																	.3	.7															
Stetsonia minuta		.3	.3	.2	.4			.1	.2	.6	.2	.2										.3	.6	.3		.6		.4	.7	1			
Textularia candeiana			.3	.3	.3	.7		.1	.4		.4	.5		.7	.7	.3		.7	.2			.1											
T conica								.3									.3		.2														
T earlandi																				.2		.1		.9									
T foliacea occidentalis																			.2														
T mayori	.3	.5		1	.6	2	2	3	3	1	2	3	4	3	4	6	.7																
Textulariella spp																	.4																
Tolypammina schaudinni																													.2				
Trifarina bradyi																.6		.4		.2									.7	.8	.8	2	2
Triloculina cf brevidentata	1	.2	.8	2	.7			.5	1	1	3	2	.2	1	.2		1	.4		.5	.1	.1											
T tricarinata																						.1											
Trochammina advena																					.1				.4								
T globulosa																									6	4	.6	.4					
T cf japonica																					.1	.1	.4		1	.9	.3		.5	.5			
T quadriloba																									.4								
T squamata & related spp								.1																									
T cf tasmanica		.3															.3									.9			.2				
Uvigerina auberiana																										.3						.2	
U hispida-costata																													5	.2	6	13	8
U laevis																			2	4	4	5	3	1					.2				
U parvula								.1				.2			.2		.3	1	4	3	1	1	.3	.6									
U peregrina																					2	6	2	14	10	3	1	3		2	8	13	9
Valvulineria minuta																			.2		.9	.8	.3		.4				.4	1		.2	.7
Virgulina advena																											.6						
V complanata	.3			.2					.2												.1	.1	1				.6		.2	.3	.2	.2	.3
V mexicana																					.1	.1	1	.3					.4	.4	.8	.2	1
V pantoni										.2												.1	.4										
V punctata	.3	.2	.5	1	1	.6		1	1	2	5	2	.2		.9	.6		.7	1	2	1		.2										
V tessellata																							.7	2	8		.3		1	2	.5		.6
Wiesnerella auriculata	.3			.3	.1	.2			.2		.2	.2																					
Miscellaneous spp	.1	1	1	3	1	2	1	2	.8	1	1	1	.4	1	1	.8		4	4	4	2	1	1	2	2	6	4	4	1	.4	3	1	2

Table 11. Percentage distribution of benthonic Foraminifera in traverse V (pt.).

TRAVERSE	VI																																		
STATION	73	72	71	70	69	68	67	66	65	64	63	62	59	58	57	56	55	54	53	52	51	50	49	48	47	46	45	44	43	42	41	40	39	38	106
DEPTH IN METERS	20	22	24	24	29	27	24	39	43	49	55	64	91		106	113	119	128	139	146	155	165	183	223	446	555	631	650	677	823	860	960	1144	1573	2697
TOTAL PLANKTONIC POPULATION	0	10	48	4	6	0	10	49	11	64	275	350	700	6 200	5 000	8 200	7 400	5 300	12 700	11 700	18 400	10 500	19 800	6 500	26 200	12 100	11 300	11 200	5 600	11 500	14 300	19 500	53 000	20 200	13 000
TOTAL BENTHONIC POPULATION	250	1 800	6 700	850	375	400	1 100	1 100	275	1 700	4 200	3 300	4 300	29 100	24 300	28 000	12 100	18 700	23 600	27 500	9 600	9 000	13 800	2 100	7 800	3 100	2 200	1 600	1 600	2 500	2 100	3 600	5 100	1 300	600
Adercotryma glomeratum																											.1		.3	.3			.3		.6
Alveolophragmium nitidum																									.1	.1					.2	.1		.2	.3
A. ringens																														.2					
A scitulum													.1																.1	.2		.2	.2	.5	.3
A wiesneri																										.1					.6	.1		.2	
A sp										.1	.2		.1																			.1	.2		
Ammobaculites sp B																														.2					.3
Ammodiscus spp							.2																		.1						.2	.1	.2		
Ammoscalaria pseudospiralis													.3																						
Amphistegina spp		.2			2	13	.2	6	28	50	48	19	15	2	.8	.9																			
Angulogerina jamaicensis							.4	.5		.1	.4	.1	.5	2	1	.7	2	1	1	.8	.3		.3					.1	.3						
Anomalinoides mexicana																								.2	.3		.1		.3	.5	.2	.2			
Asterigerina carinata	4	12	10	9	15	21	3	4	3	3	2	4	.8	.1		.5		.2	.1	.1		.4													
Astrononion tumidum																										.1									
Bigenerina irregularis		1	1	1	4	1	.9	2	4	.6	1	2	3	.8	.4	.2	.5			.2	.2														
B textularioidea		.1		.5	2	.5	.7	2	3	2	3	3	6	.5	.3			.2																	
Bolivina albatrossi													.1							.1	.3	.2	.7	5	10	4	6	7	6	7	6	4	3	.5	
B barbata																							.1												
B fragilis														.2	2	2	3	.5	3	3	2	1	2	1											
B goesii																			.1	.2		.4	.2	.4											
B lanceolata												.6	.3	.2	.1	.2	.5	2	.5	.3	1	1	2												
B lowmani							.5	.3				.1	.1	.3	1	2	3	4	4	4	8	4	7	4	2	2	2	1	.5	3	3	.4	.8		2
B minima																.5	.5		.8	1	5	6	6	7	4	.8	.1	.1			.2				
B ordinaria																.2		.2	1	2		.2		.8	4	5	8	3	.3	.8	.8	.6	.3	.3	
B paula															.1		.3																		
B pulchella primitiva		.7	.7		.5		.5	.1					.2	.9	.9	1	.3	1	.4	.7															
B pusilla																																			1
B striatula spinata															.7	.5		.7	.7	.9	.5	.2													
B subaenariensis mexicana															.1	.7	.8	.2	.5	.7	3	11	17	16	.7										
B subspinescens													.2	.6	2	.7	.3	.5	1	1	.7	1	.7	2	1	1	.9	.5	.3	.6	.2	.2			.3
B translucens																				.1	.2		.2	.6	.3	.1	.3								
B sp																												.4	.4	.6		.3	.2	.2	
Buccella hannai		.9	2	1	.5	.5	1	1		.1			.1	.7	.4		.5	.2																	
Bulimina aculeata																								.2	.7	1	3	3	1	3	2	6	7	4	.3
B alazanensis																									.7	4	6	7	8	9	7	10	5	.5	
B marginata													.1	.1	.3	.2	.8	2	3	3	2	3	1	.8	.2										
B spicata													.1			.5	.3	.7	.5	.2		.2	.3	.4	.1	.3	.3	1	1	1	.6	.8	.8	3	
B striata mexicana																								1	2	2	2	1		.2	.4	.1	.2	3	.6
Buliminella cf bassendorfensis																			.3																
Cancris oblonga						.5	.4	.2		.1			.5	.5	1	1	1	2	1	.9	.5	.9	.3	.6											
Cassidulina carinata									.4												.3	.4	.1	.6	.3	.4	.9	.1	.1	.2			.2	2	
C aff crassa																				.2		.4	.8	.4	2	.8			.3	.2			.3	2	
C curvata												.2	.6	2	1	3	2	.3	1	3	5	3	2	2	2	1	.3		.3						
C laevigata								.5		.1		.1		.7	.7	.7		.2																	
C neocarinata													.1			.2	2	1	6	7	10	4	8	4	7	4	.7	.2		.2	.6	.1			
C subglobosa & variants	.8	.2	.2	.2			1	1		.2	.2	.9	2	9	13	13	9	15	9	5	4	4	2	1	1	9	10	14	16	15	12	15	13	6	1
Cassidulinoides tenuis																										.1	.4	.5	.4	.3	.4	.3	.6		
Chilostomella oolina																			.1	.1		.2		1	.8	1	2	2	.4	.3	.4	.1	.2		.3
Cibicides corpulentus																			.3		1	4	.5	.2			.5				.2	.4	.6		
C deprimus		1	4	4	2		3	1		.1	.2	.1	.5	2	1	3	2	1	.5	.7							.1	.1							
C aff floridanus								.2				.9	3	5	2	2	4	2	5	6	2	2	3	2	2	4	4	4	3	2	3	3	5	.8	
C io												.2	.2	.5	.5	.7		.3	.3																
C kullenbergi																																.1		.5	2
C mollis											.2	1	.9	.8	.7	.5	2	.5	.3	.3															
C protuberans								1	.4	.3	.6	2	1	4	3	4	5	.7	.4	.8	3	4	.7												
C robertsonianus																									.1	.1	.3	.4	.4	.3		.4	2	.8	2
C rugosa																											.1	.1	.5	.5	.2	.4	.8	.5	
C umbonatus																	.3		.1	1	3	3	5	5	1										
C wuellerstorfi																														.5	1	2	3	3	9
Cibicidina strattoni	4	10	11	5	5	3	11	6	2	.6	.8	4	4	5	3	2	.8	.7	1	1	.2														
Conorbina orbicularis								.1						.1	.4	.5	.3				.2			.2											
Cyclammina spp																											.1	.1		.2					
Dentalina - Nodosaria													.2		.1			.2	.5					.2	.6	.1	.1	.1	.1			.1		.4	

Table 12. Percentage distribution of benthonic Foraminifera in traverse VI (pt.).

TRAVERSE	VI																																		
STATION	73	72	71	70	69	68	67	66	65	64	63	62	59	58	57	56	55	54	53	52	51	50	49	48	47	46	45	44	43	42	41	40	39	38	106
DEPTH IN METERS	20	22	24	24	29	27	24	39	43	49	55	64	91		106	113	119	128	139	146	155	165	183	223	446	555	631	650	677	823	860	960	1144	1573	2697
"Discorbis" bulbosa		.2	.2	.7	1		2	.5				.1	.1	1	.3	.9	.3	.7	.5	.6	.7	.2													
Eggerella bradyi																									.1	.4	.2	.2	.3	.5	.2	.3	.2	.8	5
Elphidium advenum		1	.2	.5	2	2	.4	.7	.4	.1	.2		.1																						
E discoidale		2	2	3	.5	4	2	3	2	.6	.8	2	2	2	.8		.3		.7																
E gunteri		.1						.1	.4																										
E poeyanum	.8	.6	1	1	2		.5	.4		.2		.1		.5	.2		.3																		
E spp	8	3	3	1	.5	2	1	1						2	4	5	6	4	4	3	.8	.9	.1												
Epistominella decorata																														.3	.8	.3	.5	22	13
E exigua																								.2	2	8	7	8	9	7	8	7	3	3	.3
E rugosa																									.6	2	.7	2	.6	3	1	4	2		
E vitrea														.7	.1	.2	.3		.1	.1	.3				.1	.4		.2		.5	.2				
Eponides antillarum						.5		.6	.4	.6	1	2	2	.4	.3	.2																			
E palius																														1	1	.9	.3		4
E regularis																				.2				.2					.9						
E repandus		.1			.5	.5		.7	.8	5	5	.9	1									.2													
E. tumidulus																											.1			.3	.2				3
E turgidus							.2					.1	.2	.2	.5	.7	.3	2	.5	2	.5	.4	1	1	.2	3	5	1	6	5	8	3	2	4	19
Pseudoeponides umbonatus												.1	.3			.2	.8	.2		.1		.2	.2		.3	.8	.8	.9	.1	.2	.4	.4	.2	2	2
Gaudryina cf aequa														.3	1	.7	.5			.3															
G (Pseudogaudryina) atlantica																						.2		.2											
G flintii																								.2									.5	.2	
G cf minuta						.5	.7	.2																		.3	1	.4	1	.6	1	.1			
Globobulimina affinis & var																						.4	.2	.2			.4	.1	.1			.1	.2	.6	
Globulina caribaea			.7	.2	.5	1	.4	.7			.6																								
Glomospira charoides																					.2				.1	.1	.4	.2	.1	.5		.1	.6	.2	
G cf. gardialis																																			.6
Guttulina australis		.3	.7	.7				.4		.1	.2	.2																							
Gypsina vesicularis		.1				.5		.3		1	1	.6	.8	.3																					
Gyroidina neosoldanii																													.3				.8	.2	
G orbicularis																						.2	.1	.6	.3	.6	1	.6	.9	1	.6	1	3	4	2
Gyroidinoides soldanii altiformis																					.2		.3		.1	.4	.2	.4	.1	.5	.6	.9	.5	.3	
Haplophragmoides bradyi																					.2					.3	1	.5	1	2	2	1	.6		2
Haglundina elegans												.2		.5	.8	.7	1	.9	.7	.9	.3	.4	.6	.4	2	.3							2	8	1
Hormosina sp																										.1	.2		.5	.5	.2	.6	.2		
Karreriella bradyi																			.1	.1	.5			.4	.5			.1	.1	.5		.2	.2	.2	.3
Lagena spp & related forms	.8						.2	.1						.8	.8	1	.8	.2	1	1	.8	.7	.5	1	2	2	2	2	1	2	2	2	1	2	5
Laticarinina pauperata																									.2	.8	1	1	.9	1	.8	.4	.9	1	.6
Lenticulina peregrina																					.2	.2	.3	.2	.5	.5	.8	.9	.7	.8	.4	.8	.2	.2	
Liebusella spp																		.2	.4	.1	.2		.6												
Loxostomum abruptum																									.1	.5	.3	.4	1	2	2	.9	.3	2	
Marginulina marginulinoides																	.3		.3		2	.7	.1		.1										
Miliolidae	7	5	6	5	6	6	6	6	10	4	3	5	4	8	10	9	4	8	7	4	.7	1	.2	.4			.1	.1							2
Nodobaculariella cassis		2	1	2	6	2	3	1	11	3	3	5	1	.5		.2			.1	.1															
Nodosaria hispida																								.4	.9										
Nonion formosum														.2	.4		.5	.2	.5	.2	1	1	.8					.2	.3			.1	.2		
N pompilioides																																			1
Nonionella atlantica		3	4	3	1	2	1	2	.8	.1		.2	.6	2	2	2	.8	1	.5	.7	.7	.4			.3										
N opima		.2	.2			.5		.1						.9	.5	.7	.3	.5	.1	.5		.1		.4			.1			.5	.4				
Osangularia cultur																										.1	1	3	6	5	5	3	2	.2	.9
Peneroplidae	.8	7	9	9	9	17	6	4	4	3	3	5	2	.2	.4				.1																
Planorbulina mediterranensis				.2				.4	.4	.6		.4	.3	.1																					
Planulina ariminensis																						.2	.5		1	1	.6	.2	.1	.5	.2				
P exorna	.8	5	5	10	9		16	2	8	2	.8	3	2	2	3	.9	1	.2	.3	.1		.2													
P foveolata																.2	.5	.3	1	2	4	5	2	1											
Plectina apicularis																										.1		.1	.5						3
Proteonina atlantica								.1				.1																							
P difflugiformis																				.1	.2	.2		.6		.3	.1	.1	.9	.6	.2	.1			.9
Pseudoclavulina mexicana													.7										.1		.5										
P aff novangliae																			.7	.2	.8		.2	.8											
Pseudoglandulina comatula																					.2	.4													
Pullenia bulloides																					.2		.5	1	1	.4	.2	.6	.3	.3	.2	1	.9	.2	.6
P quinqueloba														.2		.5			.7	.1	.5	.2	.2	.2	.1	.1	.4	.6	.6	.2	.8	1	.9	1	1
P sp																																.1			
Pyrgo murrhina								.1									.3								.1					.2	.6	.1		.6	
P cf nasutus								.2					.3	.4	.8	.7	.3	.5	.5		.3	.4	.2	.4	.2										
Quinqueloculina bicostata		.1		.2		1	.2	.8	2	.6	1	.2	.4	.1																					
Q compta		.5		.7	2	2	.7	.7	.8	.7		1	.5	.4	.1	.2	.5		.3																
Q horrida								.4		.7	.6	1	5	1	.4	.2	.5	.2	1	.7	1	.5	.7												
Q lamarckiana		2	.5	.2	2	4	.9	4	8	7	11	8	6	2	.9	.7	1		.2	.2	.8		.6												
Q cf polygona		.7	.2		.5	.5		.1		.2	.4	.7	.2	.2																					

Table 13. Percentage distribution of benthonic Foraminifera in traverse VI (pt.).

TRAVERSE	VI																																		
STATION	73	72	71	70	69	68	67	66	65	64	63	62	59	58	57	56	55	54	53	52	51	50	49	48	47	46	45	44	43	42	41	40	39	38	106
DEPTH IN METERS	20	22	24	24	29	27	24	39	43	49	55	64	91		106	113	119	128	139	146	155	165	183	223	446	555	631	650	677	823	860	960	1144	1573	2697
Quinqueloculina sabulosa	.8	.1	.2	1			.2					.2	.1	.1																					
Q venusta																																			.3
Q sp																																		.3	.6
Rectobolivina advena			.5	.2			.4	.1				.1		.8	1	.5	.3	.3	.1	.2			.1												
R dimorpha																									.1	.1	.2	.1		.2			.3		
Reophax bilocularis																									.3	.3	.1		.4	.2				.2	
R distans delicatulus																															.2				
R hispidulus															.1										.1			.7	.1	.2	.4				
R irregularis											.2	11	9		.1						.7	.2	.2												
R scorpiurus																					.2				.3										.3
R sp																										.1									
Reussella atlantica		.9	1	1	.5	2	2	5	3	.7		.7	.4	.9	2	1	.5	.5	.8	.7	.2	.2	.1												
Robertina bradyi															.1								.2											.2	
Robulus spp							.2	.6	.4	4	4	2	5	1	1	2	.8	.9	3	2	2	4	3	3	1	.3	.7	.2	.1		.2			.2	
Rosalina bertheloti														.4	.4	.9	2	.9	2	1	2	1	.8	.2											
R. cf concinna	14	15	19	23	15	5	18	7	.4	.5		.6	2	14	12	11	15	12	8	9	.8	.4	.2	.8											
R floridana	15	7	10	7	2	.5	4	2		.2	.2	.2	.4	3	3	2		.5	.7	.8															
R floridensis									.4	.8	1	2	.8	.5		.2				.1															
R parkerae	.8	.3	.2					.5				.1		.2	.9	1		.7	.8	.6		.4	.1												
R suezensis		2	.2			.5	.5	.3				.1		1	1	1	1	2	3	4	2	2	1	.4											
"Rotalia" beccarii variants	34	6	1	2	1		2	.7	.8				.2	.1	.1	.2		.2																	
"R" translucens																						.2		5	15	20	8	7	7	4	4	3	2	2	
Rotamorphina laevigata														.1				.2	.4	.2	.2	.2	.7	1	.2	.9	.8	.7	.4	1	.4	.6		.3	
Saccamminidae & related forms																								.2		.4	.5		.6	.2	.6	.1	.3		1
Seabrookia earlandi															.3				.5	.2	.2		.2			.3	.2				.2	.1		.2	
Sigmoilina distorta													.4		.8	.9	1	2	1	1	1	1	3	.6	.3										
S schlumbergeri																									.6		.5	.4	.4		.2	.1	.5	1	.3
S tenuis																									.6	.1	.2	.1	.1		.2	.1	.5	.6	
S sp						1		.2			.2	.6									.2														
Siphonina bradyana																					1	.5	.8	.4	.8	.3	.1	.2							
S pulchra								.2		.2		.4	.2	.9	1	1	2	1	2	2	3	2	.8	.6	.3		.2		.1						
Siphotextularia curta																																	.2	.2	.3
S rolshauseni																																	.3		.3
Sphaeroidina bulloides															.3		.3	.2	.4	.3	.3	.4	.2	1	4	2	2	3	3	2	2	1	.5	.6	.3
S compacta																					.2									.3		.2		.5	
Spirillina vivipara						.5		.1		.5				.8	.4	.2	.3	.7	.4	.5	.5	.2	.1												
Spiroloculina cf grata		.6	1	1			.4	.5						.4	1	.7	1	.9	.1	.2															
S soldanii		.1	.2	.2				.1					.1	.4	.4	.2		.2		.1				.2											
Spiroplectammina floridana								.1	.4	.3	.6	1	2																						
Stetsonia minuta		.5	.2				.5	.2						.3	1	1	1	1	.3	.6					.3	2	.8	.2	1	.5	.6	.3	.9	.2	.3
Textularia candeiana		1	.5	2			.9	1	.4	.3	.2	.4	.4	.3						.1			.4	.4											
T conica		.3				1	.5	1	2	2	2	.5	1	1		.2																			
T foliacea occidentalis												.6	.4	.5		.2		.5	.6	.2	.3	1			.2										
T mayori		.1	.2	.2		1	.2	1	.4	.1	.2	.5	.8	.1						.1		.4	.1												
Textulariella spp										.1		1	2	.2																					
Tolypammina schaudinni																																			
Trifarina bradyi															.1			.2							.6	.9	.5	.7	1		.8	.1	.2		
Triloculina cf brevidentata	.8	2	.5	2	.5		2	1		.2	.2		.5	.5							.3														
T tricarinata																																		.5	.3
Trochammina advena																											.4			.8					
T globulosa																																	.3		1
T. cf. japonica																													.6			.1	.2		
T squamata & related spp	5	1		.7	2		1	.1	.4																										
T cf tasmanica																											.2					.1			
Uvigerina auberiana																									.1		.2					.1	.2		
U flintii																	.3	.3	1	.7	1	2	.7												
U hispida-costata																								3	10	.6	.6								
U laevis													.2	1	3	3	3	7	4	6	4	5	7	8											
U parvula														.8	2	2	2	4	4	4	6	7	6	2	.2										
U peregrina																									2	2	7	14	10	7	10	17	25	9	
Valvulineria minuta																.2		.6			.3		.2	.6	.5	1	.1			.2		.3	.3		
Virgulina advena																																			2
V complanata													.1	.1	.3		.5	.2	.1	.1				.4	.4	.3	.4	.2	.5	.3	.4	.1	.2		
V mexicana																.2		.2							.7	.1	.7	.2	.1						
V pontoni														.1			.3				.3														
V punctulata		.2	1	.2	.5		1	1					.2	2	2	2	1	2	.8	.6															
V tessellata																									.3	1	1	.5	1	.2	1	.3			
Wiesnerella auriculata	2	.8	.7	.2		1	.7	.4						.1																					
Miscellaneous spp	.6	3	1	1	5	2	1	2	1	3	3	4	4	3	2	2	6	4	2	3	3	3	4	5	5	4	2	2	.3	.2	3	2	1	3	5

Table 14. Percentage distribution of benthonic Foraminifera in traverse VI (pt.).

TRAVERSE	VII																		
STATION	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	107
DEPTH IN METERS	22	31	46	49	86	146	183	186	237	274	274	320	347	457	585	732	878	2999	3017
TOTAL PLANKTONIC POPULATION	12	8	34	450	150	2 300	27 100	12 800	19 500	14 000	14 800	20 700	60 900	200 000	56 800	16 000	34 600	47 300	40 400
TOTAL BENTHONIC POPULATION	1 900	1 400	1 500	17 100	2 400	5 300	46 700	12 800	27 900	6 600	6 400	3 100	10 300	7 400	5 600	4 500	4 000	1 300	1 600
Adercotryma glomeratum											.1					.2	.1	2	3
Alveolophragmium nitidum													.1	.1			.2	.2	
A subglobosum																		.5	
A sp				.1															
Ammobaculites sp 8																		.9	.5
Ammodiscus spp																.1			
Ammoscalaria pseudospiralis	.2	.8																	
A tenuimargo																		1	1
Amphistegina spp	.2		5	1	11	16													
Angulogerina bella			.3	.6		.1													
A jamaicensis	.5		.3	.2	.8	.3													
Anomalinoides mexicana											.4	.3	.2	.5	.9	1	.9		
Asterigerina carinata	.8	6	3	15	7	1													
Astrononion tumidum												.1		.2	.1	.3			
Bigenerina irregularis	1	5	.7	.7	.3	.3													
B textularioidea	.2	.6	6	2	3	2													
Bolivina albatrossi							.7	.9	3	5	7	8	10	7	3	5	3		
B barbata						.1													
B fragilis				.1	.3	.7													
B goesii						.1	.3	1	1	.2									
B lanceolata			.1		.2	.6	3	2											
B lowmani	.3				.2	2	8	2	4	1	3	.9	1	.8	1	1	.7	2	1
B minima						.1	3	2	6	2	6	6	6	3	.9	.9	2		
B ordinaria						.2	4	3	7	3	4	4	15	3	8	1	.3		.5
B paula	.2	.3																.2	
B pulchella primitiva	.4		.5	.1	.3	.4	.1	.1	.1								.1	2	.5
B striatula spinata						3	.7	1	.5										
B subaenariensis mexicana							4	12	10	11	9	2	.3						
B subspinescens					.2	.3	.8	1	3	2	2	2	2	1	.9	.4	.2	.2	
B translucens										.2	.4	.8	.2	.4	.4				
B sp.														.1	.6	.5	.7		
Buccella hannai	.5	.8	.1	.2	.3		.1												
Bulimina aculeata											.1	.1	1	.8	3	2	3		
B alazanensis														1	3	5	6	.2	
B marginata							.1	1	1	.7	.3	.3	.2						
B spicata									.8			.6	.6	.2	.3	.3	.7		
B striata mexicana												.1	.1	.2					
Cancris oblonga			.3	.1	.3	.6	.1		.3										
Cassidulina carinata				.1			2		1	4	1	2	1	3					.5
C aff crassa						.4	.6	.8	.2				.9	2	.3		.1		
C curvata					.4	.7	4	5	5	1	2	1	1	4	2				.5
C laevigata												.1							
C neocarinata					.2	3	7	11	8	2	5	9	5		2	.5	.1		
C subglobosa & variants	.2		.7	.6	3	9	4	2	6	4	7	6	4	6	9	16	9	1	1
Cassidulinoides tenuis													.1	1	1	.3	.3		
Chilostomella oolina										.2		.5	.2	.8	1	.7	.4		
Cibicides corpulentus						.1	.1	1	.3	.5	.1	.4	.2	.1	.3		.1		
C deprimus	1	1	.7	.7	1	.9	.1	.4	.1			.3	.1	.2			.3		
C aff floridanus					.6	2	7	4	.9	5	2	3	2	1	3	2	1		
C io					.1														
C kullenbergi																	.6	1	.5
C mollis						.3	.1							.2					
C protuberans	.3		.5	.8	.9	4	1	4	.9	1						.3	.3		
C. robertsonianus										1	.1	.1	.1		.7	.3	.4	2	2
C. rugosa																3	.5		
C umbonatus							1	3	2	.5	2	3	1						
C. wuellerstorfi														.1	.9	.5	1	21	15
Cibicidina strattoni	9	19	5	6	2	.4													
Conorbina orbicularis					.3	.2													
Dentalina - Nodosaria										.2		.3	.4	.3		.1	.2		

Table 15. Percentage distribution of benthonic Foraminifera in traverse VII (pt.).

TRAVERSE	VII																		
STATION	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	107
DEPTH IN METERS	22	31	46	49	86	146	183	186	237	274	274	320	347	457	585	732	878	2999	3017
"Discarbis" bulbosa			.4			.1	.1												
Eggerella bradyi																.2	.4	3	1
Elphidium advenum	.5	2	.7	.6	.5														
E discaidale	2	7	.7	.6	.1	.1													
E gunteri	.8			.4															
E poeyanum	1	.6																	
E spp	4	1	1	.9	5	2	.3												
Epistominella decorata																		13	18
E exigua													.4	3	6	8	14		.5
E rugosa												.1	.9	2	1	3	2		1
E vitrea				.1		.5	.3	.2			.3	.1	.2	.4	.4	.2			
Eponides antillarum	.2		3	.6		.1													
E palius																1	.5	4	5
E regularis																			1
E. repandus		.3	.3		.3	3													
E tumidulus																		3	3
E turgidus							2	.9	4	1	4	1	.4	2	4	7	5	5	8
Pseudoeponides umbonatus								.1		1	.6	.5	.2	.3	.1	.4	.3	3	3
Gaudryina cf aequa				.2															
G (Pseudogaudryina) atlantica								.1	.1	.5									
G flintii																	.2		
G cf minuta	.5	1							.1		.1	.1	.2	.1	.1	.1	.2		
Globobulimina affinis & variant									.1								.1	.3	1
Globulina caribaea		.6	1																
Glomospira charoides								.1		.2			.3					.5	.5
G cf gordialis																		.3	1
Guttulina australis	.1	.3	.3																
Gypsina vesicularis			.5	.5	.4	.3													
Gyroidina neosoldanii								.1									.1	.8	
G orbicularis							.3		.5	.2	.6	.1	.4	.2	.4	2	2	.2	
Gyroidinoides soldanii altiformis								.2	.1		.3	.3	.2	.6	.6	.7	.3		
Hoplophragmoides bradyi													.1	.1	.1	.6	.3	2	2
Hoglundina elegans						.2	.3	1	.8	.5	.3	.5	.4	1	1		1		5
Harmosina sp											.1	.1				.2			
Karreriella bradyi								.4		.7	.3		.2			.1	.4		
Lagena spp & related forms	.2		.8	.2	.2	.6	.4	1	1	2	.8	1	.6	2	2	3	3	6	3
Laticarinina pauperata													.2		.3	.9	1	.9	
Lenticulina peregrina							.1	.1	.2		.3	.5	.5	.4	.3	.8	1		
Liebusella spp					.2	1		.6	.2	.2									
Loxostomum abruptum														.1	.1	.6	3	.3	.5
Marginulina marginulinoides								.2	.1										
Miliolidae	14	9	10	15	11	6	2	1	.8		.1	.3	.2						
Nodobaculariella cassis	.5	.3	1	7	2	.8													
Nodosaria hispida												.1	.2	.3					
Nonion formosum					.1	.1	.3	.8	.1		.3				.1				
N pompilioides																		2	2
Nonionella atlantica	2	2	1	1	1	.7					.1	.1							
N opima	.9		.3																
Nouria polymorphinoides	.1	.3	.1																
Osangularia cultur															.4	3	3	.3	.5
Peneroplidae	2	4	14	10	5	.5													
Planorbulina mediterranensis		.3	.9	.3	.6	.3													
Planulina ariminensis								1	.6	.5	.3	.4	.9	2	1	.2			
P exorna	2	13	9	8	3	2	.4	.6	.3										
P faveolata							4	3	3	3	2	.9	.2						
Plectina apicularis									.2					.1			.1	3	2
Prateonina atlantica	.1							.1		.2									1
P difflugiformis													.1					1	
Pseudoclavulina mexicana					.2		.1	.2	.3	.5	.3	.4	.1	.3					
P aff novangliae						.1	.3	.1		1	.3	.3	.1						
Pseudoglandulina comatula						.2		.1	.1										
Pullenia bulloides						.3	.3	.2	.9	.7	.9	.8	.6	.7	.3	.5	.5	1	1
P quinqueloba						.2	.3	.6	.1	.5	.4	.4	.2	.7	.8	1	2	.9	2
P sp																		.3	
Pyrgo murrhina									.1	.2	.4	.1	.3	.2		.4	.8	.6	
P cf nasutus	.4			.2		.3						.1							
Quinqueloculina bicostata	.3	.6	2	.1	.2														
Q compta	1	2	.8	.1	.2	.3													
Q horrida	.3		2	1	.5	.3			.1			.1	.1						

Table 16. Percentage distribution of benthonic Foraminifera in traverse VII (pt.).

TRAVERSE	VII																		
STATION	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	107
DEPTH IN METERS	22	31	46	49	86	146	183	186	237	274	274	320	347	457	585	732	878	2999	3017
Quinqueloculina lamarckiana	3	1	4	3	2	2	.1		.1		.1								
Q cf polygona			.3			.2													
Q sabulosa	.2	.6		.2															
Q venusta																		.9	.5
Rectobolivina advena		.3	.1	.8	.7	.6	.3												
R. dimorpha															.1	.1	.2		
Reophax bilocularis												.4	.1	.3		.4	.4		
R. distans delicatulus																		3	1
R guttifera										.2			.1						
R hispidulus			.1					.1	.1	.2	.1	.3	.2	.2				.8	.5
R irregularis			2	2	1	1													
R. scorpiurus																		.5	
Reussella atlantica	1	2	3	1	.6	1	.4	.1											
Robertina bradyi							.1					.1							
Robulus ssp			4	1	1	2	3	3	3	2	1	1	1	.8	.2	.2	.1		
Rosalina bertheloti					.1	.4	2	1	.9	.7	.3								
R cf. concinna	13	7	4	8	13	5	2	.4		1	.3	.4	.2	.1			.1		
R. floridana	3	.6	.4	.2	.9	.1	.3												
R floridensis				.3	.4	.8													
R parkerae	.4	.6		.1	.7	.6	.1		.1										.5
R suezensis		.8	.9	1	1	.9	2	2	2	1	.3	.3							
"Rotalia" beccarii variants	24	4	1	.5	.1														
"R." translucens							.1		1	10	14	16	19	25	27	11	5	.2	.5
Rotamorphina laevigata						.1	.1	.9	.7	.5	2	.3	.1	.4		.6	.9		
Saccamminidae & related forms																.1			
Seabrookia earlandi			.1		.1	.2			.1	.7	.5	.5	.1	.4	.5	.4			
Sigmoilina distorta					.2	.1	1	.5	.5	1	2	2	2	.2					
S schlumbergeri								.4			.1		.5	.5	.4	.2	.3	1	
S. tenuis												.1	.1	.1	.4	.3	.6		
S sp					1	3			.2										
Siphonina bradyana								.4				.5	.4	.6	.1				
S pulchra				.3	.1	.7	2	2	.8	1	.5	.1	.1	.4					
Siphotextularia rolshauseni																		.3	1
Sphaeroidina bulloides						.3		.5	.6	.7	1	2	.9	1	.9	2	2		.5
Spirillina vivipara	.1			.2	1	.7	.3												
Spiroloculina cf grata	.5		.3		.3	.2													
S saldanii	.1	.3	.1			.2													
Spiroplectammina floridana			.5	.2	2	.3													
Stetsonia minuta						.1	.3	.1	.3				.2	.7	.4	.5	.6		
Textularia candeiana	.8	.3	1	2	.7	.2	.3	.2	.2	1	.4	.3	.5						
T conica	.2	.8	1	.5		1		.4		.2	.3								
T foliacea occidentalis					.2	.4		.2											
T. mayori	1	2	.7	.9															
Textulariella spp				.4	2	2		.1											
Tolypammina schaudinni																			.5
Trifarina bradyi										.2		1	1	1	2	.9	.9		
Triloculina tricarinata												.1							
Trochammina globulosa																		1	
T. cf japonica						.1						.1				.2			
T. quadriloba									.1										
T squamata & related spp	1			.3	.1														
Uvigerina auberiana												.4			.1		.1	.2	
U. flintii					.3	.3	.4	.6	.4	1	.3	.1	.1						
U hispido - costata												2	6	3	.1				
U laevis					.2	1	6	4	6	9	5	3	.6	.1					
U parvula						.4	9	8	4	3	2	.8	.2						
U. peregrina									.3	2	2	3	2	1	2	6	14	.2	
Valvulineria mexicana																			.5
V minuta						.2	.3	.2	1	1	.9	.9	.7	.8	.6	.7	.3		.5
Virgulina advena																		.8	
V complanata					.1		.3	.2	.1		.5	.3	.2	.3	.7	1	.5	.2	
V mexicana												.6	.5	.3			.1		.5
V. pontoni	.2		.1																
V punctata	.9	.3	.8	.3	.6	.9		.1											
V tessellata														.6	.6	.7	.4		
Wiesnerella auriculata	.3	.3			.8	.1		.1											
Miscellaneous spp	2	1	2	1	5	3	6	4	2	6	2	3	2	3	2			5	5

Table 17. Percentage distribution of benthonic Foraminifera in traverse VII (pt.).

TRAVERSE	VIII																								
STATION	172	171	170	169	168	167	166	165	164	163	161	160	159	158	157	156	155	154	153	152	151	150	149	148	146
DEPTH IN METERS	?12	15	20	20	22	26	29	31	31	36	35	46	51	60	62	58	79	117	146	183	366	585	914	1730	3164
TOTAL PLANKTONIC POPULATION	2	0	0	0	0	0	0	0	64	200	1 700	88	175	650	1 600	500	3 000	37 200	38 500	38 500	25 900	16 200	14 900	15 700	65 000
TOTAL BENTHONIC POPULATION	800	2 100	5 400	20 500	900	2 300	5 800	36 400	29 900	18 900	60 500	4 900	3 600	5 700	17 400	22 900	7 500	19 400	19 800	23 700	11 100	3 300	3 000	1 600	1 600
Adercotryma glomeratum																									2
Alveolaphragmium nitidum																							.3	.2	
A subglobosum																							.3	.2	
A. wiesneri																							.4		
Ammobaculites sp B																								.2	2
Ammodiscus spp																							.1		
Ammoscalaria pseudospiralis																				.3					
A tenuimargo																									2
Amphistegina spp				.8	3	.4	.2		.1	3	2	2	25	4	2	3	17	1							
Angulogerina bella																	.2	.5		.3					
A jamaicensis											.1			.4	.1					.3				.2	
Anomalinoides mexicana																						.5	.5	.5	
Asterigerina carinata	5	15	36	18	24	31	28	8	5	2	.1	7	7	8	19	31	2		.3	.3					
Astrononion tumidum																					.1	.4	.4		
Bigenerina irregularis	.3		2	.8	.2	.7	.8	1	2	3	2	1	1	2	2	.6	1	.5		.6					
B textularioidea			.1			.6	.7	1	1	2	.7	2	9	9	5	.4	3			.3					
Bolivina albatrossi					.2															.3	6	4	5	.5	
B fragilis														.1	.3			.3	.3	2					
B goesii																			4	1					
B. lanceolata															.1			2	4	2	.3				
B lowmani										.2	.3	.2	.1		.1	.1	.2	2	2	4	2	2	.4	8	.8
B minima																			4	12	14	2	.1		
B. ordinaria																			.3		5	5	.8		.5
B. paula																								.7	.8
B pulchella primitiva				2			.3	.2	.4	.2		.2	.1	.4					.3			.1			
B. pusilla																								2	.2
B. striatula spinata																					.3				
B subaenariensis mexicana																			.3	.8					
B subspinescens														.3	.1	.1	.4	2	1	2	2	.6	.4		.5
B translucens																						.2			
B sp																						1	.8	.7	
Buccella hannai		.2	2	1	.4	.1	.3	1	1	2	1	.2		.3	.3	1									
Bulimina aculeata																					2	1	3	9	
B alazanensis																						2	7	3	.2
B spicata																			.6		.3	.1	1	.7	
B striata mexicana																					.1			1	
Cancris oblonga									.1	.3	.6	1	.8	.7	.7		.2	.5	2						
Cassidulina carinata											.2	.2	.2		.1		.6		.3	.8	3	.2		5	.2
C. aff crassa																				.3	2	.6			
C curvata														.7	1	.6	4	4	3	3	.3	2			
C laevigata																	6	.3						.2	
C. neocarinata																	.2	.3	5	3	6	2			
C. subglobosa & variants	.3										.3	.3	1	.6	.3	.4		8	4	5	6	10	9	10	5
Cassidulinoides tenuis																						1	.8		
Chilostomella oolina																					.4	2	.4		
Cibicides corpulentus																		.2	.6	.3		.8	.5		
C deprimus	.5	3	2	6	19	4	6	7	4	2	2	1	.5	.4	1	.4	.8	1							
C. aff floridanus																	.8	4	3	4	2	1	2	.2	
C io													.2	.4	.5	1	.4	.7							
C kullenbergi																	.4					.2	.3	1	.5
C. mollis														.3	.6	.4		1	.6						
C. protuberans							.1			.3	1	2	2	3	3	2	11	10	6	7	.4	.2			
C. robertsonianus																						.5	.9	.5	2
C. rugosa																						.1	.8	.2	
C. umbonatus										.2									.3	2	3	.4			
C. wuellerstorfi																						1	2	1	12
Cibicidina strattoni		.5	.8	5	2	3	4	8	8	8	4	2	1	4	6	3	1	2	1						

Table 18. Percentage distribution of benthonic Foraminifera in traverse VIII (pt.).

TRAVERSE	VIII																								
STATION	172	171	170	169	168	167	166	165	164	163	161	160	159	158	157	156	155	154	153	152	151	150	149	148	146
DEPTH IN METERS	212	15	20	20	22	26	29	31	31	36	35	46	51	60	62	58	79	117	146	183	366	585	914	1730	3164
Conorbina orbicularis							.3	.2	.3		1	.8	.7	.6	.3			.7	.6						
Cyclammina spp																						.1			
Dentalina - Nodosaria															.1		.2		.6			.2	.3	4	
"Discorbis" bulbosa								.3	.1		.4	.2	.1		.1		.2	1		.8					
Eggerella bradyi																				.3			.1	1	.8
Elphidium advenum	.3	.2	2	2	.7	1	.6	.3	.2	.8	.2	.7	.4		.6	.8		.3							
E discoidale	.8	.5	2	3	1	1	3	3	5	6	2	.3	.5	1	.8	.8				.3					
E gunteri	1	.3	.3	.7	.4	.4	.4	1	3	2	2	1	.4	.7	1	.3	.6	.5		.3					
E poeyanum	2	.4	1	1	.2	.1	.4	1	.4	.8	1	.3	.5	.3	.1	.1									
E spp	2	3	2	4	.2	.9	2	1	.8	1	3	1	.3	.4	.8	.1	.4	.8							
Epistominella decorata																								3	13
E. exigua																					.6	3	9	.5	3
E rugosa																					2	1	.7		
E vitrea																						.8	.4	1	
Eponides antillarum							.3	.5	.5	1	.1	.7	.8	1	1	.8	.2								
E palius																						.1	.3	.7	5
E repandus					.9	.2	.1	.1	.3	.2		.2	2	.3	.2	.3	.4								
E tumidulus																									4
E turgidus																		.3		.3	.1	3	5	3	8
Pseudoeponides umbonatus																					.3	.2	.3	.2	2
Gaudryina cf aequa											.8	.2		.4		.1	.6	.8							
G (Pseudogaudryina) atlantica																			.6						
G flintii																							.3	1	
G cf minuta																						.4	.3		
Globobulimina affinis & variant																									.2
Globulina caribaea	.5	.1		.2	.2		.2					.2				.3									
Glomospira charoides																							.5	.7	1
G cf gordialis																									1
Guttulina australis	.3	.1	.3	1		.3	.4	.4	.4	.5	.3	.5	.1	.1	.4		.2								
Gypsina vesicularis							.1	.2		.2		.7	.8	.3	.4	.1	.8								
Gyroidina neosoldanii																									.5
G orbicularis																				.3	.3	.1	2	2	2
Gyroidinoides soldanii altiformis																					.4	1	.4		.2
Haplophragmoides bradyi																						.4	.4		1
Hoglundina elegans																		.2	.3	.5	.9	1	1	4	
Karreriella bradyi																					.1	.2	.4		
Lagena spp & related forms										.2				.1	.2	.1	.2	.2		1	1	2	3	2	5
Laticarinina pauperata																					.1	.1	.8	.7	2
Lenticulina peregrina											.1				.1						.4	.8	.7		
Liebusella spp																			.3						
Loxostomum abruptum																		.3				.5	2	3	.2
Marginulina marginulinoides																		.3							
Miliolidae	42	21	9	11	5	8	16	14	14	15	20	18	5	10	13	11	6	7	3	2	.3	.1		.5	
Nodobaculariella cassis	4	2	.6	.5	.9	4	4	2	2	2	3	5	1	3	3	4	2	.5		.3					
Nodosaria hispida																					.4	.1			
Nonion formosum															.1		.2	.7		.3		.2	.1	1	
N pompilioides																									2
Nonionella atlantica		.4			.2		.8	2	2	3	4	2	.8	1	1	.6	.4	.7	.6	.3					
Nouria polymorphinoides						.1	.1		.1																
Osangularia cultur																						.2	2	1	
Peneroplidae	16	16	16	17	28	26	10	13	18	8	6	18	8	19	8	16	2	1		.3					
Planorbulina mediterranensis	.8	.1	.1	.1	.2			.1	.1	1	.6	.2	.4	.4	.6	.3	.8	.8	.6						
Planulina ariminensis																				1	1	.7			
P exorna						.1	.3	6	8	11	15	5	4	8	11	11	8	5	.6	.5	.3				
P foveolata																	.4	.7	2	2					
Plectina apicularis																						.1		.2	2
Proteonina difflugiformis													.1									.1		.2	1
Pseudoclavulina mexicana																		.2							
P aff novangliae																		.3	1		.1				
Pseudoglandulina comatula																				.3					
Pullenia bulloides																				.3	1	.5	.3	1	.8
P quinqueloba																		.2	.3	.3	.4	.7	1	.2	2
P. sp.																								.2	.2
Pyrgo murrhina																					.4	.1	.4	.5	2
P cf. nasutus								.1	.1	.3			.5	.1	.2		.2	.5	1		.7				
Quinqueloculina bicostata			.5	.3	.7	2	.8	.5	.6	1	.4	.3	2	.4	.3		.2		.3						
Q compta	1	.1	6	3	3	2	2	3	3	2	1	2	1	.7	.3	.1	.2								
Q harrida												.2	.4	.8	.9		.8	.2	.3		.9				

Table 19. Percentage distribution of benthonic Foraminifera in traverse VIII (pt.).

TRAVERSE	VIII																								
STATION	172	171	170	169	168	167	166	165	164	163	161	160	159	158	157	156	155	154	153	152	151	150	149	148	146
DEPTH IN METERS	212	15	20	20	22	26	29	31	31	36	35	46	51	60	62	58	79	117	146	183	366	585	914	1730	3164
Quinqueloculina lamarckiana	.3	.5	6	4	4	5	3	5	7	5	5	5	6	5	4	3	5	1	2						
Q cf polygona	1	.1	.6	.4		.3		.2	.3	.2	.5	.2		.4			.6	.2							
Q sabulosa			.4																						
Q venusta																									2
Q sp.																						.2	.4	1	.5
Rectobolivina advena									.2	.2	.5	.2	.2				.2				.1				
R dimorpha																						.1	.1		
Reophax bilocularis																						.6	.9		
R distans delicatulus																									.8
R hispidulus																							.3	.2	.5
R irregularis												.2	.9	1	.6	.4	2	2	6	1					
Reussella atlantica							.3	1	1	2	2	.8	2	1	1	1	4	.8	1						
Robertina bradyi																		.2			.1			.2	
Robulus spp								.1					.5	.3	.7		.6		3	2	2	.1	.3	.7	
Rosalina bertheloti											.2	.3						.7	3	3	.3				
R cf concinna	13	28	5	11	3	4	6	4	1	1	4	2	2	.4	.4	.4	.6	1	2	1			.3		
R floridana	1	4	2	5	.9	3	3	5	5	2	2	4	.2	.4	.6	.3	.6	1							
R floridensis														.1											
R parkerae						.1	.4	.3	.2	.2	.6	1	1	.1	.7		.2	.5	.6	.8		.1			
R suezensis							.4	.9	.5		1	2	2	1	.8	.7	.4	6	5	6	.1				
"Rotalia" beccarii variants	1	1	.5	.6	.2	.2	.3	.5	.1			.3	.1		.7		.2	2							
"R" translucens																					14	21	5	1	
Rotamorphina laevigata																			.3	3	.1	.5	.7		.2
Saccamminidae & related forms																									
Seabrookia earlandi																		.5			.4	.1	.3		
Sigmoilina distorta																		1	.3	.3	.6				
S schlumbergeri																						.5	2	.7	.8
S tenuis																							.4	.7	
S sp				.3	.2				.1				.4		.4		.8								
Siphonina bradyana												.2		.1	.4			.7	1	.8	.9	.6			
S pulchra											.3	.2		.4	.2		.6	.8	1	2	.1				
Siphotextularia curta																							.1		
S rolshauseni																									.2
Sphaeroidina bulloides																				.3	2	2	1		
S compacta																		.3			.4				
Spirillina vivipara							.1	.1			.2				.1		.2	.7	.6						
Spiroloculina cf grata			.2	.4		.1	.2	.3		.3	.3	2		.3				1		.8	.1	.2			
S soldanii				.1	.2	.1	.1	.2	.1		.3	.2		.3	.2		.2	1	.3	1					
Spiroplectammina floridana											.1		.2	.7	.6	.3	2	.2							
Stetsonia minuta																				.5		.4	.4	.2	
Textularia candeiana	3	.7	1	1	.4	.4	1	2	1	4	.5	1	1	2	2	1	2	2	.3	.3				.2	
T conica	.3		.2				.1	.4	.3	.8	.5	.8	1	1	.8		1	.7	.6						
T foliacea occidentalis															.1		.6	.8	1	.3				.2	
T mayori								.8	.5	1	2	.2	.2	.1	.3	.1	.2	1	.3						
Textulariella spp										.2			.7					.2		.3					
Tolypammina schaudinni																						.1		.2	.5
Trifarina bradyi														.1							2	2	2	9	
Triloculina cf brevidentata	2	.5	.7	.2		.4	.7	1	.6	1	1	.7	.8	.6	.7	.6	.6	2	.6	.5					
T tricarinata																						.2			
Trochammina globulosa																									1
T quadriloba																									.2
T squamata & related spp		.4				.2					.2	.2	.1				.2								
Uvigerina auberiana																					.1			9	.8
U flintii																		.7	5	2					
U hispido-costata																					.7				
U laevis																		2	3	5	1			.2	
U parvula																		2	1	3	.6				
U peregrina																					4	4	14	4	.2
Valvulineria mexicana																							.1		
V minuta																	.2	.3	1	.3	.7	.6	.3		
Virgulina advena																								.2	.2
V complanata																						.2	.7	.2	.2
V mexicana																					.3	.2			
V. pontoni																		.2							
V punctata		.1		.1				.7	.3	2	1	1	.4	.3	5	.1		.5	.3						
V tessellata																						1	.4		
Wiesnerella auriculata							.5	.5	.2	.2	.2	.5	.1					.2	.3						
Miscellaneous spp	1	1	.7		.7	.3	1	2	1	.7	2	2	2	1		1	2	2	6	3	2	6	1	3	4

Table 20. Percentage distribution of benthonic Foraminifera in traverse VIII (pt.).

TRAVERSE	IX								X									XI													
STATION	138	140	141	142	144	145	137	108	136	134	131	130	133	129	128	127	126	117	118	116	124	123	122	121	120	113	112	110	111	1	2
DEPTH IN METERS	183	256	320	421	914	2268	3160	3072	1051	950	1920	3200		3180	1737	2150	1317	139	146	155	914	1326	1829	2560	3246	2280	3283	3218	3251	3237	3237
TOTAL PLANKTONIC POPULATION	20 000	80 000	60 000	100 000	40 000	30 000	100 000	80 000	200 000	60 000	10 000	10 000	80 000	90 000	80 000	200 000	30 000	40 000	50 000	60 000	100 000	30 000	70 000	50 000	20 000	10 000	60 000	100 000	40 000	20 000	70 000
TOTAL BENTHONIC POPULATION	9 800	8 800	26 800	32 400	4 200	900	1 500	1 700	3 900	3 500	1 100	275	1 100	2 000	2 800	4 300	1 300	12 100	12 400	1 800	8 000	1 100	1 300	900	375	325	1 600	1 400	600	275	625
Adercotryma glomeratum						.2	2	1	.1			1	.7	5	1		.2				.1	.1	.3		5	.6	1	1	4	4	3
Alveolophragmium nitidum							1					.4					.2				.1		.6	.4							4
A. ringens										.1												.2	.2	.2							
A. scitulum																								.1							
A. subglobosum							.5	.2						.4							.1		.2	.2	.5						
A. wiesneri									.1						.4		.2														
A. sp.							.3											.1				.4		.1		.6					
Ammobaculites sp. B						.2			.1	.2		3	2		.3	.2						.3	.5	.6							
Ammodiscus spp.					.2		.3					.7		.4			.2					.1		.4						.4	
Ammoscalaria tenuimarga						.7	.3		.1	.2		.4	.4	2		.2						.1			3		.5			1	1
Amphistegina spp.	3																	6	5	5			.2				.3	.3			
Angulogerina bella										.1													.3		.3						
A. jamaicensis		.4																			.4	.1									
Anomalinoides mexicana		.1		.1	.2					.5					.1											.3					
Asterigerina carinata																		.4													
Astrononion tumidum					.2				.2								.3							.1							
Bigenerina irregularis	.8																														
B. textularioidea	2																	.1	.1	.7											
Bolivina albatrossi		1	2	.7	3				3	2	2	.4			.1		3				.5	.3	.2	.1	.3	.3					
B. fragilis		.3																.4	.5			.1									
B. goësii	.7	7	1	.2													.2	4	6	5	.2			.1							
B. lanceolata	.8	1	.5	.2	.6				.3	.1	.8						.3	2	4	.8	1	.3				1	.5	.6			
B. lowmani	.7	2	2	.9	.2	.4		1	3	2	1	1	2		2	.6	1	.2	3	.5	3	2	2	4	.5	4	2	2		.7	.6
B. minima	2	3	2	1	4				.4	.6	.7	.7	.7		.1		.2	1	2	1	.4	.2	.2		.3	.3					
B. ordinaria		2	4	1	.4			.2	.6	1			.7		.1		.2		.1		1	.6	.6	.4		1					
B. paula	.2			.3					.4						.3		.3				.3		.6		1	.3	.5	.8		.4	
B. pulchella primitiva								.2	.1	.1					.3						.2	.3	.5	.1	.5	.3	.5	.6	.7	.4	3
B. pusilla		.1				.2					.7	.4				.2	.3						.2	.6		.3	.3				
B. subaenariensis mexicana	.2	.1													.1																.6
B. subspinescens	1	2	4	2	.8				.9	2	1	1	.4		.9	.2		1	2	2	1	1	1	1						.4	
B. translucens		.1								.1												.1				.9			.7		
B. sp.				.1	.6	.2			.9	.7	.4	.7			.7		.9				.7	.1	.3	.5		.3					
Bulimina aculeata			.7	2	4		1		2	2	1	.4			1	2	10				2	.9	.8	.2		.3					
B. alazanensis				.5	15	.2			15	11	2	1	.7		.9	.7	4				7	3	.8	.2	.8	.3	.8		.7	.4	.6
B. spicata		.7	.6	.2	.6		2		2	12					.1	.9	.8			.3	.5	.2	.2	.1							.6
B. striata mexicana		.2		.3		.9	.8		.1					.4	.4	1							.3	.1							
Cancris oblonga	.2	.1								.1								.3		.5	.5					.3				.7	
Cassidulina carinata		1					1	.7	.2	.2			.4			.6															
C. aff. crassa	1	2	2	4	.2				.6	.8			.4		.3	.2	.3	2	.9	2	.9	.3	.5		.8		.5				
C. curvata	5	2	5	4						.5	1					.2		3	2	1	.8	.1	.2			.3					.6
C. laevigata																	.3	3	2	2	.3					.3	.8				
C. neocarinata	1	7	7	3	.2					.2	.4						.2	.5	.5	.3	.3									.4	
C. subglobosa & variants	3	4	10	11	7	10	3	3	10	8	7	3	9	2	14	12	9	3	.9	4	15	15	7	11	3	8	3	3	1	4	4
Cassidulinoides tenuis		.1		.1	.2					.3					.1		.5					.1				.3				.4	
Chilostomella oolina										.3						.4					.1										
Cibicides corpulentus	.2			.1	.7				.2	.3					.1		.5				.1	.6									
C. deprimus	1	1		.8	.6										.3			1	.8	2	.4			.1		.6					
C. aff. floridanus	7	.8	2	2	.8				2	1						.2	.8	.5	.8	1	1	.1									
C. kullenbergi						.2	.3		.1			2	1		.3	3						.1	.5	.3		.3		.6	.7	.4	.6
C. mollis																		.4	.1												
C. protuberans	21	9	2	.1													.2	15	17	18	.8	.2	.3								
C. robertsonianus				.7	.9	2	2	2	2	.2	1	.7	3	.4	1	.6	1			.1	2	2	.3	1	1	.6	2	.6	.7	.7	
C. rugosa						.2			.2		.4				.3	.2	.2				.2	.5	.2								
C. umbonatus	.3	2	.5	.7																	.1										
C. wuellerstorfi					.8	4	37	49	.9	.2	.4	5	5	47	2	6	2				1	1	3	1	17	.3	24	27	38	34	35
Cibicidina strattoni	.3				.2													.4													

Table 21. Percentage distribution of benthonic Foraminifera in traverses IX-XI (pt.).

TRAVERSE	IX								X									XI													
STATION	138	140	141	142	144	145	137	108	136	134	131	130	133	129	128	127	126	117	118	116	124	123	122	121	120	113	112	110	111	1	2
DEPTH IN METERS	183	256	320	421	914	2268	3160	3072	1051	950	1920	3200		3180	1737	2150	1317	139	146	155	914	1326	1829	2560	3246	2280	3283	3218	3251	3237	3237
Conorbina orbicularis																			.1	.3											
Cyclammina spp.																						.2	.2			.3	.3			.7	
Dentalina – Nodosaria	.7	.4		.1	.6		.2	.2	.1	.2			.4		.2	.2		.5	1	.1	2	.2	.6	.1			.3		.7	.4	
"Discorbis" bulbosa																					.6	.3	.3			.6					
Eggerella bradyi				.1		1	.5	.2	.4	.2	1	3	2	.8	.3	.2	.3			.1	1	.6	.2	1	2	.6	1	.6	.7	.7	.6
Ehrenbergina spinea		.4								.5								6	3	3	.8										
Elphidium spp.	.2																	.4		.1	.7		.8	.2				.3			
Epistominella decorata					.2	19	3	11			19	6	2	2	12	9	2					1	7	5	15	7	17	14	10	8	7
E. exigua			.2	1	16	.7	.5		4	7	6	2	.4		5	3	1				5	2	4	2	1	2	.3	.3		.4	.6
E rugosa		.8	11	11	1				2	2	3					.4	.2				5	.3	.2	.6			1	.3			
E vitrea				.2	.2	.4				.2											.7	.4		.2		.3		.3			
Eponides polius					.2	2	3	3	.7	.2	.4	3	.4	4	.7	.4	2					.7	.6	.3	4		4	4	6	2	4
E repandus	.2																	.5	.1												
E tumidulus						3		1			.7	7	5	1	.7	.4	1				.3	1	1	3	3	2	1	3	1	4	1
E turgidus		.5	1	.2	1	6	.5	6	2	1	11	4	5		3	2	2			.3	3	2	4	5	3	3	.3	2	.7	.4	.6
Pseudoeponides umbonatus	.5	.2	.5	.9		2	5	2	.4	.3	.7		1	2	2	2	.9		.3		.3	.5	1	.8	3	.9	3	3	.7	.4	2
Gaudryina cf aequa																		.7	.1												
G (Pseudogaudryina) atlantica	.2	.1	.1															.3		.1											
G flintii						.4			.9	.2					1	.2	.6			.3	1	1									
Globobulimina affinis & var.							2	3						1										.1	.3		1	.8			
Glomospira charoides				.2		2	1	.7	.4	.1	.7	9	10	.8	2	.4	2				.1	.9	2	2	1	4	.3	.3	3	3	2
G. cf. gordialis								.2			.7	.4	.4	.8	.7	.2	.5						.8	.4	.8	2			.7		
Gypsina vesicularis																		.3	.1	.1											
Gyroidina neosoldanii	.2	.1	.4	.4		.2	1								.3	.6					.2		.6	.1	.5	.3	.2			.7	.6
G orbicularis		.3	.4	.1	2	.4	2	.5	3	1	2	.7	.4	.8	2	3	3				.7	2	2	.3		2	.3	.3			
Gyroidinoides soldanii altiformis	.2	.5		1	.2	.4		1	.5	.3	.4				.1		.3				.5							.6	.7		
Haplophragmoides bradyi				.1		.6		.7	.1			2	2	.4		.2	.3					1	.5	.2	1	.3	1	.8	.7	1	.6
Hoglundina elegans	.3	.8	.2	1	.7	12	6		2	2	5	3	10	4	3	25	7	.1	.6	.8	1	4	3	5		10	9	3	3	5	3
Karreriella bradyi	.3	.6		.3	.4		.3		.5								.2	.5	.4	.4		.2	.2	.2							
Lagena spp & related forms	1	1	2	4	4	8	2	1	6	3	6	3	9	2	8	2	4	.8	5	.1	4	8	7	10	4	4	4	5	3	4	3
Laticarinina pauperata		.1	.4	1	.9	2	2	.2	1	1	2	.4	1		1	.9	2				1	2	.9	1	.3	.3					
Lenticulina peregrina		.3	.5	.2	1				1	.8	.7				.6		.8		.3		.9	.6	.2								
Liebusella spp.	.8	.2																.3	1	.8											
Loxostomum abruptum		.3	.7	.4		2			.5	.7	1				.7	.7					.6	.3	.2	.8		.3		.8			
Miliolidae	2	3	.8	.9				.2		.1		.4	1		2	.9	1	4	4	1	.8	6	4	3	.5	2	1	.3		.4	
Nodobaculariella cassis	.5																	.5	.5	.6											
Nodosaria hispida				.5																	.2										
Nonion formosum	.3	.3			.4													.7	.3												
N pompilioides						.4	3	3				.7	.7	4										.6	3	.3	4	8	6	3	6
Nonionella atlantica																							.2								
N opima																					.2					.3					
Nummoloculina irregularis			.4	.1											2	.7	.2				3	5	5	1		.9					
Osangularia cultur					4		.5		2	3	1	.4	.4	.4	2	2	2				2	1	2	.6	.5	.6	1	.3		1	.6
Peneroplidae																		.9		.1											
Planorbulina mediterranensis	.3																	1	2	1		.2					.3				
Planulina ariminensis	.2	.7	2	4					.2	.5										.3	.5		.2	.2							
P exorna	.5	.2																.4													
P. foveolata	3	5																2	3	2											
Plectina apicularis							1	.2				2	2	3	.1		.6					.3	.7		2		2	1	2	2	1
Proteonina difflugiformis								.2				3					.3							2	1	.6					
Pseudoclavulina mexicana	.2																	.4	.5	.4											
P aff. navangliae	.3					.2																									
Pseudoglandulina comatula		.2		.1						.1								.3	.3	.4							.3				
Pullenia bulloides		.2		.6	.6	.4	.3	.5	.5	.2	1	.4		.4	2	1	1			.1	1	2	2	.6	1	.6	.3	.3	.7	1	.6
P quinqueloba	.3	.2	.6	.4	1	.7	.8	1	1	.5	2		1	1	2	.7	2	2	.9	.9	.8	1	2	1	.8	.6	1	1	.7		1
P sp						.4		.2	.2			.4		.4	.4	.6						.5	.2	1	1	1		.8	.7	1	
Pyrgo murrhina				.5	1	3	2	.7	1	.9	1	.7	4	2	.4	1	2				.3	.6	.2	2	.5	2	2	.6	1	.4	3
P cf nasutus	.5	.2	.4															.3	1	.7							.3				
Quinqueloculina compta																				.1											
Q horrida	.7	.3																													
Q lamarckiana	.7														.1	.4		1	.4	.5											
Q cf polygona	.3																	.1													
Q venusta						.4	.5					.7	1		.3								.8	.8		.6		.3		.4	
Q sp.					.7	2	1		.8	.1		2	1	.4	.4	4	.9				.6	1	3	1		.3	.5	.3	1	1	.6
Rectobolivina advena		.1																						.2							

Table 22. Percentage distribution of benthonic Foraminifera in traverses IX-XI (pt.).

TRAVERSE	IX								X									XI													
STATION	138	140	141	142	144	145	137	108	136	134	131	130	133	129	128	127	126	117	118	116	124	123	122	121	120	113	112	110	111	1	2
DEPTH IN METERS	183	256	320	421	914	2268	3160	3072	1051	950	1920	3200		3180	1737	2150	1317	139	146	155	914	1326	1829	2560	3246	2280	3283	3218	3251	3237	3237
Rectobolivina dimorpha				.1																		.1									
Reophax bilocularis				.3								2										.5		.3		.3					
R. distans delicatulus						.4	.5	.2				3	.4	4	.3							.2	.5	1	5	2	1	.6	1	1	3
R guttifera																										.3					
R. hispidulus									.2	.3		2			.4		.2				.1	1	.2	2	1	.6	.3			1	
R. irregularis	4	.5																.4	.3												
R. scorpiurus												.7																	1		
R. sp													.4																		
Reussella atlantica	.7														.1			2	.9	1	.8										
Robertina bradyi	.2	.1	.2	.1	.9				.8	.7					2	.7	.6				.7	1	2	.4		2					
Robulus spp	2	2	2	3	.4				.1	.2	.4					.4	.2	3	3	6	.3	.4					.5				
Rosalina bertheloti	.8	1							.2									.5	.9	.5	1										
R cf concinna		.3							.6	.3							.3	2	.4	.3	2	.3	.5	.7						.4	
R floridana	.2												.4					.1	.1	.1											
R. floridensis	.7																	.5	.3	.3											
R. parkerae		.2		.2		.7		1	.1				.4	.4	.6		.2		.4		1	.4	.5	.6		.9					
R suezensis	.2	.5	.6	.3	.4																							.3			
"Rotalia" translucens		2	12	8	3	.4	.5		4	6	5	1	.4	.8	3	.9	4				3	3	1	1	.5		.8	.3			.6
Rotamorphina laevigata	.2	1		.2	.4				.8	1	1	.7	1		.4	.4	.2	.4	.4	.1	.4	.4	.5	.4		2	.3	.3			.6
Saccamminidae & related forms																										.3					
Seabrookia earlandi			.2						.4	.1		.4			.1		.9	.1	.1	.1	.1	1	.5	.9		2		.3			
Sigmoilina distorta		.4													.6			.8		.8	.4										
S schlumbergeri		.2	.4			.2	.5	2	.4	.3	.4			1	.4	.9	1				.1	.2	.6	.2	1					.7	
S tenuis	1	.8	.6						.7	.2		.4					.2	1	.9		.7	.5								.4	
S sp	.7	.7																.3		.3											
Siphonina bradyana	.2	.7	.6	.4						.1								1	.8	1											
S pulchra	.5	1	.1	.4														1	.4	.4											
Siphotextularia curta					.2				.3	.3					.1	.2	.5				.1	.4	.7	.3							
S rolshauseni												4			.1		.2							.1	1		.3	.8		.4	1
Sphaeroidina bulloides	.3	.7	.6	2	.6	.2			1		.4						.5			.1	.9	.5	.6			.6	.8				
S. compacta									.2						.3		.3		.1			.5	.2			.3					
Spirillina vivipara					.2				.1									.3	.1												
Spiroloculina soldanii	.3	.1	.1						.1										.1	.5											
Spiroplectammina floridana	.3																	.7	.5	.4											
Stetsonia minuta		.1							.5	.3			.4				.2	.3			.1			.1		.6		.3	.7		
Textularia candeiana	3	2	.4															1	1	1											
T. conica	1	.2																1	.9	2											
T foliacea occidentalis	3	1																1	.8	1											
T. mayori	.2	.2																.3	.1												
Textulariella spp	2	.4	.1															1	1	3											
Tolypammina schaudinni						.9						4	2	2	1		.6					.2	.5	3		2				.4	
Trifarina bradyi	.5	.5	6	8	3				3	2	2	.4	1		.4	.2	.2	.3	.4	.5	2	.2		.2		.9				.4	
Triloculina cf brevidentata	.5	.5														.2		.8	.1	1											
T tricarinata					.2				.2			.7			1		.2					1	.3	.9		.6			.7		
Trochammina globulosa						.4	.3		.1			1	2		.3		.8					.3	.2	1		3					
T cf japonica												.4			.3		.3						.2	.4		.3					
T quadriloba																									1						
T squamata & related spp									.1															.1							
T cf tasmanica						.2						2										.2		.9		.6				.4	
Uvigerina auberiana		.2	3	1		.7	3	.2	.7	.8	.4				.4	1	.5				.2	.2	.5	.6		.3			2	.7	.6
U flintii	3	4	.4	.2														2	3	6											
U hispida-costata		.1	.6	1					.3	2																					
U laevis	1	2		.2					.1	.3	.7		.4		.1		.2	1	1	.7	.8		.8	.1		.3	.5				
U parvula	3	6	.2															3	5	4											
U peregrina				.3	12	.9	2		5	8	.7				.9	.9	6				.8	2	.3	.3							
Valvulineria mexicana								1																			.3	.6			.6
V minuta		.4	.1	1	.9	.2			.2	.7	.7						.6		.4		.5	.4	.2	.3	.6	.3					
Virgulina advena						.9		.2					1			.4								.1		.3					1
V complanata		.1	.6	.2		.4		.2		.5			1				.2	.1		.1	.1	.3	.3								.6
V mexicana		.1										.4			.1	.2								.1							
V pontoni																						.1				.3					
V punctata										.2								.1	.1		.1	.2	.2	.4		.3					
V tessellata																					.1										
Miscellaneous spp	5	4	4	6	.1	5	4	1	3	3	3	4	3	2	5	2	4	4	4	8	3	7	9	8	7	7	3	7	5	5	.6

Table 23. Percentage distribution of benthonic Foraminifera in traverses IX-XI (pt.).

TRAVERSE	VII																		
STATION	174	175	176	177	178	179	180	181	182	183	184	185	186	187	188	189	190	191	107
DEPTH IN METERS	22	31	46	49	86	146	183	186	237	274	274	320	347	457	585	732	878	2999	3017
TOTAL PLANKTONIC POPULATION	12	8	34	450	150	2 300	27 100	12 800	19 500	14 000	14 800	20 700	60 900	200 000	56 800	16 000	34 600	47 300	40 400
Candeina nitida																.4	.2	.3	.3
Globigerina bulloides	17			4	18	5	16	17	19	13	18	13	10	6	9	12	14	14	16
G. digitata											1		.1	.1	.2	.4		.1	
G. eggeri			24	4	19	23	9	11	7	9	7	9	11	8	8	11	9	8	6
G. inflata						1	2	2	3	1	1	2	1	.9	.7			.1	
G. pachyderma																	.2	.7	
G. sp.						2	4	2	3	2	3	.8	3	4	2	1	1		1
Globigerinella aequilateralis					1	3	.7	1	2	3	4	3	3	3	5	5	2	5	6
Globigerinita glutinata				18	4	3	9	10	11	4	9	2	9	9	6	4	5	3	5
Globigerinoides conglobata					8	1	.5			.7	.4	.9	.3	.2	.3	.4	.4	.1	.5
G. rubra	50	100	64	52	27	28	36	39	34	35	34	33	32	40	40	33	33	34	35
G. sacculifera	33				3	5	3	2	3	5	4	13	10	10	13	9	13	12	10
Globorotalia hirsuta																			.1
G. menardii					10	8	3	3	2	5	5	6	5	4	4	7	6	7	6
G. punctulata				4		.8	3	1	2	2	2	3	3	3	2	1	2	2	.6
G. scitula						1	4	3	6	2	2	2	1	1	2	1	2	.5	.6
G. truncatulinoides			12	18	7	5	5	3	3	8	5	7	4	3	3	5	4	4	3
G. tumida					3	1	1	1	.8	1	.2	.9	.2	1	1	1	2	.7	.5
Hastigerina pelagica																			.1
Orbulina universa						1	.2	.7	.2	2	.1	1	.8	3	2	4	2	3	4
Pulleniatina obliquiloculata						12	4	4	4	7	3	3	6	4	2	4	4	5	4
Sphaeroidinella dehiscens						.1		.2				.2				.2	.2		.1

Table 24. Percentage distribution of planktonic Foraminifera in traverse VII.

TRAVERSE	I											II																				
STATION	211	210	209	208	207	206	205	204	202	203	201	16	17	18	19	20	21	22	23	15	24	14	13	12	11	10	9	8	7	6	5	4	3
DEPTH IN METERS	51	?86	?86	73	82	79	82	91	128	201	430	33	58	88	106	113	142	168	208	298	314	471	631	732	914	1298	1372	1417	1875	2468	2788	2972	3017
TOTAL BENTHONIC POPULATION	30	229	14	101	30	11	17	20	22	9	8	31	115	20	1	6	12	22	6	3	22	0	6	1	3	1	2	5	1	1	12	0	0
Alveolophragmium scitulum											2																						
A sp					1			1																									
Ammobaculites sp A										1						1	2	2															
Ammoscalaria pseudospiralis														1																			
Bolivina albatrossi																							1					1					
B barbata		2		19														3															
B ordinaria																		2															
B striatula spinata				6																													
Bulimina marginata																		3			1												
B striata mexicana																				1	1												
Buliminella cf bassendorfensis		1		50								1																					
Chilostomella oolina																							2								1		
Cibicides aff floridanus																												1					
C wuellerstorfi																											1						
Eponides regularis																		2															
Globobulimina affinis & var																								1	1								
Goesella mississippiensis		2	4	8	2	1	2	4	7	2				3		4	5	4	1												3		
Gyroidina orbicularis																										1	1	1					
Hormosina sp											2																						
Miliolidae																														1			
Nonionella opima	4				2																2												
Nouria polymorphinoides																															5		
N sp	24	114	3	5	9	2	14	2				25	64	10	1						1												
Osangularia cultur																							1										
Proteonina atlantica																															1		
P difflugiformis				1	3	6		5	4	5	1			2		1	1	2							1								
Reophax gracilis		26	2								1		1																				
R hispidulus					2			1	4					1			1	2	1				1					1			2		
R scorpiurus				1	2			3	2								1	1	4	1													
R spp																					6												
Robulus spp																												1					
"Rotalia" beccarii variants		33					1					5	8																				
Saccamminidae & related forms																	2																
Sphaeroidina bulloides																									1				1				
Textularia earlandi	2	50	3										42	3							1												
Trochammina cf japonica											1																						
T quadriloba					9	2		4	2	1	1																						
T cf tasmanica			2															1															
T spp (juvenile)																					7												
Valvulineria mexicana																					2												
Virgulina mexicana																				1													
V pontoni				10																	1												
V tessellata																							1										
Miscellaneous spp		1		1					3																								

Table 25. Distribution of living benthonic Foraminifera in traverses I and II (in numbers of specimens).

TRAVERSE	III													IV													V										
STATION	25	26	27	28	29	30	31	32	33	34	35	36	37	225	224	222	221	220	219	218	217	216	215	214	213	212	78	76	75	74	99	100	101	102	103	104	105
DEPTH IN METERS	22	53	77	106	155	205	373	400	1024	1262	1481	1719	2388	20	20	33	35	37	38	42	40	42	47	49	55	62	71	99	146	204	238	530	914	1097	1822	2213	1417
TOTAL BENTHONIC POPULATION	103	14	30	78	96	70	12	11	17	27	19	5	1	5	50	28	61	53	194	87	38	33	287	232	37	62	46	35	52	34	19	11	24	10	5	5	1
Ammoscalaria pseudospiralis																	3	1		2	3		5		13	1											
Angulogerina bella																	1		2			5	16	2													
Anomalinoides mexicana																																	1				
Bigenerina irregularis																			1			1	4														
Bolivina albatrossi						1		1	5	1																				2							
B barbata				21	45	10																															
B lowmani									1											1									1	1							
B ordinaria						11																															
B striatula spinata		1	7	3	1																	2	32	46					1								
B subaenariensis mexicana				32	35																							2	3	2							
Bulimina aculeata								2			2																					1			1		
B marginata					2	6																	1						2		1						
B spicata																														1							
B striata mexicana																															2	1	1			1	
Buliminella cf bassendorfensis	8	8	8	10														2	1			2	5														
Cancris oblonga																	1	2	3	2			1				8	3	2								
Cassidulina carinata							1																														
C curvata																													1	1							
C neocarinata																													2			1					
C subglobosa & variants																				2									3	1							
Chilostomella oolina									6	4																			4	5	2	6	12	2		1	
Cibicides aff floridanus																													7								
Cibicidina strattoni																8	8	5	3			2	3														
Dentalina - Nodosaria																				1			2														
Elphidium discoidale																	1		3																		
E gunteri																1							2	1													
E poeyanum																1																					
Epistominella vitrea		4	2	2	2					1				2			1		2	1		1	5	1									1				
Eponides antillarum																	3																				
E regularis						35	3																														
Pseudoeponides umbonatus																												1									
Globobulimina affinis & var									2	11	5	1																					1				
Goesella mississippiensis			1	2	3																		14		9	9	1	3									
Gyroidina orbicularis												1																									
Hormosina sp						1	1		1	1																											
Lagena spp & related forms				1	1					1		1										1															
Lenticulina peregrina																																					1
Miliolidae																	1		2			1															
Nonionella atlantica					1	1								1		5	1			2		3	4				1										
N opima	3		2		1					1				1	44	4	22	17	119	40	1	5	104	153			26	16	4	3	1						
Nouria polymorphinoides														1	1	5		7	41	31	14	1	13	10			6	1									
N sp	7																								10	8											
Planulina foveolata																													1	3							
Proteonina atlantica																	15	15	2	1	19	7	70		2		1		2		1						
P difflugiformis						1	1	2																										1			
Pullenia bulloides								1																						1					1		
P quinqueloba																																	6	1			
Pyrgo cf nasutus																			3										3								
Quinqueloculina compta																	1	1				1															
Q lamarckiana																		1																			
Reophax gracilis																								6													
R hispidulus								1		1	1																		4	2	2					1	
R irregularis																											2										
R scorpiurus																							1														
R spp																													2			1					
Reussella atlantica																			1					1													
Robulus spp				1																											2						
Rosalina bertheloti																	1																				
R cf concinna															5	2																					
R floridana																		1												2							
"Rotalia" beccarii variants	3	1															1		2	1			1														
Rotamorphina laevigata								1		1																			1					1	1	1	
Sphaeroidina bulloides										1																			1		1		1				
Textularia earlandi	11		1			1																			3	44											
T mayori																1	1		1	1																	
Trochammina advena						1																															
T spp (juvenile)	71																																				
Uvigerina laevis																												1	1	1							
U parvula																								1							5						
U peregrina								2	1				1																	1			1		2		
Valvulineria mexicana							4																														
Virgulina mexicana								1																													
V pontoni			9	3	4											1			2			1	3	11													
V punctata																		1	3	2							1	5			1						
V tessellata										4	11																							5			
Miscellaneous spp				3	1	2	2		1			2							3		1		1					3	7	8	1	1				1	

Table 26. Distribution of living benthonic Foraminifera in traverses III V (in numbers of specimens).

TRAVERSE						VI																					VII											
STATION	197	198	200	196	199	59	58	57	56	54	53	52	51	49	48	47	46	45	44	43	42	41	40	39	38	106	179	181	182	183	184	185	186	187	188	189	190	191
DEPTH IN METERS	549	549	600	713	735	91		106	113	128	139	146	155	183	223	446	555	631	650	677	823	860	960	1144	1573	2697	146	186	237	274	274	320	347	457	585	732	878	2999
TOTAL BENTHONIC POPULATION	11	16	7	11	12	15	4	4	4	15	12	1	5	3	5	6	11	5	1	9	9	5	2	1	0	1	5	5	6	4	4	6	0	4	0	5	2	6
Ammoscalaria tenuimargo																																						1
Bolivina albatrossi					1											2																						
B lanceolata						3				1																												
B minima											1																											
B striatula spinata									1	1																	5											
B subaenariensis mexicana																												1				1						
Bulimina aculeata			1	1	1																		1	1														
B alazanensis					1																																	
B spicata				2																																		
B striata mexicana		1			5																																	
Cancris oblonga						1				1																			1									
Cassidulina neocarinata																					1																	
C subgobosa & variants						1														1																1		
Chilostomella oolina	1	7		2										1		1	7	3		1												1						
Cibicides corpulentus											2																											
C aff floridanus																				1	1	1														1		
C mollis						1																																
C robertsonianus																																						1
C rugosa			1																																			
Dentalina - Nodosaria	1												1																		1			1				
Eggerella bradyi	1																																					
Epistominella decorata																					1																	
E exigua	1																1																					
E rugosa					1																																	
Eponides regularis													1																									
E turgidus	1																																					
Pseudoeponides umbonatus																				1																		
Gyroidina orbicularis																													1									
Hoglundina elegans						1		2				1																										
Karreriella bradyi																			1																			
Lagena spp & related forms					1						1										1		1															
Miliolidae											1																	1										
Nonionella atlantica						1																																
Osangularia cultur				1																1	1																	
Planulina exorna							1																															
Proteonina atlantica						1			1	2																		1		1								
P difflugiformis	1		1																	2																		
Pullenia bulloides															1	1																						
P quinqueloba						1																																
Pyrgo murrhina																										1												
P cf nasutus										1																												
Reophax bilocularis										1																						1						
R guttifera																														1								
R hispidulus	1	1												2														1	1	1	1	1						1
R irregularis						1																																
R scorpiurus	1	2													1							2																
R spp											1				1		2												1			1						
Robulus spp						1		1	1	2																					1							
Rosalina floridensis							1																															
"Rotalia" translucens	1																																					
Rotamorphina laevigata															1																							
Siphonina bradyana		1													1																							
S pulchra									1	4	2				1													1	1					1				
Sphaeroidina bulloides	1	1	2	1	1						1							2				1																
Trifarina bradyi							1													1																		
Trochammina globulosa																				1																		
Uvigerina flintii											1																											
U hispido - costata					1																											1		2				
U peregrina			2													2					2								1		1					2	1	
Valvulineria minuta																					1	1																
Virgulina tessellata	1	1		3																																		
Miscellaneous spp		2		1		3	1	1		2	2		3				1				1									1						1	1	3

Table 27. Distribution of living benthonic Foraminifera in traverses VI and VII (in numbers of specimens).

TRAVERSE	VIII								IX							X								XI										
STATION	154	153	152	151	150	149	148	146	140	141	142	144	145	137	108	136	134	131	130	129	128	127	126	124	123	122	121	120	113	112	110	111	1	2
DEPTH IN METERS	117	146	183	366	585	914	1730	3164	256	320	421	914	2268	3160	3072	1051	950	1920	3200	3180	1737	2150	1317	914	1326	1829	2560	3246	2280	3283	3218	3251	3237	3237
TOTAL BENTHONIC POPULATION	12	40	13	10	6	2	1	1	3	6	2	6	1	0	0	4	5	1	2	0	13	1	14	11	6	6	7	0	3	0	0	0	0	0
Alveolophragmium ringens																											1							
A subglobosum						1																												
A wiesneri		1																																
Ammoscalaria tenuimargo				1																														
Bolivina goësii		1																																
Bulimina aculeata																							3		1									
Cancris oblonga	1	1																																
Cassidulina subglobosa & vars												1				2					1		2	1										
Chilostomella oolina				2																														
Cibicides aff floridanus					1																													
C robertsonianus																					1					1								
C umbonatus	1																																	
C wuellerstorfi																									1									
Dentalina - Nodosaria																								2										
Epistominella decorata																										2			1					
E exigua																					1													
E rugosa											1																							
Eponides polius																	1																	
E turgidus																											1							
Gaudryina (Pseudogaud) atlantica			1																															
Gyroidina orbicularis																1	1				1					1								
Hoglundina elegans		2														1			1		1	1	1	1		1	1							
Lagena spp & related forms			1									1																						
Laticarina pauperata																									1									
Marginulina marginulinoides	1																																	
Miliolidae	2								1																		1							
Osangularia cultur												2									1		2	1										
Proteonina atlantica	1	3																																
Pullenia bulloides					1												1																	
P quinqueloba	2								1												1		1			1								
Pyrgo murrhina																											1							
P cf nasutus		2		1																														
Reophax hispidulus		2		1	2	1	1	1		1									1		1		1											
R irregularis	1	2																																
R scorpiurus																							1											
R spp	2	1		2																							1							
Robulus spp			1	3					1	1																								
"Rotalia" translucens																									1									
Rotamorphina laevigata											1																							
Seabrookia earlandi										2																								
Siphonina pulchra		18	8																															
Siphotextularia curta																								1										
S rolshauseni													1																					
Sphaeroidina bulloides	1		1									1					1				2		2	1	1									
Textulariella spp										1																								
Trifarina bradyi										1																								
Trochammina squamata & rel spp																								1										
T spp (juvenile)																								1			1							
Uvigerina flintii		5	1																															
U. peregrina					2							1						1					1		1									
Valvulineria minuta																													2					
Miscellaneous spp		2															1				3			2										

Table 28. Distribution of living benthonic Foraminifera in traverses VIII-XI (in numbers of specimens).

TRAVERSE	II						III		IV				
STATION	9	8	6	5	4	3	34	37	222	221	220	218	215
DEPTH IN METERS	1372	1417	2468	2788	2972	3017	1262	2388	33	35	37	42	47
TOTAL PLANKTONIC POPULATION	7	5	2	11	5	2	5	6	2	2	1	2	1
Globigerina bulloides	1			2			1						
G. eggeri				1			2	1					
G. (juvenile)	4	4	1	2	5		2	5		1		2	1
Globigerinella aequilateralis						1							
Globigerinita glutinata				2									
Globigerinoides rubra						1			2	1	1		
G. sacculifera	1												
Globorotalia menardii				2									
G. punctulata	1			1									
G. truncatulinoides													
Orbulina universa			1										
Pulleniatina obliquiloculata		1		1									

TRAVERSE	V									
STATION	78	76	75	74	99	100	103	104	105	198
DEPTH IN METERS	71	99	146	204	238	530	1822	2213	1417	549
TOTAL PLANKTONIC POPULATION	3	2	3	6	2	3	2	1	4	1
Globigerina bulloides										
G. eggeri										
G. (juvenile)	1	1	3	3	1	3		1	4	
Globigerinella aequilateralis				1						
Globigerinita glutinata										
Globigerinoides rubra				1	1					
G. sacculifera	1									
Globorotalia menardii	1									1
G. punctulata										
G. truncatulinoides							2			
Orbulina universa				1						
Pulleniatina obliquiloculata		1								

TRAVERSE	VI													
STATION	59	57	54	53	49	48	47	46	44	43	42	39	38	106
DEPTH IN METERS	91	106	128	139	183	223	446	555	650	677	823	1144	1573	2697
TOTAL PLANKTONIC POPULATION	2	1	1	2	2	2	2	1	5	2	3	2	3	1
Globigerina bulloides														
G. eggeri	1				1	1		1						
G. (juvenile)			1	2					5	2	3	2	2	1
Globigerinella aequilateralis							1						1	
Globigerinita glutinata														
Globigerinoides rubra					1		1							
G. sacculifera														
Globorotalia menardii	1													
G. punctulata														
G. truncatulinoides														
Orbulina universa														
Pulleniatina obliquiloculata		1				1								

Table 29. Distribution of living planktonic Foraminifera in traverses II-VI (in numbers of specimens).

TRAVERSE	VII											VIII								IX							X								XI							
STATION	181	182	183	184	185	186	187	188	189	190	191	154	153	152	151	150	149	148	146	140	141	142	144	145	137	108	136	134	131	130	129	128	127	126	124	123	122	121	113	110	111	1
DEPTH IN METERS	186	237	274	274	320	347	457	585	732	878	2999	117	146	183	366	585	914	1730	3164	256	320	421	914	2268	3160	3072	1051	950	1920	3200	3180	1737	2150	1317	914	1326	1829	2560	2280	3218	3251	3237
TOTAL PLANKTONIC POPULATION	3	6	1	1	3	1	2	2	2	8	3	5	9	2	9	5	29	4	3	9	11	3	3	6	1	4	74	21	5	4	7	32	12	32	32	6	21	7	24	2	3	3
Candeina nitida																1																										
Globigerina bulloides																	2							1			1						2	2	2			3		1		
G. digitata																												1														
G. eggeri	1																3			1						2	2					6	2	1	4		4					
G. (juvenile)		4	1		2				2	3	2		6		4		3	1		5	5	2	2	3			57	11	4	1	2	6	5	16	4		7		8		1	3
Globigerinella aequilateralis												1	1			1	7						1			1	4	1		1		10		3	4	3	2	2	4		2	
Globigerinita glutinata	1						1			1	1				1			1			2			1						1	1		1	3		1						
Globigerinoides rubra										1					1	1	4			1						1	2	2		1				2	1		1	1				
G. sacculifera																	1										1						1	1	1				1			
Globorotalia menardii		1								2		2		1		1	1				1	1		1			5	1				6	1	2	12		4		4			
G. punctulata																											1				1			1		1		1	1			
G. scitula										1																		1							2				2			
G. truncatulinoides					1		1	1					1		2		5		2	2							1	1				2		1	1	1			2			
G. tumida																1																			1							
G. (juvenile)																													1													
Orbulina universa												1	1				1		1		1							2				1								1		
Pulleniatina obliquiloculata	1	1		1		1		1				1		1	1		2	2			2				1			1			3	1					3		2			

Table 30. Distribution of living planktonic Foraminifera in traverses VII-XI (in numbers of specimens).

PLATES

PLATE 1

Fig. 1. *Proteonina atlantica* Cushman. X 42. Sta. 222.

Fig. 2. *Proteonina difflugiformis* (H. B. Brady). X 62. Sta. 208.

Fig. 3. *Reophax bilocularis* Flint. X 39 Sta. 187.

Fig. 4. *Reophax distans delicatulus* Cushman. X 42. Sta. 37.

Fig. 5. *Reophax guttifera* H. B. Brady. X 42. Sta. 15.

Figs. 6, 7. *Reophax hispidulus* Cushman. X 42. (6) Sta. 191; (7) Sta. 121.

Fig. 8. *Hormosina* sp. X 70. Sta. 13.

Figs. 9, 10. *Reophax irregularis* n. sp. Sta. 59. (9) Holotype, X 33; (10) Paratype, X 39.

Fig. 11. *Reophax scorpiurus* Montfort. X 39. Sta. 24.

Fig. 12. *Reophax* sp. X 42. Sta. 23.

Fig. 13. *Glomospira* cf. *gordialis* (Jones and Parker). X 42. Sta. 24.

Fig. 14. *Glomospira charoides* (Jones and Parker). X 62. Sta. 36.

Fig. 15. *Tolypammina schaudinni* Rhumbler. X 62. Sta. 121.

Fig. 16. *Haplophragmoides bradyi* (Robertson). X 70. Sta. 36.

Fig. 17. *Alveolophragmium nitidum* (Goës). X 39. Sta. 8.

Fig. 18. *Adercotryma glomeratum* (H. B. Brady). X 42. Sta. 8.

Fig. 19. *Alveolophragmium ringens* (H. B. Brady). X 42. Sta. 5.

Figs. 20, 21. *Alveolophragmium scitulum* (H. B. Brady). X 42. (20) Sta. 8; (21) Sta. 5.

Fig. 22. *Alveolophragmium* sp. X 62. Sta. 35.

Fig. 23. *Alveolophragmium wiesneri* (Parr). X 64. Sta. 33.

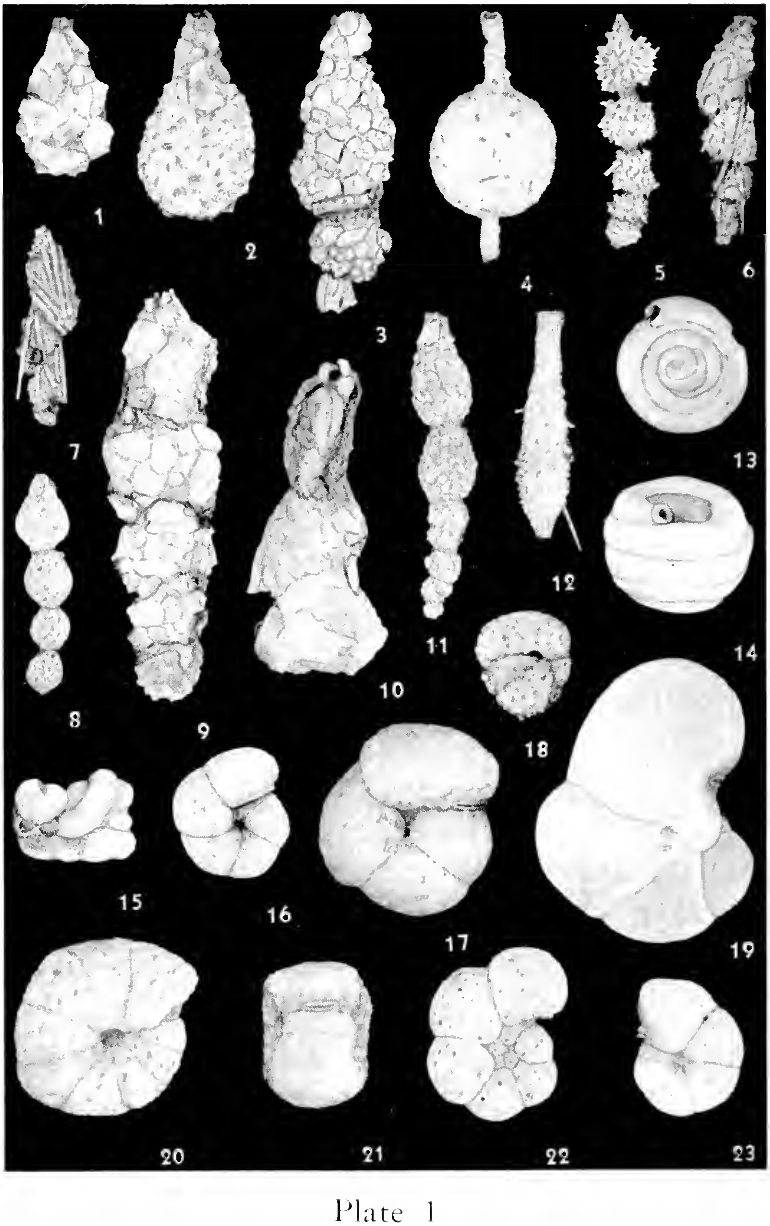

Plate 1

PLATE 2

Figs. 1, 2. *Alveolophragmium subglobosum* (G. O. Sars). X 33. (1) Sta. 4; (2) Sta. 191.

Figs. 3, 4. *Ammoscalaria pseudospiralis* (Williamson). X 42. (3) Sta. 225; (4) Sta. 208.

Fig. 5. *Ammoscalaria tenuimargo* (H. B. Brady). X 42. Sta. 107.

Fig. 6. *Ammobaculites* sp. B. X 70. Sta. 104.

Figs. 7, 8. *Ammobaculites* sp. A. (7) X 42. Sta. 203; (8) X 31. Sta. 202.

Fig. 9. *Spiroplectammina floridana* (Cushman). X 42. Sta. 156.

Fig. 10. *Textularia foliacea occidentalis* Cushman. X 39. Sta. 116.

Fig. 11. *Textularia mayori* Cushman. X 33. Sta. 92.

Fig. 12. *Textularia earlandi* Parker. X 70. Sta. 30.

Fig. 13. *Textularia conica* d'Orbigny. X 39. Sta. 117.

Fig. 14. *Siphotextularia rolshauseni* Phleger and Parker. X 62. Sta. 191.

Fig. 15. *Siphotextularia curta* (Cushman). X 42. Sta. 121.

Figs. 16, 17. *Textularia candeiana* d'Orbigny. (16) X 42. Sta. 116; (17) X 31. Sta. 85.

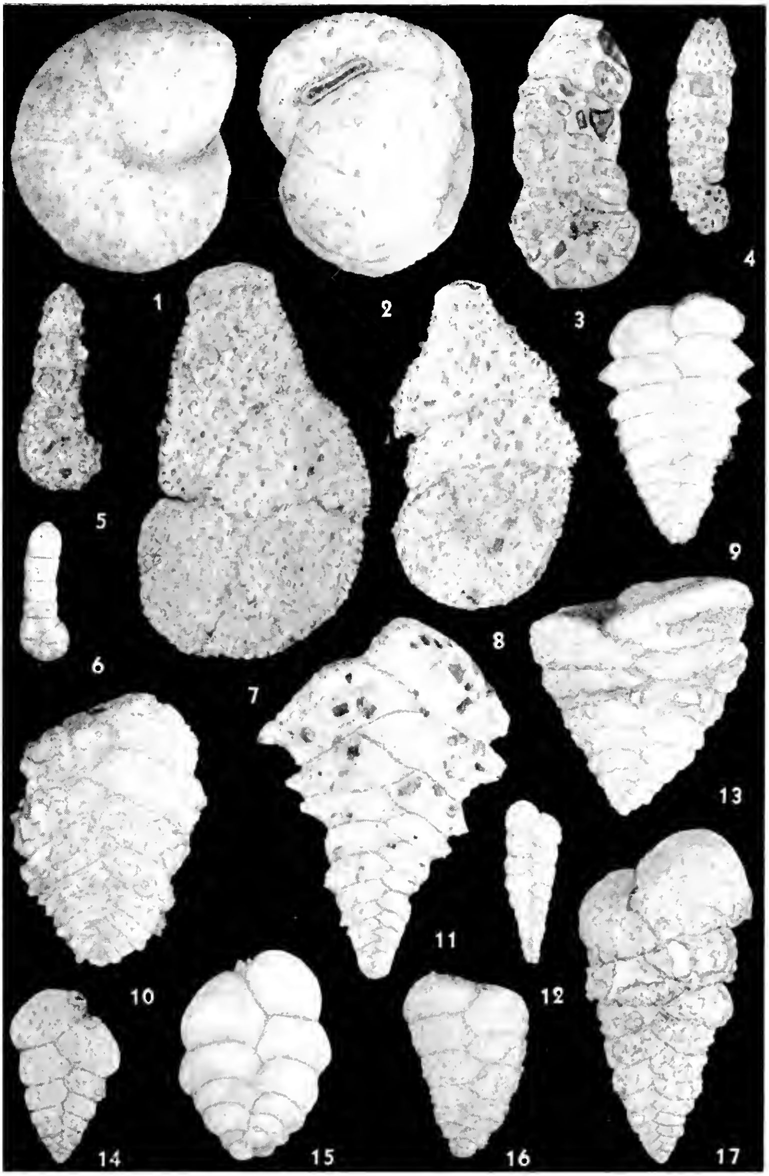

Plate 2

PLATE 3

Figs. 1, 2, 3. *Bigenerina irregularis* Phleger and Parker. X 39. (1, 2) Side views; (3) Edge view. Sta. 164.

Figs. 4, 5. *Bigenerina textularioidea* (Goës). (4) X 22. Side view; (5) X 42. Edge view. Sta. 90.

Fig. 6. *Gaudryina flintii* Cushman. X 24. Sta. 128.

Fig. 7. *Gaudryina* (*Pseudogaudryina*) *atlantica* (Bailey). X 22. Sta. 181.

Fig. 8. *Pseudoclavulina mexicana* (Cushman). X 24. Sta. 181.

Figs. 9, 10. *Pseudoclavulina* aff. *novangliae* Cushman. X 24. Sta. 52.

Fig. 11. *Karreriella bradyi* (Cushman). X 47. Sta. 116.

Fig. 12. *Gaudryina* cf. *aequa* Cushman. X 62. Sta. 77.

Figs. 13, 14, 19. *Goësella mississippiensis* n. sp. (13, 14) X 62. Paratypes; (19) X 42. Holotype. Sta. 28.

Figs. 15, 16. *Gaudryina* cf. *minuta* Earland. X 70. (15) Sta. 12. (16) Sta. 11.

Fig. 17. *Eggerella bradyi* (Cushman) X 42. Sta. 191.

Fig. 18. *Plectina apicularis* (Cushman). X 42. Sta. 191.

Figs. 20, 21. *Quinqueloculina compta* Cushman. X 42. Sta. 214.

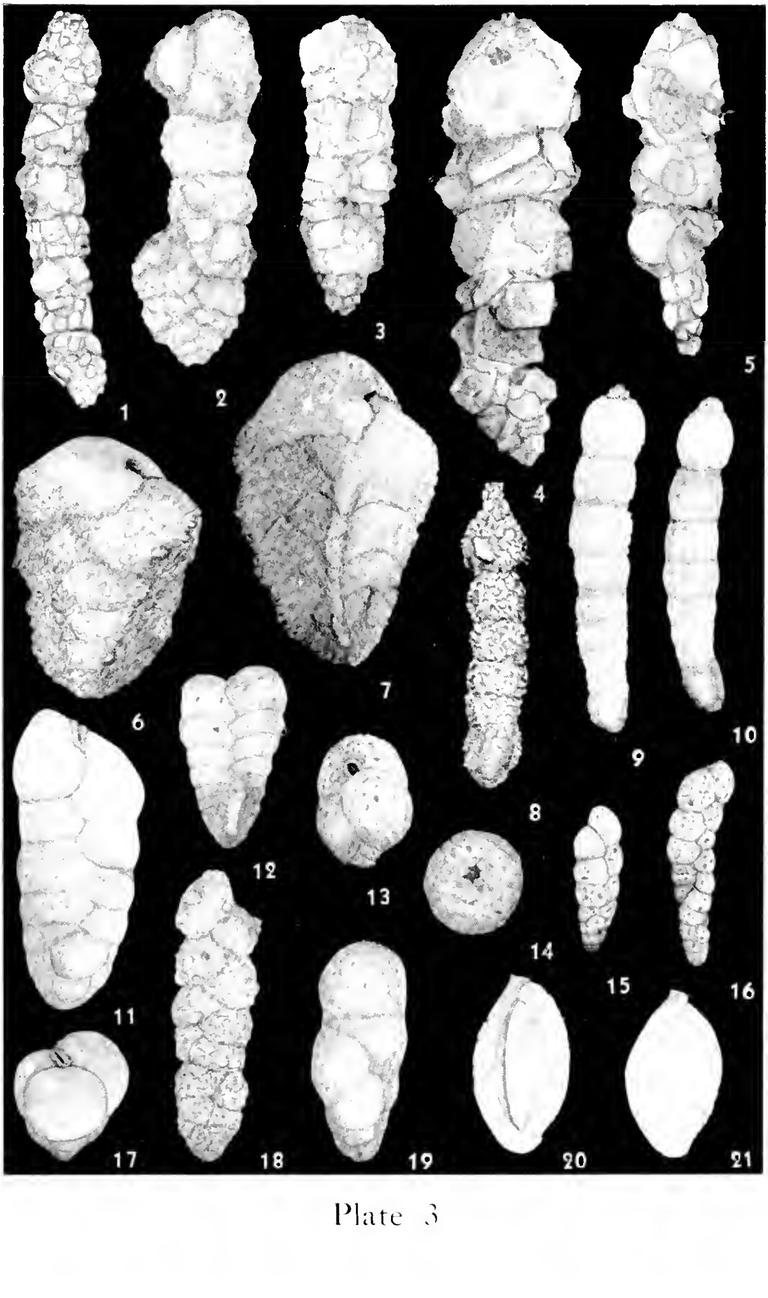

Plate 3

PLATE 4

Figs. 1, 2. *Quinqueloculina bicostata* d'Orbigny. X 39. Sta. 93.

Figs. 3, 4. *Quinqueloculina horrida* Cushman. X 42. (3) Sta. 66; (4) Sta. 62.

Figs. 5, 6. *Quinqueloculina lamarckiana* d'Orbigny. X 39. Sta. 164.

Figs. 7, 8. *Quinqueloculina* cf. *polygona* d'Orbigny. X 42. Sta. 93.

Figs. 9, 10. *Quinqueloculina sabulosa* Cushman. X 42. (9) Sta. 214; (10) Sta. 93.

Figs. 11, 12. *Quinqueloculina* sp. X 42. Sta. 124.

Figs. 13, 14. *Quinqueloculina venusta* Karrer. X 42. Sta. 191.

Fig. 15. *Spiroloculina* cf. *grata* Terquem. X 42. Sta. 58.

Fig. 16. *Spiroloculina soldanii* Fornasini. X 42. Sta. 154.

Figs. 17, 21. *Sigmoilina distorta* Phleger and Parker. (17) X 70. Sta. 218; (21) X 62. Sta. 184.

Fig. 18. *Sigmoilina schlumbergeri* Silvestri. X 41. Sta. 107.

Fig. 19. *Sigmoilina tenuis* (Czjzek). X 62. Sta. 116.

Fig. 20. *Nummoloculina irregularis* (d'Orbigny). X 62. . Sta. 124.

Fig. 22. *Triloculina tricarinata* d'Orbigny. X 42. Sta. 121.

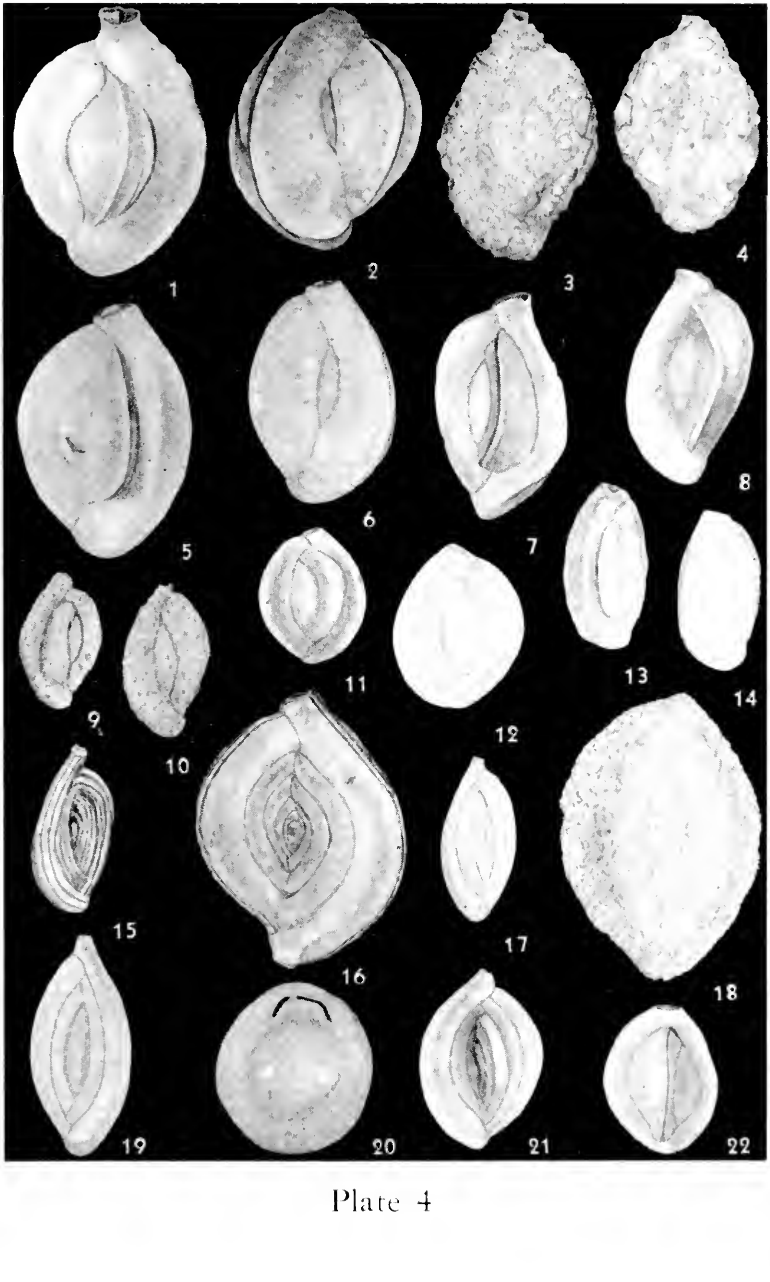

Plate 4

PLATE 5

Fig. 1. *Sigmoilina* sp. X 33. Sta. 59.

Figs. 2, 3. *Triloculina* cf. *brevidentata* Cushman. X 42. Sta. 93.

Fig. 4. *Pyrgo* cf. *nasutus* Cushman. X 42. Sta. 93.

Figs. 5, 6. *Trochammina advena* Cushman. X 70. Sta. 24.

Fig. 7. *Pyrgo murrhina* (Schwager). X 39. Sta. 133.

Fig. 8. *Nodobaculariella cassis* (d'Orbigny). X 47. Sta. 93.

Figs. 9, 10. *Trochammina* cf. *japonica* Ishiwada. X 70. Sta. 24.

Figs. 11, 12. *Trochammina globulosa* Cushman. X 42. Sta. 36.

Fig. 13. *Wiesnerella auriculata* (Egger). X 70. Sta. 93.

Figs. 14, 15. *Trochammina quadriloba* Höglund. X 70. Sta. 191.

Figs. 16, 17. *Trochammina* cf. *tasmanica* Parr. X 70. Sta. 24.

Fig. 18. *Lenticulina peregrina* (Schwager). X 47. Sta. 199.

Fig. 19. *Nouria polymorphinoides* Heron-Allen and Earland. X 42. Sta. 225.

Fig. 20. *Nouria* sp. X 62. Sta. 27.

Fig. 21. *Marginulina marginulinoides* (Goës). X 33. Sta. 154.

Fig. 22. *Pseudoglandulina comatula* (Cushman). X 39. Sta. 116.

Fig. 23. *Globulina caribaea* d'Orbigny. X 62. Sta. 93.

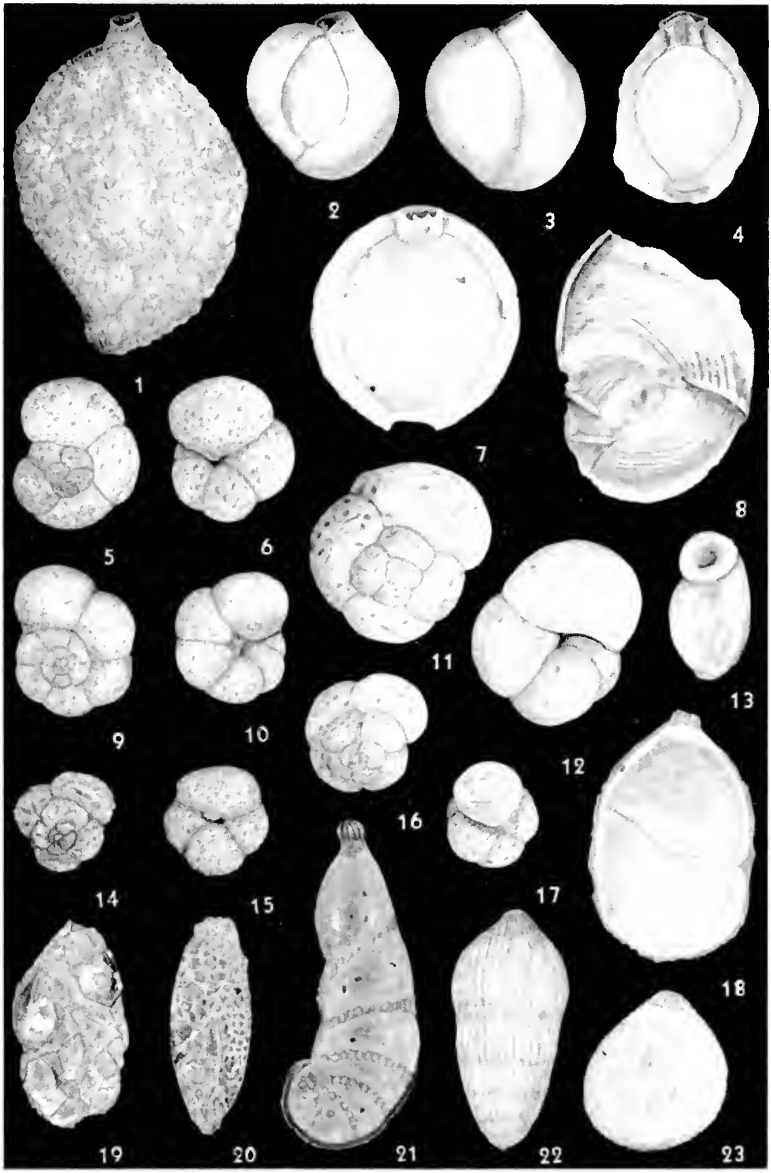

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PLATE 6

Fig. 1. *Nodosaria hispida* d'Orbigny. X 31. Sta. 187.

Fig. 2. *Guttulina australis* (d'Orbigny). X 42. Sta. 225.

Fig. 3. *Nonion formosum* (Seguenza). X 42. Sta. 154.

Fig. 4. *Nonion pompilioides* (Fichtel and Mol.). X 42. Sta. 2.

Fig. 5. *Astrononion tumidum* Cushman and Edwards. X 62. Sta. 189.

Figs. 6, 7. *Nonionella atlantica* Cushman. X 62. Sta. 222.

Figs. 8, 9. *Nonionella* sp. X 62. Sta. 224.

Figs. 10, 11, 12. *Nonionella opima* Cushman. X 62. Sta. 224.

Fig. 13. *Buliminella* cf. *bassendorfensis* Cushman and Parker. X 62. Sta. 28.

Fig. 14. *Elphidium advenum* (Cushman). X 42. Sta. 177.

Fig. 15. *Elphidium discoidale* (d'Orbigny). X 42. Sta. 222.

Fig. 16. *Elphidium gunteri* Cole. X 42. Sta. 93.

Fig. 17. *Elphidium poeyanum* (d'Orbigny). X 42. Sta. 93.

Fig. 18. *Robertina bradyi* Cushman and Parker. X 42. Sta. 124.

Fig. 19. *Bulimina aculeata* d'Orbigny. X 42. Sta. 105.

Fig. 20. *Bulimina marginata* d'Orbigny. X 62. Sta. 30.

Fig. 21. *Bulimina alazanensis* Cushman. X 62. Sta. 199.

Figs. 22, 23. *Bulimina spicata* Phleger and Parker. X 62. Sta. 32.

Fig. 24. *Bulimina striata mexicana* Cushman. X 42. Sta. 193.

Fig. 25. *Globobulimina affinis* (d'Orbigny). X 42. Sta. 34.

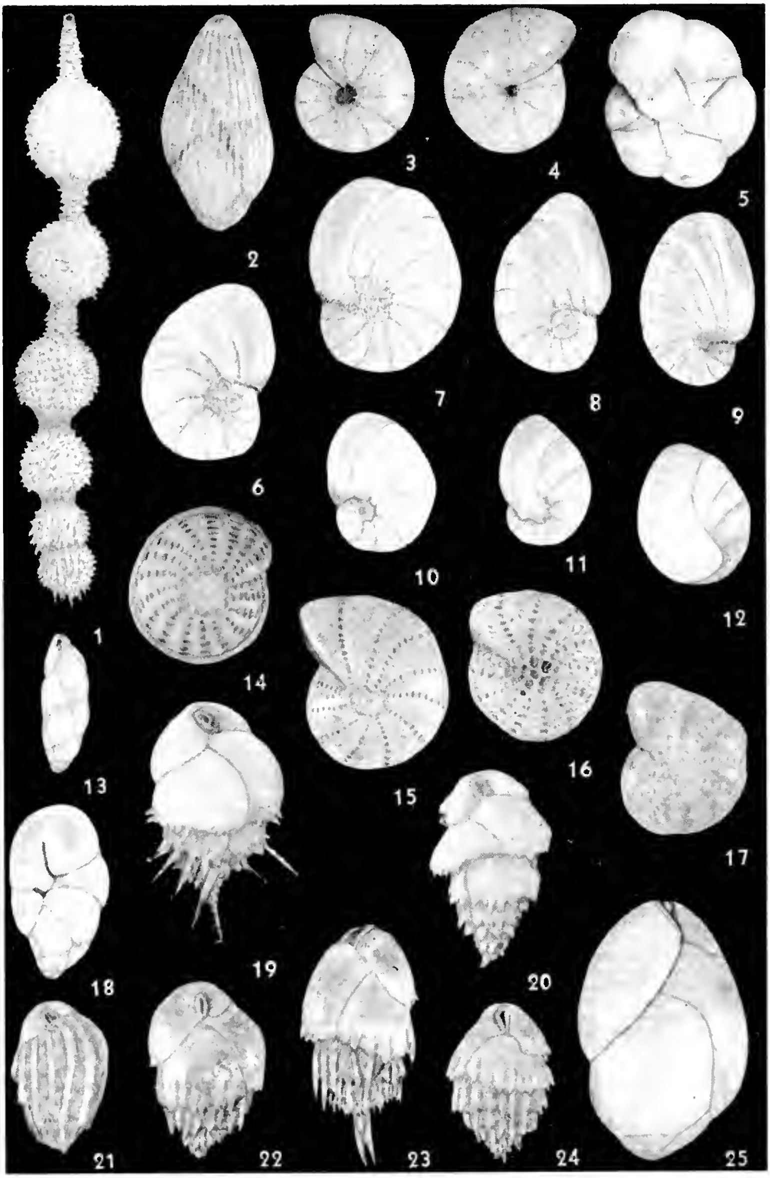

Plate 6

PLATE 7

Fig. 1. *Globobulimina affinis* (d'Orbigny). X 46. Sta. 12.

Fig. 2. *Globobulimina affinis* (d'Orbigny) var. X 42. Sta.. 8.

Figs. 3, 4, 10. *Globobulimina mississippiensis* n. sp. X 62. Sta. 29. (3) Holotype; (4, 10) Paratypes.

Fig. 5. *Virgulina advena* Cushman. X 42. Sta. 191.

Fig. 6. *Virgulina complanata* Egger. X 62. Sta. 36.

Figs. 7, 8. *Virgulina mexicana* Cushman. X 42. Sta. 199.

Fig. 9. *Virgulina pontoni* Cushman. X 62. Sta. 214.

Fig. 11. *Virgulina punctata* d'Orbigny. X 42. Sta. 93.

Fig. 12. *Virgulina tessellata* Phleger and Parker. X 62. Sta. 33.

Fig. 13. *Bolivina albatrossi* Cushman. X 62. Sta. 184.

Fig. 14. *Bolivina barbata* Phleger and Parker. X 62. Sta. 28.

Fig. 15. *Bolivina fragilis* Phleger and Parker. X 60. Sta. 76.

Fig. 16. *Bolivina goësii* Cushman. X 62. Sta. 116.

Figs. 17, 18, 19, 20. *Bolivina lanceolata* n. sp. X 62. Sta. 180. (17) Holotype; (18, 19, 20) Paratypes.

Fig. 21. *Bolivina lowmani* Phleger and Parker. X 70. Sta. 184.

Figs. 22, 23. *Bolivina minima* Phleger and Parker. X 62. Sta. 184.

Fig. 24. *Bolivina ordinaria* Phleger and Parker. X 70. Sta. 30.

Fig. 25. *Bolivina* sp. X 42. Sta. 190.

Fig. 26. *Bolivina paula* Cushman and Cahill. X 70. Sta. 122.

Fig. 27. *Rectobolivina advena* (Cushman). X 42. Sta. 57.

Fig. 28. *Reussella atlantica* Cushman. X 62. Sta. 58.

Fig. 29. *Bolivina striatula spinata* Cushman. X 62. Sta. 27.

Figs. 30, 35. *Bolivina subspinescens* Cushman. X 42. Sta. 116.

Fig. 31. *Bolivina pusilla* Schwager. X 62. Sta. 121.

Fig. 32. *Loxostomum abruptum* Phleger and Parker. X 70. Sta. 144.

Fig. 33. *Bolivina subaenariensis mexicana* Cushman. X 42. Sta. 184.

Fig. 34. *Bolivina translucens* Phleger and Parker. X 62. Sta. 184.

Fig. 36. *Bolivina pulchella primitiva* Cushman. X 70. Sta. 74.

Fig. 37. *Rectobolivina dimorpha* (Parker and Jones). X 62. Sta. 190.

Fig. 38. *Uvigerina auberiana* d'Orbigny. X 42. Sta. 128.

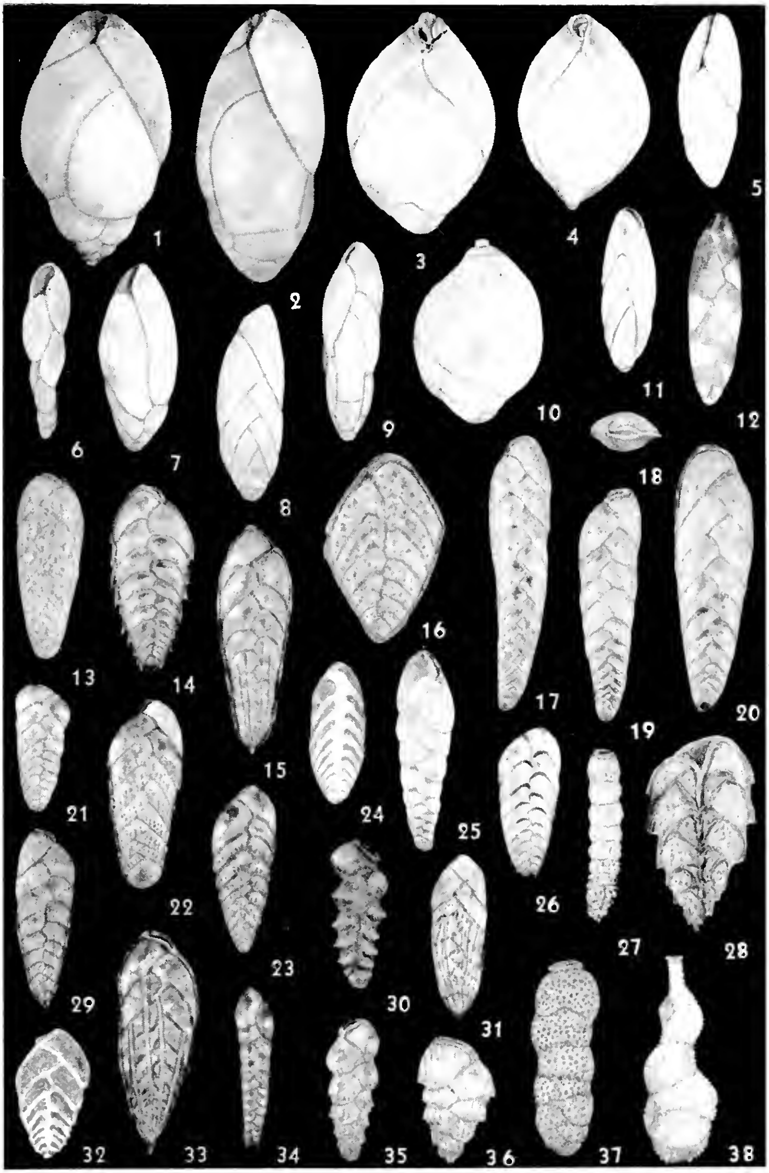
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Plate 7

PLATE 8

Fig. 1. *Uvigerina auberiana* d'Orbigny. X 39. Sta. 128.
Fig. 2. *Uvigerina flintii* Cushman. X 42. Sta. 116.
Fig. 3. *Uvigerina hispido costata* Cushman and Todd. X 42. Sta. 187.
Fig. 4. *Uvigerina laevis* Goës. X 62. Sta. 76.
Fig. 5. *Uvigerina peregrina* Cushman. X 42. Sta. 128.
Fig. 6. *Uvigerina parvula* Cushman. X 62. Sta. 116.
Fig. 7. *Angulogerina bella* Phleger and Parker. X 62. Sta. 214.
Fig. 8. *Angulogerina jamaicensis* Cushman and Todd. X 70. Sta. 58.
Fig. 9. *Trifarina bradyi* Cushman. X 42. Sta. 141.
Figs. 10, 11, 12. "*Discorbis*" *bulbosa* n. sp. X 70. Sta. 220. (10) Holotype; (11, 12) Paratypes.
Figs. 13, 14. *Conorbina orbicularis* (Terquem). X 70. Sta. 161.
Figs. 15, 16. *Spirillina vivipara* Ehrenberg. X 70. Sta. 154.
Figs. 17, 18. *Rosalina* cf. *concinna* (H. B. Brady). X 62. Sta. 93.
Figs. 19, 20. *Rosalina floridana* (Cushman). X 62. Sta. 224.
Figs. 21, 26, 27. *Rosalina suezensis* (Said). (21) X 70; (26, 27) X 62. Sta. 52.
Figs. 22, 23. *Rosalina bertheloti* d'Orbigny. X 42. Sta. 179.
Figs. 24, 25. *Rosalina parkerae* (Natland). X 62. Sta. 154.
Figs. 28, 29. *Rosalina floridensis* (Cushman). X 30. Sta. 138.

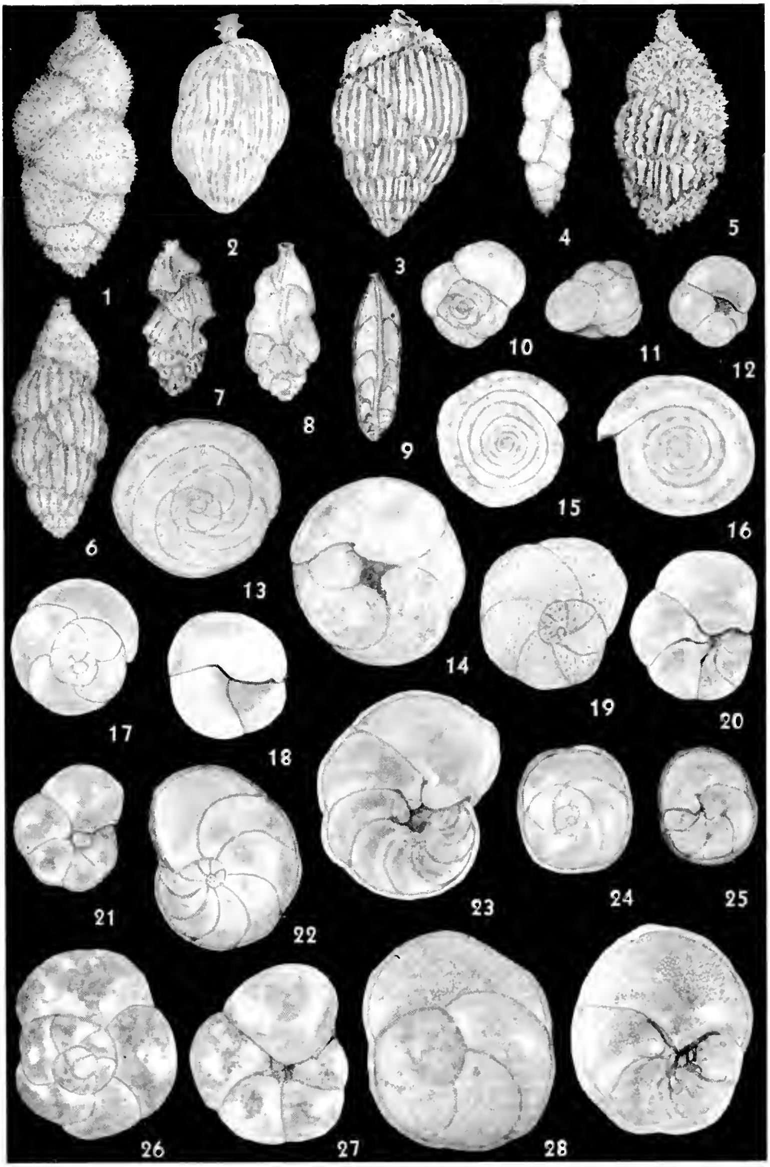

Plate 8

PLATE 9

Figs. 1, 2, 3. *Valvulineria mexicana* n. sp. (1, 2) X 62; (3) X 70. (1, 3) Paratypes; (2) Holotype. Sta. 31.

Figs. 4, 5, 6. *Valvulineria minuta* n. sp. X 70. (4, 6) Paratypes; (5) Holotype. Sta. 184.

Figs. 7, 8. *Gyroidinoides soldanii altiformis* R. E. and K. C. Stewart. X 42. Sta. 190.

Figs. 9, 10 *Gyroidina neosoldanii* Brotzen. X 42. Sta. 191.

Figs. 11, 12. *Eponides polius* Phleger and Parker. X 62. Sta. 107.

Figs. 13, 18. *Gyroidina orbicularis* d'Orbigny. X 62. Sta. 184.

Figs. 14, 15. *Eponides antillarum* (d'Orbigny). (14) X 39; (15) X 42. Sta. 93.

Figs. 16, 17. *Eponides regularis* Phleger and Parker. X 70. Sta. 30.

Figs. 19, 24. *Eponides tumidulus* (H. B. Brady). X 94. Sta. 191.

Figs. 20, 21. *Pseudoeponides umbonatus* (Reuss). X 42. Sta. 107.

Figs. 22, 23. *Eponides turgidus* Phleger and Parker. X 70. Sta. 191.

Figs. 25, 26. *Buccella hannai* (Phleger and Parker). X 62. Sta. 93.

Figs. 27, 28. *Eponides repandus* (Fichtel and Moll). (27) X 39; (28) X 33. Sta. 179.

Figs. 29, 30. *Osangularia cultur* (Parker and Jones). X 42. Sta. 124.

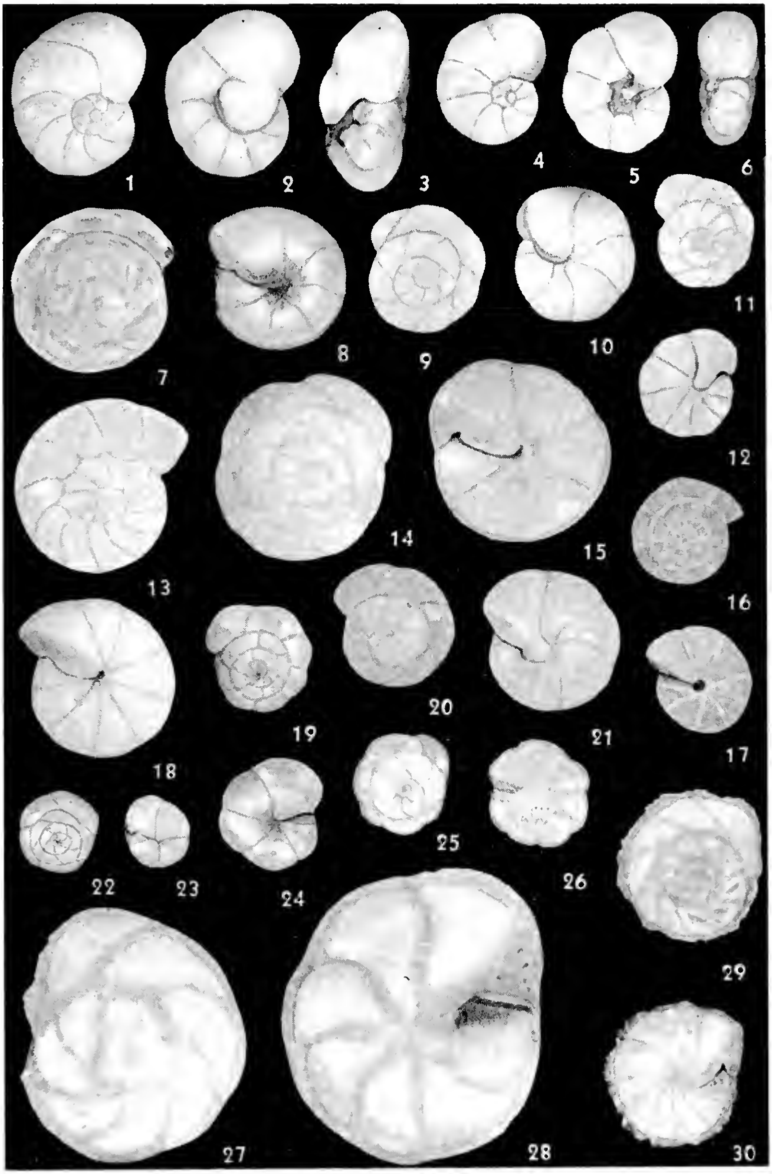
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Plate 9

PLATE 10

Figs. 1, 2, 5, 6. "*Rotalia*" *beccarii* (Linné) vars. X 62. Sta. 93.

Figs. 3, 7. "*Rotalia*" *translucens* Phleger and Parker. X 70. Sta. 99.

Figs. 4, 8. *Höglundina elegans* (d'Orbigny). X 42. Sta. 116.

Figs. 9, 10. *Siphonina bradyana* Cushman. X 42. Sta. 141.

Figs. 11, 12. *Siphonina pulchra* Cushman. X 42. Sta. 179.

Figs. 13, 14. *Cancris oblonga* (Williamson). X 42. Sta. 52.

Figs. 15, 21. *Cancris sagra* (d'Orbigny). X 42. Sta. 93.

Figs. 16, 17. *Asterigerina carinata* d'Orbigny. X 42. Sta. 170.

Figs. 18, 19. *Epistominella decorata* (Phleger and Parker). X 70. Sta. 191.

Figs. 20, 26. *Epistominella vitrea* Parker. X 62. Sta. 27.

Figs. 22, 23. *Epistominella exigua* (H. B. Brady) X 62. Sta. 124.

Figs. 24, 25. *Epistominella rugosa* (Phleger and Parker). X 62. Sta. 141.

Figs. 27, 28, 29. *Stetsonia minuta* n. sp. X 94. (27) Holotype; (28, 29) Paratypes. Sta. 218.

Fig. 30. *Cassidulina carinata* Silvestri. X 42. Sta. 100.

Fig. 31. *Cassidulina* aff. *crassa* d'Orbigny. X 62. Sta. 116.

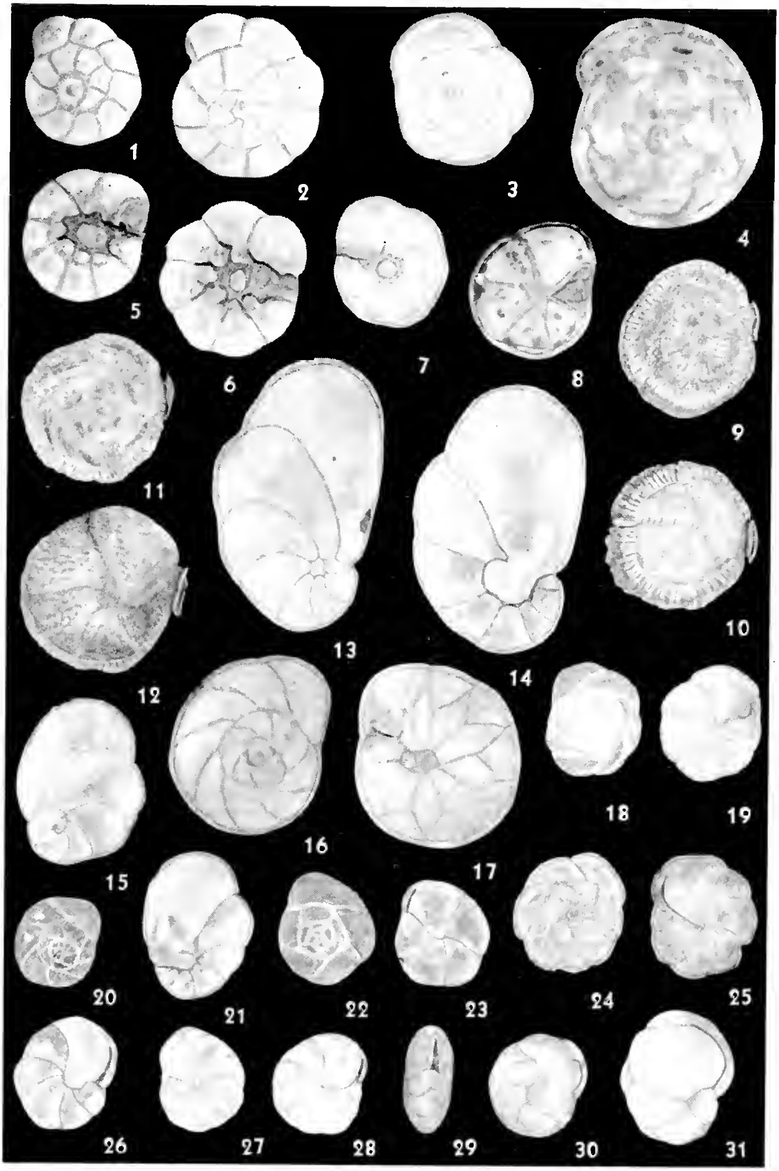
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Plate 10

PLATE 11

Fig. 1. *Cassidulina curvata* Phleger and Parker. X 42. Sta. 116.

Fig. 2. *Cassidulina laevigata* d'Orbigny. X 62. Sta. 78.

Fig. 3. *Cassidulina neocarinata* Thalmann. X 62. Sta. 184.

Figs. 4, 5. *Cassidulina subglobosa* H. B. Brady. X 62. Sta. 124.

Figs. 6, 7, 8, 9. *Cassidulina subglobosa* H. B. Brady vars. X 70. (6) Sta. 74; (7, 8, 9) Sta. 124.

Figs. 10, 11. *Rotamorphina laevigata* (Phleger and Parker). X 70. Sta. 184.

Fig. 12. *Ehrenbergina spinea* Cushman. X 62. Sta. 116.

Fig. 13. *Seabrookia earlandi* Wright. X 70. Sta. 179.

Fig. 14. *Cassidulinoides tenuis* Phleger and Parker. X 62. Sta. 188.

Fig. 15. *Chilostomella oolina* Schwager. X 62. Sta. 189.

Fig. 16. *Pullenia quinqueloba* Reuss. X 62. Sta. 179.

Fig. 17. *Pullenia bulloides* (d'Orbigny). X 42. Sta. 107.

Fig. 18. *Sphaeroidina bulloides* d'Orbigny. X 42. Sta. 116.

Fig. 19. *Sphaeroidina compacta* Cushman and Todd. X 39. Sta. 128.

Figs. 20, 24. *Pullenia* sp. X 70. Sta. 121.

Figs. 21, 22, 23. *Anomalinoides mexicana* n. sp. X 62. (21) Holotype; (22, 23) Paratypes. Sta. 184.

Figs. 25, 26. *Planulina foveolata* (H. B. Brady). X 42. Sta. 181.

Figs. 27, 30. *Planulina ariminensis* d'Orbigny. (27) X 30; (30) X 42. Sta. 141.

Figs. 28, 29. *Planulina exorna* Phleger and Parker. X 42. Sta. 93.

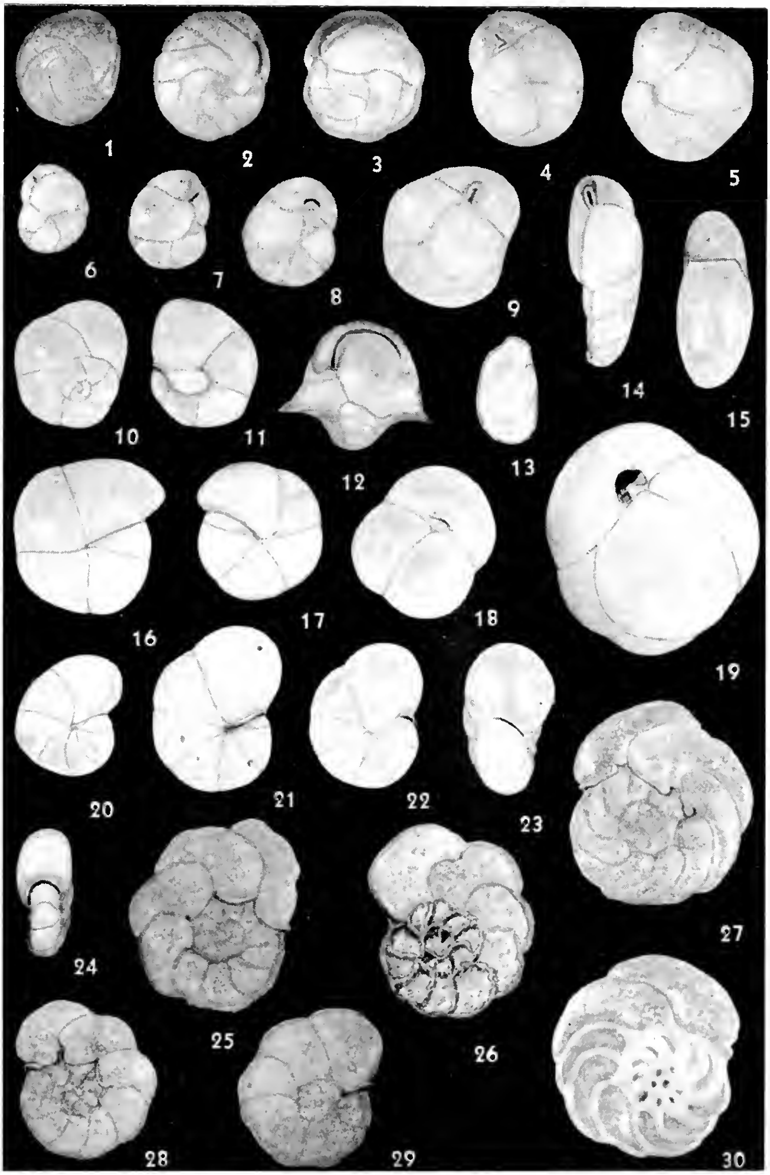
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Plate 11

PLATE 12

Figs. 1, 2. *Cibicides deprimus* Phleger and Parker. X 42. Sta. 154.

Fig. 3. *Laticarinina pauperata* (Parker and Jones). X 30. Sta. 191.

Figs. 4, 8. *Cibicides corpulentus* Phleger and Parker. X 39. Sta. 181.

Figs. 5, 9. *Cibicides* aff. *floridanus* (Cushman). X 42. Sta. 31.

Figs. 6, 7. *Cibicides io* Cushman. X 42. West of Sta. 78, at 62 m.

Figs. 10, 11. *Cibicides kullenbergi* Parker. X 42. Sta. 191.

Figs. 12, 15. *Cibicides mollis* Phleger and Parker. X 42. Sta. 76.

Figs. 13, 14, 16. *Cibicides protuberans* n. sp. (13, 14) X 39; (16) X 42. (13) Holotype; (14, 16) Paratypes. Sta. 116.

Figs. 17, 18. *Cibicides umbonatus* Phleger and Parker. (17) X 42; (18) X 39. Sta. 181.

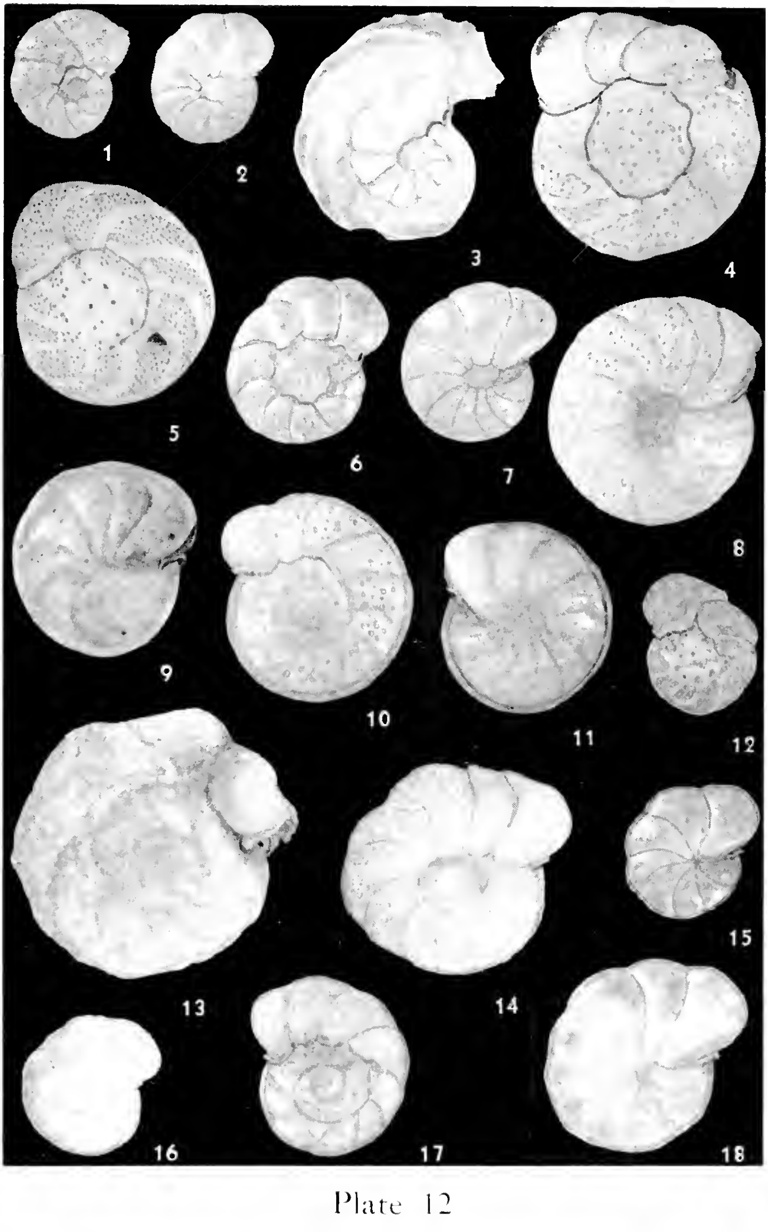


Plate 12

PLATE 13

Figs. 1, 4. *Cibicides rugosa* Phleger and Parker. X 30. Sta. 124.

Figs. 2, 5. *Cibicides robertsonianus* (H. B. Brady). (2) X 42; (5) X 39. Sta. 191.

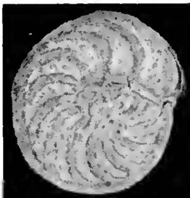
Figs. 3, 6. *Cibicides wuellerstorfi* (Schwager). X 42. Sta. 191.

Figs. 7, 10. *Cibicidina concentrica* (Cushman). X 42. Sta. 58.

Figs. 8, 11. *Cibicidina strattoni* (Applin). (8) X 42; (11) X 39. Sta. 93.

Fig. 9. *Planorbulina mediterranensis* d'Orbigny. X 30. Sta. 138.

Fig. 12. *Gypsina vesicularis* (Parker and Jones). X 34. Sta. 64.



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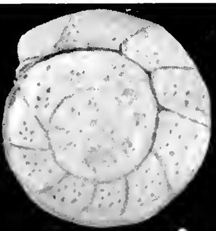

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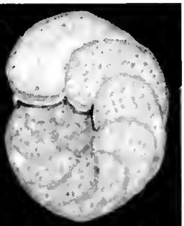

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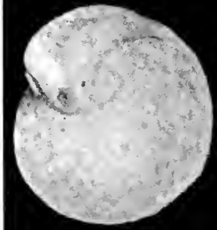

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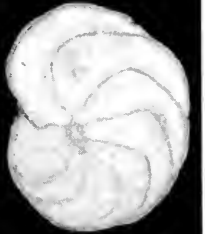

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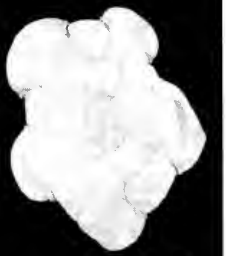

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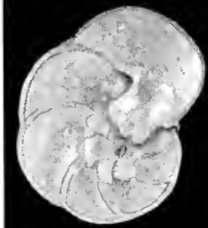

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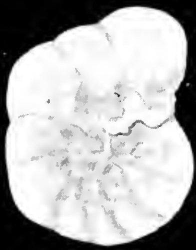

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Plate 13

ERRATA

The following corrections should be made in Figures 3-9.

Figure 3. *Bolivina albatrossi* does not occur in traverse I.

Figure 4. *Caneris oblonga* does not occur in traverses II-III.
Cassidulinoides tenuis does not occur in traverses IV-V.
Cibicides kullenbergi occurs once in traverse V (not in IV).

Figure 5. "*Discorbis*" *bulbosa* occurs in traverse XI.
Elphidium gunteri occurs in traverse III (once).
Epistominella rugosa does not occur in traverse I. It occurs once in traverses II and III.

Figure 6. *Liebusella* spp. occurs in traverses II-III (once).
Marginulina marginulinoides occurs once in traverse V (not in IV).
Nodosaria hispida occurs deeper than 146 m.
Nonion pompilioides does not occur in traverses IV-V.
Nonionella opima occurs in traverse I.

Figure 7. *Quinqueloculina compta* occurs in traverse XI (once).
Q. sp. occurs in traverses II-III.
Rectobolivina advena occurs in traverse XI (once).

Figure 8. "*Rotalia*" *beccarii* vars. occurs in traverse I more than once.
Sigmoilina tenuis occurs in traverse III (once), V (more than once).
Siphonina pulchra occurs in traverse II (once).
Siphotextularia rolshauseni occurs in traverse II.
Sphaeroidina bulloides occurs in traverses II-III.

Figure 9. *Textularia earlandi* does not occur in traverses VI-VII.
Trochammina quadriloba occurs once in traverse VII (not in VI).
Valvulineria minuta occurs more than once in traverse II.
Virgulina pontoni occurs in traverse XI.
Wiesnerella auriculata occurs in traverse I (once), III (once).