

## A LOWER PERMIAN TEMNOSPONDYLOUS AMPHIBIAN FROM THE ENGLISH MIDLANDS

by ROBERTA L. PATON

**ABSTRACT.** The holotype skull of *Dasyiceps bucklandi* (Lloyd, 1850) from the Lower Permian (Autunian) Kenilworth Breccia is redescribed and its relationships with other members of the family Zatrachyidae are discussed. The two species of the American genus *Zatrachys*, the type species *Z. serratus* Cope, 1878 and *Z. microphthalmus* Cope, 1896 are considered. *Z. microphthalmus* is transferred to the genus *Dasyiceps* as a new species *D. microphthalmus*, leaving *Z. serratus* as the only species of the genus *Zatrachys*. It is shown that *Acanthostomatops* Kuhn, 1961 is not the larval form of *Dasyiceps*, but may instead be the larva of *Z. serratus*. It is suggested that *Dasyiceps* was a terrestrial labyrinthodont, and a possible function for its enormous median nasal vacuity is put forward.

THE unique skull (Warwick County Museum, no. Gz 42) is the holotype of the species *Labyrinthodon bucklandi* Lloyd, 1850. It was more fully described by Huxley (1859) who recognized it as a form distinct from other known labyrinthodonts and separated it as a new genus *Dasyiceps*. Von Huene (1910) studied it further, giving the most complete description to date. Case (1911) was the first to note its close relationship to the aberrant family of labyrinthodonts, the Zatrachyidae. The other generally recognized members of this family are *Stegops* Moodie, 1909, a primitive form from the Westphalian D of Linton, Ohio (Romer 1930); *Acanthostomatops* Kuhn, 1961 (previously known as *Acanthostoma* Credner, 1883, but Kuhn pointed out that this name was preoccupied by a polychaete), a small form found in the lower Permian Niederhässlich deposits of Saxony (Steen 1937); and *Zatrachys* Cope, 1878 from the lower Permian of Texas and New Mexico. The poorly known genus *Platyhystrix* Williston, 1911, from the lower Permian of New Mexico, was thought to belong in this family at one time, but this was because Williston (1911, 1916) figured what is almost certainly a *Z. microphthalmus* skull (Langston, 1953) in artificial association with long-spined *Platyhystrix* vertebrae, believing the two to belong to one genus. This has given rise to the erroneous belief that some zatrachyids possessed 'sails' of pelycosaurian type on their backs. The affinities of *Platyhystrix*, which did have a 'sail', are uncertain, and are irrelevant to the present topic; for a good discussion of them see Langston (1953).

The Zatrachyidae have always been considered as rhachitomous labyrinthodonts, and Romer (1947, 1966) placed them in the superfamily Eryopoidea. The differences used by Case (1911) to distinguish *Dasyiceps* from *Zatrachys* will be discussed later. *Dasyiceps* has been briefly discussed by Romer (1930, 1939, 1945), but a detailed study of it has not been attempted since von Huene (1910) examined it. Some authors (e.g. Romer 1947, p. 172) have suggested that *Acanthostomatops*, which appears to be a juvenile form, is in fact the larva of *Dasyiceps*. At the same time Romer suggested that *Dasyiceps* and *Zatrachys* might be synonymous, a view also held by Broom (1913). These points will be discussed later.

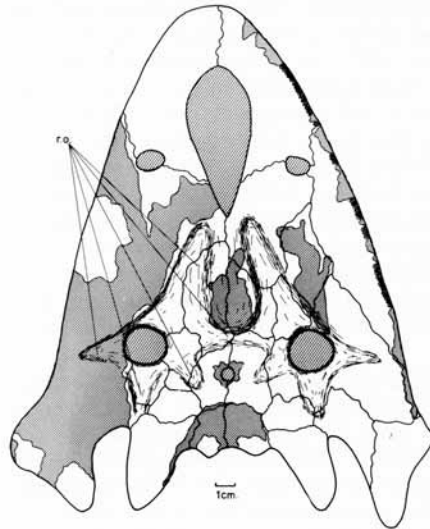
The specimen, an almost complete skull, is in two pieces, part and counterpart.

Much of the skull roof has adhered to one portion, so exposing the ventral surface of the bones with some impressions of their dorsal surfaces. The other portion shows some of the skull roof, but anteriorly a considerable part of the dorsal surface of the palate is exposed. The occiput has at some time been destroyed. Further preparation of the specimen would appear to be impossible owing to its extremely fragile nature, but the thick coat of dark shellac which covered both parts of the specimen, obscuring all detail, has been removed. The skull has been crushed dorso-ventrally but it must in life have been shallow anteriorly and of a moderate depth posteriorly.

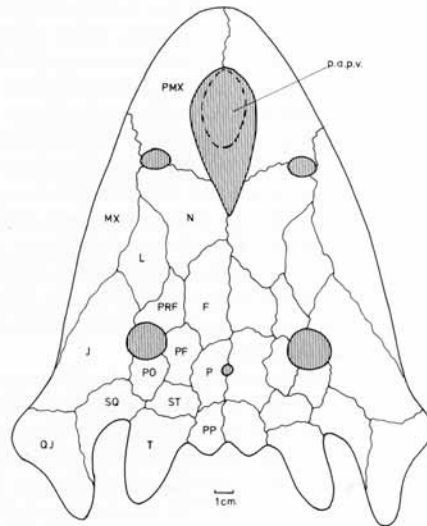
The skull was found in a quarry close to Kenilworth itself (grid ref. SP 290720); the quarry has long been disused and its exact location cannot now be determined. The matrix is a coarse, red, loosely cemented sandstone containing pellets of red clay. The horizon of the specimen is probably Autunian (Paton 1974b).

#### DESCRIPTION

Von Huene (1910) described and figured the specimen fairly accurately, although his plates show that it was then covered by the above-mentioned shellac. The skull is much larger than those of other known zatrachydids, being twice as large as the largest known specimen of *Zatrachys*; its maximum length is 298 mm and the maximum width is 230 mm. Its general shape, and the arrangement of the bones, is typical of a rhachitomous temnospondyl, as can be seen from text-figs. 1-4 and Plates 98 and 99. Several features of interest are apparent.



TEXT-FIG. 1. Specimen Gz 42, *Dasyceps bucklandi* (Lloyd), showing the ventral surface of the skull roof. Stippled areas indicate where bone is missing. (For abbreviations see p. 837.)



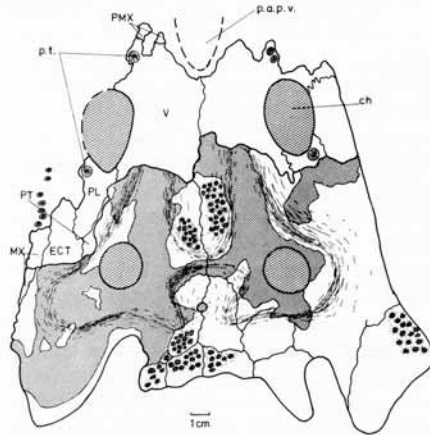
TEXT-FIG. 2. Reconstruction of skull roof of *Dasyceps bucklandi* (Lloyd). (For abbreviations see p. 837.)

The triangular skull is constricted slightly at the level of the maxillary/quadratojugal suture, so that it appears to be swollen across the maxillae. Posterior to this constriction, the quadratojugals flare outwards in a lateral flange which shows signs of having carried a bony frill at the edge. The quadratojugals also have posterior extensions, which extend further back than the tabular horns. The latter rise to a level somewhat above the rest of the skull surface. The postparietals are unusual in having small posterior extensions; they are not, however, as prominent as was shown in previous reconstructions. This feature has also been seen in '*Platyhystrix*' (Williston 1916), *Zatrachys* (Broom 1913), and, to a much lesser extent, in *Stegops* (Romer 1930). The orbits are very small and are situated in the posterior third of the skull. They are elevated above the general skull surface and lie at the apices of two quite sharply defined bony prominences, connected by a transverse ridge 16 mm in front of the pineal foramen. Four other ridges radiate out from each prominence (these are best seen as depressions on the ventral surface of the skull roof). The largest of these extends forward antero-medial to the orbit to the level of the posterior edge of the median nasal vacuity. The other three are of approximately equal size, one extending laterally from the orbit to about the centre of the jugal, another extending posteriorly from the orbit, and the third postero-medially to the middle of the parietal. The height of these prominences and ridges is exaggerated antero-lateral and postero-lateral to the orbit by two depressions: a particularly deep one on the jugal and lachrymal, and a shallower one on the squamosal and jugal, the two being separated by the bony ridges on the jugal. Case (1911) noted similarly situated preorbital depressions in *Zatrachys*, although they were not at that time known to be present in *Dasyceps*. Identically positioned ridges and depressions can be seen on the skulls of the terrestrial labyrinthodonts *Eryops* (Cope 1877) and *Peltobatrachus* (Panchen 1959). Sawin (1941) has suggested that they were occupied by the trabecular cartilages in life.

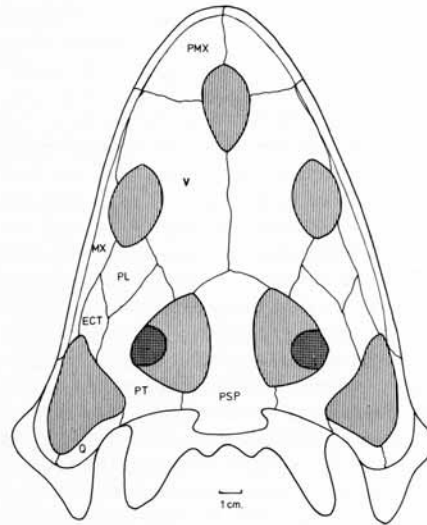
The nares are small, oval, with their long axes transverse, and lie far back, at the junction of the premaxillae, maxillae, and nasals. Their posterior position is caused by the very great enlargement of the premaxillae, which occupy approximately one-third of the total skull length. The main zones of intensive growth (Bystrow 1935), which determine the adult skull shape, are confined to (i) the premaxillae and maxillae; (ii) the jugal and quadratojugal; (iii) the tabular horns. There is a lesser zone across the nasals and maxillae just posterior to the nares. There are no signs of these zones posterior to the orbits. The pineal foramen, which is small, is thus situated very close behind the level of the posterior edges of the orbits.

Probably the most dominant feature of the skull is the very large median vacuity situated between the premaxillae and the nasals. It is drop-shaped, with the blunt end facing anteriorly, and is 86 mm long and 38 mm wide. The edge of this median nasal vacuity, where preserved, is smooth. The anterior part of the broken palate shows the posterior edge of the median anterior palatal vacuity, which corresponds in position to the dorsal vacuity, although the palatal vacuity is considerably smaller.

Only a small part of the dorsal surface of the palate is visible (text-fig. 3), but it shows that the longitudinal elongation of the premaxillae also affected the palate. In addition, the vomers are very large, extending into the posterior half of the skull. This means that the interpterygoid vacuities, although not visible, must be relatively



TEXT-FIG. 3. Specimen Gz 42, *Dasyceps bucklandi* (Lloyd), showing parts of the palate and skull roof. Stippled areas indicate where bone is missing; rest of cranial surface damaged except where ornament is shown. (For abbreviations see p. 837.)



TEXT-FIG. 4. Reconstruction of palate of *Dasyceps bucklandi* (Lloyd). (For abbreviations see p. 837.)

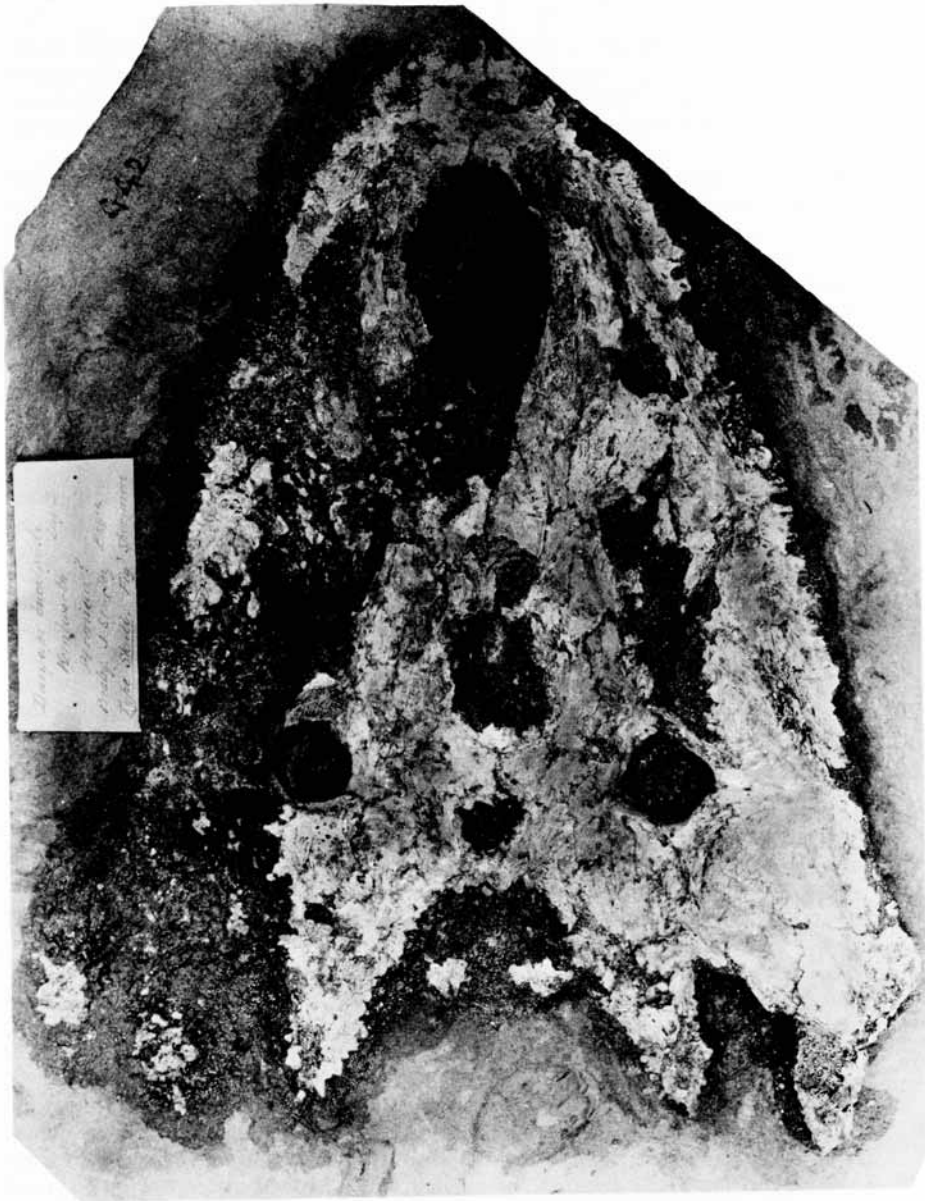
very small. Portions of the palatine and ectopterygoid bones can be seen, as well as the posterior palatal extension of the maxilla, which extends back to about the level of the squamosal/quadratojugal suture. The bases of three vomerine tusks can be seen, one on the left side, and two on the right side; one palatine tusk on each side can be seen just posterior to each choana. The choanae are, in contrast to the external nares, very large—they are oval in shape with the long axis antero-posterior and 38 mm in length, and the transverse axis 24 mm long. Because of the elongation of the anterior part of the snout, they are situated about half-way along the skull.

Only a few marginal teeth are preserved, on the left premaxilla and maxilla. The exact number is very difficult to determine because of the fragmentary nature of the specimen in this region, but remains of eighteen teeth and seven sockets are thought to be present in a maxillary length of 149 mm. Most of the teeth are broken off close to the jaw, but two are almost complete. They are situated at the level of the choanae and are 5 mm long, curving slightly inwards while being directed slightly outwards. For their position and the over-all skull size, the teeth are small. The palatal tusks are also relatively small.

The dorsal surface of the cranial bones is very poorly preserved, and only a small

#### EXPLANATION OF PLATE 98

*Dasyceps bucklandi* (Lloyd). Kenilworth. Ventral surface of skull roof,  $\times \frac{1}{2}$ . Warwick County Museum, Gz 42.



PATON, Permian amphibian

part of the ornamentation is intact. It apparently consisted of very small, fairly shallow pits separated by wide ridges which form blunt, upwardly directed points at junctions of two or more ridges, thus giving the bone surface a pustular appearance. A similar slightly pustular type of ornament can be seen in *Stegops*, '*Platyhystrix*', and *Zatrachys*.

No trace of any lateral-line system can be seen, and it seems likely that von Huene (1910) was incorrect in figuring parts of it in his reconstruction. The only other member of the family in which this system has been figured is *Stegops*, and even here there is some doubt about its presence.

No other material of *Dasyceps bucklandi* is known, although part of a rib in the Institute of Geological Sciences, GSM 90490, from the lower Permian of Kenilworth, is labelled as '? *Dasyceps*'. It appears to be a labyrinthodont rib, but is so poorly preserved that further identification is impossible.

#### DISCUSSION

Case (1911) noted the similarities between *Dasyceps* and *Zatrachys*, but distinguished between them because of the apparent lack of the deep preorbital pits in *Dasyceps*, and the apparent absence of the median nasal vacuity in *Zatrachys*. These features were in fact later found in both genera, and Broom (1913) concluded that the two were congeneric. This conclusion does not appear to have been widely accepted and Romer (1966) still recognized both genera.

Langston (1953) has discussed the genus *Zatrachys* in considerable detail, based upon a study of a large number of specimens of *Z. serratus*. A cast of one of the best specimens used by Langston was available to the author. Case (1911) suggested that *Z. serratus* and *Z. microphthalmus* were conspecific. Langston (1953), however, gives fairly conclusive evidence that they are in fact distinct species. He cites many differences in the skulls of the two species of *Zatrachys*, and goes on to list various skull characters in these, and in *Dasyceps bucklandi*, *Acanthostomatops*, and *Stegops*. A modified version of this table, omitting *Stegops* and bringing the information on *Dasyceps* up to date, is given here (Table 1). Some of the points Langston included are left out, as they are considered irrelevant to the discussion on *Dasyceps*; these are the basal articulation, ossifications in palatal roof, occiput, sclerotic plates, and scutes.

This table again emphasizes the differences between *Z. serratus* and *Z. microphthalmus*. Of the 17 characters listed here, they differ in 9 and agree in 5, while 3 are unknown in one or the other. When *Z. microphthalmus* is compared with *D. bucklandi*, there are only 2 differences, 4 unknown characters (the cultriform process in *Dasyceps* is hypothetical and therefore considered here as an unknown character), and 11 similarities. Some of the characters are dependent upon the over-all size of the specimen, e.g. orbital size, depth of orbital pit, quadratojugal spikes, otic notch depth, size of interpterygoid vacuities. The two features in which *D. bucklandi* differs from *Z. microphthalmus* (the narrower otic notch and narrower internasal vacuity) are here considered to be growth factors probably affected by the much larger size of *D. bucklandi*. That *Z. microphthalmus* resembles *D. bucklandi* much more than it

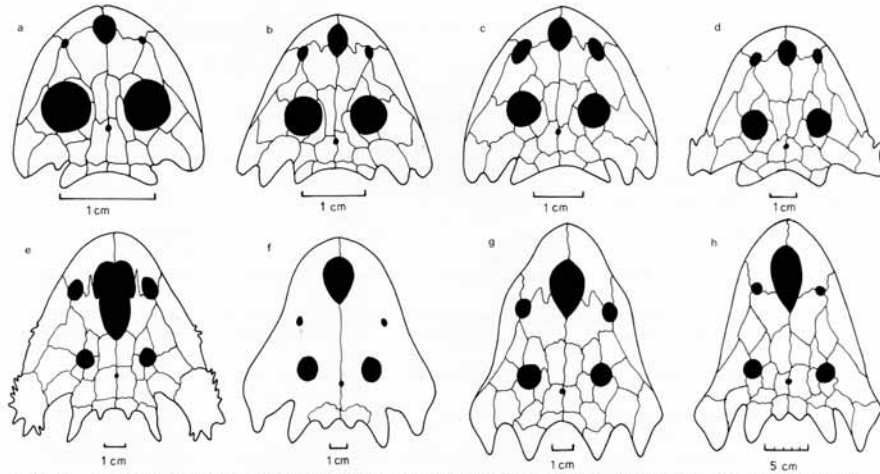
TABLE 1. Comparative osteology of the Zatrachydidae. Modified after Langston (1953).

	<i>Dasyceps bucklandi</i>	<i>Zatrachys microphthalmus</i>	<i>Zatrachys serratus</i>	<i>Acanthostomatops vorax</i>
Dorsal outline	Acute U-shape, slight max. exp.	Acute U-shape, max. exp.	Broad U-shape, no max. exp.	Broad U-shape, no max. exp.
Jaw articln.	Post. to occiput	Post. to occiput	In line with occiput	In line with occiput
Dermal bone ornament	Pits+ridges, low bosses on ridges	Similar to <i>D. bucklandi</i>	Pits+ridges, prominent spikes+bosses	Similar to <i>Z. serratus</i> , but less complex
Preorb. pit	Deep	Deeper	Deep	Shallower
L.l.g.	Not known	Not known	Not known	Not known
Cornua	Broad T and PP cornua	Broad T and PP cornua	Slender T and PP cornua	Weak T cornua only
QJ spikes	Lateral QJ flange and postartic. proc.	Like <i>D. bucklandi</i> but less pronounced	Many long spikes on QJ and postartic. proc.	3 spikes on QJ, small postartic. proc.
Orbits	Small, rims elevated	Small, rims elevated	Slightly larger, rims less elevated	Large, rims slightly elevated
Nares	Small, far posterior	Small, posterior	Large, posterior	Large, more anterior
Otic notch	Narrow, deep	Broad, deep	Broad, deep	Broad, shallow
Median nasal vacuity	Long, fairly narrow, partly separates Ns.	Shorter, wider, partly separates Ns.	Very large, separates Ns., partly divides Fs.	Small, hardly separates Ns.
Choanae	Larger than nares, post. to nares	Not known	Same size as nares, post. to nares	Same size as nares, posterior to nares
Interpt. vacuities	Widely triangular, very short (?)	Widely triangular	Widely triangular	Widely triangular, relatively large
Cultr. proc.	? short, broad	Broad, ? longer	Short, broad	Short, narrow
Ant. pal. vac.	Large	Not known	Not known	Large
Mandible	Not known	Not known	ANG.+SA. ridged, low bosses on ANG.	5 long spines on ANG.
Dentition	Marginal teeth small, 3 tusk pairs	Marginal teeth small, tusk pairs not known	Marginal teeth small, 3 tusk pairs	Marginal teeth small, 3 tusk pairs

## Abbreviations used in text-figures and in Table 1

ANG	angular	PO	postorbital
ant. pal. vac.	anterior palatal vacuity	postartic. proc.	postarticular process
ch	choana	PP	postparietal
cultr. proc.	cultriform process	preorb. pit	preorbital pit
ECT	ectopterygoid	PRF	prefrontal
F	frontal	PSP	parasphenoid
interpt. vac.	interpterygoid vacuity	PT	pterygoid
J	jugal	p.t.	palatal tusk
L	lachrymal	Q	quadrate
l.l.g.	lateral line groove	QJ	quadratojugal
max. exp.	maxillary expansion	r.o.	ridges around orbit
MX	maxilla	SA	surangular
N	nasal	SM	septomaxilla
P	parietal	SQ	squamosal
p.a.p.v.	position of anterior palatal vacuity	ST	supratemporal
PF	postfrontal	T	tabular
PL	palatine	V	vomer
PMX	premaxilla		





TEXT-FIG. 5. *a-d*: growth stages in skulls of '*Acanthostomatops vorax*' (Credner), after Steen (1937). *e*, *Zatrachys serratus* Cope, after Langston (1953). *f*, '*Platyhystrix*' (probably *Dasyceps microphthalmus*), after Williston (1911). *g*, '*Zatrachys*' *microphthalmus* Cope, after Broom (1913). *h*, *Dasyceps bucklandi* (Lloyd).

resembles *Z. serratus* can also be seen quite clearly from text-fig. 5. The positions of the various sutures in *Z. microphthalmus* and *D. bucklandi* are very similar (although Broom's 1913 figure of the former shows a large lachrymal and small jugal, the suture between these bones is dotted in, so presumably there is some doubt about its position). The tabular meets the squamosal, excluding the supratemporal from the otic notch, only in *Z. microphthalmus* and *D. bucklandi*.

Since the differences between *Z. serratus* and *Z. microphthalmus* are of a much greater order than those between *Z. microphthalmus* and *D. bucklandi*, it is felt that this confirms Broom's (1913) decision that the latter two species belong to the same genus. The name of *Dasyceps* Huxley, 1859 antedates that of *Zatrachys* Cope, 1878 and *Z. microphthalmus* must therefore become a species of *Dasyceps*, *D. microphthalmus*. It was thought advisable to retain this as a distinct species, separate from *D. bucklandi*, because of the poor illustrations of *D. microphthalmus*, the imperfections of the specimen of *D. bucklandi*, and the difference in size between the specimens.

Langston (1953) considered that it would serve no useful purpose to synonymize *Zatrachys* and *Dasyceps*. This is not the case, if only from a stratigraphical point of view. The presence of two very closely related, possibly even conspecific, forms, one in North America and the other in England, provides yet more evidence for the lower Permian age of the Kenilworth Breccia and for the proximity of the two countries at this time.

EXPLANATION OF PLATE 99

*Dasyceps bucklandi* (Lloyd). Kenilworth. Part of dorsal surface of skull roof and palate,  $\times \frac{1}{2}$ . Warwick County Museum, Gz 42.





PATON, Permian amphibian

*Z. serratus* shows so many differences from the two species of *Dasyceps* that it is considered necessary to retain it in a separate genus.

The other point put forward by previous authors is the possibility of *Acanthostomatops* being the juvenile form of *Dasyceps*. Probably the most complete growth series known in fossil Amphibia is that shown by the skull of *Benthosuchus sushkini* (Bystrow and Efremov 1940; Westoll 1950) in which most stages between skull lengths of 30 mm and 600 mm are known. The development of the fairly elongated skull can be seen easily when specimens of different sizes are reduced to a standard width (Westoll 1950, fig. 26). A similar diagram has been produced for some growth stages of *Acanthostomatops*, and for the skulls of *D. bucklandi*, *D. microphthalmus*, and *Z. serratus* (text-fig. 5). From this diagram it can be seen that 'Platyhystrix' (almost certainly a badly preserved skull of *D. microphthalmus*) and *D. microphthalmus* are only slightly larger than the largest known specimen of *Acanthostomatops* and that there are substantial differences between the two forms in the skull shape and in the positions of bones. Other differences are apparent from Table 1. The skulls of *D. microphthalmus* and *D. bucklandi*, however, although very different in size, are very similar in shape and bone arrangement. Thus it seems most unlikely that *Acanthostomatops* can be the larva of either species of *Dasyceps*.

However, a different picture emerges when *Acanthostomatops* and *Z. serratus* are compared. Even the largest specimens of *Acanthostomatops* are believed to be juvenile, and no true adult of this genus is known (Romer 1947; Langston 1953). The converse is true of *Z. serratus*; many specimens are known, all are of similar size and all are undoubtedly adults. Langston (1953, p. 396) states that 'this suggests that near adulthood was attained elsewhere, but nothing is known of the habitat'. The skull width of the largest known *Acanthostomatops* specimen is 92 mm measured across the quadratojugals, while that of the smallest *Z. serratus* is approximately 117 mm. It can be seen from Table 1 that, in a comparison between these two forms, there are 11 similarities, 5 differences, and 1 unknown character. The only significant difference between them is the apparent absence of the anterior palatal vacuity in *Z. serratus*. Other differences (i.e. no postparietal cornua, small internasal vacuity, short premaxillae and therefore more anteriorly placed nares, shallower otic notch) are features which are likely to be associated with growth. Since juveniles of *Z. serratus* are unknown, it is obvious that its larval stages grew and metamorphosed elsewhere—perhaps this was a mechanism to prevent possible cannibalism by the adults. Equally, no adults of *Acanthostomatops* are known, therefore metamorphosis occurred elsewhere and the adult form inhabited a different environment. Because of this and the many similarities between *Acanthostomatops* and *Z. serratus*, it is suggested that the former is the juvenile form of *Z. serratus*. It would appear that, just before metamorphosis occurred, the juvenile migrated and only moved to the adult habitat after it had reached a definite size. A possible reason for the large and relatively rapid increase in size of the median nasal vacuity at metamorphosis is given later (p. 844). It is not suggested that the juvenile *Z. serratus* migrated the considerable distance which would separate Niederhässlich and New Mexico even when the effects of continental drift are taken into account and the two placed on a single Laurasian continent. It is merely thought to indicate that *Z. serratus* was fairly widespread over the whole of Laurasia (see later, p. 843), but that larva and adult, inhabiting different

environments, would have been preserved under differing conditions, and therefore would not have been preserved together.

*Z. serratus* Cope, 1878 has priority over *A. vorax* (Credner, 1883) so the species remains *Z. serratus*. The apparent absence of the anterior palatal vacuity in the adults of *Z. serratus* is most surprising in view of its large development in other members of the family. Langston (1953) has indicated that a very small vacuity might perhaps be present in the adult *Z. serratus*. He states, however, that the vomer is not usually preserved and is in no case intact, so there is possibly some doubt about this point.

The author (1974a) has suggested that minor differences in the normal labyrinthodont ornamentation pattern of pits and ridges may be of taxonomic value, and it is therefore interesting to note that the patterns found in the four groups discussed above fall into two distinct types. That in *Dasyceps bucklandi* and *D. microphthalmus* consists of very small, shallow pits separated by wide ridges which have low bosses on them at their junctions. Langston (1953) describes that of the adult *Z. serratus* as having prominent spikes and bosses superimposed on the ridges, which also appear to be wide, separating small, shallow pits. He states that the ornament of '*Acanthostomatops*' is very similar to that of *Z. serratus* but is less complex. This is what would be expected, as Bystrow and Efremov (1940) have shown that the juvenile pattern of dermal bone ornamentation is less complex than that in the adult. This division of the ornament into distinct groups confirms the conclusions reached above that *D. bucklandi* and *D. microphthalmus* are closely related, as are *Z. serratus* and '*Acanthostomatops*', the two groups being separate.

Normal rhachitomous vertebrae are found in all the genera of Zatrachydidae (the vertebral structure of *D. bucklandi* is unknown, but there can be little doubt that it too was rhachitomous). *Stegops* is the earliest zatrachydid known but is considered to be too aberrant to be ancestral to other members of the family, and Milner (pers. comm.) suggests that it constitutes a separate family of specialized early dissorophoids. The ancestry of the Zatrachydidae is unknown, but it seems probable that it was derived from an early edopoid. It was included by Romer (1966) in the superfamily Eryopoidea and it is not proposed to remove it from this superfamily, which contains many widely divergent families and which is probably a polyphyletic assemblage of advanced rhachitomes.

#### SYSTEMATIC PALAEOLOGY OF THE ZATRACHYDIDAE

##### Order TEMNOSPONDYLI Superfamily ERYOPOIDEA Family ZATRACHYDIDAE

for family diagnosis see Langston (1953)

##### Genus DASYCEPS Huxley, 1859

Zatrachydids with acutely U-shaped skulls showing slight expansion across maxillae; large median nasal vacuity; premaxillae much expanded antero-posteriorly; nares far posterior; orbits small, in posterior third of skull, with rims much elevated; pronounced lateral and posterior flanges on quadratojugal; tabulars broad; small

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postparietal process; supratemporal excluded from otic notch; ornament of pits and ridges but with low bosses on the ridges; jaw articulation posterior to occiput.

*Dasyceps bucklandi* (Lloyd)

1850 *Labyrinthodon bucklandi* Lloyd, p. 56.

Very large zatrachydid with drop-shaped median nasal vacuity; orbits and nares relatively very small; lachrymal excluded from both orbit and naris.

*Dasyceps microphthalmus* (Cope)

1896 *Zatrachys microphthalmus* Cope, p. 436.

Small zatrachydid with oval median nasal vacuity; lachrymal excluded from naris but not from orbit; quadratojugal flanges less pronounced than in *D. bucklandi*.

Genus ZATRACHYS Cope, 1878

1878 *Zatrachys serratus* Cope, p. 523.

*Zatrachys serratus* Cope

Small zatrachydids with broad U-shaped skulls; no maxillary expansion; very large median nasal vacuity in adult; premaxillae with moderate antero-posterior expansion; nares slightly posterior and large; orbits small, in posterior half of skull, with slightly elevated rims; lachrymal forms part of orbital border; quadratojugal flanges ornamented with long spikes; tabulars narrow; small postparietal process present in adult; supratemporal forms part of edge of otic notch; ornament of pits and ridges with prominent spikes and bosses on ridges; jaw articulation in line with occiput.

MODE OF LIFE

*Dasyceps* and *Zatrachys* have always been considered as aquatic forms. The reason for this is not clear and it seems possible that at least one species of *Dasyceps* was terrestrial. Lateral-line grooves seem to be unknown in *Dasyceps* and *Zatrachys*, and the skull appears to have been protected by an outstanding bony frill on the postero-lateral edges; this was probably present in all members of the family but is not often preserved complete. Such a bony frill would seem to be a distinct disadvantage to a purely aquatic animal, as it would impede its progress through the water. In addition, the skull shape, shallow anteriorly but moderately deep posteriorly and with ridges radiating outwards from the orbits, is very similar to that found in known terrestrial labyrinthodonts such as *Eryops* and *Peltobatrachus*. Advanced procolophonids and the pareiasaurs, particularly *Elginia*, which were certainly terrestrial, also had spiny edges on the posterior margins of the skull. Similar spines are found in present-day lizards, e.g. *Moloch horridus* and *Phrynosoma*, where their function may be camouflage as they break up the skull outline (Walker, pers. comm.; Langston 1953). Thus from an anatomical point of view it seems likely that *Dasyceps* and *Zatrachys* were terrestrial forms. This view is confirmed by the nature of the sediments in which *D. bucklandi*

occurs. The Kenilworth Sandstone or Breccia is a coarse, red, terrestrial deposit of lower Permian (Autunian) age (Hains and Horton 1969; Paton 1974b). These deposits are almost barren, the only other fossils known being three genera of pelycosaurs (Paton 1974b), a species of the conifer *Lebachia* (*Walchia*) (Hains and Horton 1969), and some reptilian and amphibian footprints (Haubold 1970, 1971, 1972). Thus *D. bucklandi* occurs in deposits of terrestrial origin and in association with a completely terrestrial fauna and flora. It therefore seems most unlikely that the species was aquatic. Anatomical similarities in the skulls of *D. bucklandi*, *D. microphthalmus*, and the adults of *Z. serratus* indicate that all three were probably terrestrial. Milner and Panchen (1973) suggest that terrestrial animals were able to move freely over the single continent of Laurasia during the lower Permian while a partial barrier seems to have separated the aquatic tetrapods of the eastern and western parts of the supercontinent. If, as suggested here, *D. bucklandi* and *D. microphthalmus*, and *Z. serratus* and '*Acanthostomatops*' form two genera, the fact that the members of these two genera are found widely apart on what was the Laurasian continent is added evidence for their being considered terrestrial.

This leads to a consideration of the function of the relatively enormous median nasal vacuity found in all zatrachydids except *Stegops*. The occurrence of a very small interpremaxillary foramen is widespread among labyrinthodonts, and it is generally accepted that this foramen was connected to a mucus-producing gland which had another opening into the mouth in the anterior palatal vacuity. The mucus presumably lubricated the edges and inside of the mouth, and it has also been suggested that it may have functioned either to attract prey or to repel predators (see Langston 1953). In all cases the interpremaxillary foramen is situated wholly between the premaxillae and is in the vertical overhang of these bones above the mouth—a position whence gravity would aid the mucus to run downwards to the mouth.

This is not the case in *Dasyceps*. The vacuity is situated between the premaxillae and nasals, is very large, and lies horizontally on the dorsal surface of the snout. The anterior palatal vacuity is positioned directly below it but is considerably smaller, its position relative to the median nasal vacuity is shown in text-fig. 2. The appearance of the two vacuities suggests that they were in fact confluent in life. Confluent foramina between snout and palate are known, for example in *Mastodonsaurus* where they accommodate the relatively enormous symphyseal tusks of the lower jaws. This is obviously not their function in *Dasyceps*. While it is possible that a small part of the vacuity may still be glandular in function, it seems most unlikely that such an enormous area could be given over entirely to mucus production. Assuming that *Dasyceps* was terrestrial, such vast quantities of mucus spilling on to the skull surface would cause considerable evaporation and consequent heat loss, and thus might be disadvantageous.

*D. bucklandi* probably inhabited a fairly hostile environment. Its teeth are not large and suggest a diet of small, fairly inactive animals. But it in turn may have been hunted by predators including the large carnivorous pelycosaur *Sphenacodon britannicus* which occurs at the same locality near Kenilworth. In common with other large terrestrial labyrinthodonts, it was probably a ponderous animal which would have to rely upon forms of protection other than a speedy retreat. No postcranial material is associated with *D. bucklandi* but evidence (admittedly poor) from the

other species of zetrachydids suggests that little armour was present on the body. The skull, however, possesses a prominent bony frill around the posterior edge which may have helped to camouflage the animal but which, in view of its size, also suggests that the head could be used as a means of defending the whole animal. For this reason it is very tentatively suggested that the large median nasal vacuity which is thought to connect directly with the mouth may have been the site of an expandable sac which could be inflated as an aggressive defence mechanism. The anterior palatal vacuity, situated directly below and approximately in the centre of the median nasal vacuity, but being much smaller, may have been the site of a valve which could cut off the inflated sac from the mouth, thus enabling it to remain inflated independent of respiration. This suggestion may appear unlikely at first sight, but such forms of defence mechanisms occur in modern amphibians and reptiles and are known to deter relatively large predators very effectively (see references in Cott 1940). It is also possible that the throat could be inflated as in some modern frogs and the resultant apparent increase in size combined with the visual effect of the bony frill round the skull would probably be quite effective as a psychological deterrent.

The bony frill and internasal vacuity are relatively undeveloped in the juvenile *Zatrachys serratus* although their development can be traced in the larger specimens. If the functions for these structures suggested above are correct, they would of course be unnecessary in the aquatic larval form, although the median nasal vacuity would probably be glandular at this time.

*Acknowledgements.* I wish to thank Dr. A. D. Walker most sincerely for his continued help throughout this work, and for his constructive criticisms of the manuscript. I am also grateful to Dr. S. M. Andrews for reading the manuscript and for helpful suggestions, and Dr. A. R. Milner for useful discussions. I wish to thank Miss J. Morris, Dr. W. Allen, and the Trustees of Warwick County Museum for their help and permission to borrow and study *Dasyceps bucklandi*, and Mr. D. E. Butler of the Institute of Geological Sciences, London, for the loan of specimens.

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Original typescript received 22 November 1974

Revised manuscript received 17 February 1975