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The first tetrapod finds from the Devonian (Upper Famennian) of Latvia

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CONTENTS

SUMMARY

Ventastega curonica, from the Upper Famennian Ketleri Formation, is the first tetrapod find from the Upper Devonian of Latvia, and only the fourth adequately represented Devonian tetrapod genus to be described. The taxon is represented by disarticulated cranial and postcranial elements from two localities, Ketleri on the Venta River and Pavāri on the Ciecere River. A second tetrapod, represented by a single mandibular fragment, appears to be present at Ketleri. The lower jaw of *Ventastega* is strikingly primitive in retaining fangs on the coronoid series, but shares many characters with those of other known Devonian tetrapods. Some of these features are interpreted as basal tetrapod synapomorphies; they provide a new data set for the identification of isolated tetrapod jaw fragments, and confirm the (previously disputed) tetrapod status of *Metaxygnathus*. The upper jaw bones of *Ventastega* are broadly similar to those of *Acanthostega*, *Ichthyostega* and *Tulerpeton*, as is the narial region. The lateral rostral bone is either very small or absent. A preopercular bone is present in the cheek, and the lacrimal is excluded from the orbit. The palate is closed. Palatine and vomer bear fangs which are set in the marginal tooth row. An isolated iliac blade from Pavāri, probably attributable to *Ventastega*, resembles that of *Acanthostega* but may not have carried a dorsal process. Two clavicles from Pavāri and Ketleri which may also belong to *Ventastega* are of a typical early tetrapod pattern, similar to *Greerpeton* but with a broader ventral blade. Non-attributable or doubtfully attributable bones from Ketleri include a probable tetrapod postorbital and a possible limb bone. *Ventastega* appears to be a tetrapod of the same broad 'grade' as *Ichthyostega* and *Acanthostega*, but is arguably more primitive than either.

1. INTRODUCTION

Ichthyostega, the first Devonian tetrapod, was discovered more than 60 years ago (Säve-Söderbergh 1932). However, although the Devonian genera are of crucial importance to the study of tetrapod origins and basal systematics, progress in the field has not been rapid. Disregarding the questionable genus *Ichthyostegopsis* (Säve-Söderbergh 1932) which is probably synonymous with *Ichthyostega*, and the Lower Frasnian *Elpistostege* (Westoll 1938) which has been shown to be a panderichthyid fish (Schultze &

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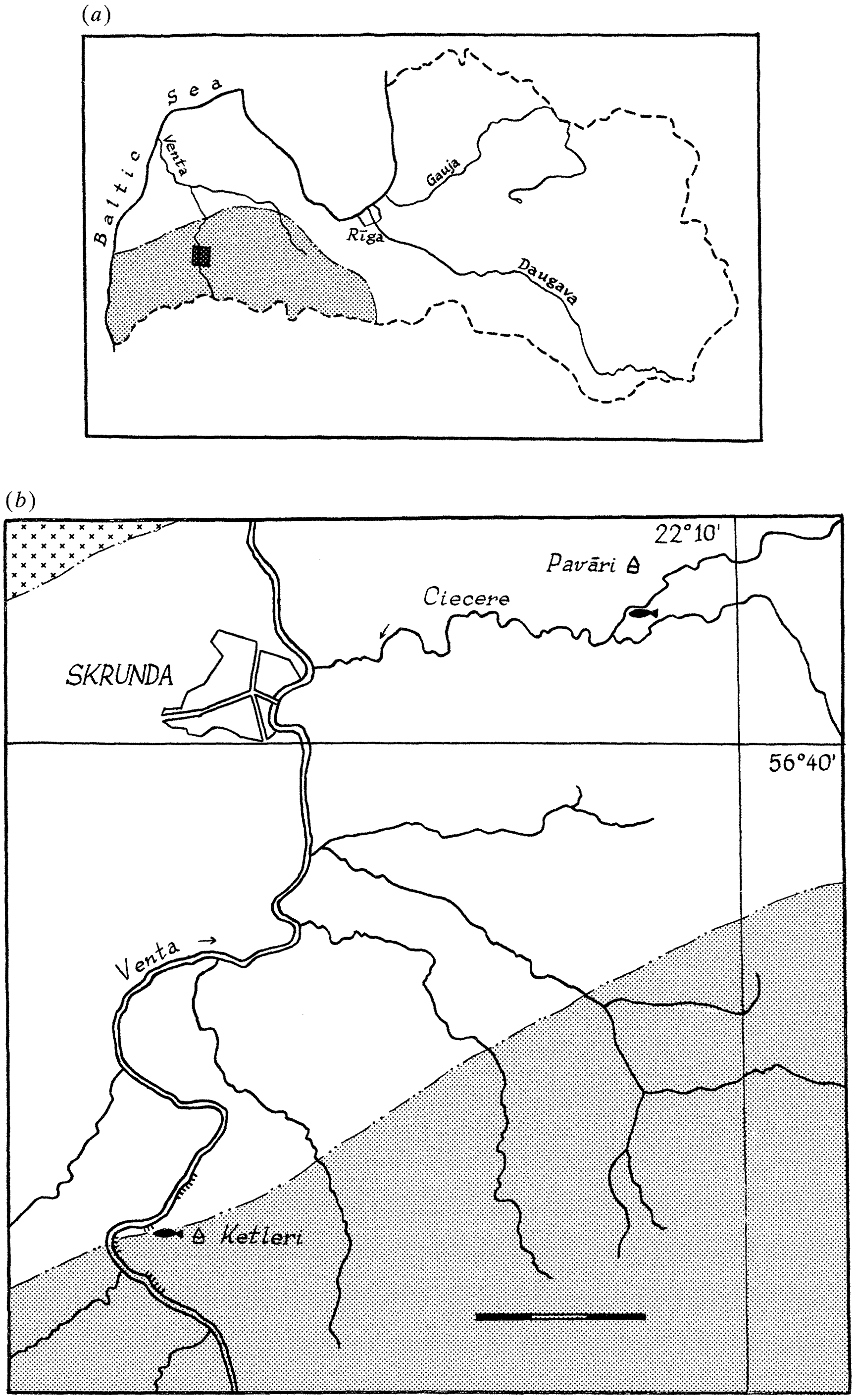

Figure 1. (*a*) Map of Latvia; the area of light shading indicates the extent of Famennian and later deposits, the square of dark shading is the area of the next map. (*b*) Detail map of the Skrunda area showing the localities of Pavāri and Ketleri. The house symbols indicate Pavāri and Ketleri hamlets, whereas the stylised fishes mark the fossil localities. Crosses, Žagare formation; no shading, Ketleri formation; light shading, Šķervelis formation. The fossil locality at Ketleri lies just below the top of the Ketleri formation. Scale bar 3 km.

Arsenault 1985), only three further Devonian tetrapod genera have been formally described. These are *Acanthostega* from East Greenland (Jarvik 1952), *Metaxygnathus* from Australia (Campbell & Bell 1977) and *Tulerpeton* from Russia (Lebedev 1984). *Metaxygnathus* is based on a single lower jaw and has not universally been accepted as a tetrapod (Schultze 1987).

We present below a case of mistaken identity which for several decades has concealed an undescribed Devonian tetrapod from Latvia.

In 1933, Walter Gross described some teeth and scales of an osteolepiform fish under the name *Polyplocodus wenjukovi*. The material had been collected by him in 1931 at a site on the right bank of the Venta River close to Ketleri hamlet in the southwestern part of Latvia (Gross 1933). This locality is of Upper Famennian age (Savvaitova & Žeiba 1981). Later, Gross (1941) reascribed these fragments to *Panderichthys bystrowi*, a newly erected taxon based on a lower jaw fragment (Latvian Museum of Natural History, LDM 15/49) from the same locality. Vorobyeva (1960, 1962) assigned a premaxilla (Palaeontological Institute of the Russian Academy of Sciences, PIN 54/180b) and incomplete maxilla (PIN 54/180) from Ketleri to the same species, along with several scales from various localities.

It has recently become clear, partly due to the discovery of additional specimens, that PIN 54/180 and 54/180b cannot be attributed to *Panderichthys bystrowi*, but belong instead to a previously unrecognized Devonian tetrapod. This is not the first discovery of its kind; in 1991, one of us (Ahlberg 1991*a*) described a number of tetrapod-like cranial and postcranial fragments from the Upper Frasnian of Scat Craig near Elgin, Scotland which had lain unrecognized in collections for more than a century. Ahlberg (1991*a*) also tentatively re-interpreted the supposed panderichthyid *Obruchevichthys* (Vorobyeva 1977), as a tetrapod, as the lower jaw of this poorly known animal is very similar to those from Scat Craig. However, the new Latvian material is better preserved than any of these specimens and provides a considerably clearer insight into basal tetrapod anatomy.

2. MATERIAL

The bulk of the new material derives not from Ketleri but from a new locality discovered during the 1970s and initially excavated by Lyubov Lyarskaya (Lyarskaya & Savvaitova 1974). This site lies on the left bank of the Ciecere River (a tributary of the Venta) opposite Pavāri hamlet in the Saldus District, about 15 km from the Ketleri locality (figure 1). The authors collected specimens at this locality in 1988 (E.L. and O.L.) and 1991 (E.L., P.E.A. and O.L.). Both localities lie in the Ketleri formation, which is of late Devonian (Upper Famennian) age and comprises about 45 m of sands, sandstones, clays and dolomite marls. These strata overlie the calcareous rocks of the Žagare Formation. The Ketleri formation is divided into three subformations (Lyarskaya & Savvaitova 1974; Savvaitova & Žeiba 1981); the Pavāri locality lies in the middle subformation, whereas Ketleri represents the upper subformation. The Devonian strata of Latvia dip gently to the south but have not suffered significant tectonic disturbance. The extent of the Ketleri formation is thus likely to be considerable. However, exposures are rare, being limited to low and generally overgrown streamside cliffs.

Both of the sites are characterized by a rich fish assemblage (Lukševičs 1991) which includes the placoderm *Bothriolepis ciecere* Lyarskaya, the acanthodians *Devononchus ketleriensis* Gross and *D. tenuispinus* Gross, the porolepiform *Holoptychius* cf. *nobilissimus* Agassiz, the osteolepiforms *Cryptolepis grossi* Vorobyeva and *Panderichthys bystrowi* Gross, the lungfish *Orlovichthys* cf. *limnatis* Krupina, and the unusual ?sarcopterygian *Ventalepis ketleriensis* Schultze. Personal observations by the authors indicate that a large eusthenopterid (represented by the lower jaw PIN 54/180d) is also present in the fauna. Most of the bone material from Pavāri consists of detached plates from the trunk shield of *Bothriolepis*, complete head shields of the same fish, and detached cranial and postcranial bones of porolepiforms and osteolepiforms. Sarcopterygian scales and teeth are much less common at Pavāri than at Ketleri, as are acanthodian remains. Dipnoan fragments are rare at both sites. At Pavāri the bones are almost unworn, whereas larger bones from Ketleri are generally both worn and broken. The preservation is three-dimensional and there appears to be very little distortion. At both localities the bones are preserved in virtually unconsolidated pale sand; the overburden can easily be removed with spades and shovels. The Pavāri fossils are extremely fragile and need to be carefully 'pedestalled' by means of a trowel or knife, and consolidated with a plastic lacquer before jacketing with plaster and bandages. At Ketleri, on the other hand, the bones are so robust that they can be exposed by pouring river water over the exposure face until the sand washes away. Laboratory preparation is done by mounted needle, and is relatively straightforward due to the softness of the matrix.

3. LIST OF ABBREVIATIONS USED IN TEXT AND FIGURES

ad.fos.	adductor fossa
al.proc.	alar process
ang.	angular
ant.cho.mar.	anterior margin of choana
bas.art.	basal articulation
clav.	clavicle
clav.ol.	overlap for clavicle
cor.fang	precoronoid and intercoronoid fang(s)
cor.fos.	coronoid fossa
cor.teeth	coronoid teeth
den.fang	dentary fang(s)
dentic.prart.	denticulated part of prearticular
dors.sens.can.	dorsal opening of sensory canal
epipt.	epipterygoid scar
fac.lam.	facial lamina
for.	foramina
icl.	interclavicle
il.neck	'iliac neck'
infraorb.sens.line	infraorbital sensory line
internas.em.	embayment for internasal
intercor.fos.	intercoronoid fossa
ju.	jugal
la.	lacrimal
lat.psym.for.	lateral parasymphysial foramen
LDM	Latvian Museum of Natural History
mar.sub.fos.	margin of subtemporal fossa
max.ol.	overlap for maxilla
max.sut.	sutural area for maxilla
Meck.fen.	Meckelian fenestra
mes.psym.for.	mesial parasymphysial foramen
nas.ol.	overlap for nasal
orb.mar.	orbital margin
orn.prart.	ornamented part of prearticular
pal.sut.	sutural area for palatine

parasph.gr.	groove for edge of parasphenoid
PIN	Palaeontological Institute of the Russian Academy of Sciences
pi.	pit line
pit.	pitted surface on ilium
pmx.sut.	sutural area for premaxilla
po.ol.	overlap for postorbital
pop.	preopercular
po.sens.line	postorbital sensory line
post.sens.can.	posterior opening of sensory canal
postspl.	postsplenial
precor.fos.	precoronoid fossa
prf.ol.	overlap for prefrontal
psym.fang	fang(s) on parasymphysial plate
psym.plate	parasymphysial plate
psym.teeth	teeth on parasymphysial plate
pter.	pterygoid
pter.ol.	overlap area for pterygoid
qj.	quadratojugal
sens.line	pores sensory line pores
spl.	splenial
sq.	squamosal
surang.	surangular
sym.	symphysis
tec.ol.	overlap for anterior tectal
vo.sut.	sutural area for vomer

4. SYSTEMATIC PALAEONTOLOGY

Superclass Tetrapoda Goodrich, 1930

Remarks. The group Tetrapoda is a clade characterized by many cranial and postcranial autapomorphies. Some, such as the possession of manus, carpus and digits (Panchen & Smithson 1987; Godfrey 1989), persist in most members of the group. Others can only be recognized in primitive members, as they are modified beyond recognition in later tetrapods. This group of characters includes a characteristic type of dermal ornament (Godfrey 1989), and several features of the lower jaw (Ahlberg 1991*a*) which are considered in detail later in the paper (see §§5 and 7).

Some of the earliest known taxa which exhibit tetrapod autapomorphies (*Obruchevichthys*, *Metaxygnathus*) are represented only by isolated elements and cannot yet be shown to have possessed limbs (Campbell & Bell 1977; Ahlberg 1991*a*), but we nevertheless refer them to the clade Tetrapoda. This decision simply reflects the derived characters they possess, and does not imply any assumptions about unknown aspects of their anatomy. Given our limited knowledge of the earliest and most primitive members of the clade, we regard this usage as preferable to ill-defined terms such as 'proto-tetrapods'. When the term 'Scat Craig tetrapod' is used in the text, it refers to the taxon represented by the mandibular material (Ahlberg 1991*a*); the limb elements from the site may well belong to the same animal, but this cannot yet be demonstrated. We will not attempt to place these basal tetrapods in any lower suprageneric categories, as their relationships to each other and to the 'higher' tetrapods are not sufficiently well understood.

Genus *Ventastega*, new genus

Generic definition. A tetrapod in which the anterior and middle coronoids of the lower jaw carry distinct fang pairs that are set in the marginal tooth row. The parasymphysial tooth plate lacks fangs but carries a single tooth row which is continuous with that of the coronoids. The sutures between the splenials are complex double overlaps. If the cranial material associated with the lower jaws is assumed to belong to the same genus, the following features can be added to the definition: In the upper jaw, the premaxilla has a tooth count of around 17, and the infraorbital sensory canal does not enter the maxilla. The middle part of the infraorbital canal is developed as an open furrow, but other parts are enclosed. The lacrimal does not reach the orbital margin. A preopercular is present. The vomer and palatine carry fangs similar to those on the coronoids. The pterygoid is denticulated and clasps the lateral edge of the parasphenoid, forming a closed palate. Although none of these features can be shown to be autapomorphies, *Ventastega* can be distinguished from the other known Devonian tetrapods by the combination of characters present in the lower jaw. The cranial features conform to this picture. A more detailed justification of the assignation of *Ventastega* to the Tetrapoda is given in § 7.

Type species. *Ventastega curonica*, new species.

Horizon. Ketleri Formation, Upper Famennian, Upper Devonian.

Derivation of name. The generic name refers to the Venta River, on which the Ketleri site is located; the specific name is derived from Curonia, the Latin form of Kurzeme, the historical name for the western part of Latvia.

Specific definition. Same as for genus.

Synonymy.

1960 *Panderichthys bystrovi* Gross *non*; Vorobyeva, 92.
1962 *Panderichthys bystrovi* Gross *non*; Vorobyeva, 89, fig 33, plXX1 fig 1, pl XXVII fig 4 (partim).

Holotype. Latvian Museum of Natural History LDM 81/521, a right lower jaw ramus.

Referred material. An articulated partial cheek and palate, a number of upper and lower jaw elements, and some pectoral and pelvic girdle bones from Pavāri and Ketleri can be referred to *Ventastega curonica*. These are held by the Latvian Museum of Natural History in Riga (LDM) and the Palaeontological Institute of the Russian Academy of Sciences in Moscow (PIN). The referred specimens from Pavāri are LDM 81/185 (right premaxilla), LDM 81/188 and 81/553 (right and left maxillae) LDM 81/551 (maxillary fragment), LDM 81/359 and 81/517 (right lower jaws), LDM 81/552 (isolated right dentary), LDM 81/528 and 81/532 (incomplete right palatines), LDM 81/550 (left pterygoid and partial cheek), LDM 81/522 (left ilium) and LDM 81/531 (right clavicle). The Ketleri specimens are LDM 57/2600 (incomplete posterior part of left lower jaw), PIN 1491/85 (fragment of angular), PIN 54/180 (anterior part of right maxilla), PIN 54/180c (right premaxilla), PIN 1491/82 (incomplete left suspensorium), PIN 1491/86 (incomplete right vomer), PIN 1491/83 (incomplete palatine), LDM 57A/1978 (incomplete interclavicle),

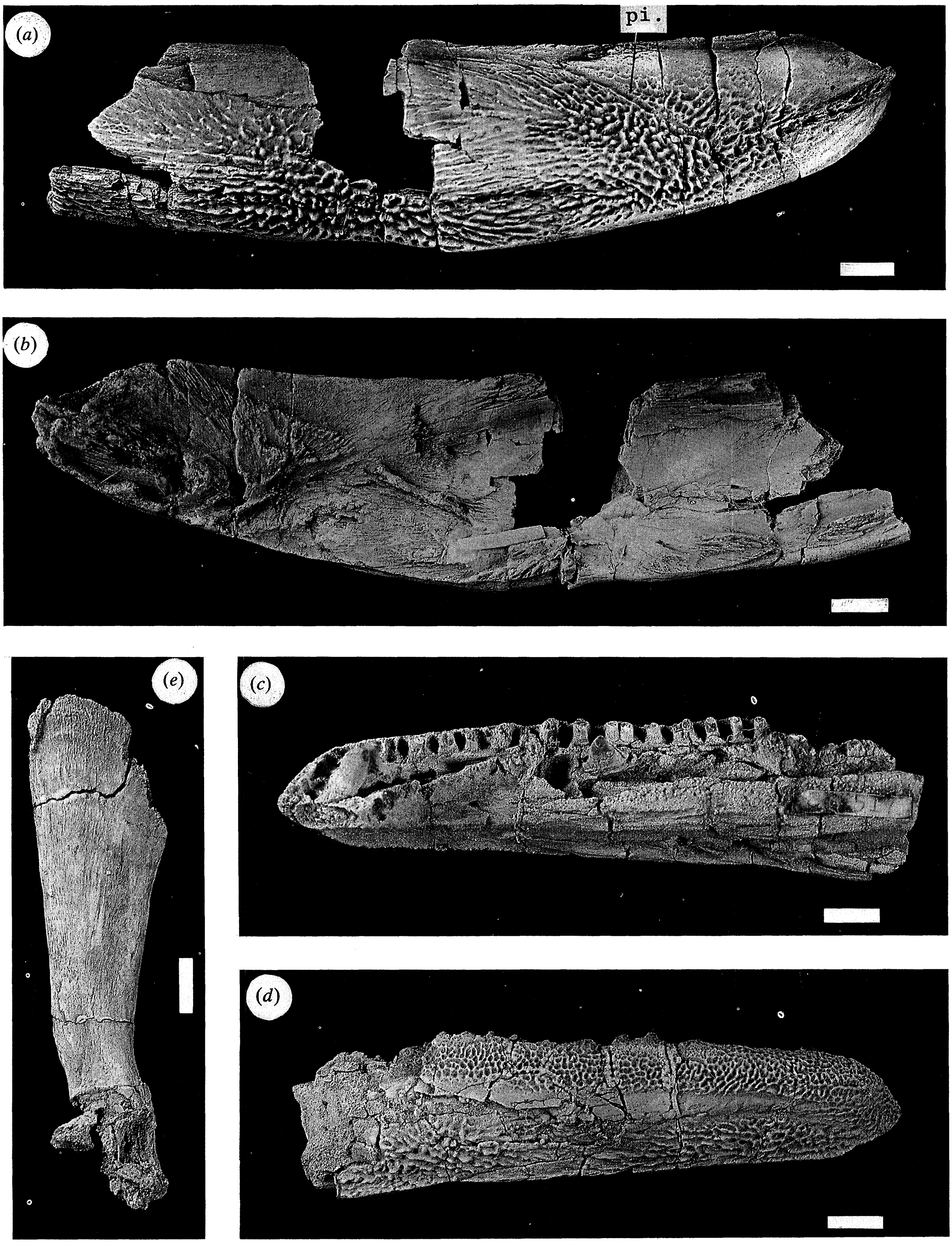

Figure 2. (*a*,*b*) LDM 57/2600, incomplete posterior part of left lower jaw ramus from Ketleri in lateral and mesial views, attributed to *Ventastega curonica*. In (*a*), note the surangular pit line (pi.). (*c*,*d*) LDM 81/517, anterior part of right lower jaw ramus of *Ventastega curonica* from Pavāri, in mesial and lateral views. (*e*) LDM 81/522, left ilium from Pavāri in mesial view, attributed to *Ventastega curonica*; same specimen as figure 13. All scale bars 10 mm.

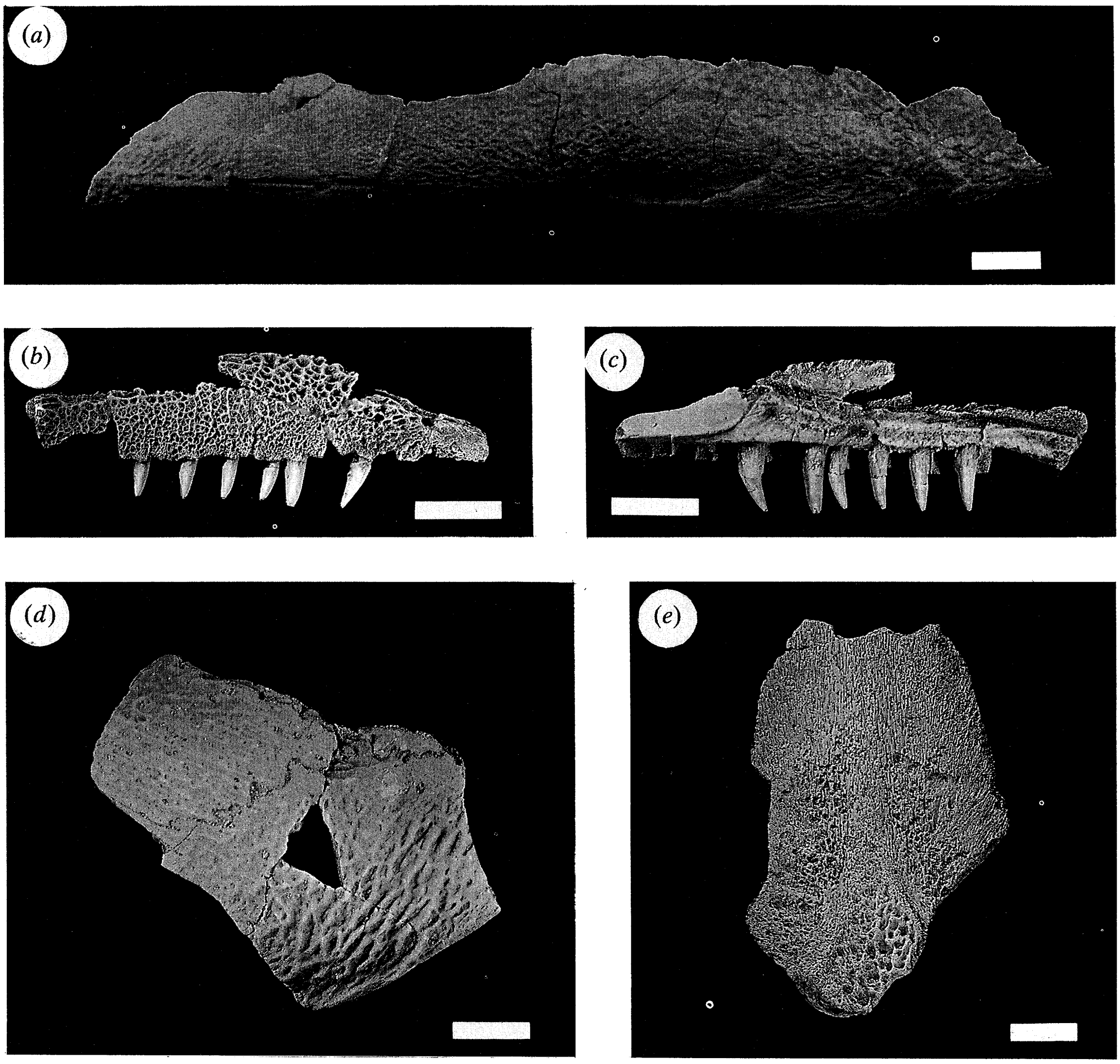

Figure 3. (*a*) LDM 81/550, incomplete left cheekplate of *Ventastega curonica* from Ketleri in lateral view; same specimen as figure 7. (*b,c*) PIN 54/180, anterior part of right maxilla of *Ventastega curonica* from Ketleri in lateral and mesial view. (*d*) PIN 1491/92, incomplete left suspensorium from Ketleri, attributed to *Ventastega curonica*, in lateral view; same specimen as figure 8*a,b*. (*e*) LDM 57/1978, anterior part of interclavicle from Ketleri in ventral view, attributed to *Ventastega curonica*; same specimen as figure 12*e*. All scale bars 10 mm.

LDM 57A/1984 (iliac fragment) and PIN 1491/81 (clavicle fragment). Ketleri has also yielded tetrapod bones which cannot be securely attributed *Ventastega*, and one jaw fragment which appears to represent a second tetrapod taxon. These will be discussed in detail later in the paper.

Type locality. Pavāri, left bank of Ciecere River, Saldus District, Latvia.

5. DESCRIPTION OF *VENTASTEGA*

(*a*) *Lower jaw*

The lower jaw is long and low (figure 4). Although no complete jaw ramus has been discovered to date, the total length appears to have been over 200 mm. This conforms to the size of other cranial and postcranial elements from the two sites; *Ventastega* seems to have been a large animal, somewhat bigger than *Ichthyostega*. The mandible is widest anterior to the first coronoid fang and deepest in the region of the adductor fossa. The anterior part of the lateral surface is strongly twisted in relation to the posterior region, resulting in a dramatic reduction in the depth of the symphysial region. The dentary is long and shallow; it reaches its maximum depth close to the first coronoid. Posteriorly, the dentary reaches almost to the posterior wall of the adductor fossa. The ventral margin of the dentary forms a smooth, simple overlap on the infradentary bones, and the contact with the coronoid series is a simple butt joint. As a result, the dentary is only loosely attached to the jaw. The lateral surface of the dentary is ornamented dorsally, but a smooth strip runs along the ventral margin of the bone. A similar pattern occurs in the tetrapod dentaries associated with *Tulerpeton* (Lebedev & Clack 1993), and in *Acanthostega* (J. A. Clack, personal communication), whereas in *Obruchevichthys* and the Scat Craig tetrapod the ventral margin of the dentary is recessed into a distinct furrow. Vorobyeva (1977, text-fig. 46) des-

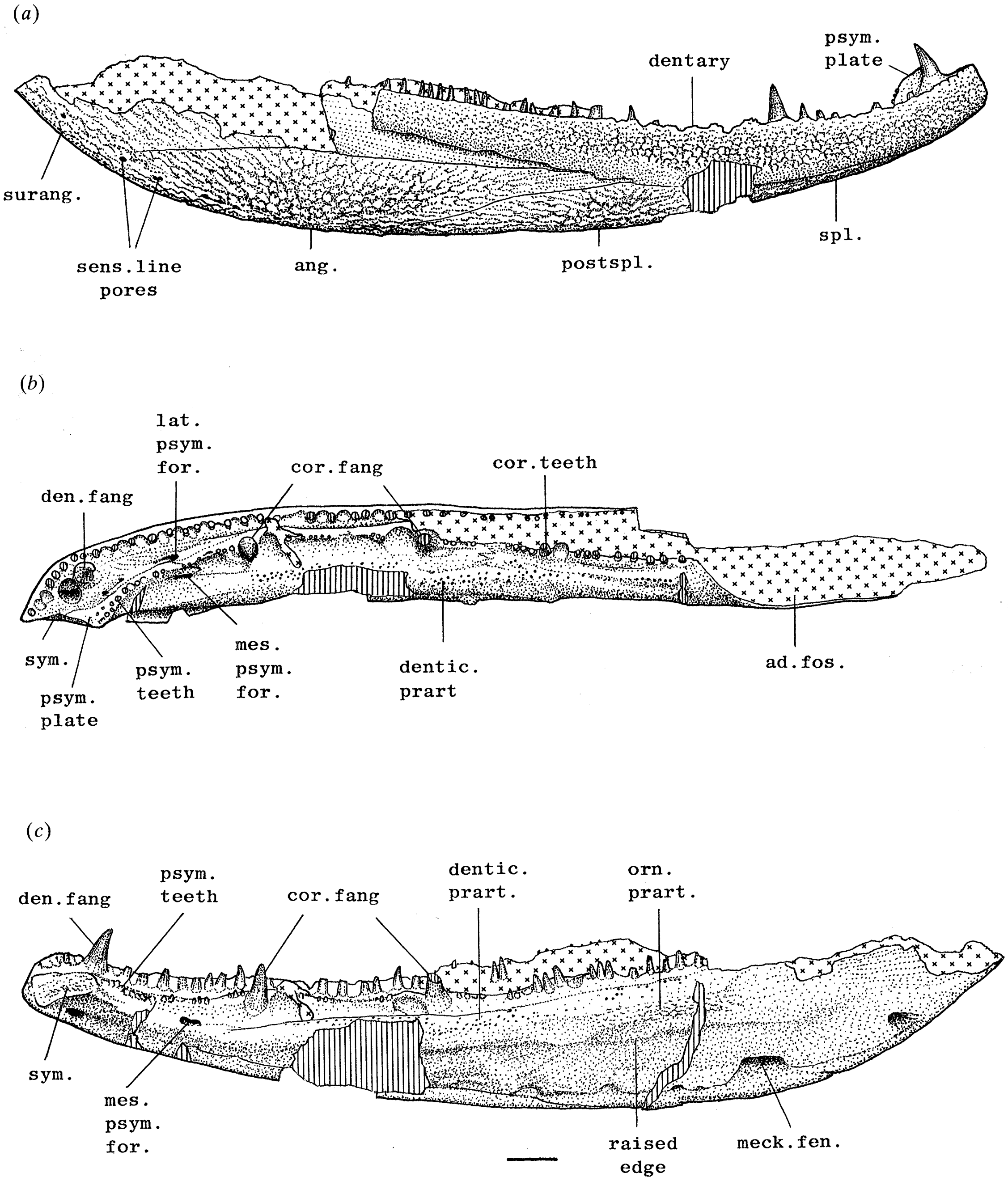

Figure 4. LDM 81/521, right lower jaw ramus from Pavāri, holotype of *Ventastega curonica*. (*a*) Lateral view, (*b*) dorsal view, (*c*) mesial view. Vertical hatching, broken bone; crosses, matrix. Scale bar 10 mm. The jaw ramus is complete except for the articular region and the posterior part of the dentary. In (*a*) note that the dentary is loosely attached and has become separated from the underlying surangular. The precoronoid and intercoronoid carry prominent fangs (cor.fang) and small marginal teeth, whereas on the coronoid the marginal teeth are larger, and the fang and replacement pit (cor.teeth) hardly distinguishable. Denticles are restricted to the raised dorsal part of the prearticular (dentic.prart).

cribed the furrow in *Obruchevichthys* as the postsplenial pit line, but the more complete Scat Craig material does not bear out this interpretation. The coarsest ornament is found on the middle part of the dentary; the dorsal margin, which adjoins the marginal tooth row, bears only tiny pores and ridges.

The only known complete dentary, LDM 81/552, carries 89 approximately even-sized marginal teeth, decreasing in height a little caudally. A pair of large fangs is situated close to the symphysis, inside the main tooth row. Fangs in this position are also found in *Panderichthys* (Gross 1941), some osteolepiforms (Jarvik 1952, 1972; Vorobyeva 1977), *Ichthyostega* (Jarvik 1980), the dentaries associated with *Tulerpeton* (Lebedev & Clack 1993), the un-named tetrapod from Parrsboro, Nova Scotia (Godfrey & Holmes 1989), and apparently in *Proterogyrinus* (Holmes 1984) as well as in most of the Palaeozoic and early Mesozoic temnospondyls. A corresponding but rather smaller pair of teeth is present in *Pholiderpeton* (Clack

1987*b*) and some individuals of *Archeria* (Holmes 1989).

The surangular (figures 2*a*,*b* and 4*a*) is of a generalized sarcopterygian shape. There is no surangular crest, and the bone makes no significant contribution to the mesial face of the jaw. A large patch of radially disposed irregular pit-and-ridge ornament is developed in the middle of the lateral face of the bone, but the anterior end and dorsal margin are unornamented.

In addition to a segment of the enclosed mandibular canal, the lateral face of the surangular also carries an l-shaped, open furrow which originates near the middle of the bone; the short limb of this furrow runs posterodorsally, whereas the long limb runs anterodorsally towards the dentary suture (figure 2*a*). This is the surangular pit line, a structure which is present in most sarcopterygians (Jessen 1980, fig. 1; Jarvik 1980, fig. 125A and 186, 'pl.Id.4') but not known in any other tetrapods. Pit lines are in fact generally unknown in tetrapods, with the exception of discosauriscids (Klembara 1992).

The anteroventral margin of the surangular is divided into internal and external laminae, separated by a deep groove which receives the dorsal margin of the angular. This creates a very firm suture, in marked contrast to the loose attachment of the dentary. The structure of the more anterior infradentary sutures is not revealed by the available material.

The mesial lamina of the angular is low and is embayed by the edge of a large Meckelian foramen approximately in the middle of its length. The ornament in the centre of the lateral surface consists of deep pits and curved ridges; towards the margins the ridges diverge and develop into an irregular, radially disposed network. The splenial and postsplenial are ornamented in essentially the same fashion as the angular. The splenial does not appear to contribute to the symphysis.

Unlike the great majority of early tetrapods, *Ventastega* has a wholly enclosed mandibular sensory canal which opens to the outside through a single row of pores (figures 2*a*,*e* and 4*a*). This is a primitive characteristic shared with fishes, but it is also developed in *Ichthyostega* (Säve-Söderbergh 1932; Jarvik 1980) and the Scat Craig tetrapod (P. E. Ahlberg & O. Lebedev, personal observation). Colosteids have a partially enclosed mandibular canal in which the pores are very large and closely spaced (Smithson 1982), whereas the degree of closure in *Obruchevichthys* appears to vary between individuals (P. E. Ahlberg, personal observation).

On the mesial face of the jaw, the coronoids, prearticular and parasymphysial tooth plate are closely joined together (figure 4*b*,*c*), so that sutures are difficult to trace. The Meckelian bone is not exposed in the bottom of the shallow precoronoid fossa, although it can be seen as a rough unfinished area on the mandibular symphysis. This pattern appears to be a tetrapod autapomorphy (see §7). There is a single row of teeth on the parasymphysial plate, which is continuous with the marginal tooth row of the coronoids. The anterior teeth of the row are somewhat enlarged, but they are situated within the row and do not form a distinct fang pair. In LDM 81/521 there is a short secondary row of small teeth outside the anterior end of the main tooth row. This difference can probably be put down to individual variation. The parasymphysial plates of Devonian and Carboniferous tetrapods, where known, always carry large teeth; those of osteolepiforms on the other hand are generally covered with denticle shagreen. In *Ichthyostega* the parasymphysial plate carries three large teeth which appear to be in line with the marginal coronoid dentition (P. E. Ahlberg, personal observation). *Obruchevichthys* (Vorobyeva 1977; Ahlberg 1991*a*), *Metaxygnathus* (P. E. Ahlberg, personal observation), the Scat Craig tetrapod (Ahlberg 1991*a*) and *Acanthostega* (J. A. Clack, personal communication) have both marginal teeth and a fang pair on the plate, whereas in the Parrsboro tetrapod (Godfrey & Holmes 1989) it carries only a fang pair. *Ventastega* is thus in some ways similar to *Ichthyostega*. A conspicuous, anterolaterally directed canal opens on the floor of the precoronoid fossa; it is apparently connected to another similar foramen which lies outside the marginal coronoid tooth row. Similar pairs of foramina are developed in *Obruchevichthys*, the Scat Craig tetrapod (Ahlberg 1991*a*) and probably *Metaxygnathus* (Campbell & Bell 1977), as well as *Acanthostega* (J. A. Clack, personal communication).

The coronoid series consists of three bones, the precoronoid, intercoronoid and coronoid (*sensu* Gross 1941). The two former carry moderately large fang pairs, which are set within the marginal row of teeth on the dorsal edge of the vertical coronoid lamina (figure 4*b*,*c*). There is no distinct fang pair on the coronoid, but two teeth in the middle of the row are somewhat enlarged. This pattern resembles that of osteolepiforms, particularly long-jawed forms (see below), but in osteolepiforms (and porolepiforms and rhizodonts) the fangs are always separate from, and mesial to, the marginal tooth row.

The only tetrapods known to possess fangs on the coronoid series are *Metaxygnathus* (Campbell & Bell 1977), *Obruchevichthys* (Vorobyeva 1977) and the Scat Craig animal. The exact relationship between the fangs and marginal teeth is uncertain in the two former genera. In the Scat Craig tetrapod the fangs are separate from the marginal tooth row, but those marginal teeth which lie immediately lateral to the fangs are minute. *Ichthyostega* (Jarvik 1980) and the Carboniferous tetrapod '*Doragnathus*' (probably synonymous with *Spathicephalus*; O. Lebedev, personal observation) have coronoid series which carry a single row of teeth (Smithson 1980), probably corresponding to the marginal row of osteolepiforms. In most other early tetrapods the coronoid series carries shagreen, sometimes with a few irregularly arranged teeth (Romer & Witter 1942; Beaumont 1977; Holmes 1984; Panchen 1985). It is not clear to which row of teeth in Devonian tetrapods or sarcopterygians those of later tetrapods may be homologous. *Greererpeton* (Smithson 1982) carries a fang pair and a pair of smaller teeth on the so-called 'anterior coronoid', whereas the longer 'posterior coronoid' is covered in

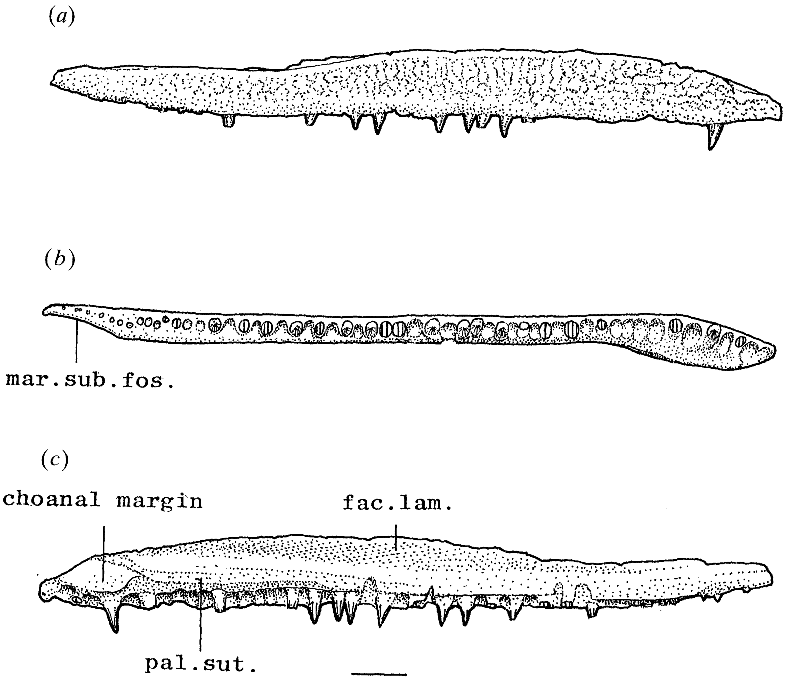

Figure 5. LDM 81/188, right maxilla of *Ventastega curonica* from Pavāri. (*a*) Lateral view, (*b*) ventral view (anterior end to right), (*c*) mesial view. Vertical hatching, broken teeth. Scale bar 10 mm. In (*b*) note the slight curvature of the bone – lateral margin concave – and the contribution to the subtemporal fossa by the mesial margin (mar.sub.foss.). The mesial view (*c*) shows the smooth choanal margin and the sutural area for the palatine (pal.sut.).

denticles. However, comparison with Devonian tetrapods and the Westphalian tetrapod jaw from Parrsboro (Godfrey & Holmes 1989) suggests that the 'anterior coronoid' is in fact the parasymphysial plate.

On the prearticular the shagreen field starts anteriorly as in the osteolepiforms, below the anterior coronoid (figure 2*c*), and extends posteriorly along the dorsal margin of the bone as a comparatively narrow strip. The ventral part of the prearticular is smooth and bears very faint radial striations. A raised strip of dermal ornament lies between the shagreen field and the smooth ventral area; anteriorly and posteriorly it consists of longitudinal striations, whereas the middle part is broadly similar to the ornament of the external dermal bones (figure 4*c*). There are several Meckelian foramina of modest size along the line of contact between the prearticular and infradentaries. The largest of these is approximately ventral to the anterior edge of the adductor fossa.

(*b*) *Dermal skull bones*

Several dentigerous bones from the upper jaw can be attributed to *Ventastega* with reasonable confidence, as they match the lower jaws very closely with respect to tooth structure, tooth arrangement, gross morphology and dermal ornament. This material includes maxillae, premaxillae, palatines and a vomer. A large skull fragment from Pavāri, consisting of a partial cheekplate in articulation with a pterygoid (LDM 81/550), can be assigned to *Ventastega* on similar criteria. Ketleri has yielded a partial suspensorium, an incomplete prefrontal and a probable postorbital fragment, which all clearly derive from tetrapods. The suspensorium closely resembles that of LDM 81/550 and thus probably represents *Ventastega*. The same may be true of the prefrontal and postorbital, but the apparent presence of a second tetrapod at Ketleri (see below) makes the attribution less certain.

The maxilla (LDM 81/188 and 81/553, PIN 54/180) is very low and long (figures 3*b*,*c* and 5). Unlike in osteolepiforms, the facial lamina does not increase in height towards the rear; the posterior third is the lowest part of the bone. The anterodorsal part of the external surface is covered with typical pit-and-ridge ornament, but ventrally and posteriorly the sculpturing consists of tiny pits. A narrow but continuous horizontal shelf, which carries the sutural surfaces for the ectopterygoid and palatine, is developed mesial to the tooth row. This shelf is widest just behind the choanal margin, where the maxillary teeth are also somewhat enlarged. The teeth are otherwise almost equal in size except at the posterior end where they decrease rapidly in size. LDM 81/188 and 81/553, the only known complete maxillae, carry respectively 55 and 60 teeth. The posterolateral margin of the choana is represented by a conspicuous smooth area with a slight dorsolateral slope (figures 3*c* and 5*c*). There was evidently a loose and probably ligamentous contact with the premaxilla, as no sutural surface is developed on either bone. On the anteriormost part of the external surface the dermal ornament gives way to a smoother area which slopes dorsomesially (figure 3*b*).

The premaxilla (LDM 81/185, PIN 54/180c; figure 6) closely resembles those of *Ichthyostega* (Jarvik 1980) *Acanthostega* (Clack 1988*b*, 1994*a*) and *Tulerpeton* (Lebedev & Clack 1993). In dorsal or ventral view the region of maximum curvature can be seen to lie

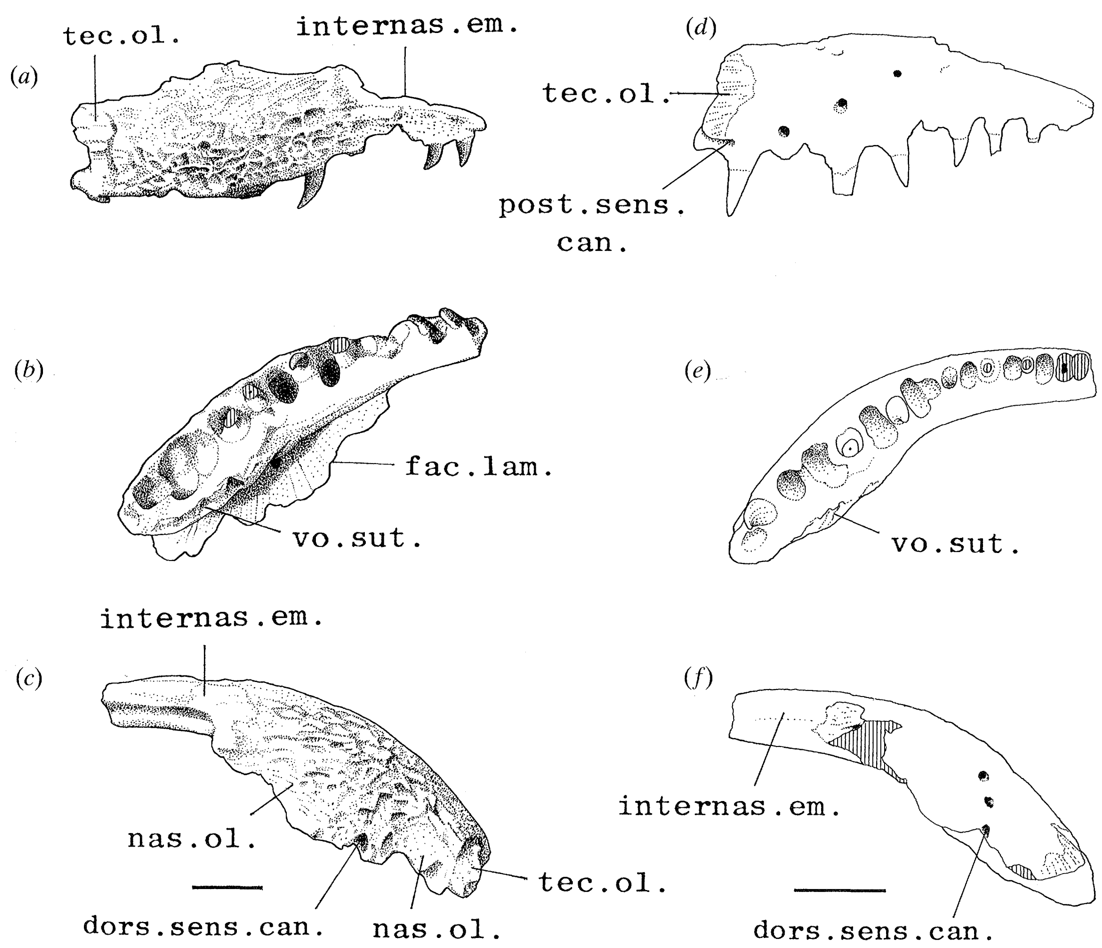

Figure 6. Two right premaxillae of *Ventastega curonica*. (*a–c*) LDM 81/185 from Pavāri in anterolateral, posteroventral and dorsal views. (*d–f*) PIN 54/180c from Ketleri in anterolateral, ventral and dorsal views (ornament omitted). Vertical hatching, broken bone. Scale bars 10 mm. LDM 81/185 has a complete facial lamina carrying overlap areas for the nasal bone (nas.ol.) and the exit of the supraorbital sensory line (dors.sens.can.), but the dentition and sensory line pores are better preserved in PIN 54/180c. Note the large overlap for the anterior tectal bone (tec.ol.) in (*a*) and (*d*), ventral to which lies the posterior opening of the infraorbital sensory canal (post.sens.can.).

approximately halfway along the bone. This suggests that, as in *Ichthyostega* and *Acanthostega*, the snout was broad and spade-shaped rather than pointed. Seventeen teeth are carried by the premaxilla, compared with thirteen in *Acanthostega* (Clack 1994*a*) and nine in *Ichthyostega* (Jarvik 1980). They increase considerably in size from the tip of the snout to the region of maximum curvature, beyond which point they decrease very slightly again.

Mesial to the tooth row, the bone is developed into a horizontal ledge similar to that observed in the maxilla. The posterior third of this ridge carries a large and fairly complex suture area for the vomer (figure 6*b*,*e*). In *Acanthostega* (Clack 1994*a*) and *Greererpeton* (Smithson 1982), the anterior palatal fenestra is divided in two by a pair of processes from the vomers, which reach forward along the midline to suture with the anterior ends of the premaxillae. The premaxilla of *Ventastega* has no such sutural surface near the anterior end, so the anterior palatal fenestra was probably undivided as in *Ichthyostega* (Jarvik 1980), *Panderichthys* (Vorobyeva 1960) and most osteolepiforms.

The anterior part of the premaxilla is very low and carries a large smooth embayment for an internasal ('median rostral') bone (figures 6*c*,*f* and 11). This region resembles that in *Acanthostega* very closely, though it is unclear whether one or two internasals were developed in *Ventastega*. The anterior opening of the infraorbital sensory canal lies on the symphysis. Its posterior exit from the premaxilla is marked by a slot-shaped opening near the posteroventral corner of the bone (figure 6*d*).

The supraorbital canal runs anteroventrally from the dorsal margin of the premaxilla and joins the infraorbital canal in the middle of the bone; both canals are fully enclosed and open to the surface through rows of pores. This pattern is nearly identical to that of *Acanthostega* (Clack 1994*a*), and also resembles the osteolepiform condition (Jarvik 1980). The dermal ornament consists of deep pits separated by sharp ridges.

The posterior margin of the premaxilla carries a large overlap area for a bone which lay dorsal to the external nostril (figure 6*a*,*d*). This bone is also developed in *Ichthyostega* and *Acanthostega*; there has been some debate about its identity (Clack 1994*a*), but it is probably homologous with the osteolepiform anterior tectal. It is much more doubtful whether *Ventastega* carried a lateral rostral bone below the nostril.

Jarvik (1952, 1980) stated that *Ichthyostega* has a small lateral rostral bone which carries the infraorbital sensory canal from the premaxilla to the lacrimal, but in *Acanthostega* the lateral rostral is absent and the canal extends into the maxilla. In *Ventastega*, the infraorbital canal does not penetrate the maxilla. The smooth area on the lateral face of this bone (see above), which lies immediately ventral to the presumed position of the external nostril, may represent an overlap area for a lateral rostral but could equally well just be part of the narial margin. As the premaxilla carries a conspicuous posterior opening for the infraorbital canal, it seems unlikely that the canal was interrupted below the nostril. It may, however, have run through soft tissue between the lacrimal and the premaxilla. Thus, while the narial region of *Ventastega* appears similar to those of *Ichthyostega* and *Acanthostega*, it is not yet possible to determine whether it contained a lateral rostral bone.

The partial cheekplate of LDM 81/550 (figures 3*a* and 7*a–c*) comprises the whole jugal, most of the lacrimal and quadratojugal, somewhat less than half the squamosal and a tiny fragment of the preopercular. The specimen also exhibits sutural areas for the maxilla, postorbital and prefrontal. Additional information about the squamosal and preopercular is given by PIN 1491/82, the partial suspensorium from Ketleri (figures 3*d* and 8*a–c*). The cheekplate is markedly convex in the vertical plane, suggesting that the skull was low. Below the orbit this curvature is so pronounced that the infraorbital sensory line pores face ventrally and the jugal must have projected laterally above the maxilla. This is a surprising feature, but the cheekplate is well preserved and does not seem to have suffered significant distortion.

The suture between the jugal and lacrimal follows a zig-zag course. Dorsally, both the lacrimal and the adjacent part of the jugal show smooth overlap areas for the prefrontal (figure 7*a*). The lacrimal was thus excluded from the orbital margin as in many early tetrapods. The outline of the jugal is comparable to those of embolomeres; it carries a long orbital margin which indicates that the orbit was relatively large, although not so large as in *Proterogyrinus*. Rather than being smoothly curved, the orbital margin has pronounced ventral and posteroventral angles. Posterior to the orbit, the jugal carries a smooth overlap area for the postorbital. The contact for the maxilla is a simple butt joint; there is a broad alar process which is overlapped by the lateral margin of the pterygoid.

Only the ventral part of the squamosal is preserved. It is a relatively featureless element with a convex ventral margin, interrupted in one place by an anterodorsally directed process of the quadratojugal. As in all primitive tetrapod cheekplates there is a broad contact between the jugal and quadratojugal. The latter appears similar in shape to those of many early tetrapods, notably anthracosaurs. The anterior part of its ventral margin carries a notch for the posterior end of the maxilla. In PIN 1491/82 the free ventral margin of the quadratojugal is somewhat swollen, but this is not so in LDM 81/550. The suture between the quadratojugal and jugal seems to be a rather simple overlap, suggesting some degree of flexibility between the two bones.

The posterior end of the cheek is better preserved in PIN 1491/82 than in LDM 81/550. The former specimen (figures 3*d* and 8*a*,*b*) comprises parts of the quadratojugal, squamosal and preopercular. Very little remains of the latter bone, but the dorsal margin of the squamosal is clearly sutural and pieces of the preopercular survive in places all along this margin. The specimen has a complex curvature, gently convex as well as slightly twisted. This compares well with the curvature in LDM 81/550, and suggests that the external face of the suspensorium was oriented dorsolaterally.

The most interesting feature of PIN 1491/82 is the presence of a preopercular, a primitive character otherwise only known in *Ichthyostega* (Säve-Söderbergh 1932; Jarvik 1980), *Acanthostega* (Clack 1988b) and *Crassigyrinus* (Panchen 1985). LDM 81/550 retains only a tiny fragment of the preopercular. As far as can be determined (figure 8*c*), the preopercular of PIN 1491/82 lay posterodorsal to the squamosal and had only a short contact with the quadratojugal. In this respect the suspensorium appears to resemble that of *Crassigyrinus*; the preoperculars of *Ichthyostega* and *Acanthostega* occupy a more posterior position, and the preopercular-quadratojugal sutures of these genera are long. There is no exposure of the preopercular on the mesial face of PIN 1491/82. The mesial surface of the quadratojugal carries a large and conspicuous scar (figure 8*a*) which, by comparison with osteolepiforms (P. E. Ahlberg & O. Lebedev, personal observation), most probably represents the sutural surface for the quadrate.

Suspensorial shape is very variable in early tetrapods. In some forms such as *Crassigyrinus*, *Proterogyrinus* and *Acanthostega* the suspensorium is strikingly elongated, whereas microsaurs (Carroll & Gaskill 1978), colosteids (Smithson 1982; Godfrey 1989) and most early amniotes (Carroll & Baird 1972) possess short suspensoria with near-vertical posterior margins. There is some correlation between these patterns and the presence or absence of an 'otic' notch (more plausibly interpreted as a spiracular notch in basal tetrapods: Clack 1983, 1989; Panchen 1985). Those tetrapods which have elongate suspensoria with sloping posterodorsal margins invariably also possess otic/spiracular notches, whereas many of the forms with short suspensoria are notchless. Both in LDM 81/550 and PIN 1491/82 the posterodorsal margin has been lost. However, if it is assumed that the preopercular was narrow and approximately parallel-sided as in osteolepiforms (Long 1985) and the other basal tetrapods (Jarvik 1980; Panchen 1985; Clack 1988*b*), the posterodorsal margin must have had a distinct slope (figures 8*c* and 9). It thus appears that *Ventastega* had a suspensorium of essentially the same type as *Ichthyostega*, *Acanthostega* and *Crassigyrinus*: in all likelihood it was also associated with a spiracular notch.

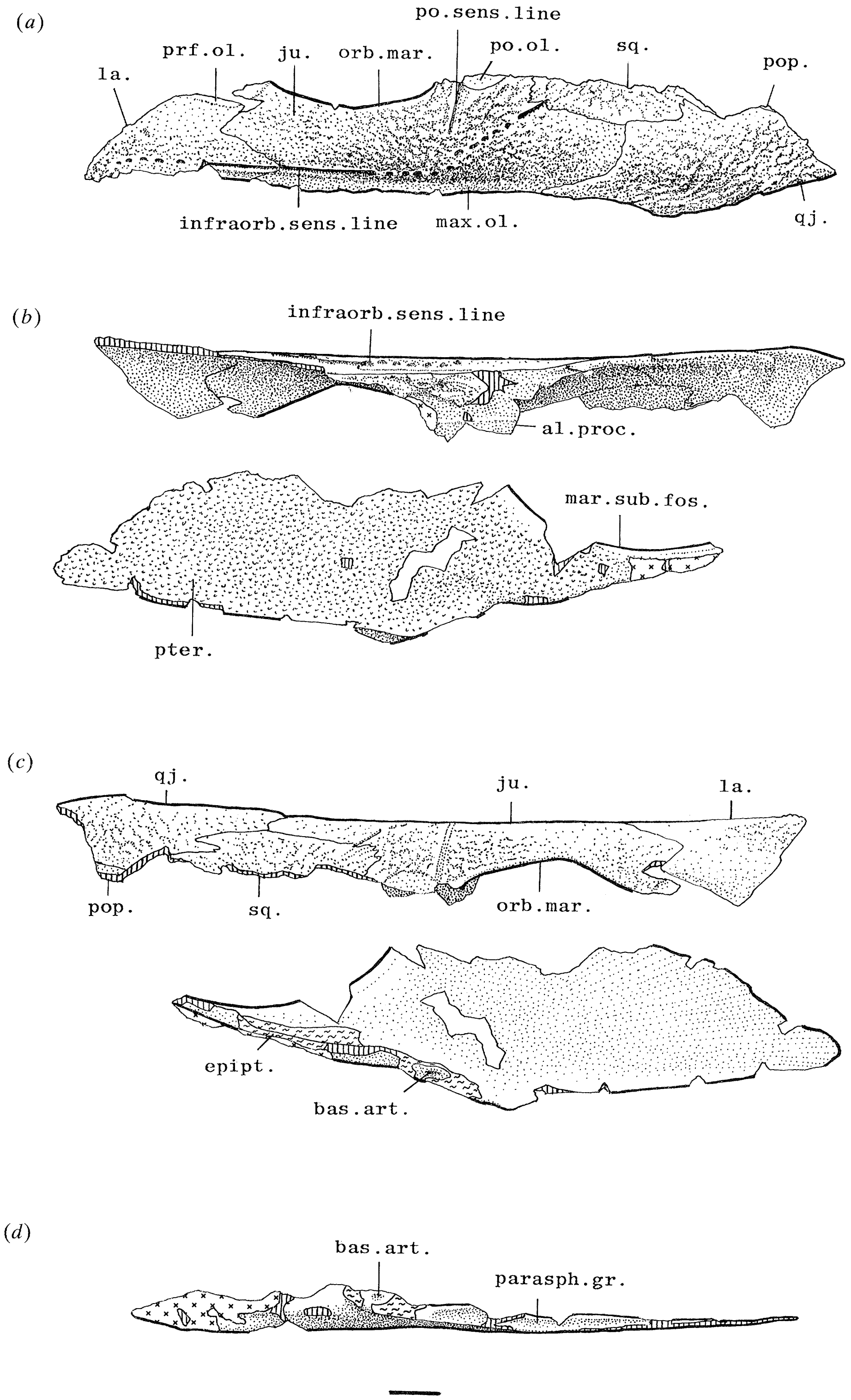

Figure 7. LDM 81/550, incomplete left cheekplate and pterygoid of one individual of *Ventastega curonica* from Pavāri. The two elements are depicted in approximate life positions. (*a*) Lateral view of cheekplate, (*b*) ventral view, (*c*) dorsal view, (*d*) mesial view of pterygoid. Vertical hatching, broken bone; crosses, matrix; thick outline, true margin; thin outline, broken edge. Scale bar 10 mm. Prefrontal and postorbital overlaps (prf.ol., po.ol.) are present on the cheekplate. Note the gently concave lateral margin of the cheekplate in ventral and dorsal view, and how the partly open infraorbital sensory line faces ventrally. The posteromesial margin of the pterygoid (pter.) carries the attachment scar for the epipterygoid (epipt.); anterior to the basal articulation (bas.art.), the pterygoid margin carries a groove (parasph.gr.) for the lateral edge of the parasphenoid.

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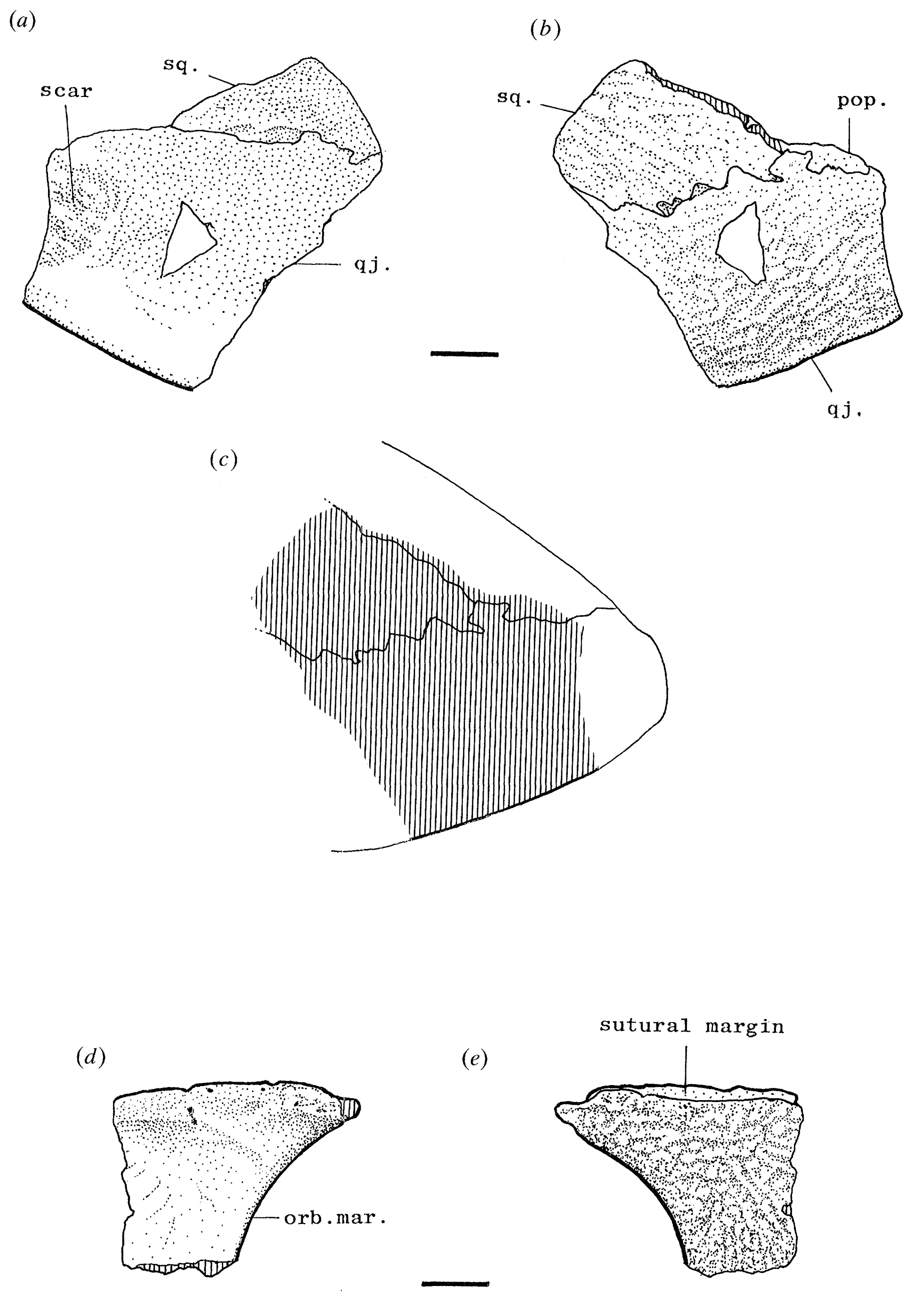

Figure 8. Isolated cranial elements from Ketleri attributed to *Ventastega curonica*. (*a*,*b*) PIN 1491/82, incomplete left suspensorium in internal and external views. Vertical hatching, broken bone; thick outline, true margin; thin outline, broken edge. The suspensorium contains a preopercular bone (pop.) which is only exposed on the external surface. (*c*) Attempted reconstruction of suspensorium; vertical hatching, preserved area. (*d*,*e*) PIN 1491/84, incomplete right prefrontal in internal and external views. Same conventions as (*a*) and (*b*). Both scale bars 10 mm.

The prefrontal (PIN 1491/84; figure 8*d*,*e*) has a straight dorsal margin. The anterior end of the element is lost, but as the centre of the ornament 'starburst' lies on the preserved part it seems likely that the missing region was relatively short. Very little bone seems to have been lost from the ventral margin. In overall appearance the prefrontal resembles those of *Acanthostega* (Clack 1988*b*), *Crassigyrinus* (Panchen 1985), *Eoherpeton* (Smithson 1985) and embolomeres (Holmes 1984; Clack 1987*b*). *Ichthyostega* (Jarvik 1980) also appears to be broadly similar, whereas the prefrontal of *Greererpeton* (Smithson 1982) is of a very different shape. There was clearly no loxommatid-like anterior extension to the orbit (compare Beaumont 1977). The relatively great ventral extent of the bone probably indicates that the lacrimal was excluded from the orbit. All the characteristics of PIN 1491/84 are consistent with it belonging to *Ventastega*, and we have accordingly decided to incorporate it in the tentative skull reconstruction (figures 9 and 11). However, we recognize that this element cannot be as securely attributed as the other cranial bones.

There are considerable collections from Ketleri in the Museum für Naturkunde, Berlin, that were brought there by Walter Gross. One of the uncatalogued specimens, unfortunately incomplete, carries

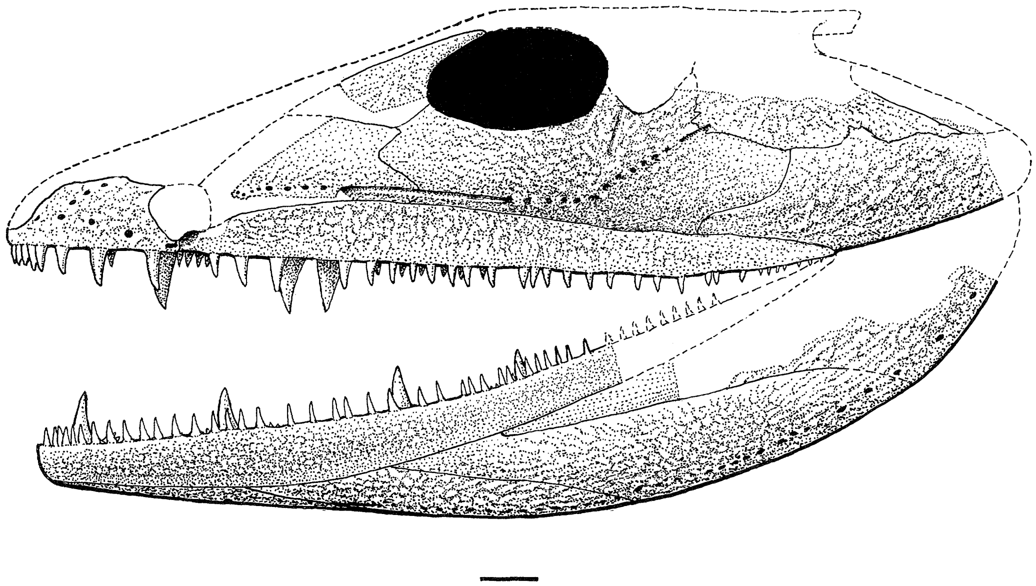

Figure 9. Compound skull reconstruction of *Ventastega curonica* in left lateral view. Shaded areas, preserved bone; dashed line, conjectural outline. Scale bar 10 mm. The reconstructed round bone between the premaxilla and lacrimal is the anterior tectal; the small external nostril lies between the ventral margin of this bone and the anterior end of the maxilla.

characteristic radially disposed tetrapod ornament and appears to represent a postorbital (O. Lebedev, personal observation). The (assumed) anterior edge is smooth and slightly concave as would be expected for part of the orbital margin. The dorsal margin is also smooth; it carries a longitudinal furrow accompanied by a narrow shelf, a pattern characteristic of kinetic margins in early tetrapod skulls. The most prominent feature of the lateral surface is a well developed sensory canal which passes obliquely from the anteroventral corner in a posterodorsal direction. Its dorsal part is marked by four prominent foramina, whereas the ventral part lies in an open furrow. Like the prefrontal, this interesting bone may well belong to *Ventastega* but cannot as yet be securely attributed.

The dermal ornament of the cheek is similar in character to that of the lower jaw (figures 3*a* and 7*a*). It is deep and quite coarse in the middle of the jugal, on the preserved parts of the squamosal and prefrontal, and on most of the quadratojugal. In these areas it consists of sharp ridges separating irregular polygonal pits; the jugal, squamosal and prefrontal have radially disposed ornament, whereas the quadratojugal ornament has an anteroventral–posterodorsal trend. The ornament fades away almost completely on the anterior and posterior ends of the jugal, the dorsal part of the lacrimal, and the posterodorsal margin of the quadratojugal. This contrasts with the pattern in *Ichthyostega* and *Acanthostega* (P. E. Ahlberg, personal observation; J. A. Clack, personal communication), where the skull bones are completely covered by ornament. Among Carboniferous tetrapods, patchy ornament broadly comparable to that in *Ventastega* occurs in anthracosaurs and *Crassigyrinus* (Panchen 1985), whereas the ornament of temnospondyls, loxommatids and colosteids is more complete.

The sensory canals of the cheek are only partly enclosed in *Ventastega* (figure 7*a*). The infraorbital canal is represented by a row of pores on the premaxilla and the anterior part of the lacrimal, but then breaks into an open furrow which continues onto the jugal. Ventral to the posterior part of the orbit this canal becomes enclosed again. It continues posterodorsally across the jugal as a row of pores until, just below the squamosal suture, the canal opens into a short furrow once more. Neither pores nor an open canal are visible on the squamosal. The postorbital commissure is represented by an open and very shallow groove which seems to come to a blind end ventrally.

The dermal cheek bone pattern of *Ventastega* is in most respects comparable to those of *Ichthyostega* (Jarvik 1980), *Acanthostega* (Clack 1988*b*), *Crassigyrinus* (Panchen 1985), *Eoherpeton* (Smithson 1985) and embolomeres (Panchen 1972; Clack 1987*b*). Although the pattern could be subjectively described as 'anthracosaur-like', the similarities are almost certainly symplesiomorphies. A possible exception is the exclusion of the lacrimal from the orbit, which must be judged as a derived character on the basis of outgroup comparison with sarcopterygians (compare Jarvik 1972, 1980; Schultze & Arsenault 1985). The lacrimal contributes to the orbital margin in colosteids (Smithson 1982), loxommatids (Beaumont 1977) and the 'lepospondyl' groups (Carroll 1988; Andrews & Carroll 1991). However, this character is variable within temnospondyls (Carroll 1988, figures) and anthracosaurs (Panchen 1977; Clack 1987*a*), and may be of limited taxonomic value.

The most interesting features of *Ventastega*'s cheekplate are the presence of a preopercular, the structure of the narial region and the development of the lateral lines. The preopercular is a primitive tetrapod feature otherwise only known in *Ichthyostega*, *Acanthostega* and

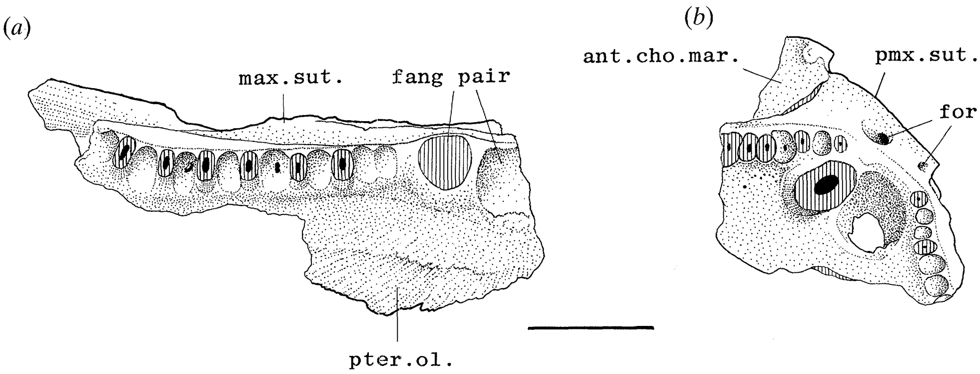

Figure 10. Palatal bones of *Ventastega curonica*. (*a*) LDM 81/528, incomplete right palatine from Pavāri in ventral view, anterior to right. Note the concave lateral margin of the tooth row and the broad overlap area for the pterygoid (pter.ol.). (*b*) PIN 1491/86, incomplete right vomer from Ketleri in ventral view, anterior to right. The premaxillary process is pierced by two nerve foramina (for.) and forms the anterior margin of the choana (ant.cho.mar.). Vertical hatching, broken teeth and bone; thick outline, true margin; thin outline, broken edge. Scale bar 10 mm.

Crassigyrinus. The narial region, though incomplete, appears to have contained a large anterior tectal bone dorsal to the external naris. This pattern is again shared with *Ichthyostega* and *Acanthostega*, but not with other early tetrapods; loxommatids (Beaumont 1977) have a septomaxilla which may be homologous with the anterior tectal, but this bone lies posterior to the naris, and other tetrapod groups differ even more from the condition in the Devonian forms. Both the presence of the preopercular and the apparent structure of the narial region thus indicate that *Ventastega* is a very primitive tetrapod.

The cephalic lateral lines tell a slightly different story. The primitive condition, seen in fishes and *Ichthyostega*, is to have the lateral lines fully enclosed in canals; in temnospondyls, loxommatids and embolomeres, on the other hand, they are represented by open grooves. *Ventastega* occupies an intermediate position, as does *Greererpeton* (Smithson 1982) and the cranial material associated with *Tulerpeton* (Lebedev & Clack 1993). The exact distribution of enclosed and open lateral lines differs between these taxa, and the phylogenetic significance of the variation cannot as yet be determined. It does, however, seem as though *Ventastega* is less primitive than *Ichthyostega* in this respect.

A compound reconstruction of the skull and lower jaw of *Ventastega* in lateral view is shown in figure 9. This incorporates the prefrontal PIN 1491/84 but not the Berlin postorbital fragment. The shaded region of the lower jaw represents the preserved part of LDM 81/521; the curvature of the anterior part of the ramus has been modified in an attempt to compensate for slight post-mortem distortion.

The palatal bones of *Ventastega* so far recovered include one vomer (PIN 1491/86) from Ketleri, three palatines from Ketleri (PIN 1491/83) and Pavāri (LDM 81/528, 81/532), and a pterygoid which articulates with the cheekplate described above (LDM 81/550). The vomer (figure 10*b*) is much abraded dorsally and has lost its anterior, mesial and posterior margins, but the ventral surface is well preserved. At first sight it is strikingly like that of an osteolepiform; a large fang and replacement pit dominate the middle of the bone, which also has a prominent, curving vertical lamina which carries a marginal tooth row. Unlike in many early tetrapods (Carroll 1967; Beaumont 1977) there is no shagreen field. However, it is interesting to note that the marginal tooth row is interrupted lateral to the fang pair, which thus relates to the marginal row in much the same way as the coronoid fangs. In osteolepiforms the marginal tooth row extends unbroken round the fang pair. The vomer contacts the premaxilla by means of a broad but low premaxillary process, which bears a groove that holds the corresponding ridge and rugose area on the latter bone. The posterior tip of the premaxillary process is bent dorsolaterally to form the anterolateral margin of the choana. Anteriorly, the premaxillary process is pierced by two canals which pass obliquely from the ventral to the dorsal side of the bone and might represent passages for branches of the r. palatinus VII. Similar canals are developed in *Ichthyostega* (P. E. Ahlberg, personal observation). Although the anterior and mesial edges of the vomer have been lost, it seems clear that there was a large anterior palatal fenestra which was most probably undivided (see above). A small posterolateral extension of the premaxillary process (figure 10*b*) may have formed a loose contact with the maxilla, but the two bones were clearly not sutured together. The Ketleri vomer is broadly similar to that of *Acanthostega*, but the latter carries an anteromesial process (Clack 1994*a*).

None of the palatines is complete; the description given below is based on information from LDM 81/528 (figure 10*a*), LDM 81/532 and PIN 1491/83. LDM 81/532 has a choanal notch at the anterior end and can thus be identified as a palatine rather than an ectopterygoid. The other two specimens conform to the shape of LDM 81/532 and are therefore also interpreted as palatines. The horizontal plate of the bone is rather broad and bears a broad overlap area for the pterygoid; the tooth-bearing vertical lamina is low. A pair of fangs are developed at the anterior end of the main tooth row, which in LDM 81/528 contains 14 even-sized teeth. Anterior to these fangs, the vertical lamina of the bone extends into a process which forms the posteromesial margin of the choana. The lateral surface of the palatine is strongly rugose dorsally and bears a deep groove for the contact with the corresponding crest on the mesial surface of the maxilla. The groove for the postchoanal anastomosis runs obliquely across the anterior part of the dorsal surface.

The pterygoid of LDM 81/550 is less well preserved than the cheek but still very informative (figure 7*b*–*e*). When the specimen was discovered the cheekplate and pterygoid were in articulation, united by the alar process of the jugal (see above). Unfortunately, the fragile pterygoid suffered some damage during transport from the field; it became detached and can no longer be fitted precisely against the cheekplate. There is thus some uncertainty about the precise positional relationship between the two elements, although not by more than a few millimetres.

One of the most striking features of the pterygoid is that it is not, unlike those of most early tetrapods (Beaumont 1977; Smithson 1982; Clack 1987*b*), co-ossified with the epipterygoid. The latter element may have been unossified and is not preserved; its attachment is represented by areas of unfinished bone. The most anterior of these represents the basal articulation. It consists of two patches of unfinished bone on the mesial margin of the pterygoid, separated by a shallow pit lined with smooth bone (figure 7*d*). The posteroventral margin of the basal articulation is sharply demarcated and slightly raised. Posterior to the articulation, the dorsal face of the bone carries a long strip of unfinished surface and broken bone. This is presumably the attachment for the posterior part of the epipterygoid.

The pterygoid itself is almost completely flat. This appears to be the natural shape of the bone, and correlates with the apparently flattened shape of the skull. Anterior to the basal articulation, the mesial margin of the bone is essentially straight, but can be divided into two distinct sections. The posterior section carries a longitudinal furrow lined with finished bone surface, which presumably clasped the lateral margin of the parasphenoid (figure 7*d*). This furrow becomes shallower anteriorly and eventually dies out; at this point begins the anterior section of the margin, which is less well preserved but appears to be a simple straight edge. It seems likely that this part of the pterygoid was in contact with its counterpart on the other side of the palate, anterior to the parasphenoid. In all likelihood the palate was thus completely closed, with the pterygoids meeting anteriorly to separate the parasphenoid from the vomers. This pattern also occurs in *Acanthostega* (Clack 1988*a*), *Ichthyostega* (Jarvik 1980) and loxommatids (Beaumont 1977). Anthracosaurs (Holmes 1984; Clack 1987*b*) and colosteids (Smithson 1982) have a similar palatal structure, but narrow palatal vacuities are developed between the pterygoids and parasphenoid. The ventral surface of the pterygoid is covered with denticles (figure 7*b*); this is generally true in early tetrapods, with the exception of *Ichthyostega* which lacks denticles altogether.

In morphological terms the vomer and palatine of *Ventastega* are broadly comparable to those of many early tetrapods. The presence of an anterior palatal fenestra is however a strikingly primitive characteristic, present in osteolepiforms and panderichthyids (Jarvik 1942; Vorobyeva 1960; Vorobyeva & Schultze 1991) but known among early tetrapods only in *Acanthostega* (Clack 1994*a*), *Ichthyostega* (Jarvik 1980), *Tulerpeton* (Lebedev & Clack 1993), *Crassigyrinus* (Clack 1994*b*), colosteids (Smithson 1982) and possibly some loxommatids (Beaumont 1977). An anterior palatal fenestra is also developed in urodeles, but this is probably an independently acquired structure. The palatal dentition of *Ventastega* is also rather fishlike, in that it combines a well-developed marginal tooth row with distinct fang pairs on the dermopalatine and vomer. Palatine and vomerine fangs are common in early tetrapods (Sawin 1941; Carroll 1967; Beaumont 1977; Smithson 1982; Clack 1987*b*), but marginal teeth are less frequently seen on these bones. The Carboniferous tetrapods *Greererpeton* and *Eoherpeton* possess marginal palatine teeth (Smithson 1982, 1985), but in embolomeres the tooth row is restricted to the ectopterygoid (Panchen 1972; Clack 1987*b*), and many early tetrapods lack such teeth altogether (Sawin, 1941; Carroll 1967; Beaumont 1977). *Ventastega* resembles Carboniferous tetrapods in that the fangs are set into the marginal palatine-vomerine tooth row. In osteolepiforms and other sarcopterygians with paired palatal fangs (Gross 1941; Jarvik 1972; Jessen 1980), the marginal tooth row is unbroken and lies lateral to the fang pairs. *Acanthostega* seems to show an intermediate condition (Clack 1994*a*; P. E. Ahlberg, personal observation). *Ichthyostega* has a single palatal tooth row which, in the published reconstruction (Jarvik 1980) appears as a row of uniform teeth. In fact the tooth size is quite variable (P. E. Ahlberg, personal observation); the vomerine and palatine tooth rows each contains a pair of noticeably enlarged teeth, which are proportionately smaller than the fangs of *Ventastega* but seem to correspond to them in other respects. The palatal dentition of *Ichthyostega* thus appears to be broadly comparable to those of *Ventastega* and many Carboniferous tetrapods.

A compound dorsal and ventral reconstruction of the skull of *Ventastega* is shown in figure 11. The overall proportions of the skull can be extrapolated with some confidence from the cheekplate and pterygoid of LDM 81/550 (figure 7). The curvature of the reconstructed maxilla is greater than that of LDM 81/188 (figure 5), but compares well with LDM 81/553; it has been reconstructed to match the sutural area on the cheekplate and the curvature of the palatine (LDM 81/528, Figure 10). The proportions of the snout are heavily dependent on the presumed size of the premaxilla and thus somewhat tentative. However, we feel confident that the reconstructed pattern of the palate is essentially correct.

(*c*) ***Pectoral and pelvic girdles***

One incomplete interclavicle, LDM 57A/1978

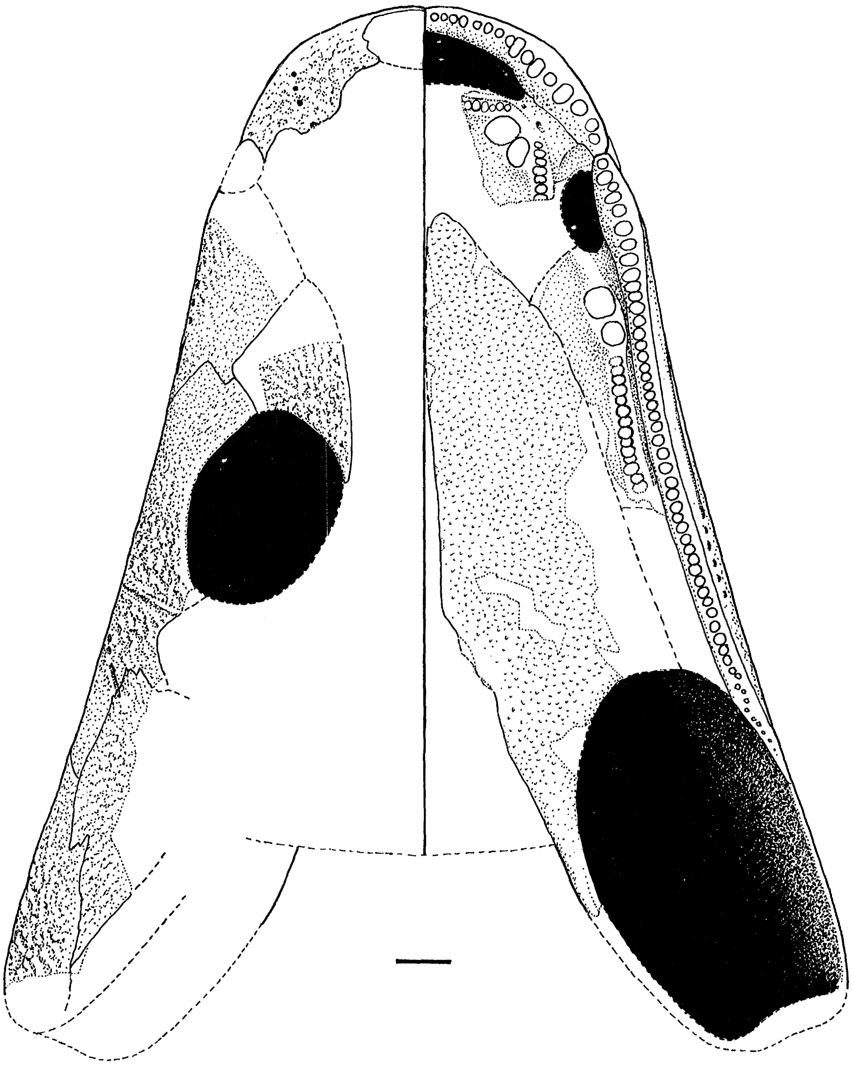

Figure 11. Compound dorsal and ventral skull reconstruction of *Ventastega curonica*. Shaded area, preserved bone; dashed line, conjectural outline. Scale bar 10 mm. On the ventral view the tooth positions are shown as empty outlines, and the anterior palatal fenestra, choana and subtemporal fossa are rendered in black.

(figures 3*e* and 12*e*) has been recovered from Ketleri. The anterolateral edges of the bone are relatively well preserved, and although the anterior margin is broken it is unlikely that much bone has been lost. Posteriorly, however, the element is broken just anterior to the 'centre of radiation'. The dorsal surface of the bone is featureless. Ventrally, the most conspicuous features are the large overlap areas for the clavicles. These almost meet anteriorly, but posteriorly they are separated by an area of rather eroded ornament.

Two clavicles are known, one from each locality. The best preserved, LDM 81/531 (figure 12*a–d*), is an apparently undistorted and virtually complete right clavicle from Pavāri. (The other specimen, PIN 1491/81 from Ketleri, is much less complete but agrees with LDM 81/531 in all significant respects. It is however somewhat larger.) LDM 81/531 lacks only a part of the posterior margin, a small area on the lateral face of the clavicular stem, and some chips off the very thin mesial margin. The general appearance of the bone, a broad ventral blade with a narrow and sharply offset stem, is characteristic of early tetrapods. In sarcopterygian fishes the clavicular stem is less distinct from the ventral part (Jarvik 1972, text-fig. 52; Andrews 1985, fig. 13). The ventral blade of LDM 81/531 is gently ventrally convex in the anteroposterior plane, so that the bone rocks when resting on a flat surface, and the dorsal surface of the blade is concave to a corresponding degree. The mesial margin is smoothly curved. As in many early tetrapods, the clavicular stem consists of a thick anterior rod and a much thinner posterior lamina which merges into the lateral surface of the rod (figure 12*b*,*d*). In cross-section, the stem thus comes to resemble the letter 'P'. The ventral part of the lamina is bowed outwards into a distinct embayment which presumably housed part of the scapulocoracoid. Most of the ventral surface of the clavicle is covered with dermal ornament consisting of sharp-edged, anastomosing ridges and quite deep pits which become finer and shallower towards the mesial edge. Along the anterior margin runs a fairly broad strip of smooth bone which may represent an overlap area for the gular region of a gill cover (figure 12*a*). Dorsolaterally, the ornamented area ends in a rela-

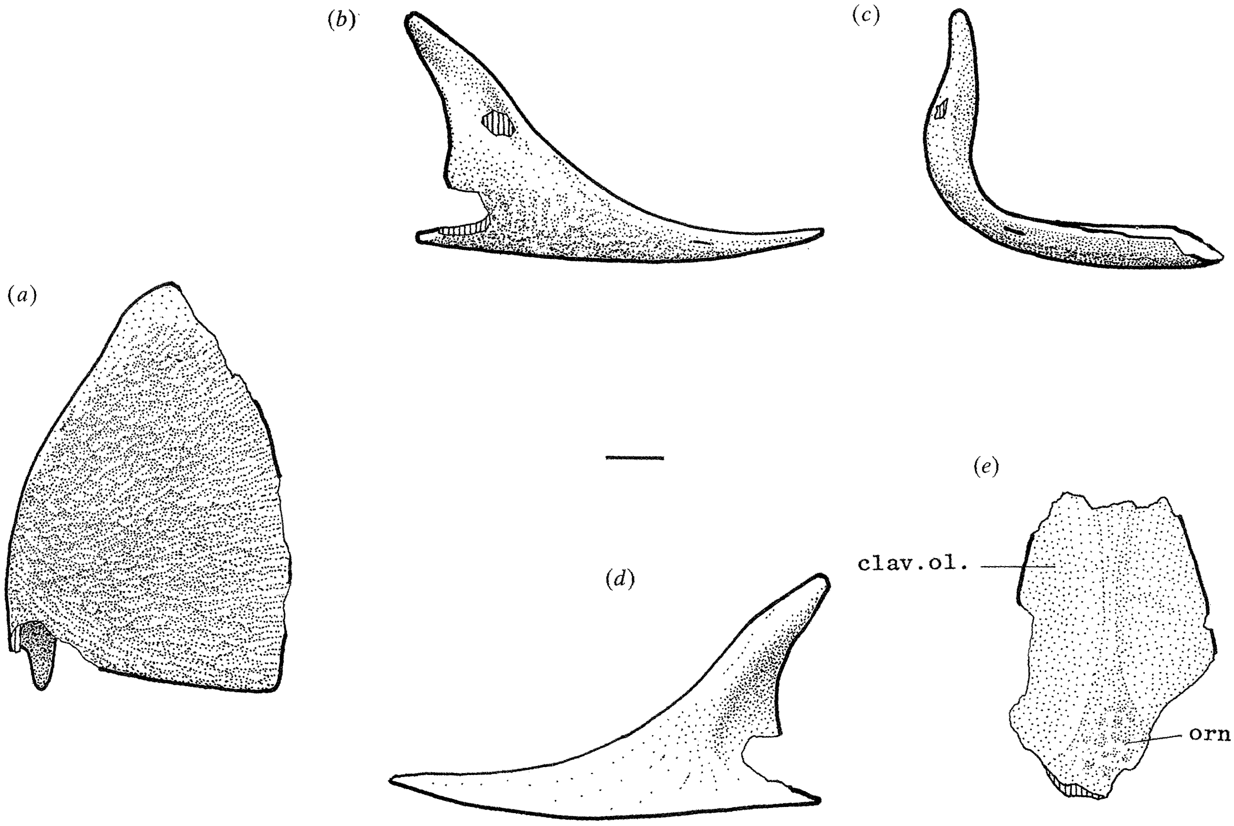

Figure 12. **Pectoral girdle elements attributed to** *Ventastega curonica*. (*a–d*) LDM 81/531, right clavicle from Pavāri in ventral, (antero)lateral, anterior and (postero)mesial views. In (*d*), note that the clavicle stem consists of a thick anterior rod and a thin posterior lamina. (*e*) LDM 57A/1978, an incomplete interclavicle from Ketleri in ventral view (anterior at top). The specimen represents the anterior part of the bone; note the overlap areas for the clavicles (clav.ol.) and the small field of eroded dermal ornament (orn.). Vertical hatching, broken bone; thick outline, true margin; thin outline, broken edge. Scale bar 10 mm.

tively distinct curving margin across the base of the clavicular stem. This pattern is very reminiscent of that in *Greererpeton* (Godfrey 1989).

Two postcranial elements, one from Pavāri (LDM 81/522) and one from Ketleri (LDM 57A/1984) were at first interpreted as cleithra. LDM 81/522, which is the best preserved specimen, consists of a rather narrow, laterally compressed shaft which widens distally into a thin blade (figure 13). Proximally the shaft ends in a mass of crushed endoskeletal bone. There is a pronounced bend in the shaft about one third of the way along from the proximal end. LDM 57A/1984 is a small fragment of the shaft, but resembles LDM 81/522 in all significant respects.

These elements resemble the cleithra of *Ichthyostega* (Jarvik 1980) and *Acanthostega* (Coates & Clack 1991) to some extent, and were initially interpreted in the same way. The broken bone at the base of LDM 81/522 was taken to represent the dorsal end of a low scapulocoracoid without a distinct scapular blade. However, during the refereeing process, Michael Coates discovered that LDM 81/522 more closely resembles the figured (Clack 1988*b*) but not yet fully described iliac blade of *Acanthostega*. Personal observation of the *Acanthostega* specimens by one of us (P.E.A.) confirms this reinterpretation. It should be added that 'iliac blade' in this context is used *sensu* Godfrey (1989) to refer to the large, posterodorsally directed blade of the ilium. In anthracosaurs and similar forms, this blade is often referred to as the 'postiliac process' (Smithson 1985; Panchen & Smithson 1990), while 'iliac blade' is used for the dorsal process of the ilium.

As mentioned above, there is a pronounced bend or kink in the iliac blade about one-third of the way from the proximal end; the distal part of the blade is deflected dorsally (figure 13*a*,*c*,*e*) and mesially (figure 13*b*,*d*) with respect to the proximal part. A similar dorsal bend to the blade is seen in *Greererpeton* (Godfrey 1989) and *Proterogyrinus* (Holmes 1984), but the accompanying mesial deflection does not appear to be developed in Carboniferous tetrapods. In the region of the bend, the lateral surface of the iliac blade carries a patch of pitted 'ornament'. This is probably a muscle attachment (M. I. Coates, personal communication), and closely resembles the 'ornament' on the ischium of *Crassigyrinus* which led Panchen & Smithson (1990) to suggest a dermal origin for this bone (O. Lebedev, personal observation).

The mass of broken bone at the proximal end of LDM 81/522 fortunately preserves a small area of true surface which appears to define the posterior margin of the 'neck' of the ilium (figure 13*a*,*e*). Interestingly, there is no trace of the dorsal process which rises immediately dorsal to this region in anthracosaurs,

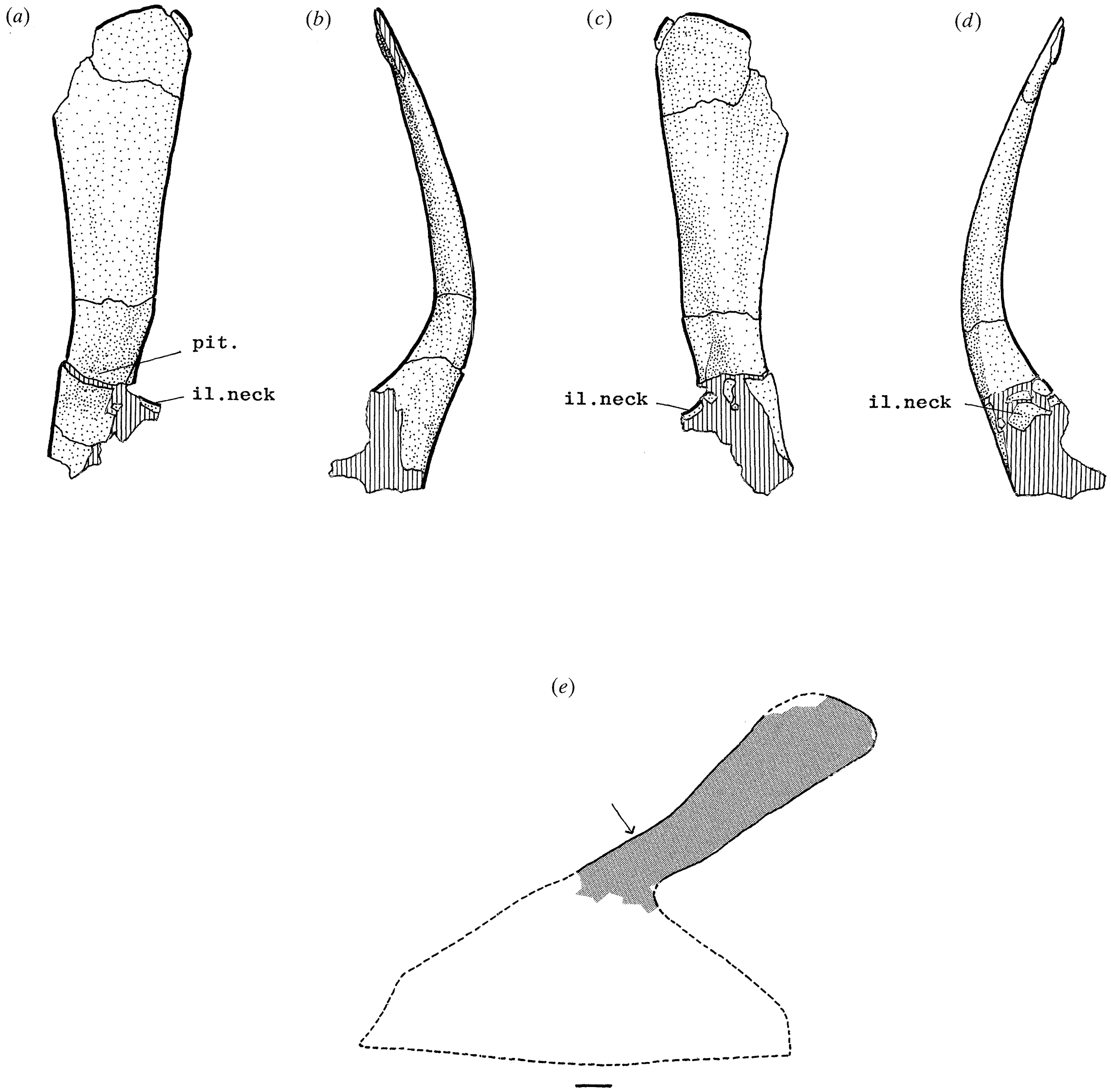

Figure 13. LDM 81/522, left ilium from Pavāri, attributed to *Ventastega curonica*. (*a–d*) Lateral, anterodorsal, mesial and posteroventral views. Vertical hatching, broken bone; thick outline, true margin; thin outline, broken edge. In this figure thin lines within specimen indicate major cracks, rather than sutures as in other drawings. Scale bar 10 mm. The lateral surface carries a patch of faint pitting (pit.) which may represent a muscle attachment. A fragment of the posterior margin of the 'iliac neck' (il.neck) can be seen in (*a,c*) and (*d*). (*e*) Sketch reconstruction in left lateral view showing the probable relationship between the iliac blade and the rest of the pelvis. Shading, preserved area; the arrow indicates the most posterior possible position for the posterior margin of a dorsal iliac process. Scale bar 10 mm.

and also in *Crassigyrinus* and *Ichthyostega* (Holmes 1984; Smithson 1985; Jarvik 1980; Panchen & Smithson 1990). The dorsal process was either absent as in *Greererpeton* and temnospondyls generally, or more anterior in position; the latter condition would be unique among known tetrapods.

Before comparing the pectoral and pelvic girdle elements with those of other early tetrapods, we must consider whether they are all likely to belong to the same taxon. In the first place it can be noted that the clavicles and ilia from Ketleri, though incomplete, seem to be virtually identical to those from Pavāri. They thus probably represent either one tetrapod genus which occurs at both sites, or two genera with that distribution. As all the tetrapod cranial material from Pavāri and most of that from Ketleri can be assigned to *Ventastega*, it seems most probable that the clavicles and ilia in fact belong to this genus.

The overlap areas on the single known interclavicle are a strikingly good 'fit' for the mesial edge of the clavicle, although the interclavicle appears to be proportionately about 25% smaller than the clavicle. Early tetrapod clavicles and interclavicles show considerable morphological variability (Jarvik 1980; Holmes 1984; Clack 1987*b*; Godfrey 1989), so the close correspondence of form between LDM 81/531 and 57A/1978 probably indicates that the two bones belong to the same genus, albeit to individuals of somewhat different size. The circumstantial evidence clearly suggests that all the pectoral and pelvic girdle elements pertain to *Ventastega*. We accordingly feel justified in assigning them, with a degree of caution, to that genus.

The clavicle is of a general type seen in many early tetrapods. It particularly resembles that of the Carboniferous colosteid *Greererpeton* (Godfrey 1989), but the clavicles of the embolomeres *Pholiderpeton* (Clack 1987*b*) and *Archeria* (Holmes 1989) are also fairly similar. All these genera have tapering clavicular stems with P-shaped cross-sections, similar to that of LDM 81/531, but this morphology is not universal among early tetrapods (Jarvik 1980, fig 169; Holmes 1980, 1984). Clack (1987*b*) suggests that a narrow tapering clavicular stem is primitive for tetrapods. Outgroup comparison with osteolepiforms (Jarvik 1944) and other osteichthyans (Gardiner 1984) supports this interpretation, but more detailed character polarities are difficult to establish. The most noteworthy features of the *Ventastega* clavicles, visible in both LDM 81/531 and PIN 1491/81, are the unusual width of the ventral blade and the presence of an unornamented strip along the anterior margin of the bone. The latter could represent an overlap area for an opercular flap, but may simply indicate that the edge of the bone was buried in soft tissue.

The interclavicle from Ketleri is too incomplete to reconstruct in detail. The preserved part resembles the interclavicle of *Greererpeton* rather closely, suggesting that the complete outline of the bone was rhomboidal or kite-shaped. This general pattern is seen in many early tetrapods including *Greererpeton*, *Crassigyrinus* (Panchen 1985) and embolomeres (Holmes 1980, 1984; Clack 1987*b*). A different morphology with a broad anterior plate and slender posterior stem occurs in *Ichthyostega* (Jarvik 1980), most microsaurs (Carroll & Gaskill 1978), seymouriamorphs (Holmes 1980) and early amniotes (Carroll 1988). The systematic significance of this character distribution is obscure.

It is clear from the development of the overlap areas on the Ketleri interclavicle that the anterior parts of the clavicles approached each other very closely. This condition is widespread among early tetrapods, including amniotes, and outgroup comparison with osteolepiforms (Jarvik 1944) indicates that it is primitive for the group as a whole. A different pattern is present in certain anthracosaurs such as *Proterogyrinus* (Holmes 1980, 1984), where the clavicles are completely separated by a broad expanse of ornamented bone.

On the whole, the clavicle and interclavicle attributed to *Ventastega* are not phylogenetically very informative. Although they resemble those of many Carboniferous and later tetrapods in a general way, they appear to share no derived characters with any specific post-Devonian group: the similarities are probably basal autapomorphies of the Tetrapoda.

Probably the most interesting aspect of the iliac blade is that it does not resemble that of *Ichthyostega*. In the latter genus the blade ('posterior iliac process'; Jarvik 1980) is horizontal, slender and gently curved, while the dorsal process is massive. By contrast, the blade attributed to *Ventastega* has a distinct dorsal bend, appears to have been directed posterodorsally (figure 13*e*), and is certainly not associated with a massive dorsal process (it may lack such a process altogether). It is far more similar to the ilia of *Greererpeton* (Godfrey 1989), anthracosaurs (Holmes 1984; Smithson 1985) and *Acanthostega* (Clack 1988*a*; M. I. Coates, personal communication) than to that of *Ichthyostega*. This underlines the morphologically isolated position of *Ichthyostega*, which is particularly interesting in view of the suggestion that *Ventastega* may be a more primitive animal than *Ichthyostega* (see § 7). The unusual pelvic morphology of *Ichthyostega* may thus be derived in some respects.

6. OTHER TETRAPOD MATERIAL

(*a*) *A second tetrapod from Ketleri?*

Although most of the tetrapod jaw material from Ketleri and Pavāri can be either identified as belonging to *Ventastega* or dismissed as indeterminable, one small mandibular fragment from Ketleri (LDM 57/900) appears to represent a second tetrapod genus. The specimen (figure 14) consists of the symphysial region of a lower jaw, and comprises most of the parasymphysial plate together with short sections of the dentary and splenial. It is distinguishable from *Ventastega* by the presence of a well-developed fang and replacement pit on the parasymphysial plate, similar to those seen in *Obruchevichthys*, the Scat Craig tetrapod, *Acanthostega* and the Parrsboro jaw (see above). No marginal teeth can be seen on the parasymphysial plate, but this may be an artefact as the specimen is rather worn. The presence of large teeth and replacement pits rather than shagreen on the parasymphysial plate appears to be a derived tetrapod character (see §§ 5*a* and 7). This suggests that LDM 57/900 represents a tetrapod, but unfortunately the incompleteness of the specimen makes it impossible to determine whether it is a new genus or represents one of the previously known Devonian taxa. All that can be said with certainty is that it is neither *Ventastega* nor *Ichthyostega*.

(*b*) *A possible limb bone*

A small endoskeletal element from Ketleri, LDM 57/2003, may represent a tetrapod limb bone (figure 15). Superficially it resembles the ulnae of *Acanthostega* (Coates & Clack 1990) and *Ichthyostega* (Jarvik 1980),

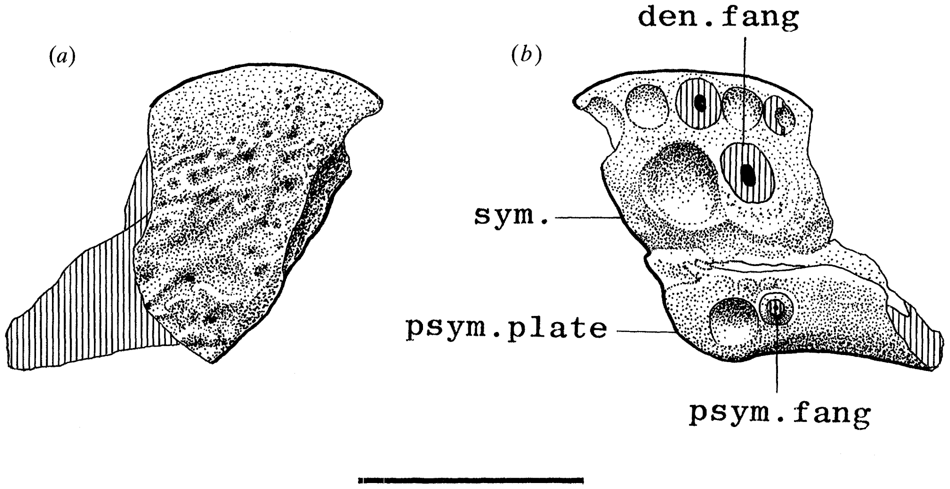

Figure 14. LDM 57/900, tetrapod jaw fragment from Ketleri in ventral and dorsal views. The parasymphysial plate of this jaw carries a fang (psym.fang) and replacement pit: some faint structures along the dorsal margin may represent very worn marginal teeth, but this is by no means certain. Vertical hatching, broken bone; thick outline, true margin; thin outline, broken edge. Scale bar 10 mm.

but it is a rather stout bone and carries a pronounced process on what would be (by analogy with the ulna) the proximal end of the flexor surface (figure 15*a*,*d*). The authors are divided in their interpretations of this bone, viewing it either as a possible ulna (P.E.A.) or a tibia (O.L.); it is presented here in order to bring it into the public domain and to facilitate comparison with other specimens.

7. DISCUSSION AND CONCLUSIONS

(*a*) *The tetrapod status of* Ventastega curonica

Given that no fully articulated specimens of *Ventastega curonica* have been found, and that no limb elements can be confidently assigned to the taxon, it may legitimately be asked how it can be identified as a tetrapod. A number of authors (Gaffney 1979; Panchen & Smithson 1987; Godfrey 1989) have recently examined the systematic status of the tetrapods. All agree that the group Tetrapoda is a clade which can be characterized by a number of autapomorphies. The longest list of proposed tetrapod autapomorphies is that of Godfrey (1989), which includes 41 characters. Some of these are present in the great majority of recent tetrapods, but several are only recognizable in early members of the group. In addition, several of Godfrey's characters are in fact lacking in very primitive tetrapods. These include character 16 (some lateral line canals in open grooves) which is absent in *Ichthyostega* (Säve-Söderbergh 1932) and character 23 (large dorsally expanded scapular blade) which is absent in *Ichthyostega* (Jarvik 1980) and *Acanthostega* (Coates & Clack 1991; J. A. Clack, personal communication).

A great many of Godfrey's derived tetrapod characters are of course indeterminable in the specimens attributed to *Ventastega*, due to their incompleteness. However, the material unambiguously shows the following characters from Godfrey's list:

5: Jugal forms at least half of lower orbit margin.
6: Median abutment of pterygoids below cultriform process.
16: Some lateral line canals in open grooves.
17: Characteristic dermal ornament (see below).
25: Large interclavicle.

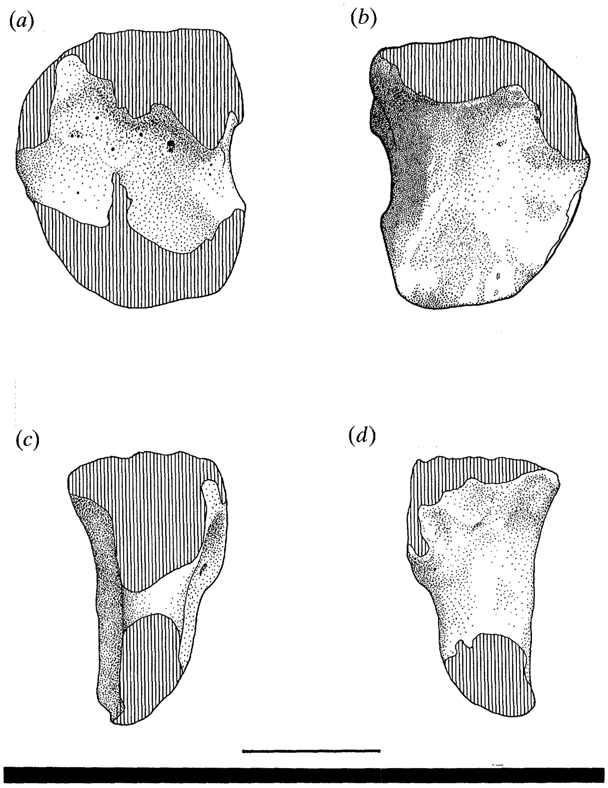

Figure 15. LDM 57/2003, unidentified endoskeletal bone from Ketleri, possibly a tetrapod limb bone. The two broad faces of the bone, (*a*) and (*b*), are both concave, and (*a*) is pierced by several foramina for nerves or blood vessels. The ends of the bone are unfinished and may be somewhat eroded. Vertical hatching, broken or unfinished bone. Scale bar 10 mm.

33: A pubis, ischium and ilium form each half of the pelvic girdle. (Only the ilium is known, but it clearly belongs to a tetrapod pelvis.)

In addition, the cheekplate has a broad jugal-quadratojugal contact, a character which was regarded as a tetrapod autapomorphy by Panchen & Smithson (1987) but is apparently also developed in some panderichthyids (Vorobyeva & Schultze 1991).

Character 17 requires some further discussion; it attempts to define the characteristic appearance of early tetrapod ornament, but is not completely successful in this respect. Godfrey (1989) describes early tetrapod ornament as composed of 'deep polygonal pits or troughs surrounded by raised ridges'. This definition omits one of the most striking differences between tetrapod and other sarcopterygian ornament, namely that tetrapod ornament tends to radiate from the centre of a bone, forming an irregular 'starburst' pattern. This phenomenon is not equally developed on all bones, but is usually obvious on the squamosal and jugal as well as on the infradentary series (see figures in Beaumont 1977; Smithson 1982; Panchen 1985). Devonian fish ornament, by contrast, almost never radiates from the centre of bones in this way and often extends across sutures without any interruption.

This assemblage of characters clearly supports the identification of *Ventastega* as a tetrapod, particularly as it possesses character 16 unlike *Ichthyostega*. The gross morphology of the known elements is also strikingly close to that of *Ichthyostega* and *Acanthostega* (P. E. Ahlberg & O. Lebedev, personal observation). The only feature at odds with this general picture is the dentition of the lower jaw, which is surprisingly fishlike.

The lower jaw of *Ventastega* carries characteristic tetrapod ornament which is particularly similar to that of *Acanthostega* (P. E. Ahlberg & O. Lebedev, personal observation). However, well developed fangs are present on the precoronoid and intercoronoid. There are no distinct fangs on the coronoid, but this pattern also occurs in some long-jawed osteolepiforms such as *Platycephalichthys* (P. E. Ahlberg, personal observation). The lower jaw of *Ventastega* thus possesses Godfrey's character 17 but lacks character 15 (loss of fang and replacement pit on at least one bone in coronoid series). The dentition of the coronoid series is not however completely fishlike, as the fangs are set in the marginal coronoid tooth row rather than mesial to it as in sarcopterygians.

In addition to those listed by Godfrey, the lower jaw shows three further features which we suggest are derived tetrapod characters: (i) the exclusion of the Meckelian bone from the floor of the precoronoid fossa; (ii) the extension of the coronoid tooth row onto the parasymphysial plate; and (iii) the presence of two conspicuous foramina lateral and mesial to the suture between the parasymphysial plate and the precoronoid.

(i) *Meckelian bone*

In all those lobe-fins where the coronoid series is known, the Meckelian bone is exposed on the mesial face of the jaw anterior to the precoronoid, and often between the more posterior coronoids as well. In osteolepiforms (Jessen 1966, Fig. 5B; Vorobyeva 1977, Pl. 7:6), porolepiforms (Gross 1941, Fig. 7; Ahlberg 1991*b*, Fig. 8) and panderichthyids (Gross 1941, Fig. 18), Meckelian bone thus forms the floor of the precoronoid fossa and is usually also exposed in the intercoronoid and coronoid fossae (figure 16*a*,*b*). Tetrapods completely lack these exposures of Meckelian bone. The coronoid series, prearticular and (if present) parasymphysial plate are closely sutured together, and if the parasymphysial plate is absent the ventral margin of the precoronoid is sutured to the splenial (Beaumont 1977; Carroll & Gaskill 1978; Smithson 1982; Clack 1987*b*, 1988*a*; Godfrey & Holmes 1989). *Ventastega* shows unambiguously the tetrapod condition (figures 4 and 16*b*).

Clack (1988*a*) interpreted the presence of a short prearticular and associated coronoid/splenial suture as a 'neotetrapod' autapomorphy. *Ventastega*, like *Ichthyostega*, has a long prearticular which separates the splenial from the anterior coronoid. If Clack is correct in her suggestion, *Ventastega* thus falls outside the neotetrapod clade.

Primitive actinopterygians superficially resemble tetrapods in that their coronoids are sutured together without exposure of Meckelian bone (Gardiner 1984). There is however little reason to doubt that tetrapods are derived from sarcopterygians with a lower jaw of the porolepiform-osteolepiform-panderichthyid type (Schultze & Arsenault 1985; Panchen & Smithson 1987; Ahlberg 1991*a*,*b*), and that the tetrapod ossification pattern is autapomorphic.

(ii) *Parasymphysial dentition*

The situation is similar with respect to the dentition of the parasymphysial tooth plate. In sarcopterygians this plate carries either shagreen (in osteolepiforms and panderichthyids: Jessen 1966; Jarvik 1980, Fig. 125; Vorobyeva 1962, Pl. 18:3) or tooth whorls (in onychodonts and porolepiforms: Jessen 1966; Jarvik 1972). By contrast, all known parasymphysial plates of Devonian and Carboniferous tetrapods carry large teeth with replacement pits (Jarvik 1980; Godfrey & Holmes 1989; Ahlberg 1991*a*). *Ventastega* conforms to the early tetrapod pattern (figures 4*b* and 16*d*). Well-developed marginal teeth also occur on the parasymphysial plates of early actinopterygians (Gardiner 1984, Figs. 91 and 92) and the Carboniferous osteolepiform *Lamprotolepis* (Vorobyeva 1977, Fig. 39), but again it seems likely that the tetrapod condition is derived independently of these.

(iii) *Foramina*

The final character, two relatively large and apparently connected foramina which lie lateral and mesial to the posterior end of the parasymphysial plate (figure 4*b* and 16*d*), is at present only known in *Ventastega*, *Metaxygnathus* (Campbell & Bell 1977; P. E. Ahlberg, personal observation), *Obruchevichthys* (Vorobyeva 1977; Ahlberg 1991*a*) the Scat Craig tetrapod (Ahlberg 1991*a*) and *Acanthostega* (J. A. Clack, personal communication). This could indicate that these

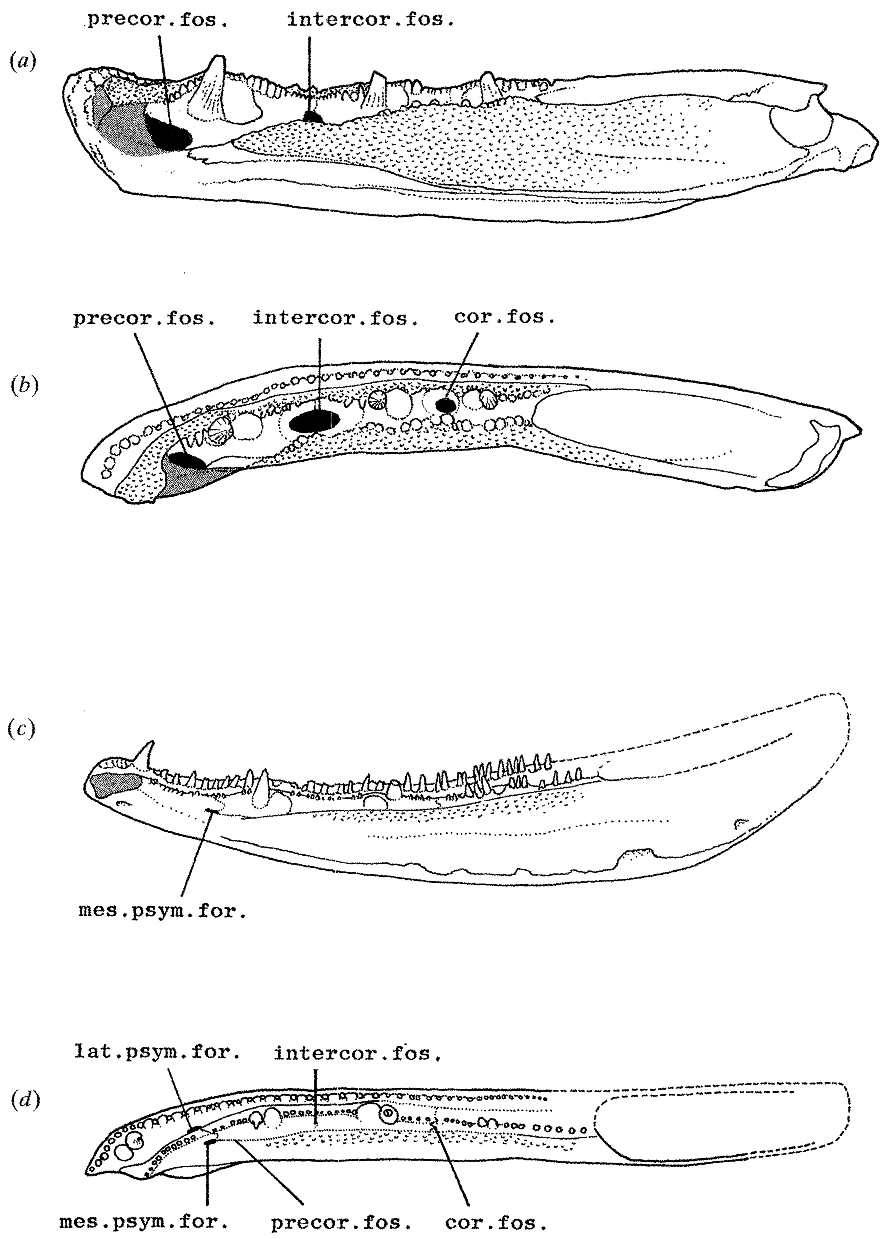

Figure 16. **Comparison between osteolepiform and tetrapod lower jaws.** (*a*,*b*) Lower jaw of an osteolepid from Russia (Lebedev 1994) in mesial and dorsal views. The precoronoid, intercoronoid and coronoid fossae are floored with Meckelian bone (black), and Meckelian bone also forms a stout mentomandibular buttress (grey). The parasymphysial plate is covered by shagreen. Large and distinct dentary fangs like those in *Ventastega* are present in many derived osteolepiforms. (*c*,*d*) Lower jaw of *Ventastega* in mesial and dorsal views. There is no exposure of Meckelian bone in the precoronoid, intercoronoid and coronoid fossae (which are also much shallower than in osteolepiforms). Nor is there an exposed mentomandibular buttress; the only visible Meckelian bone in this region is the actual symphysis. The parasymphysial plate carries a continuation of the coronoid tooth row, and is 'bracketed' posteriorly by a pair of foramina which are absent in osteolepiforms. It is also worth noting the difference in overall shape between the jaws.

animals form a clade, but it is also possible that the character is a basal tetrapod autapomorphy secondarily lost in post-Devonian genera.

As can be seen there are good reasons for identifying *Ventastega* as a tetrapod, albeit a very primitive member of the group. The skull, pectoral girdle and pelvis appear to be closely similar to those of other Devonian tetrapods, while the lower jaw displays a number of probable tetrapod autapomorphies.

(*b*) *Relationships to other early tetrapods*

Although *Ventastega curonica* remains poorly understood in several respects, it is possible to draw some conclusions about its relationships to other early tetrapods. In particular, it casts valuable light on the taxonomic position of the Lower Famennian, Australian genus *Metaxygnathus* (Campbell & Bell 1977).

Metaxygnathus, which is known from a single lower jaw ramus, was described as a tetrapod, but has been dismissed as an osteolepiform fish by Schultze & Arsenault (1985) and Schultze (1987). They reject the supposed tetrapod characters of *Metaxygnathus* as providing inadequate evidence of tetrapod affinities, and claim that the presence of an enclosed mandibular canal and a parasymphysial ('adsymphysial') tooth plate identify the jaw as that of a fish.

The latter argument is easily refuted; both the enclosed canal and the tooth plate are present in *Ichthyostega* (Säve-Söderbergh 1932; Jarvik 1980), *Acanthostega* (J. A. Clack, personal communication; P. E. Ahlberg, personal observation) and *Ventastega*. However, Campbell & Bell's suggested tetrapod characteristics for *Metaxygnathus* (narrow dentary, small coronoid fangs, retroarticular process, overall shape of jaw) do not appear very convincing.

In 1991, one of us (P.E.A.) had the opportunity to examine *Metaxygnathus* in some detail. The study confirmed most aspects of Campbell & Bell's reconstruction, but in addition the jaw proved to exhibit all three of the new derived tetrapod characters recognized in *Ventastega*. There is no Meckelian bone exposed in the precoronoid fossa; the parasymphysial tooth plate carries both a continuation of the marginal coronoid tooth row (shown but not labelled in Campbell & Bell's reconstruction) and at least one large fang, and is thus apparently similar to that of *Obruchevichthys* and the Scat Craig tetrapod (Ahlberg 1991*a*); and the large foramen illustrated by Campbell & Bell (1977, fig. 6B, 'psymp.f') is clearly the lower one of the pair of foramina bracketing the coronoid/parasymphysial plate suture (the site of the upper, or lateral, foramen is obscured by matrix). Campbell & Bell's (1977) interpretation of the specimen as a tetrapod jaw appears to be correct.

Clack (1988*a*) pointed out that *Metaxygnathus*, in Campbell & Bell's reconstruction, appears to possess a coronoid/splenial suture. If this is accepted as a 'neotetrapod' autapomorphy, *Metaxygnathus* would thus be a more derived tetrapod than *Ichthyostega* or *Ventastega*. However, the anterior extension of the first coronoid shown in the reconstruction is in fact the parasymphysial plate; the coronoid ends dorsal to the large foramen ('psymp.f.'), and there is no coronoid-splenial contact.

Given that important parts of the anatomy of *Acanthostega* have yet to be published, and that the Scat Craig tetrapod material has not been fully described, the time is not yet ripe for a cladogram of basal tetrapods. However, some conclusions can already be drawn about the position of *Ventastega* within the Tetrapoda. The most informative characters are the preopercular bone, the sensory canals and pit lines, the structure of the lower jaw, and the coronoid fangs.

Among other tetrapods, a preopercular bone is known only in *Crassigyrinus* (Panchen 1985), *Ichthyostega* (Säve-Söderbergh 1932) and *Acanthostega* (Jarvik 1952; Clack 1988*b*). The degree of enclosure of the cephalic sensory line system is greater in *Ventastega* than in any other known tetrapods except *Ichthyostega* (Säve-Söoderbergh 1932; Jarvik 1980) and *Acanthostega* (J. A. Clack, personal communication). The surangular pit line of *Ventastega*–a common sarcopterygian feature–is not known in any other tetrapod. (The only other tetrapods in which pit lines are known to occur are discosauriscids; Klembara 1992.) *Ventastega* also lacks the proposed neotetrapod synapomorphy of splenial/coronoid contact (Clack 1988*a*). These characters establish beyond doubt that *Ventastega* is one of the most primitive known tetrapods.

The presence of coronoid fangs in *Ventastega* is particularly interesting, as this is a primitive feature which has been lost in *Ichthyostega* (Jarvik 1980; P. E. Ahlberg, personal observation), *Acanthostega* (J. A. Clack, personal communication) and probably *Tulerpeton* (Lebedev & Clack 1993). It may thus be that *Ventastega* – together with *Metaxygnathus* and the Scat Craig tetrapod, which also possess this feature – occupies a less crownward position on the tetrapod tree than *Ichthyostega*, *Acanthostega* or *Tulerpeton*. This inference is supported by the presence of a surangular pit line in *Ventastega*, but is apparently contradicted by the more fully enclosed nature of the lateral line canals in *Ichthyostega*.

The excellent preservation and relative abundance of the material makes *Ventastega curonica* one of the most important Devonian tetrapod discoveries of recent decades. Future work at Ketleri and Pavāri will hopefully provide more information about this intriguing and extremely primitive animal.

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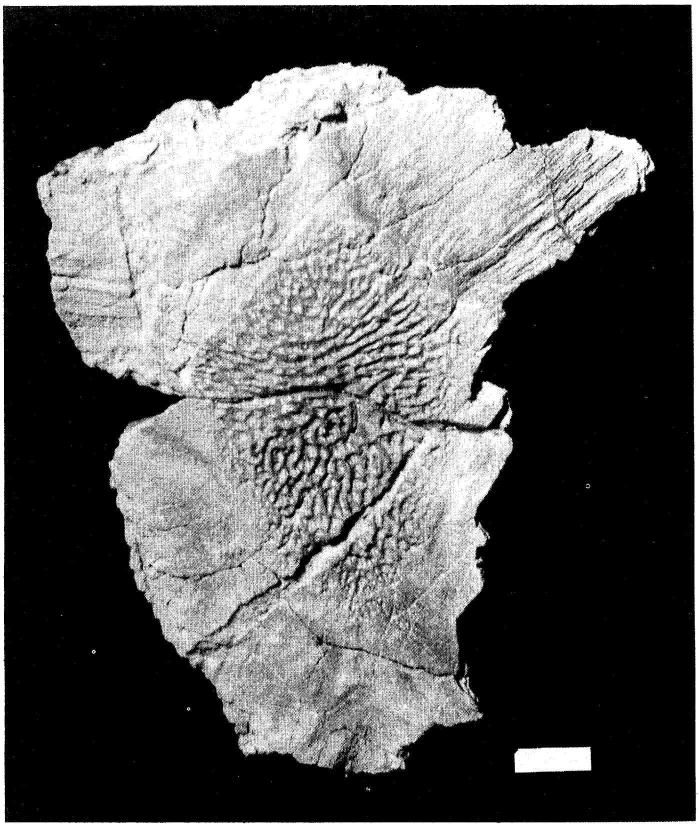
Note added in proof (10 January 1994): A nearly complete tetrapod interclavicle, LDM 81/557, was recently discovered in an unprepared block from Pavāri. It has not been examined in detail, but seems to differ in shape from LDM 57/1978. The figure below shows a ventral view. Scale bar, 10 mm.



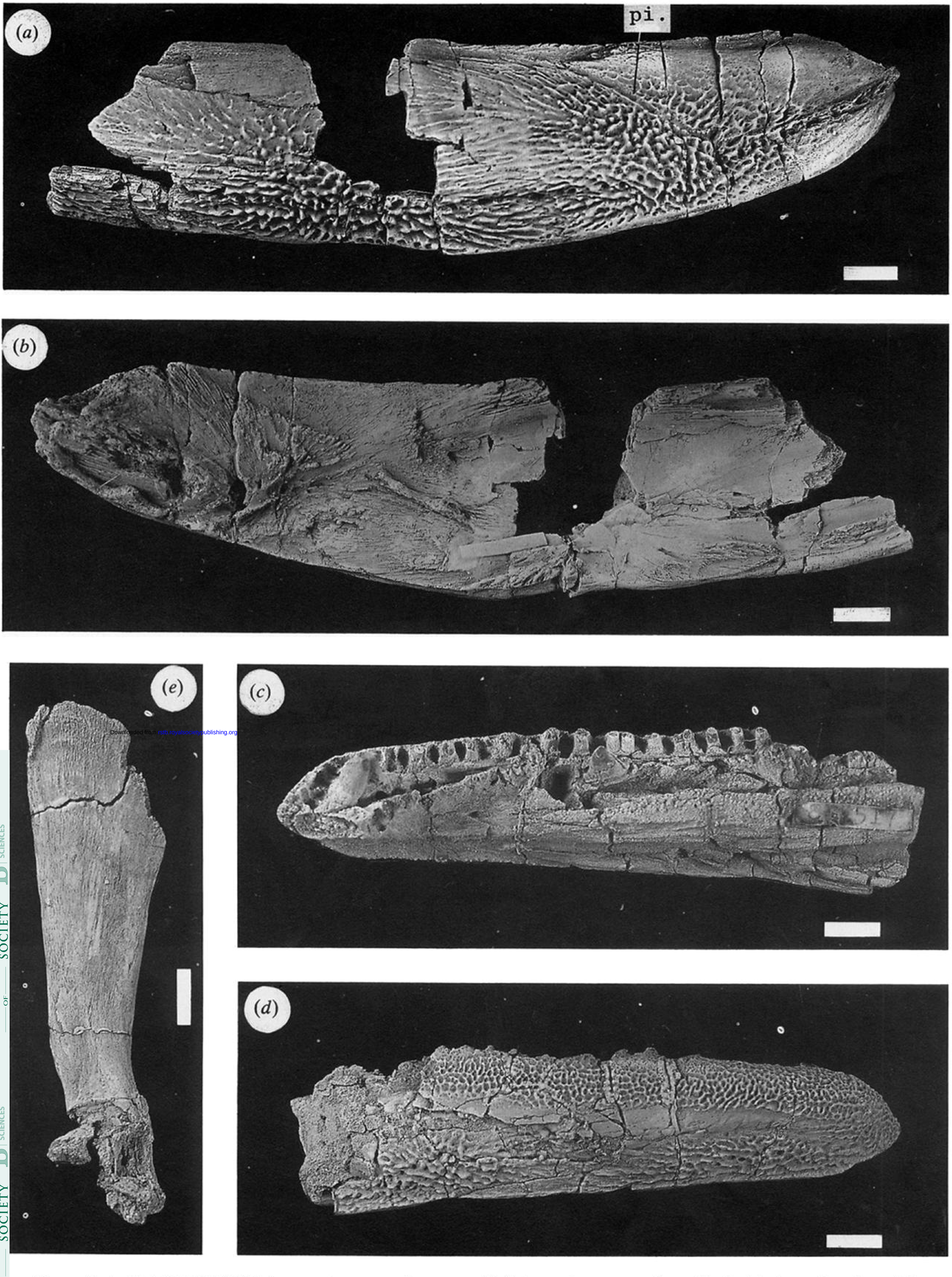
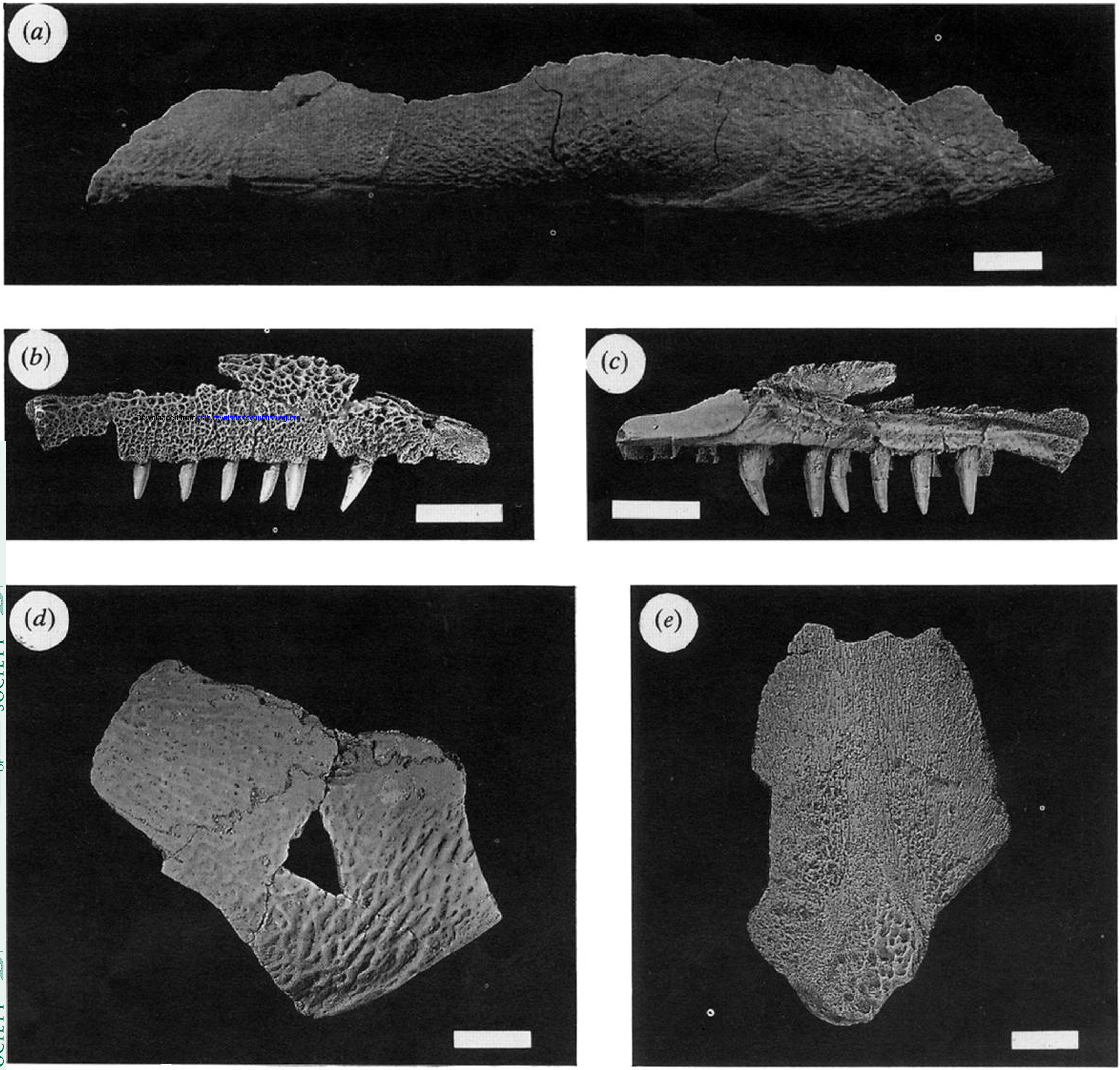


Figure 2. (*a*,*b*) LDM 57/2600, incomplete posterior part of left lower jaw ramus from Ketleri in lateral and mesial views, attributed to *Ventastega curonica*. In (*a*), note the surangular pit line (pi.). (*c*,*d*) LDM 81/517, anterior part of right lower jaw ramus of *Ventastega curonica* from Pavāri, in mesial and lateral views. (*e*) LDM 81/522, left ilium from Pavāri in mesial view, attributed to *Ventastega curonica*; same specimen as figure 13. All scale bars 10 mm.



gure 3. (*a*) LDM 81/550, incomplete left cheekplate of *Ventastega curonica* from Ketleri in lateral view; same
pecimen as figure 7. (*b*,*c*) PIN 54/180, anterior part of right maxilla of *Ventastega curonica* from Ketleri in lateral and
esial view. (*d*) PIN 1491/92, incomplete left suspensorium from Ketleri, attributed to *Ventastega curonica*, in lateral
ew; same specimen as figure 8*a*,*b*. (*e*) LDM 57/1978, anterior part of interclavicle from Ketleri in ventral view,
tributed to *Ventastega curonica*; same specimen as figure 12*e*. All scale bars 10 mm.

Note added in proof (10 January 1994): A nearly complete tetrapod interclavicle, LDM 81/557, was recently discovered in an unprepared block from Pavāri. It has not been examined in detail, but seems to differ in shape from LDM 57/1978. The figure below shows a ventral view. Scale bar, 10 mm.