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The brachyopoid *Hadrokkosaurus bradyi* from the early Middle Triassic of Arizona, and a phylogenetic analysis of lower jaw characters in temnospondyl amphibians

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The holotype of the brachyopoid temnospondyl *Hadrokkosaurus bradyi*, represented by a right lower jaw ramus, is re-examined based upon new data and revision of various morphological features. Additional fragmentary jaw material referred to this species is briefly described. Prominent features are a large postsymphyseal foramen that is anteriorly open, and prearticular and surangular buttresses for support of the articular. Brachyopoid characters include a long and robust postglenoid area formed by surangular and prearticular, anterior and posterior keels on at least some marginal dentary teeth, and subtriangular outline of the adductor fossa in dorsal view. Five features of the holotype ramus, long thought to be at odds with its brachyopoid or temnospondyl nature, are critically re-evaluated. A phylogenetic analysis of lower jaw characters in temnospondyls retrieves most of the clades found in more comprehensive data sets, but the statistical node support is low. Brachyopoids are monophyletic, with *Hadrokkosaurus* emerging as their most basal taxon.

Key words: Temnospondyli, Brachyopidae, Chigutisauridae, lower jaw, phylogeny, characters, evolution.

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Introduction

Lower jaws provide much potential in phylogenetic analyses of early tetrapods, given their complexity and variation (e.g., Nilsson 1943, 1944; Ahlberg and Clack 1998; Bolt and Lombard 2001, 2006; Clack and Ahlberg 2004; Lombard and Bolt 2006). However, this potential remains largely unexplored due to the fact that only very few jaws—particularly those of Devonian and some Lower Carboniferous stem tetrapods—have been studied within a phylogenetic context (see Ahlberg and Clack 1998, Ruta et al. 2001, and Clack and Ahlberg 2004). Recent works have elucidated the pattern of character acquisition and transformation in the jaws of various Palaeozoic groups (see Bolt and Lombard 2001 on colosteids, Lombard and Bolt 2006 on whatcheeriids, and Clack and Ahlberg 2004, Bolt and Lombard 2006 on some tetrapods of uncertain affinities). However, there is no comparable level of phylogenetic scrutiny for the jaws of other groups, notably temnospondyls, which are the most species-rich of early tetrapods.

We have recently initiated a detailed survey of temnospondyl jaws. Species represented by abundant and well-preserved material (the Lower Permian *Trimerorhachis* from North America is a well-known example; Ruta and Bolt, work in progress) exhibit a remarkable amount of variation both in overall jaw morphology and in details of its constituent bones. In the present paper, we both test the utility of lower jaw data in phylogenetic studies of early tetrapods and employ a preliminary data matrix of mandibular characters to evaluate the interrelationships of *Hadrokkosaurus bradyi* (Welles, 1947), a controversial tetrapod from the early Anisian of Arizona.

Hadrokkosaurus is based mainly upon an almost complete right lower jaw ramus (Welles and Estes 1969), generally (although not universally) thought to belong to a brachyopoid temnospondyl. Further mechanical preparation and cleaning of the ramus and examination of undescribed lower jaw fragments attributed to *Hadrokkosaurus*, have produced additional information. Redescription of *Hadrokkosaurus* is thus appropriate and made necessary by the fact that the temnospondyl nature of the holotype ramus has sometimes been questioned (see historical account), based upon characters purportedly indicating amniote affinities (Jupp and Warren 1986).

Brachyopoids (Early Triassic to late Early Cretaceous) have been recorded almost exclusively from Gondwana. They are characterised by broad and spade-like skulls with relatively small, widely spaced, and anteriorly positioned orbits, strongly vaulted palates bearing massive fangs, and markedly elongate postglenoid areas in the lower jaw (Watson 1956; Warren 1981; Warren and Hutchinson 1983; Dong 1985; Jupp and Warren 1986; Shishkin 1991; Sengupta 1995; Damiani and Warren 1996; Warren et al. 1997; Warren and Marsicano 1998, 2000; Marsicano 1999, 2005; Damiani and Jeannot 2002; Damiani and Kitching 2003). They consist of two families, Brachyopidae and Chigutisauridae, and a handful of species placed as immediate sister groups to these families (Warren and Marsicano 2000; Damiani and Kitching 2003). Yates and Warren (2000) assigned brachyopoids to Stereospondyli, the most diverse of all temnospondyls. According to other workers, brachyopids and chigutisaurids are not closely related, but rather members of different temnospondyl groups. Thus, Milner (1990) placed brachyopids within Dvinosauria, whilst Schoch and Milner (2000) and Yates and Warren (2000) presented two conflicting positions of chigutisaurids within stereospondyls.

Historical background

Welles (1947) described the lower jaw ramus currently referred to as *Hadrokkosaurus bradyi* under the binomen *Taphrognathus bradyi*. However, as the genus name was preoccupied by a conodont (Branson and Mehl 1941), Welles (1957) introduced his new genus *Hadrokkosaurus*. Over a decade later, Welles and Estes (1969) described additional material attributed to *Hadrokkosaurus*, in particular a very large, almost complete skull. In the same paper, they also reproduced Welles' (1947) account of the holotype. However, it was not until 1986 that the taxonomic equivalence of the skull and ramus was questioned. Thus, Jupp and Warren (1986) noted that the skull shows relatively smaller teeth than the jaw, despite being about 50% larger. Also, the skull and jaw were retrieved from two different localities, more than 160 km apart (see Warren and Marsicano 2000). Jupp and Warren (1986) discussed five features of the holotype ramus that, in their opinion, would either preclude its assignment to Brachyopidae or exclude it from temnospondyls. Those features will be re-examined critically following the descriptive account below. Schoch and Milner (2000) hypothesized that the holotype ramus belongs to a primitive archosaur, specifically a proterosuchian. Warren and Marsicano (2000) assigned the skull described by Welles and Estes (1969) to a separate brachyopoid taxon, *Vigilius wellesi*, and regarded the jaw ramus as Brachyopoidea incertae sedis. More recently, Damiani and Kitching (2003) placed *Hadrokkosaurus* among Brachyopidae proper, but did not discuss its phylogenetic position. In the same paper, *Vigilius* formed the sister taxon to their new South African Lower Triassic brachyopid *Vanastega plurimidens*.

Institutional abbreviations.—NSM, Nova Scotia Museum, Halifax, Canada; QM, Queensland Museum, Brisbane, Australia; UCMP, University of California Museum of Paleontology, Berkeley, USA.

Other abbreviations.—adf, adductor fossa; adpr, adductor process; aMeckfen, anterior Meckelian fenestra; ANG, angular; CO1, anterior coronoid; CO2, middle coronoid; CO3, posterior coronoid; CO3t, posterior coronoid teeth; DEN, dentary; DENfang, dentary fang; PEA, prearticular; PEAbut, prearticular buttress for articular support; PGA, postglenoid area; pMeckfen, posterior Meckelian fenestra; psymfor, postsymphyseal foramen; PTS, postsplenial; SPL, splenial; SUR, surangular; SURbut, surangular buttress for articular support.

Methods

The holotype was prepared mechanically under a binocular microscope using a Microjack #2/4 ® tool. Given the fragile nature of some structures (particularly marginal dentary teeth), a mount of ethafoam was built. Cyanoacrylate glue was used in places (e.g., on dentary tooth crowns; inside various cracks in the body of the jaw). In the posterior portion of the prearticular, epoxy was applied for support.

Systematic palaeontology

Amphibia Linnaeus, 1758

Temnospondyli Zittel, 1888

Brachyopoidea Lydekker, 1885

Genus *Hadrokkosaurus* Welles, 1957

Type species: *Hadrokkosaurus bradyi* (Welles, 1947), only known species.

Hadrokkosaurus bradyi (Welles, 1947)

Figs. 1–3, 4A, 5B–D.

1947 *Taphrognathus bradyi*; Welles 1947: 246, figs. 3–6.
1957 *Hadrokkosaurus*; Welles 1957: 982.
1969 *Hadrokkosaurus bradyi* (Welles), 1957; Welles and Estes 1969: 41, fig. 20.
1986 *Hadrokkosaurus bradyi*; Jupp and Warren 1986: 118, fig. 11.
2000 *Hadrokkosaurus bradyi* (Welles, 1947) Welles, 1957; Schoch and Milner 2000: 169.
2000 *Hadrokkosaurus bradyi* (Welles, 1947); Warren and Marsicano 2000: 472.
2002 *Hadrokkosaurus bradyi* Welles and Estes 1969; Damiani and Jeannot 2002: 66.
2003 *Hadrokkosaurus bradyi*; Damiani and Kitching 2003: 72.

Holotype: UCMP 36199, an almost complete right lower jaw ramus.

Type locality: V3922, Geronimo (Holbrook) fossil vertebrate quarry near Holbrook, Coconino County, northeastern Arizona. Welles and Estes (1969) provided coordinates both for the type locality and for a second locality that produced a nearly complete skull (*Vigilius wellesi*; see Warren and Marsicano 2000 and data in Lucas 1993). Accounts of Holbrook Member vertebrates can be found in Welles (1947), Morales (1987), Hunt (1993), Hunt et al. (1998), Cuny et al. (1999), Lucas and Schoch (2002), and Nesbitt (2003), among others.

Type horizon: Uppermost channel sandstone of Holbrook Member, Moenkopi Formation; early Anisian, lowermost Middle Triassic.

Referred material.—UCMP 36200, anterior extremity of right dentary; UCMP 36201, partial right dentary; UCMP 36202-3, partial left dentaries; UCMP 36205, partial left prearticular;

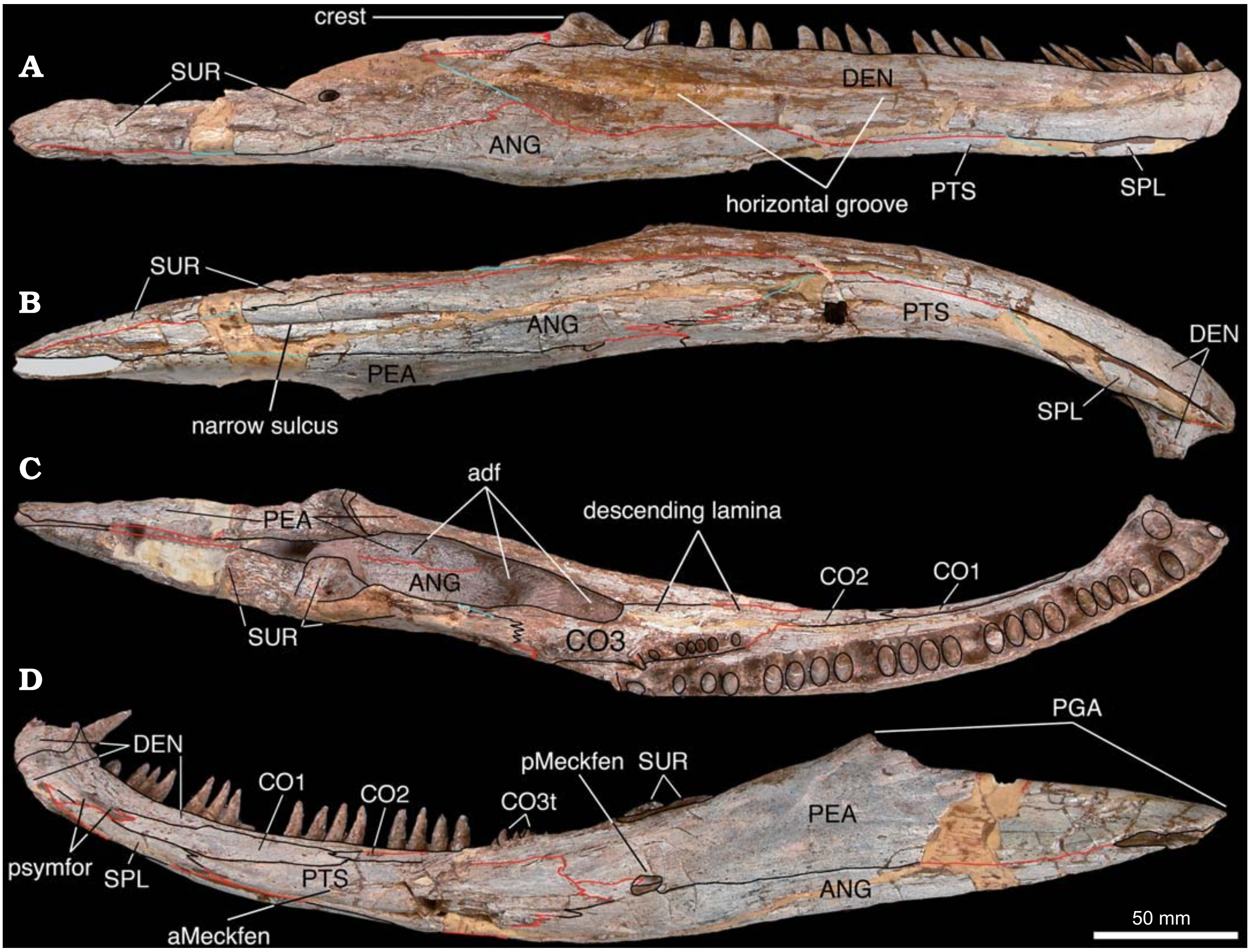

Fig. 1. Temnospondyl amphibian *Hadrokkosaurus bradyi* (Welles, 1947), holotype (UCMP 36199), early Anisian, northeastern Arizona. Right lower jaw ramus in lateral (**A**), ventral (**B**), dorsal (**C**), and slightly mesioventral (**D**) views. See text for explanation of colour-coded sutures.

UCMP 36210, right angular (may not be *Hadrokkosaurus*; see also below); UCMP 36833, approximately anterior one-third of right lower jaw ramus missing tip of symphysial area; UCMP 36834, approximately anterior three-quarters of right dentary; UCMP 36835, partial right dentary; UCMP 36836, UCMP 36838, partial left prearticulars; UCMP 36839, ?right surangular (catalogued as left prearticular; uncertain identity); UCMP 75434, anterior extremity of left dentary (may not be *Hadrokkosaurus*); UCMP 152390-1, fragmentary right and left dentaries (although UCMP 152391 may not be *Hadrokkosaurus*).

Revised diagnosis.—Autapomorphies: in lateral view, total length of angular ventral margin greater than, or nearly equal to, half of total jaw length; greatest depth of angular lateral surface situated in the anterior one-third of bone; in lateral view, angular posteriormost margin straight; greatest depth of angular lateral surface equal to, or less than, greatest depth of dentary lateral surface; ventral margin of posterior Meckelian fenestra formed only by angular; anterior Meckelian fenestra in middle one-third of postsplenial mesial lamina; dorsal surface of coronoid 3 posterodorsal process with subrectangular blunt-topped (in lateral view) crest.

Synapomorphies with other brachyopoids: greatest depth of angular lateral surface smaller than, or equal to, greatest depth of surangular lateral surface; surangular lateral surface occupying more than 40% of total projected jaw length; in lateral view, rearmost portion of surangular dorsal margin ventral to posterior end of dentary postdental process; foramen for chorda tympani indiscernible; anterior and posterior keels on marginal dentary teeth; adductor fossa outline tapering anteriorly and subtriangular in dorsal view; posterior triangular projection of articular wedged between surangular and prearticular on dorsal surface of postglenoid area.

Plesiomorphies relative to other brachyopoids: in lateral view, angular ventral margin smoothly curved; greatest depth of angular mesial lamina greater than one-third of greatest depth of adjacent prearticular surface; angular-surangular suture interdigitating; posterior Meckelian foramen subcircular or elliptical; anterior Meckelian foramen on postsplenial mesial lamina; adductor fossa length smaller than, or equal to, two-thirds of jaw ramus length anterior to fossa; glenoid surface of articular not forming deep notch along prearticular dorsal margin; combined length of coronoids 1 and 2 greater than coronoid 3 length.

Remarks.—The list of characters above is based upon accelerated transformations of state changes (ACCTRAN) in PAUP* (see cladistic analysis).

Orientation and measurements.—A convenient way of providing a standard orientation is to allow the flared, anteriormost region of the dentary to face dorsally. When the jaw is observed in dorsal view (i.e., in occlusal aspect), a horizontal line parallel to the nearly straight lateral surface of the posterior half of the ramus marks the direction of its greatest elongation. "Labial" or "lateral" (interchangeable) refer to structures oriented towards, or pertaining to, the external jaw surface. "Lingual" or "mesial" (once again interchangeable) refer to structures oriented towards, or pertaining to, the internal jaw surface. For the adductor fossa, "labial" and "lingual" refer, respectively, to external and internal surfaces in the fossa.

Four views of the ramus are shown (Fig. 1) with superimposed tracings of sutures. These are colour-coded as follows: black indicates exact course; red indicates uncertainty in tracing the exact course but with circumstantial evidence for suggested paths (e.g., parts of a suture are visible on the two sides of a plaster filling); blue indicates extrapolation of the course, i.e., our best guess.

General features.—We highlight characters that indicate temnospondyl (in particular, brachyopoid) affinities for UCMP 36199, as well as features that distinguish it from other brachyopoids. The ramus is rather gracile despite its large size (Fig. 1A), slightly compressed labiolingually, especially anterior to the level of coronoid 3 (Fig. 1B–D), and with a large symphysis (Fig. 2) and robust postglenoid area (PGA hereafter; synonymous with retroarticular process; Fig. 3A). The PGA, slightly shorter than the adductor fossa, resembles an isosceles triangle in outline in dorsal view (Warren 1981; Warren and Hutchinson 1983; Damiani and Warren 1996; Warren et al. 1997; Damiani and Jeannot 2002; Damiani and Kitching 2003). The jaw shows a distinct change in the curvature of its lateral surface occlusally.

A conspicuous and elongate postsymphyseal foramen (Figs. 1D, 2) is visible on the lingual surface, posterior to the symphysis. The clearly defined posterior margin of the foramen forms a dorsoventrally narrow notch excavated in the anterior part of coronoid 1, and aligned transversely with the base of the 10th dentary tooth position. Anterior to the latter, the foramen is narrow, almost parallel-sided, bounded dorsally by the dentary and ventrally by the splenial. Its dorsal margin appears intact; its ventral margin is somewhat damaged anteriorly. It is uncertain whether this damage greatly altered the outline of the foramen. We point out, however, that the dorsal margin shows no sign that the foramen was originally closed anteriorly. We conclude that the foramen retains its original relationships in being broadly open anteriorly and confluent with the Meckelian canal immediately posterior to the symphysis. The canal is filled with matrix posteriorly and up to the level of the 6th dentary tooth position. Anterior to this, the splenial forms the floor and the ventral portion of the lateral wall of the canal up to about the level of the dentary fang. Anterior to the fang, the tip of the splenial is broken, and obscured by a small patch of plaster. Also anterior to this level, the horizontal shelf of the dentary broadens markedly toward the symphysis, producing a nearly horizontal and strongly vaulted "ceiling" in the anteriormost portion of the Meckelian canal immediately ventral to the symphysis.

The elongate adductor fossa (Fig. 1C) has a roughly triangular outline in dorsal aspect, and narrows rapidly anteriorly. Most of its lingual and labial walls, and a considerable part of its floor, have been exposed further. The floor is covered in fine, closely spaced, straight longitudinal striations. We are not aware of published descriptions of similar striations in the lower jaws of other brachyopoids or, indeed, of any other temnospondyl species. There is no trace of an adductor process on the floor of the fossa, such as is observed in some temnospondyls (e.g., *Aphaneramma*, Nilsson 1943; *Dvinosaurus*, Shishkin 1973; *Archegosaurus*, Gubin 1997; it is also observed in *Acroplous* and *Trimerorhachis*: Bolt and Ruta, work in progress). A cast of QM F14493, a brachyopid lower jaw from the Lower Triassic of Australia (Damiani and Warren 1996) also fails to reveal an adductor process in the exposed portion of the fossa.

Sutures.—Most sutures are traceable (Fig. 1). Strongly interdigitating patterns are not unexpected, given the large size of UCMP 36199 (e.g., at the junction between coronoids 1 and 2, coronoid 3 and surangular, postsplenial and angular, and prearticular and postsplenial). An almost linear sutural junction is seen between prearticular and surangular on the dorsal side of the PGA. We note the slight separation between angular and prearticular on the rearmost one-third of its ventral side (Fig. 3).

Description of individual bones.—The deep and robust dentary compares well in proportions to the dentaries of other brachyopoids. It differs from the latter in that it does not show a wide horizontal shelf mesial to the tooth row and in the fact that its mesial surface, immediately dorsal to the anterior half of coronoid 1, is subvertical. At the level of, and

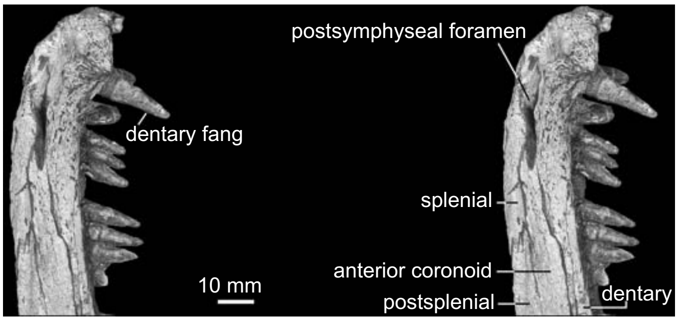

Fig. 2. Temnospondyl amphibian *Hadrokkosaurus bradyi* (Welles, 1947), holotype (UCMP 36199), early Anisian, northeastern Arizona. Stereopair of anterior part of lower jaw in mesial view; note large postsymphyseal foramen.

anterior to the 6th or 7th anterior dentary tooth, the bone widens considerably. This condition, observed in most other brachyopoids and in other temnospondyls, is associated with the presence of a pair of robust fangs (or a fang plus replacement pit) set off mesially relative to the marginal tooth row. As in *Vanastega*, the dorsal margin of the symphysis is shallowly concave in occlusal view. This concavity corresponds to a small subcentral depression on the symphysis. The symphysial surface is almost entirely dorsal to the anteriorly open Meckelian canal, displays an intact border on all sides, and appears to be formed entirely by the dentary.

The lateral surface of the angular is proportionally lower than that of other brachyopoids. However, as in other brachyopoids, it forms a dorsoventrally narrow lamina on the mesial surface of the jaw (the depth of the lamina appears conspicuous in Fig. 1D because the jaw is shown in ventromedial aspect). Laterally, the bone forms a long, narrow strip that contributes to the ventralmost portion of the lateral surface of the PGA and can be traced almost to the level of the rearmost extremity of the latter (Figs. 1A, B, 3B). The angular borders a rather small posterior Meckelian fenestra framed dorsally by the prearticular and with no contribution from the postsplenial, as in basal archegosauriforms but unlike in higher stereospondyls (Schoch and Milner 2000).

The surangular dominates the lateral aspect of the PGA and clasps the broadly wedge-like postdental process of the dentary, dorsal to which a strap-like portion of surangular contacts coronoid 3 (Fig. 1A, C). The surangular is slightly more robust and elongate than in other brachyopoids, proportionally less deep and with a shallower, sigmoid dorsal profile in lateral aspect.

A noteworthy feature is the presence of a lamella projecting from the internal (lingual) surface of the surangular at the posterolabial corner of the adductor fossa (Figs. 1C, 3A). This lamella was noted by Welles (1947: 250), who described it as "… a process from the surangular that curves lingually to meet the prearticular", which in fact it does not do. In dorsal view (Fig. 3A), the lamella arises from the surangular in a smooth curve, widens gradually from ventral to dorsal, and shows free mesial and dorsal edges. It stands at approximately 90° to the lingual wall of the adductor fossa, and at its broadest (dorsal) extremity, it spans about two-thirds of the distance from the lingual to the labial wall. Its free dorsal edge is oriented roughly horizontally. The lamella slopes rearward from bottom to top at about 45° from the horizontal. Its anterior surface is flat to slightly concave anteriorly, whilst its posterior surface is apparently free along its mesial one-half (however, details are obscured by matrix).

Laterally, the other one-half of the posterior surface of the lamella is free only along its dorsal three to four millimetres. Ventral to that, it slopes down quickly into a markedly broadened area of the dorsal border of the surangular, with which it is apparently continuous. Considering that there appears to be a certain amount of distortion in this region of the jaw, and given the unusual appearance of this region, it might be thought that this flat-topped area is mainly due to crushing. However, this is most unlikely, because the adjoining area of the prearticular shows a similar condition, which is confirmed as original by several separated, partial but undistorted prearticulars as described below. Even though no separated surangulars are known, there is no reason to doubt that this flattened region is natural. We propose that these broad, flat portions of surangular and prearticular supported the articular, and will refer to them, in both the surangular and the prearticular, as the "articular buttresses".

The surangular articular buttress in the holotype is approximately two centimetres wide as preserved and with roughly parallel sides. Its width may have been accentuated by crushing, but this is uncertain. As preserved, it is 25 mm long, as measured from its junction with the flat-topped surangular dorsal margin. Posteriorly, it ends against a lump of mixed plaster and matrix, left in place to provide support for the PGA. We could not find a description of a similarly positioned transverse lamella in the lower jaws of other brachyopoids, as the area occupied by the lamella is either disrupted or covered by the articular. In *Siderops*, "… in front of the articular, on the labial side of the mandible, the surangular is expanded to form a wide shelf beside the adductor fossa." (Warren et al. 1997: 24). However, the shelf of *Siderops* is certainly not homologous with the lamella of *Hadrokkosaurus*, in which it detaches lingually from the surangular and projects into the fossa. Similarly, we are not aware of descriptions of a surangular articular buttress in any other temnospondyl.

Thus, *Hadrokkosaurus* provides unique insights into the pattern of insertion of the articular between surangular and prearticular. In numerous brachyopoids, the portion of articular that lies posterior to the glenoid surface is a narrow triangular splinter tightly wedged between prearticular and surangular on the dorsal surface of the PGA (Warren 1981; Jupp and Warren 1996; Damiani and Kitching 2003). The presence of such a configuration in *Hadrokkosaurus* is uncertain, because the articular is missing along with much of the anterior dorsal surface of the PGA. About 35 mm of this surface are preserved on the posterior extremity of the PGA. Here, a narrow gap between surangular and prearticular may represent an original condition; if correct, it would indicate a long posterior extension of the articular. Whether or not this is the case, the prearticular-surangular gap or suture runs to the posterior end of the PGA with a moderately oblique course. As a result, the rearmost part of the dorsal surface of the PGA is formed by unequal contributions from surangular (smaller) and prearticular (greater) (Fig. 3).

Splenial and postsplenial, partially preserved in lateral view (Fig. 1A), appear almost undisrupted in mesial view (Fig. 1D). The splenial compares well with those of other brachyopoids particularly in its degree of anteroposterior shortening. The anterior end of the splenial is broken, but it appears that little bone was lost. In its anteriormost part, the splenial is thin and we think it unlikely that it contributed to the symphysis (other specimens are not informative in this respect, because the holotype is much better preserved in this area). The bone borders the postsymphyseal foramen ventrally and floors the anterior part of the Meckelian canal. Its anterior border is also damaged from its anterodorsal extremity to the border of the postsymphyseal foramen. Here, too, loss of bone has been slight. The postsplenial is quite extensive compared to that of other brachyopoids and dominates almost two-thirds of the anterior half of the mesial surface of the jaw. A tiny foramen, tentatively identified as a reduced anterior Meckelian fenestra, occurs near the center of the mesial lamina of the postsplenial; it may represent a foramen for the arteria mylohyoidea anterior (e.g., Witzmann 2006).

Hadrokkosaurus displays a pronounced twist in the orientation of the three coronoids, relative to the axis of greater elongation, on the mesial side of the jaw. The coronoid series sweeps from anteromesial (coronoid 1) to more distinctly dorsal (coronoid 3). Coronoid 1 is remarkably elongate, unlike in other brachyopoids in which it is considerably foreshortened. A row of robust teeth on coronoid 3 (coronoids 1 and 2 are smooth) is shared with *Vanastega*, although the coronoid 3 dentition in the latter is less well preserved than that of *Hadrokkosaurus* (*Vanastega* shows five eroded teeth sitting on a ridge of bone), and the teeth are proportionally smaller. A robust posterodorsal process extends for half of the length of the adductor fossa from the tooth-bearing region of coronoid 3. This region is set off at a sharp angle from a narrow, ventrally descending lamina of coronoid 3 on the mesial surface of the jaw, situated anteroventral to the adductor fossa (Fig. 1C, D). Unlike in other brachyopoids, the process is more clearly delimited from the tooth-bearing region. An elongate, mesiolaterally compressed crest with a blunt-topped subtrapezoidal profile is visible in lateral view (Fig. 1A) in the anterior two-thirds of the posterodorsal process. A similar crest occurs in the unnamed brachyopid described by Damiani and Warren (1996). In other brachyopoids, the crest is rounded and merges smoothly into coronoid 3.

The prearticular has a tall dorsal process, visible immediately anterior to the glenoid region. The tip of this process is slightly curled over toward the adductor fossa. As a result, it delimits a short, shallow trough oriented anteroposteriorly in the lateral surface of the prearticular. The articular buttress begins near the anteroposterior level of the tip of the dorsal process and forms the floor of the trough. Posterior to its origin, the buttress widens rapidly, and reaches its greatest width at the posterior extremity of the dorsal process. The articular buttress in the *Hadrokkosaurus* holotype is clearly broken posteriorly, and its surface preserves no clear indication of its precise relationship to the articular. However, three other partial prearticulars of *Hadrokkosaurus* from the type locality preserve some indication of the articular-prearticular contact: UCMP 36838 (left), UCMP 36836 (left), and UCMP 36205 (right). The latter was also figured by Welles (1947: fig. 6) and, together with UCMP 36836, illustrates the best preserved contact area for the articular (Fig. 4A). In both specimens, this contact area is flat dorsally, and distinctly set off from the surrounding bone surface. Beginning at the base of the dorsal process as well as slightly posterior to it, the contact area is an elongate triangle, showing a straight medial border coinciding with the medial border of the buttress and a lateral border gradually converging on the medial border of the buttress.

UCMP 36205 preserves much of the prearticular contribution to the PGA and shows that, especially posterior to the articular buttress, the prearticular formed the mesial wall of the large, thin-walled canal within the PGA. Part of its dorsolateral border occurs posterior to the articular buttress, at about mid-length of the PGA. At this level, it is thin and rounded and has a few faint striations but no other sutural morphology. The holotype jaw shows that, at least in the posterior one-third of the PGA, prearticular and surangular are separated by a narrow matrix-filled gap in dorsal view (Fig. 3A). Thus, they may or may not have had a dorsal contact; if they did contact one another, then, aside from the straight dorsal surface expression of this possible suture, there is no additional information on its shape.

The unusual morphology of the PGA in *Hadrokkosaursaurus* makes it possible and useful to discuss the relationships of the articular, even though the bone itself is not preserved in the holotype and cannot be recognized among the separated bones. First, the glenoid presumably lay directly above the articular buttresses, the presence of which suggests large forces acting on the articular. Second, despite obvious distortion of the holotype, there was certainly a gap between the articular buttresses of both prearticular and surangular. This is demonstrated by the position of the transverse lamella on the surangular, which would require such a gap even if the lamella were restored as being in contact with the lateral surface of the prearticular within the adductor fossa. Thus, it appears that the articular occupied this gap in life, and might have extended some unknown distance posteriorly within the PGA. This conclusion is not entirely conjectural: it has long been known (Jupp and Warren 1986) that in some brachyopoids, the articular separates the prearticular from the surangular throughout the depth of the PGA, and extends nearly to the posterior end of the latter. The ventral gap between the angular and the prearticular (Fig. 3B) might well have left a narrow portion of the articular exposed along the PGA, as might the narrow dorsal gap between surangular and prearticular, as described above.

We thus suggest that the articular of *Hadrokkosaurus* was strongly integrated with the dermal bones of the jaw, as in other brachyopoids. Its absence in the holotype may thus seem surprising as there is no evidence for severe distortion and the PGA in particular is largely intact. The logical explanation is that the articular might have been largely cartilaginous in the holotype, presumably because it belonged to a small and perhaps somewhat immature individual, as suggested by comparisons with other specimens. This explanation is plausible, as the articular usually ossifies at a late stage in temnospondyl ontogeny (e.g., *Cheliderpeton*: Boy 1993; *Sclerocephalus*: Schoch 2003). As for size comparisons, UCMP 36834 is a partial right dentary with most of the symphysis preserved; the greatest width across the symphysis is 36 mm dorsally; the same measurement is 28 mm in

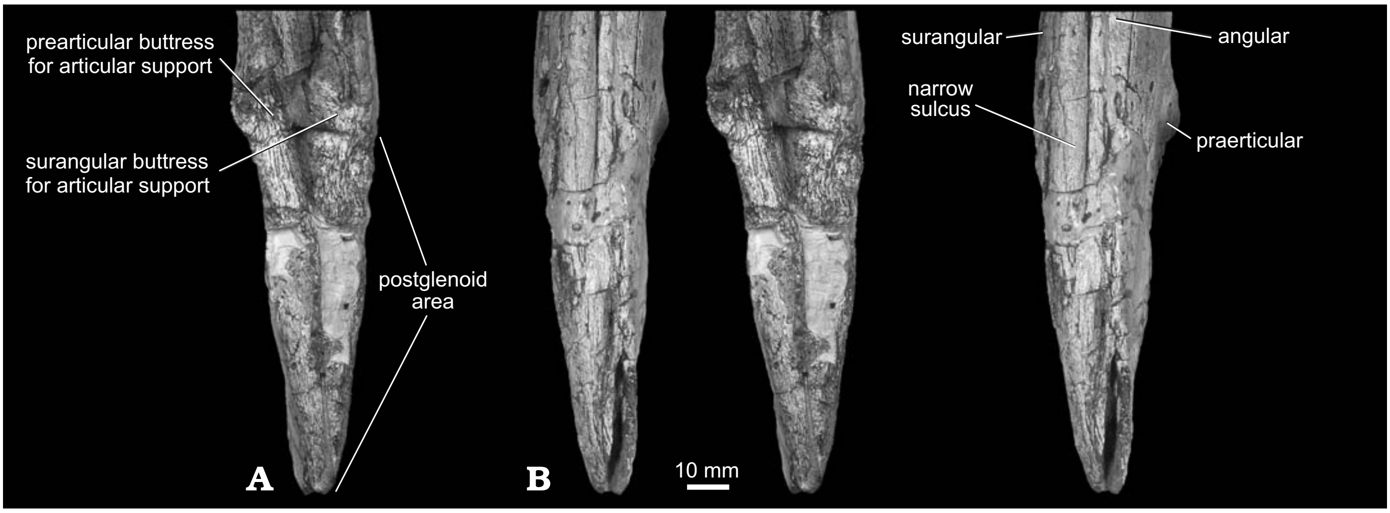

Fig. 3. Temnospondyl amphibian *Hadrokkosaurus bradyi* (Welles, 1947), holotype (UCMP 36199), early Anisian, northeastern Arizona. Stereopairs of the posterior part of the lower jaw in dorsal (**A**) and ventral (**B**) views. Note buttresses for articular (missing) projecting from prearticular and surangular, and proportions of postglenoid area.

the holotype. UCMP 36836 is a left prearticular; the minimum distance from the tip of its dorsal process (broken) to the angular-prearticular suture is 54 mm in lateral view; the same measurement is 43 mm in the holotype.

Loss of the largely cartilaginous articular may have left the PGA susceptible to distortion, the results of which could be misleading. Thus, the proximity of the prearticular to the surangular in the posterior region of the PGA could be secondary. In life, the PGA may have possessed a wider and open suture through which the articular was visible dorsally, as it apparently was ventrally along the posterior part of the prearticular-angular suture. Given that even minor crushing or distortion might have occurred, these suggestions are plausible rather than certain, but the totality of available evidence indicates that *Hadrokkosaurus* had a Type II PGA (Jupp and Warren 1986), with an extensive exposure of articular wedged between prearticular and surangular posterior to the glenoid; the articular might or might not have reached the posterior extremity of the PGA.

Sculpture.—In common with other brachyopids (e.g., *Vanastega*), the dermal sculpture is subdued on all bones of the holotype, and consists of fine and closely spaced ridges and striations in lateral aspect (Fig. 1A). On its mesial surface, the jaw is smooth or finely pitted (Fig. 1D). The sculpture is most pronounced on the lateral surfaces of angular and surangular, but nearly absent on the dentary, where weak longitudinal furrows occur (this pattern is seen frequently in temnospondyls; e.g., *Benthosuchus*: Bystrow 1935; *Archegosaurus*: Witzmann 2006). This appears consistent with the surface appearance of separated bones found in the holotype locality. Most of the material collected with the holotype was found in a channel deposit, and "the bones consist largely of water-worn fragments" (Welles 1947: 242). Some separated jaw bones of *Hadrokkosaurus* (not shown) are severely worn. The only apparent exception to the widespread occurrence of subdued sculpture is seen in UCMP 36210, catalogued as a right angular (Fig. 4B). This does indeed appear to be a temnospondyl infradentary but is fairly heavily sculptured. From available evidence, we cannot confirm whether it is an angular or even if it pertains to *Hadrokkosaurus*. Of more immediate interest is the fact that its inner surface has a stout protuberance that could indeed represent an adductor process (consistent with the interpretation of the specimen as an angular); as noted above, this process is absent in the holotype. The latter is not heavily water-worn, and we conclude that its subdued sculpture is mostly or entirely original.

Lateral line system.—A straight narrow sulcus ("longitudinal inflection"; Welles 1947: 250) runs on the ventral surface of the angular, opposite the posterior portion of the adductor fossa (Figs. 1B, 3B). It appears to have a V-shaped profile in cross section, rather than the broadly rounded profile typical of lateral line sulci, although its position corresponds, in part, to that of the mandibular lateral line sulcus (the broadly rounded condition may be derived relative to the narrow condition of numerous primitive tetrapods; Florian Witzmann, personal communication 2008). The sulcus terminates posteriorly in a large area filled with plaster; just posterior to this area, the angular surface is smooth and without any sign of a sulcus. Any possible anterior extension of the sulcus is mostly obscured by additional plaster as well as by broken bone, although the sulcus does not appear to be present near the jaw symphysis.

At the posterior end of the PGA, the angular carries a short and deep sulcus, adjacent to the angular-surangular suture. This sulcus terminates abruptly anteriorly in an area of fragmented bone, anterior to which the angular surface is smooth. The sulcus appears to be floored by bone (instead of opening into the Meckelian canal), but its irregular border and abrupt anterior termination indicate that it is unlikely to be associated with the lateral line system. On the lateral surface of the holotype ramus, much of the posterior area that might have

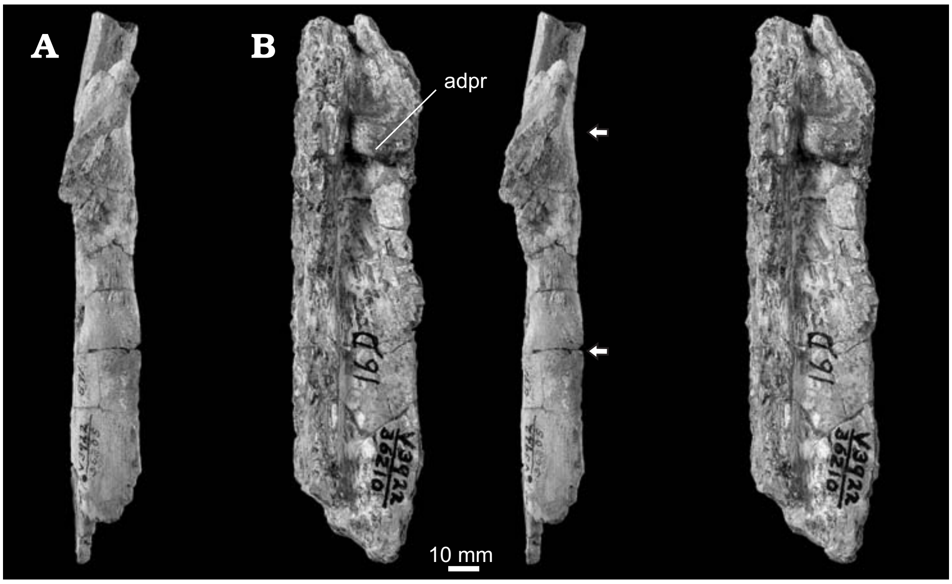

Fig. 4. **A**. Stereopair of UCMP 36205, early Anisian, northeastern Arizona; incomplete prearticular in dorsal view attributed to *Hadrokkosaurus bradyi*; arrows mark position and extent of lateral edge of contact area for articular. **B**. Stereopair of UCMP 36210, early Anisian, northeastern Arizona; broken angular in dorsal view presumably incorrectly attributed to *Hadrokkosaurus bradyi*; note pronounced boss-like adductor process.

been occupied by an oral sulcus is damaged, or heavily reconstructed in plaster. Welles (1947) noted the presence of what he called "a horizontal groove" on the dentary, which widens posteriorly (Fig. 1A). This groove is clearly pronounced in many of the separate dentaries (not shown here). Both its cross-section shape and its great variation in size from anterior to posterior make it unlikely that it represents a lateral line sulcus. We think that there is no evidence for an oral sulcus either; the wide dentary groove may have housed the external mandibular artery (Morales and Shishkin 2002). Damiani and Kitching (2003: 72) note that in *Vanastega plurimidens*, "[a]s in all brachyopids, the oral sulcus is the only sensory canal present on the mandible". However, the sulcus of *Vanastega* is broad and deep anteriorly, as in *Hadrokkosaurus*. The homology of this canal/ groove in all brachyopids is sufficiently clear, but its precise identity is questionable.

Dentition.—Twenty-two dentary teeth are preserved (there are 32 tooth positions). They appear labiolingually compressed in the upper one-third of the crown and curve gently lingually (Figs. 1, 2). The basal portion of the crown is slightly compressed anteroposteriorly. The anterior and posterior margins of the upper one-third of the crown form sharp weakly undulating (but not precisely serrated) edges, seen in a few of the larger teeth from the middle part of the jaw. The tallest teeth are about 2.5 times higher than wide (maximum width near tooth base). The posterodorsolingually oriented dentary fang resembles a larger and more slender version of the marginal dentary teeth and is likewise slightly compressed. The conical teeth on coronoid 3 (10) do not curve lingually. All teeth display faint but traceable striations (labyrinthodont pattern barely discernible in broken crown of 14th dentary tooth) extending for almost the entire height of the crown.

Hypothesized archosaurian features of UCMP 36199.—Jupp and Warren (1986) discussed a number of features of UCMP 36199 that indicate possible archosaurian affinities for this taxon. The presence of three coronoids, a splenial, and a postsplenial (all primitive tetrapod characters) suffice to rule out such affinities. For the sake of completeness, however, the features in question are re-evaluated here.

(1) Foramen between dentary and surangular on labial surface of jaw. *Comment*: Close inspection shows that this "foramen" is a product of damage (Fig. 5D). It is surrounded by plaster along its posterodorsal, posterior, and ventral borders. Anterodorsally and anteriorly, it continues as a depression in the lateral surface of the jaw rather than as a window excavated in the thickness of the bone.

(2) Splenial excluded from symphysis. *Comment*: This condition is known in other temnospondyls (e.g., *Vanastega*: Damiani and Kitching 2003; *Trimerorhachis*: MR and JRB, unpublished data).

(3) Prearticular-surangular suture posterior to glenoid area. *Comment*: This feature is observed in other brachyopoids, and has a wider distribution in temnospondyls. It describes the mutual relations of bones on the dorsal surface of PGA, whereby a narrow portion of the articular posterior to the glenoid surface appears as a triangular splint of bone tightly wedged between prearticular and surangular. Just posterior to the apex of this splint of bone, prearticular and surangular abut against each other, forming a nearly straight suture. Although the articular is not preserved in *Hadrokkosaurus*,, there is a clear indication of the part of dorsal surface of PGA where it was probably wedged between prearticular and surangular.

(4) Protothecodont (= subthecodont) tooth implantation. *Comment*: Welles (1947: 247) characterized the dentary teeth as follows: "The posterior teeth incline inward more than the anterior 6 and are fused to the thin external edge of the dentary, a condition that Broili (1899) described for *Eryops* and termed 'protothecodont'." Welles (1947) also claimed that these posterior teeth "lie in a long groove". But the groove in question is not so visible to us, although the contiguous, large resorption pits noted in places by Welles (1947) bear resemblance to a groove. His description fits Edmund's (1969: 127) definition of protothecodonty: in this kind of implantation, "the base of

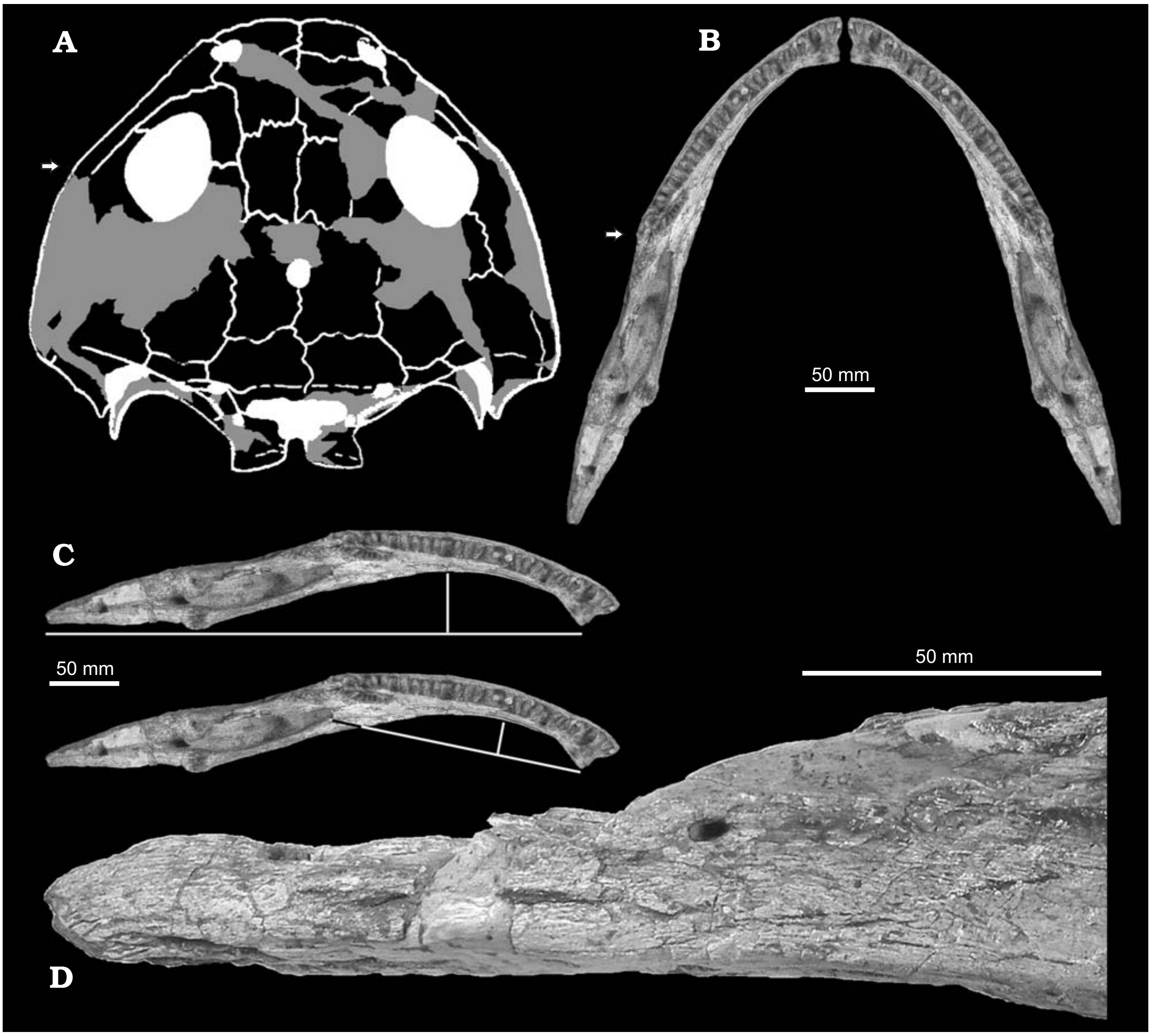

Fig. 5. **A**, **B**. Comparisons between the skull of *Vigilius wellesi* Warren and Marsicano, 2000 (**A**) and the lower jaw of *Hadrokkosaurus bradyi* (Welles, 1947) (**B**) drawn to the same proportions; arrows point to changes in degree of curvature of the skull and jaw (skull modified from Warren and Marsicano 2000). **C**. Right lower jaw ramus of *Hadrokkosaurus bradyi* (Welles, 1947) in dorsal view showing lengths of segments used for calculating the degree of curvature of the ramus (see text for details). **D**. Close-up view of posterior part of UCMP 36199, early Anisian, northeastern Arizona.

each tooth is ankylosed into a more or less deep socket by the deposition of cementum. The sockets themselves are arranged in a row in the dental groove, a depression between a labial and a more lingual wall or ridge. The labial wall is usually higher than the lingual". Note that this and similar definitions rely upon the observations of cementum as well as a dental groove, data which are rarely available in temnospondyls, at least as far as the cementum is concerned. In practice, modalities of tooth attachment in temnospondyls are generally assessed by eye. By that criterion, we entirely agree with Jupp and Warren's (1986) description of tooth attachment in *Hadrokkosaurus*, but by the same criterion, it does not differ from that in various other temnospondyls.

(5) Reduced sculpture. *Comment*: A subdued dermal sculpture of the lateral jaw surface is seen in a few brachyopids (Damiani and Warren 1996; Damiani and Jeannot 2002), though not to the extent found in *Hadrokkosaurus*. We suspect that the sculpture of the latter is genuinely weakly developed (see above).

Comparisons

Revision of UCMP 36199 and rebuttal of its supposed archosaurian features invites a comparison with the lower jaws of other brachyopoids (see also cladistic analysis). The most distinctive trait shared by *Hadrokkosaurus* and all other brachyopoids is the development of a conspicuous PGA. The latter in *Hadrokkosaurus* may have received a more substantial contribution from the prearticular to its dorsal surface (based upon the preserved part of the prearticular-surangular suture). In common with other brachyopids (and unlike in chigutisaurids), a sudden change in the curvature of the lateral surface (best seen in dorsal view) is observed just posterior to the tooth-bearing portion of the dentary. Posterior to this point, the lateral profile of the jaw is almost straight whereas anterior to it, the jaw is smoothly and gently curved. In dorsal aspect, the curvature of the *Hadrokkosaurus* jaw bears a striking resemblance to those of *Bathignathus*, *Vanastega*, and QM F14493. The degree of curvature (measured on a dorsal projection of the ramus as the percentage ratio between the lengths of the shorter and the longer white segments in Fig. 5C) is 12.12%, thus smaller than the values in *Koolasuchus* (12.87%), *Vanastega* (15.4%), *Siderops* (16.82%), and *Compsocerops* (17.4%) but larger than in *Bathignathus* (8.4%) and QM F14493 (11.63%). The degree of curvature thus measured applies to the portion of the ramus anterior to the adductor fossa. We also considered the curvature excluding PGA. Again in a dorsal projection of the ramus, the curvature in *Hadrokkosaurus* (14.41%) is smaller than that of other brachyopoids (e.g., *Bathignathus*: 15.1%; *Vanastega*: 18.42%; QM F14493: 19.02%; *Compsocerops*: 19.54%; *Siderops*: 20.4%; *Koolasuchus*: 20.9%). Mean values of jaw curvature do not differ significantly between brachyopids and chigutisaurids (two-sample Wilcoxon test; $p = 0.6286$ with PGA; $p = 0.8571$ without PGA).

If the *Hadrokkosaurus* jaw is rescaled to match the size of the *Vigilius* skull (i.e., estimated position of the articular glenoid in *Vigilius* situated at the same level as the quadrates in *Hadrokkosaurus*; Fig. 5A, B), then the degrees of curvature of jaw and skull do not coincide. Specifically, the points at which the lateral margins of the skull show a sudden change in curvature are anterior to the point at which the ramus shows an analogous change. This lends partial, but not conclusive, support to the hypothesis that *Hadrokkosaurus* and *Vigilius* are distinct. Although part of the *Vigilius* skull is reconstructed in plaster, there can be no doubt that its profile (particularly its anterior half) is clearly less smoothly rounded than the tooth-bearing part of the *Hadrokkosaurus* jaw.

The postsymphyseal foramen of *Hadrokkosaurus* is similar, in terms of its anteroposterior extension and relationships with surrounding bones, to the narrow elongate foramen in *Bathignathus* (Damiani and Jeannot 2002). Damiani and Jeannot (2002: 66) characterize the foramen as "massive", and note that it is "considerably larger than in all other brachyopid mandibles". They do not describe it further; it is thus uncertain from Damiani and Jeannot (2002: fig. 4) whether it is open anteriorly. It appears to have a narrow opening on the medial side of the symphysis, not the broadly open configuration seen in *Hadrokkosaurus*. The recently described jaw of *Vanastega* (Damiani and Kitching 2003: 72) "shows a well expressed post-symphyseal foramen as in other brachyopid mandibles". The foramen may well be illustrated in ventral view in Damiani and Kitching (2003: fig. 5d) as a sulcus, with its anterior end forming a notch along the ventral margin of the symphysis. If so, it differs from the foramina of the above taxa in showing no contact with coronoid 1. Damiani and Warren's (1996) unnamed jaw shows a small foramen in the same position as is occupied by the much larger foramina in *Bathignathus* and *Hadrokkosaurus*.

As described above, the symphysis is formed only by the dentary (e.g., as in *Vanastega*; Damiani and Kitching 2003), and lies almost entirely dorsal to the open Meckelian canal. Consistent with its limited extent, the symphysis seems to be small relative to jaw size, compared to that of other brachyopids or indeed other temnospondyls, in which the symphysis usually extends some distance down the lateral side of the jaw. The small apparent size of the *Hadrokkosaurus* symphysis, however, applies only to its dentary contribution. In view of its position dorsal to a widely open Meckelian canal, we suggest that much—or perhaps most—of the symphysis was formed by Meckelian cartilage, which thus had a significant structural role.

As in other brachyopoids, the elongate adductor fossa of *Hadrokkosaurus* tapers abruptly anteriorly. In dorsal view, the dorsal margins of both surangular and prearticular and the estimated position of the anterior margin of the articular (not preserved), confer a subtriangular outline to the adductor fossa.

Teeth on coronoid 3 are also seen in *Vanastega* and *Siderops*, whereas *Bathignathus* shows a sharp toothless keel on coronoid 3. *Hadrokkosaurus* is similar to *Bathignathus*, *Siderops*, and *Koolasuchus* in having sharp anterior and posterior keels on at least some marginal dentary teeth. The presence of such keels cannot be confirmed in *Compsocerops*, *Vanastega*, and QM F14493 due to poor preservation.

Cladistic analysis of lower jaw characters

Data from *Hadrokkosaurus* and other temnospondyls forms the basis for a detailed cladistic treatment of lower jaw characters that aims to address two questions. First, are lower jaw data alone sufficient to retrieve clades that are supported by more comprehensive data sets? Second, do lower jaws represent a reliable indicator of phylogeny for early tetrapods?

Taxon sampling.—The taxonomic sample is necessarily limited, at least in the case of temnospondyls. This is for various reasons. First, although several species are known from many specimens, there is a dearth of well-preserved, fully prepared lower jaw material that could be satisfactorily coded. Although we tried to include representative species from as many temnospondyl groups as possible, information on the jaws of various taxa is limited or unavailable. Second, jaw characters are not well-represented in many recent cladistic analyses (e.g., Yates and Warren 2000; Ruta et al. 2003; Ruta and Coates 2007).

Outside temnospondyls, outgroup choice was based upon recent analyses (Ahlberg and Clack 1998; Clack and Ahlberg 2004), with several modifications involving exclusion of taxa which either possess incomplete (e.g., *Elginerpeton*; *Metaxygnathus*; *Obruchevichthys*; *Tulerpeton*) or poorly preserved jaws (*Eoherpeton*; *Proterogyrinus*), or appear to be too derived (*Eocaptorhinus*; *Ophiacodon*; *Sauropleura*). Of the four temnospondyls in Ahlberg and Clack's (1998) analysis, only *Platyrhinops* was excluded, as its lower jaw is incomplete (*Platyrhinops* is currently being redescribed by Jennifer A. Clack and Andrew R. Milner, personal communication to MR, 2006). Relative to Ahlberg and Clack's (1998) analysis, the outgroup sample was augmented by inclusion of eight taxa whereas the number of ingroup taxa (temnospondyls) was increased to 34. All characters were coded from: (i) first-hand observation of specimens (wherever possible); (ii) surveys of published data matrices and descriptive accounts (see Supplementary Online Material at http://app.pan.pl/SOM/app53-Ruta_SOM.pdf).

Parsimony analysis.—The matrix was processed in PAUP* v. 4.0b10 (Swofford 1998) using heuristic search with characters unordered and unweighted (3,000 random stepwise addition sequences followed by tree bisection-reconnection branch-swapping, saving one tree with score greater than or equal to 1 at each replicate; swapping was performed on all trees recovered from this run with the option of multiple tree saving in effect). PAUP* retrieved 38 shortest trees (length = 745 steps; C.I. = 0.216 excluding one uninformative and two constant characters; R.I. = 0.577; R.C. = 0.125). In the strict consensus (Fig. 6), loss of resolution affects those outgroups that occupy a phylogenetically intermediate position between *Crassigyrinus* and stem amniotes. The agreement subtree (a pruned tree which includes the largest set of taxa for which all the shortest trees agree upon relationships; not shown) contains 48 out of 56 taxa; the excluded taxa encompass: *Doragnathus*, *Occidens*, NSM 987GF65.1, *Caerorhachis*, *Diploceraspis*, *Edops*, *Ecolsonia*, and QM F14493. Reweighting characters by their rescaled consistency index results in five trees (C.I. = 0.421; R.I. = 0.734; R.C. = 0.313) (not shown).

Results.—The arrangement of Devonian and Permo-Carboniferous taxa agrees to a large degree with some recent hypotheses of tetrapod phylogeny (e.g., Ruta et al. 2003; Clack and Finney 2005; Ruta and Coates 2007). A sister group relationship between *Sigournea* and *Occidens*, and between *Doragnathus* and *Greererpeton*, is found in 74 and 53% of all shortest trees, respectively. The "reptiliomorph" clade with *Caerorhachis* as its most basal taxon occurs in 89% of the shortest trees. In all trees, microsaurs (*Microbrachis* and *Pantylus*), seymouriamorphs (*Discosauriscus*), anthracosaurs (*Archeria* and *Pholiderpeton*), and gephyrostegids (*Gephyrostegus*) are grouped together.

Excluding the equivocal placements of certain taxa, the interrelationships of representatives of major early tetrapod groups support the hypothesis of a deep phylogenetic split between stem lissamphibians (temnospondyls) and stem amniotes (Ruta and Coates 2007). Several temnospondyl superfamilies and families are supported by jaw data. However, we also have examples of novel groupings (see below).

Lower jaw features and large-scale temnospondyl interrelationships.—In agreement with currently accepted, higher-level temnospondyl phylogenies (Milner 1990), Edopoidea form the basalmost clade, represented by two *Cochleosaurus* species (a third edopoid, *Edops*, is one of three temnospondyl taxa that appear unstable in our analysis). Also, note the basal position of *Balanerpeton*. Of the three taxa in the Dissorophoidea, *Ecolsonia* is unstable (see above), whereas each of the other two taxa, *Phonerpeton* and *Micromelerpeton*, branches near the base of a distinct clade. The next clade consists of members of three groups: (i) a monophyletic Zatracheidae (*Acanthostomatops*; *Zatrachys*) form the sister taxon to a clade including (ii) a paraphyletic basal Archegosauriformes (Schoch and Milner 2000; *Sclerocephalus*, *Archegosaurus*, and *Cheliderpeton*) and (iii) a monophyletic Eryopidae (*Eryops*; *Onchiodon*). The proximity of zatracheids, eryopids, and one dissorophoid (*Phonerpeton*) generally agrees with Milner's (1990) phylogenetic hypothesis. Unlike in Milner's analysis, however, all these taxa occupy a basal instead of a derived position in temnospondyl phylogeny (see Yates and Warren 2000). The present results conflict with both Schoch and Milner's (2000) and Yates and Warren's (2000) placement of basal archegosauriforms as close relatives of Stereospondyli. The latter are represented by most of the remaining species in our analysis, with the exclusion of the dissorophoid *Micromelerpeton*, the basal archegosauriform *Tryphosuchus*, and two dvinosaurs, i.e. *Trimerorhachis* and *Dvinosaurus*). Although our data do not support a monophyletic Dvinosauria, *Trimerorhachis* and *Dvinosaurus* are close to stereospondyls, thus providing partial support for Yates and Warren's (2000) Limnarchia. Except for the position of the basal stereospondyl *Rhineceps*, all remaining stereospondyls form a clade. In the latter, Brachyopoidea (*Hadrokkosaurus*, *Vanastega*, *Bathignathus*, QM F14493, *Compsocerops*, *Koolasuchus*, and *Siderops*) and Trematosauroidea (*Inflectosaurus*, *Dutuitosaurus*, *Benthosuchus*, and *Thoosuchus*) emerge as two monophyletic groups. Finally, we note a polyphyletic Capitosauroidea (*Kupferzellia*, *Mastodonsaurus*, *Parotosuchus*, and *Xenotosuchus*) and a monophyletic Rhytidostea (*Lydekkerina*; *Chomatobatrachus*). Most interesting is the grouping of eryopids (*Eryops*, *Onchiodon*) with stem-stereospondyls (*Sclerocephalus*, *Archegosaurus*, and *Cheliderpeton*). Although eryopids are separate from Stereospondyli *sensu stricto*, this finding agrees, in part, with much current discussion about the position of eryopids. For instance, Witzmann et al. (2007) have found evidence for placing eryopids near the base of the Stereospondylomorpha.

The Brachyopidae (*Hadrokkosaurus*, *Vanastega*, *Bathignathus*, and QM F14493) are paraphyletic relative to Chigutisauridae (*Compsocerops*, *Koolasuchus*, and *Siderops*). Differences in the relative positions of brachyopoids revolve around two topologies: in some trees, QM F14493 and *Bathignathus* are sister taxa; in others, *Bathignathus* is more closely related to chigutisaurids than QM F14493 is. For topological constraint experiments, see Supplementary Online Material at http://app.pan.pl/SOM/app53-Ruta_SOM.pdf.

Fig. 6. Strict consensus of 38 most parsimonious trees with bootstrap percentages based upon 10,000 replicates.

Discussion

The large and strikingly similar postsymphyseal foramina of *Hadrokkosaurus* and *Bathignathus* appear as plausible homologues. A variety of foramina, described under a variety of names, occur posterior to the symphysis on the mesial surface of the jaw in numerous other temnospondyls. For instance, *Eryops* has a single "mental foramen" communicating with a branch of the Meckelian canal (see Sawin 1941). *Mastodonsaurus* may show several "parasymphyseal foramina", but a "larger foramen exactly situated on the suture between dentary and precoronoid is throughout present" (Schoch 1999: 86). Foramina ("postsymphyseal foramina" is their common designation) are frequently overloooked or described in passing. Their phylogenetic significance remains obscure, particularly as a result of variation in many species. Yet the examples above show that they may be sources of useful characters (e.g., see foramen for arteria mylohyoidea anterior on the postsplenial; *Dvinosaurus*: Shishkin 1973; *Eryops*: Sawin 1941; *Sclerocephalus*, *Onchiodon*, *Cheliderpeton*: Boy 1988, 1990, 1993; *Archegosaurus*: Witzmann 2006).

The articular buttresses appear unique to *Hadrokkosaurus*, so far as we can determine; their rarity is, however, more likely due to scarcity of well-preserved jaws and to the common presence of articulars in situ in the jaws studied so far. In any case, the articular-supporting bones deserve more attention than they have received. Here, too, there is an opportunity to find systematically useful characters.

Hadrokkosaurus is one of the stratigraphically youngest brachyopoids, together with the coeval and geographically co-occurring *Vigilius* (Warren and Marsicano 2000; Damiani and Kitching 2003). In the present analysis, however, *Hadrokkosaurus* is basal relative to remaining brachyopoids. This find has a number of implications. Thus, *Hadrokkosaurus* might represent a very late surviving representative of a lineage of brachyopoids that probably originated in the Southern Hemisphere, before dispersing into Laurasia in the Early/Middle Triassic. This scenario, however, necessitates stringent and independent evidence. In particular, unequivocal association of a *Hadrokkosaurus* jaw with cranial material is likely to provide a more reliable guide to the phylogenetic position of this taxon. Also, if a strong case could be made for considering *Hadrokkosaurus* and *Vigilius* as a single taxon, then it would be interesting to re-evaluate the analysis of Damiani and Kitching (2003), to see if jaw and cranial data yield conflicting solutions (*Vigilius* appears as a fairly derived brachyopoid in their study). Thus, the results of our study might ultimately reflect paucity of taxa and the limited power of jaw characters to retrieve patterns of relationship that match those based on more comprehensive sets of characters.

In at least one recent study (Ruta et al. 2003), removal of lower jaw data had little impact on overall tree shape. Another study (Ruta et al. 2001) showed that jaw data can retrieve traditional groups when a sufficient number of characters are included. The cladistic analysis undertaken here highlights both the potential and the limitations of data from morphofunctional complexes. A sufficient degree of character "atomisation" is a necessary prerequisite for the purpose of covering as much variation in the jaw as possible. However, we emphasize the importance of considering these characters in all-encompassing data matrices. We are not able to predict the effectiveness (or otherwise) of data sets based upon single morphofunctional complexes, as any conclusion in this respect must rely upon empirical evidence (i.e., construction of matrices subjected to parsimony analysis). Despite this, we note that lower jaw data, at least for the taxon sample considered in this paper, provide excellent resolution in certain portions of the tree (e.g., stem tetrapods and stem amniotes). In the case of temnospondyls, the resolution offered by jaw characters is good for high taxonomic units (superfamilies), but more limited for interspecific relationships when compared to results generated by more complete matrices. Importantly, we showed that certain anatomical complexes appear to be underexplored. The potential for character discovery in fossil vertebrates is seemingly high, and a thorough treatment of morphological data at all anatomical levels represents a valuable asset for future phylogenetic undertakings.

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