The Age of Dinosaurs in Russia and Mongolia

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Procolophonoids from the Permo-Triassic of Russia

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Introduction

The Procolophonoidea is an important group of early amniotes currently placed in the subclass Parareptilia (Laurin and Reisz, 1995; Lee 1995). The procolophonoids arose in the Late Permian (Tatarian) and survived until the Late Triassic (Rhaetian or latest Norian; Benton, 1993), and during the Triassic formed a large component of many of the complex terrestrial assemblages of the period (Benton, 1983). The more derived Triassic forms had a world-wide distribution, with specimens known from European Russia, Western Europe, North America, South America, South Africa, Madagascar, Australia, China, and Antarctica.

The procolophonoids have been rather difficult to define, owing largely to dispute over the position of the primitive Late Permian genera *Barasaurus* and *Owenetta*. Ivakhnenko (1979), for example, placed both *Barasaurus* and *Owenetta* in the Russian taxon Nyctiphruretidae Efremov, 1938, while, Laurin and Reisz (1991) placed *Owenetta* in the Procolophonidae. Such discussions have largely ignored the status of the Owenettidae, a family erected by Broom (1939) on the basis of the monotypic South African species *Owenetta rubidgei*. Nevertheless, there is now evidence that *Barasaurus* and *Owenetta* may be closely related, comprising a morphologically more primitive taxon than the Procolophonidae (Meckert, 1993; Spencer, 1994). Lee (1995, 1997) has noted three postulated synapomorphies which support the inclusion of *Barasaurus* in the Owenettidae, and which distinguish the group from the Procolophonidae: postfrontal–supratemporal contact, median spur on back of skull table, and absence of entepicondylar foramen. The validity of the Family Owenettidae, and its inclusion in Procolophonoidea as sister group to Procolophonidae, have been accepted in recent cladistic analyses of basal amniotes (Laurin and Reisz, 1995; DeBraga and Rieppel, 1997; Lee, 1997).

The monophyly of the Triassic family Procolophonidae was defined by Lee (1995) on the basis of two features: the exclusion of the parietal from the orbital margin, and the presence of enlarged palatal denticles, sparsely arranged in single rows. Unfortunately, however, the first character has a polymorphic distribution in many procolophonids, in which a small exposure of the parietal in the orbital margin may be present, and its polarity is presently undefined. The second character could apply to a plethora of basal amniotes (e.g. Captorhinidae, *Protorothyris*). Alternative potential synapomorphies supporting the Procolophonidae (Spencer, 1994) include: a splint-like postfrontal, confined to the orbital margin; postparietal much reduced or absent; fewer than four premaxillary teeth; fewer than nine maxillary teeth; a thickened layer of enamel restricted to the upper half of the crown of mid-row maxillary and dentary teeth; and lateral tooth base on the pterygoid and palatine reduced in length and aligned anteroposteriorly to anteromedially.

Lee (1995) defined the Procolophonoidea (Romer, 1956, *emend.* Lee, 1995), the most recent common ancestor of the Owenettidae and Procolophonidae, and all its descendants, on the basis of three unequivocal characters: posterior spur on prefrontal antorbital buttress; ventral embayment of the cheek; occipital flange of parietal. Other possible synapomorphies of procolophonoids (*sensu* Lee; Spencer, 1994) are: jugal–squamosal contact greatly reduced or absent, and elements of the scapulocoracoid unfused in mature specimens, a trait acquired convergently in mesosaurids and the 'protorothyridid' *Cephalerpeton*. In this chapter, we provisionally accept the Procolophonoidea as a taxon embracing the Owenettidae and Procolophonidae.

Within the Procolophonidae, three subfamilies of procolophonids, the Spondylolestinae, Procolophoninae, and Leptopleuroninae, are currently distinguished, based primarily on features of the skull and the marginal dentition (Ivakhnenko, 1979). Representatives of the first two subfamilies are found in the Permo-Triassic of Russia in four successive procolophonid assemblages which characterize the Triassic of the East European platform and Cis-Urals region (Chapter 7). The phylogeny of procolophonoids has been re-analysed in detail by Spencer and Sues (2000).

Russian procolophonids have been described in a number of papers (Chudinov and V'yushkov, 1956; Ochev, 1958, 1967, 1968; Ochev and Danilov, 1972; Ivakhnenko, 1973a,b, 1974, 1975, 1979, 1983; Novikov, 1991, 1994; Novikov and Orlov, 1992). Chudinov and V'yushkov (1956) established the genera *Phaanthosaurus* and *Tichvinskia*, based on partial skull and dentary remains from the Lower Triassic of various parts of European Russia. Ochev (1958) added the species *Tichvinskia burtensis*, later made the type of the genus *Burtensia* by Ivakhnenko (1975). Ivakhnenko also described a number of new genera, *Contritosaurus* Ivakhnenko, 1974, *Kapes* Ivakhnenko, 1975, *Macrophon* Ivakhnenko, 1975, *Orenburgia* Ivakhnenko, 1975, and *Microphon* Ivakhnenko, 1983, also based on incomplete skull remains. Novikov (1991) carried out further revisions of Russian procolophonids, and erected the genera *Timanophon* and *Lestanshoria* for new forms from the northern region of European Russia and *Samaria* for another specimen from the South Urals. Novikov and Orlov (1992) erected a further genus, *Insulophon*, for a specimen from Kolguev Island, north of the Arctic Circle. Two further genera were described as procolophonids, *Vitalia* Ivakhnenko, 1973a, and *Coelodontognathus* Ochev, 1967, but these are probably wrongly attributed to the group.

Russian procolophonid remains have been found in continental sediments, largely in fluvial settings. The elements are typically isolated and often abraded, and there is a preservational bias towards tooth-bearing bones in the museum collections. While this is true in general, some articulated skeletons have been recovered, most notably the type specimens of *Tichvinskia vjatkensis* (PIN 954/1; Figure 9.7) and *Timanophon burtensis* (PIN 3359/11). These specimens are preserved in a 'rolled-up' attitude which could indicate that the animals were located in burrows, or burrow systems. Supporting evidence for this suggestion comes from the recent discovery of flask-shaped burrow structures in the southern African *Lystrosaurus*/*Procolophon* assemblage zone that contained rolled-up, articulated skeletons of the procolophonine *Procolophon* (J. Welman, pers. comm. to P.S.S., 1991).

In the following overview, the Russian procolophonids are described in order of the two subfamilies, and in approximate stratigraphic order.

Repository abbreviations

PIN, Palaeontological Institute, Moscow; SGU, Saratov State University; TsNIGRI, Tsentralny Nauchno-Issledovatelskii Geologo-Razvedochnyi Muzei, Sankt Peterburg.

Systematic survey

Subclass PARAREPTILIA Olson, 1947
Suborder PROCOLOPHONOIDEA Romer, 1956
Family PROCOLOPHONIDAE Seeley, 1888
Subfamily SPONDYLOLESTINAE Ivakhnenko, 1979

Type genus. Spondylolestes Broom, 1937, *Lystrosaurus*/*Procolophon* Zone, South Africa.
Diagnosis. The most primitive procolophonids; orbits elongated as a rule, not enlarged; teeth usually simple, conical, relatively weakly differentiated, more than ten on each jaw (Ivakhnenko, 1979).

Comments. Ivakhnenko (1979, p. 11) divided the Family Procolophonidae into two subfamilies, the Spondylolestinae and Procolophoninae, on the basis that the spondylolestines were more primitive than the procolophonines. His diagnosis of the Spondylolestinae, given above, differentiated this subfamily in broad terms from the procolophonine procolophonoids with their elongated orbits, their bicuspid marginal teeth, and the presence of fewer than ten teeth on each jaw. However, the features listed appear to be plesiomorphic for procolophonoids as a whole, and it is difficult to find autapomorphies supporting spondylolestine monophyly *sensu* Ivakhnenko (1979).

Ivakhnenko (1979, pp. 11–14) included a number of genera in the subfamily, some Russian (*Phaanthosaurus*, *Contritosaurus*), and others from South Africa (*Spondylolestes*, *Procolophonoides*), Brazil (*Candelaria*), and China (*Neoprocolophon*). These genera are all Early Triassic in age, except *Candelaria* from the Middle Triassic. *Procolophonoides* was erected by Ivakhnenko (1979, p. 13) for some South African materials previously assigned to *Procolophon*, but, according to him, not procolophonine.

The status of the Spondylolestinae is unclear. *Spondylolestes* appears to be a *nomen dubium*, and it may be difficult even to distinguish it as an amniote based on Broom's (1937) description and figures.

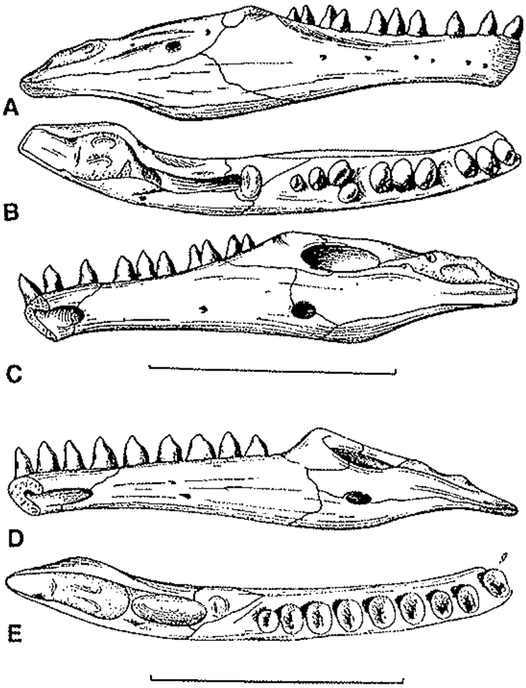

Figure 9.1. Lower jaws of the basal procolophonids *Phaanthosaurus ignatjevi* Tchudinov and Vjuschkov, 1956 (PIN 1025/1, 20; A–C) and *Contritosaurus simus* Ivakhnenko, 1974 (PIN 3355/1; D, E) in lateral (A), medial (B, D), and occlusal (C, E) views. Scale bars = 10 mm. (Modified from Ivakhnenko, 1979.)

Phaanthosaurus Tchudinov and Vjuschkov, 1956
Phaanthosaurus ignatjevi Tchudinov and Vjuschkov, 1956

See Figures 9.1A–C and 9.2A, B.

Holotype and locality. PIN 1025/1, a dentary; Spasskoe village, Vetluga River, Nizhnii Novgorod Province.

Horizon. Vokhmian Gorizont, Lower Triassic.

Paratypes. PIN 1025/21, a dentary; PIN 1025/20, postdentary portion of a lower jaw; and further jaw fragments, all from around Spasskoe village.

Diagnosis. Eleven almost undifferentiated teeth on the lower jaw. Adductor notch narrow and long. Coronoid process of lower jaw massive and low (Ivakhnenko, 1979).

Comments. Phaanthosaurus is also characterized by the tendency for the marginal teeth to form rare closely positioned pairs with replacement teeth, arranged diagonally (Figure 9.1B).

The manner of tooth wear in *Phaanthosaurus* and *Contritosaurus* is distinct. While most teeth show small terminal tooth-to-food wear facets, as in *Procolophon* for example, these are associated with extensive and steeply inclined facets. On the upper teeth these face inwards, and correspondingly on the lowers, these face outwards. This manner of wear in teeth that rarely occlude in a tooth-to-tooth fashion, as in all procolophonids (*contra* Gow, 1985) seems to be determined, as seen in unworn teeth, by the alternate displacement of the terminal cusp labially in uppers and lingually in lower teeth. It probably also corresponds to the differential thickness of the enamel of the tooth

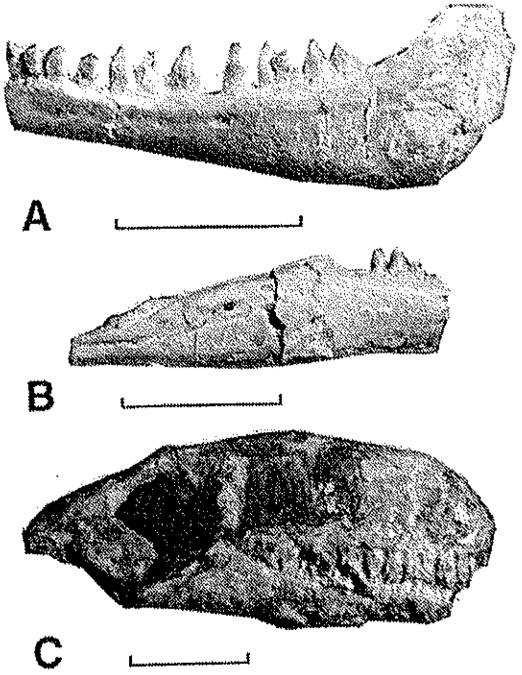

Figure 9.2. Partial lower jaws of *Phaanthosaurus ignatjevi* Tchudinov and Vjuschkov, 1956, PIN 1025/1 (A) and PIN 1025/20 (B), both in lateral view. C, Skull of *Contritosaurus simus* Ivakhnenko, 1974, PIN 3355/1, in lateral view. Scale bars = 5 mm.

crown, although this has yet to be determined by sectioning of the teeth. This character, not noted by Ivakhnenko or Novikov, seems to be a synapomorphy shared by *Phaanthosaurus* and *Contritosaurus*. Other similarities include: antorbital region of skull very high; maxillary lateral depression extends dorsally on to ventral part of nasal; anterodorsal region of prearticular, viewed medially, is bifurcated by the posteroventral ramus of the coronoid; and, base of each maxillary tooth has a small triangular distolingual flange, so that these teeth appear to be inclined anteroventrally in lingual view. Indeed, these taxa are so similar that they may well be conspecific, as is also suggested by their stratigraphic and geographic distribution.

Contritosaurus Ivakhnenko, 1974

Diagnosis. 'A very small procolophonid (length of skull reaching 2 cm). Skull high. Preorbital portion high and short. Orbits very large, rounded-trapezoidal, drawn out rearward. Fossa of lateral nasal gland very considerable, nostrils small. Lacrimal not extending to margin of nostril; postfrontal not fused with parietal. Upper margin of orbit formed by the joining of the prefontal and postfrontal bones. Teeth differentiated: front teeth (5–6 in upper jaw and 3 in lower jaw) conical, with slightly dilated and lingually recurved crowns, rear 7–8 teeth on both jaws with heavily dilated bases and pointed crowns, frequently with oblique wear surfaces. There are four rows of teeth on the palate, pterygoid, palatine, and two vomerine (perichoanal and medial); the perichoanal row of teeth is double.' (Ivakhnenko, 1974, p. 347).

Comment. *Contritosaurus* shares the same mode of tooth wear as *Phaanthosaurus*, but seems to lack the occasional diagonal pairing of marginal teeth. Most of the characters noted above are primitive. Ivakhnenko (1974, p. 347) notes that *Contritosaurus* is 'most similar to the genus *Phaanthosaurus*, but distinguished from it by the slightly shorter adductor fossa, relative to the length of the jaw, the longer and narrower retroarticular process, the thinner and higher coronoid process, and the lack of a crest on the outer face of the dentary.' In addition, the type specimen of *C. simus* (below) has a lacrimal with a narrow posteriorly directed process, resting on the dorsal surface of the extopterygoid, just medial to the foramen palatinum posterius, and a double row of vomerine teeth bordering the choana ('perichoanal tooth row' of Ivakhnenko, 1979). These features, however, are not preserved in any material assigned by Ivakhnenko to *Phaanthosaurus*. Ivakhnenko (1974) described two species of *Contritosaurus*, but these may be minor variants of a single species, *C. convector*.

Contritosaurus convector Ivakhnenko, 1974

Diagnosis. 'In contradistinction to *C. simus* the teeth in the upper jaw are slightly inclined, the adductor fossa is broader (the length of the adductor fossa is one-quarter greater than in *C. simus*, while its width is

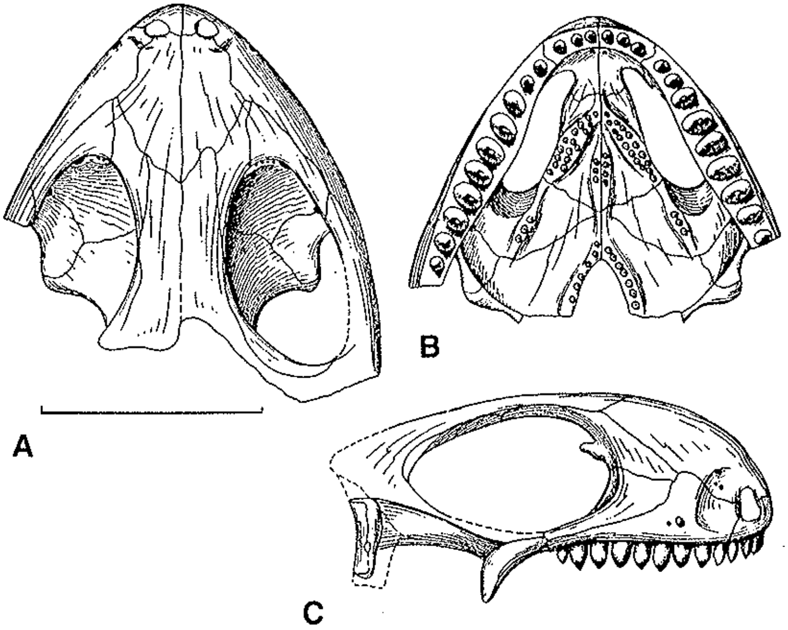

Figure 9.3. Holotype skull of *Contritosaurus simus* Ivakhnenko, 1974 (PIN 3355/1) in dorsal (A), ventral (B), and lateral (C) views. Scale bar = 10 mm. (Modified from Ivakhnenko, 1979.)

practically twice as great), the posterior margin of the dentary is sharply bent upwards, and of the two crests on the postdentary portion of the lower jaw, the outer crest is far more weakly expressed, while the other is completely absent.' (Ivakhnenko, 1974, p. 351).

Holotype and locality. PIN 3357/1, lower jaw fragment; Krasnie Baki village, Vetluga River, Nizhnii Novgorod Province.

Paratype. PIN 3357/2, a part of an upper jaw, from the same locality.

Horizon. Vokhmian Gorizont, Lower Triassic.

Contritosaurus simus Ivakhnenko, 1974

See Figures 9.1D, E, 9.2C and 9.3.

Diagnosis. [See *C. convector.*]

Holotype and locality. PIN 3355/1, an incomplete skull with lower jaw fragment; Lipovo village, Vetluga River, Nizhnii Novgorod Province.

Horizon. Vokhmian Gorizont, Lower Triassic.

Paratypes. PIN 2890/5, an incomplete skull from the Kasyanovtsy site in Kirov Province; PIN 3356/1, an incomplete skeleton and skull from the Sarafanikha site in Nizhnii Novgorod Province.

Microphon Ivakhnenko, 1983

Microphon exiguus Ivakhnenko, 1983

See Figure 9.4.

Diagnosis. 'Very small form, length of skull not more than 1 cm. Upper jaw short, maxilla with high ascending lamina. About 12 teeth in maxillary bone, teeth conical, with longitudinally compressed bases.' (Ivakhnenko, 1983, p. 136).

Holotype and locality. PIN 3583/31, lower jaw fragment; Donguz VI locality, Donguz River, Orenburg Province.

Horizon. Severodvinskian Gorizont, Upper Tatarian, Upper Permian.

Comments. It is unclear whether *Microphon* is a valid taxon or not. Among the characters listed by Ivakhnenko (1983, p. 136), only one seems to be acceptable, namely 'longitudinally compressed crowns'. The others are primitive for procolophonids

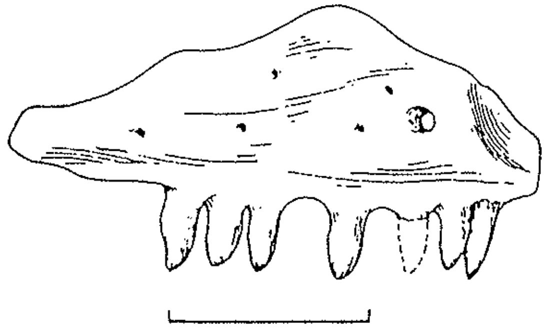

Figure 9.4. Partial right maxilla, holotype of *Microphon exiguus* Ivakhnenko, 1983 (PIN 3538/31) in lateral view. Scale bar = 25 mm. (Modified from Ivakhnenko, 1983.)

(presence of a maxillary depression) or for various basal amniotes (high maxillary process, prominent maxillary foramen: Lee, 1995). Ivakhnenko (1983) also argued that the small size of *Microphon*, the feature that gave rise to its name, is a further diagnostic feature. However, with only a single incomplete specimen, *Microphon* could be a juvenile of another taxon, although this is a unique Russian procolophonid record from the Late Permian.

The presence of single-cusped maxillary teeth is apparently primitive for procolophonoids, but would not exclude *Microphon* from the Spondylolestinae. Ivakhnenko (1983, p. 136) correctly points out similarities in the structure of the maxillary foramen, shared at least with *Phaanthosaurus*. Ivakhnenko (1983, p. 136) also lists 12 teeth as present in the maxilla of *Microphon*, according to him a spondylolestine feature, but one shared also with owenettids. However, his illustration (Figure 9.4 here) only shows seven teeth, although there may be space for 12.

Subfamily PROCOLOPHONINAE Seeley, 1888
emend. Ivakhnenko, 1979

Diagnosis. 'Skull usually high, orbits strongly elongated. Teeth differentiated into incisiforms and molariforms. Crowns of molariforms usually very complex, bicuspid. Ten or fewer teeth on the jaw' (Ivakhnenko, 1979, p. 14).

Comments. Ivakhnenko (1979, p. 14) erected this subfamily to distinguish a group of procolophonids that he saw as distinctive from the spondylolestines. He included in the subfamily a number of Russian taxa (*Tichvinskia*, *Burtensia*, *Macrophon*, *Orenburgia*, *Kapes*, *Vitalia*), as well as some from South Africa (*Procolophon*, *Microtheledon*, *Thelegnathus*, *Myocephalus*), and Germany (*Anomoiodon*, *Koiloskiosaurus*). These taxa are all Early Triassic in age, except *Anomoiodon* and *Orenburgia*, which are Early to Middle Triassic.

Ivakhnenko's subfamilies Spondylolestinae and Procolophoninae were distinguished by him from a third, Leptopleuroninae, diagnosed as (Ivakhnenko, 1979, p. 21): 'Specialized procolophonids with strong elongation backwards of the orbits and with spines on the bones of the cheek complex. Teeth differentiated a little.' This subfamily, including *Leptopleuron* from the Late Triassic of Scotland and *Hypsognathus* from the Late Triassic of North America, is distinguished by clear synapomorphies (e.g., V-shaped incursion or embayment on the anterolateral surface of the jugal; strap-like process arising from medial side of descending process of prefrontal sutured to suborbital ridge on the frontal; pair of obtusely conical, laterally directed quadratojugal processes, each with an annular basal flange), unlike the Spondylolestinae and Procolophoninae, which are probably paraphyletic assemblages of outgroups to the Leptopleuroninae. Ivakhnenko (1979) included two additional Late Triassic taxa in Leptopleuroninae, *Sphodrosaurus* from North America and *Paoetodon* from China, but these are incorrectly assigned.

Tichvinskia Tchudinov and Vjuschkov, 1956

Diagnosis. Medium-sized procolophonines; interorbital depression slight; no lateral process on the quadratojugal; prominent supraorbital ridge formed by the frontal, postfrontal, and parietal; postfrontal fused to parietal; two conical teeth form the anterior part of the maxillary tooth row; a dorsomedially directed intermediate molariform (m7) sometimes forms the end of the dentary tooth row; posteromedial enamel ridge on the lower molariforms truncated dorsally by the distal occlusal basin (*emend.* from Ivakhnenko, 1979).

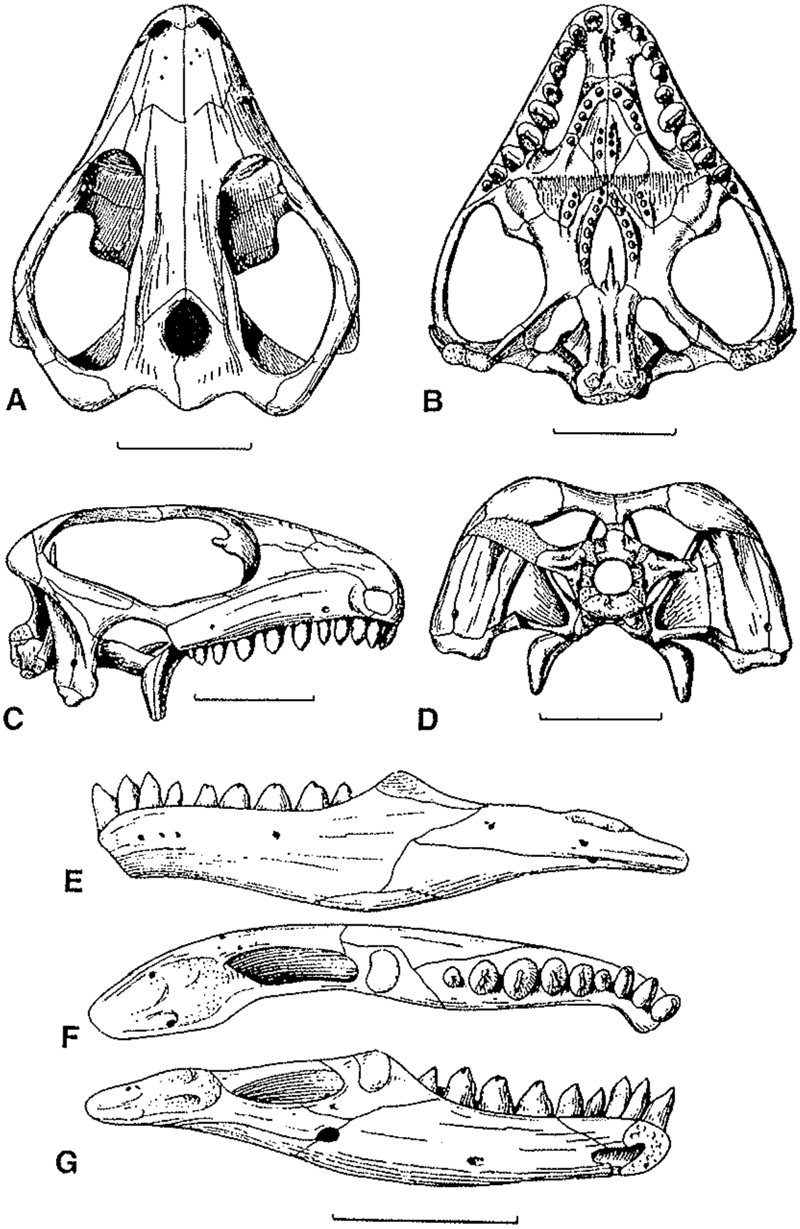

Figure 9.5. Skull (A–D) and lower jaw (E–G) of *Tichvinskia vjatkensis* Tchudinov and Vjuschkov, 1956 (PIN 954/1) in dorsal (A), ventral (B), lateral (C, E), occipital (D), occlusal (F), and medial (G) views. Scale bars = 10 mm. (Modified from Ivakhnenko, 1979.)

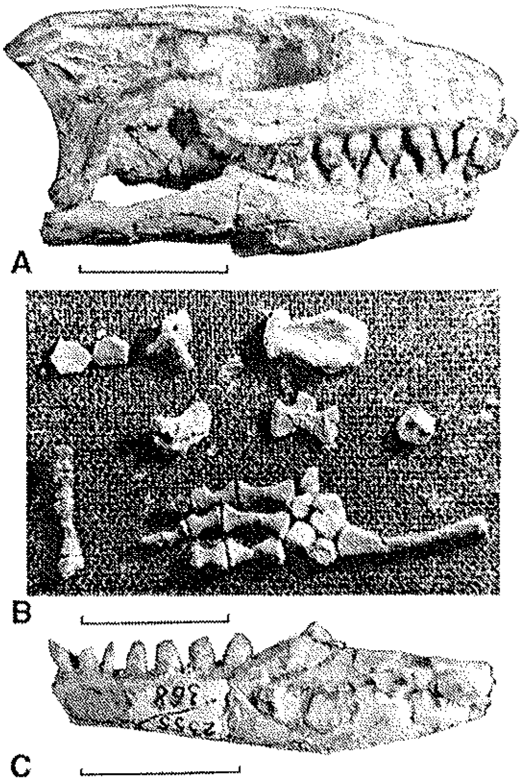

Figure 9.6. *Tichvinskia vjatkensis* Tchudinov and Vjuschkov, 1956, skull in lateral view, PIN 954/1 (A); skeletal remains, PIN 954/1, a partial foot and hindlimb and other elements (B); lower jaw of '*T. jugensis*' Vjuschkov and Tchudinov, 1956, PIN 2355/368 in lateral view (C). Scales bars = 10 mm.

Tichvinskia vjatkensis Tchudinov and Vjuschkov, 1956

See Figures 9.5, 9.6A, B and 9.7.

Diagnosis. 'Height of teeth exactly the same as the height of the dentary. Coronoid process of the lower jaw low and wide, adductor pit narrow. Post-dentary part of the mandible narrow and long.' (Ivakhnenko, 1979, p. 15).

Holotype and locality. PIN 953/1, skull; Okunevo, Fedorovka River, Vyatka River basin, Kirov Province.

Horizon. Yarenskian Gorizont, Lower Triassic.

Paratypes. Complete skeleton, series of skulls.

Comment. The holotype is lost. Ivakhnenko's (1973b) description was based on four skulls, including one with an associated postcranial skeleton (PIN 954/1; Figures 9.6 and 9.7), and other tooth-bearing elements. The species almost certainly includes the genus *Burtensia* Ivakhnenko, 1975, founded on the species *T. burtensis* Otschev, 1958 (holotype, PIN 2394/12, formerly SGU 104/2, a dentary from Kzyl-Sai ravine at Andreevka settlement, Kzyl-Oba River, Ural River basin, Orenburg Province; Petropavlovskaya Svita, Yarenskian Gorizont, Lower Triassic; and paratypes, PIN 2394/11, right mandible from the type locality; PIN 4400/1, a right dentary, from the Meshcheryakovka locality; PIN 3359/11, a skull and lower jaw, from Pizhmo-Mezen' River, Arkhangel'sk Province). *Burtensia* was said to differ from *Tichvinskia* and other procolophonines by the 'small, relatively high dentary, differentiation of lower-jaw dentition, number and shape of quasi-molar teeth' (Novikov, 1991, p. 92). However, inspection of the specimens reveals no distinguishing characters in the dentition or skull shape (Spencer and Sues, 2000). Ivakhnenko (1975) referred another specimen (PIN 3359/11, a skull and lower jaw, from Pizhmo-Mezen' River, Arkhangel'sk Province) to *Burtensia*, but Novikov (1991) assigned it to a new genus, *Timanophon* (see below).

Tichvinskia jugensis Vjuschkov and Tchudinov, 1956

See Figure 9.6C.

Diagnosis. 'In lower jaw, height of double-peaked teeth is less than height of dentary. Coronoid process low, postdentary part of the jaw high and wide, adductor pit wide.' (Ivakhnenko, 1979, p. 16).

Holotype and locality. PIN 2252/308, skull fragment with lower jaw; Vakhnevo, Sharzhenga River, Vologda Province.

Horizon. Rybinskian Gorizont, Lower Triassic.

Paratypes. Parts of skulls.

Comment. On the basis of our re-examination of the currently limited material, this taxon is here distinguished only as Procolophonidae *incertae familiae*. It exhibits features that are absent in spondylolestine procolophonoids (*sensu* Ivakhnenko, 1979), including bicuspid molariform cheek teeth, and the lingual cusp of dentary molariforms positioned directly opposite

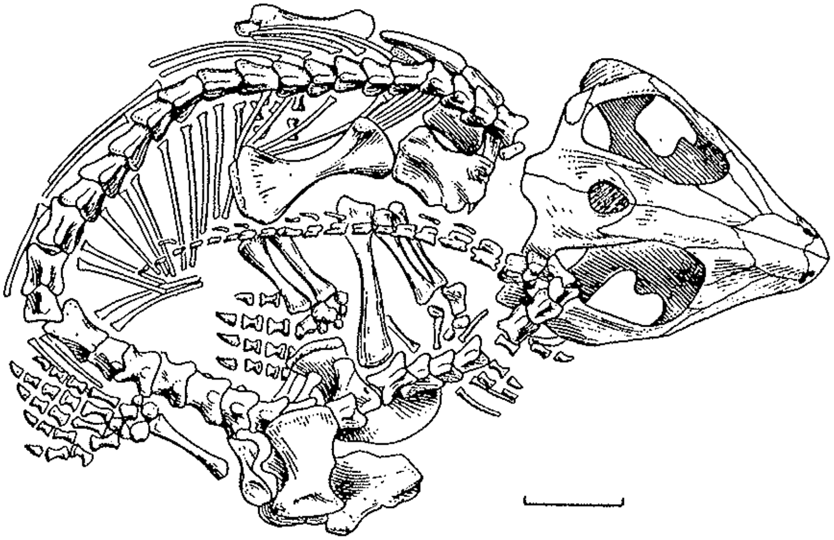

Figure 9.7. Skeleton of *Tichvinskia vjatkensis* Tchudinov and Vjuschkov, 1956 (PIN 954/1) in dorsal view, as found. Scale bar = 10 mm. (Modified from Ivakhnenko, 1979.)

the labial cusp, with both cusps of subequal size, but it lacks derived features of later procolophonoids, such as the Late Triassic leptopleuronines. Nevertheless, it is perhaps the sole published record from the Rybinskian Gorizont.

Kapes Ivakhnenko, 1975

Diagnosis. Maxillary teeth: four to five molariforms, one mesial intermediate molariform. Molariforms 1–4 of upper and lower jaws becoming progressively larger backwards. Lingual cusp in lower teeth subequal in height to labial cusp; labial and lingual cusps relatively close together.

Comments. Kapes was erected by Ivakhnenko (1975, pp. 87–88) for isolated remains of procolophonids that were larger than *Tichvinskia*, and differed by the number and shape of the teeth, and by the possession of a very large tooth on the lower jaw. This, and the characters listed in the diagnosis (Spencer and Storrs, 2000) justify the validity of this genus.

These medium to large procolophonines show a number of other characters (Novikov, 1991, p. 98) that are shared also with *Orenburgia*, *Samaria*, and *Lestanshoria*, namely: premaxillary teeth, at least one incisiform; dentary teeth, one mesial intermediate molariform (Figure 9.8), three molariforms, distal intermediate molariform absent or present, two incisors. Lower intermediate molariforms unicuspid, or bicuspid, with a labial and lingual cusp connected by a weak transverse crest. Molariforms 1–4 bicuspid and with shallow distal and mesial basins. Lower distal intermediate molariform absent, unicuspid, or bicuspid, lower than m4. Upper molariforms broader than long; bicuspid. Lower molariforms sub-conical, equidimensional to slightly longer than broad. Coronoid process not expanded transversely.

Macrophon is probably synonymous with *Kapes*, and it is possible that *Orenburgia*, *Samaria*, and *Lestanshoria*, are also synonyms, although these last three lack the enlarged penultimate molariform of *Kapes*, and they may all be better assigned to *Orenburgia* as a distinct genus. When traits that are susceptible to intraspecific variation are excluded, these three genera are based primarily on primitive character states (Spencer and Storrs, 2000). Further study is necessary to confirm which, if any, of these genera are distinctive, and to

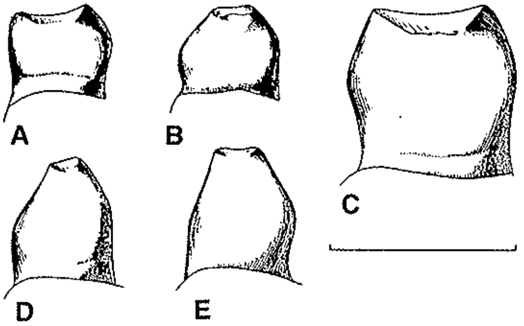

Figure 9.8. Molariform teeth, shown as the penultimate tooth on the left side, in posterior view, from the lower jaws of *Tichvinskia* (A), '*Burtensia*' (B), *Macrophon* (C), *Orenburgia* (D), and *Kapes* (E). Scale bar = 5 mm. (Modified from Ivakhnenko, 1979.)

determine which of the species that are synonymous with *Kapes* are distinct species of that genus.

Kapes amaenus Ivakhnenko, 1975

See Figure 9.9A, B.

Diagnosis. Adult mandible is 1.4–1.7 times the length of m3 beneath the distal end of m3. Upper part of molariform crowns compressed strongly distomesially; ratio of distance between labial and lingual cusp tips and maximum width of m3 is about 0.55 (Spencer and Storrs, 2000).

Holotype and locality. PIN 3361/2, dentary; Zheshart settlement, Vychegda River, Komi Republic.

Horizon. Gamskaya Svita, Yarenskian Gorizont, Lower Triassic.

Syntypes PIN 3361/4, right dentary; PIN 3361/15, 10, 11, fragments of left dentaries; PIN 3361/1, 6, 7, 12, fragments of right maxillae; PIN 3361/8, 9, 13, fragments of left maxillae; PIN 3361/14, a tooth, all from the Zheshart site (Novikov, 1991, p. 98).

Kapes majmesculae (Otschev, 1968)

See Figure 9.9C.

Diagnosis. Adult mandible is *c.* 2.0 times length of m3 beneath the distal end of m3. A weak cingulum occurs in middle height of all lower molariforms (Spencer and Storrs, 2000).

Holotype and locality. PIN 4365/5 (formerly SGU 104/3824), dentary; Petropavlovka, Sakmara River, Ural River basin, Orenburg Province.

Horizon. Yarenskian Gorizont, Lower Triassic.

Comment. This species was originally ascribed to *Tichvinskia* by Ochev (1968), and it was included in the new genus *Orenburgia* by Ivakhnenko (1975, p. 89). It was later re-assigned to *Kapes* by Ivakhnenko (1983), a view accepted by Novikov (1991) and Spencer and Storrs (2000).

Kapes serotinus Novikov, 1991

Diagnosis. Teeth widely spaced; ratio of maximum length of tooth row to maximum height of dentary is 2.7 (Novikov, 1991, p. 99).

Holotype and locality. PIN 1579/23, dentary; Berdyanka River, Ural River basin, Orenburg Province.

Horizon. Donguz Gorizont, Middle Triassic.

Comment. This specimen was originally described as *Tichvinskia* cf. *majmesculae* by Ochev and Danilov (1972), and was renamed as a distinct species by Novikov (1991, p. 99) on the basis of its less massive and widely spaced teeth. However, this is not a valid taxon, and is probably synonymous with *K. majmesculae* (Spencer and Storrs, 2000). The two diagnostic characters are both subject to individual variation in procolophonids. Indeed, spacing of the teeth varies within the holotypes of *K. serotinus* and *K. majmesculae* (Novikov, 1991, fig. 3c, e).

Macrophon Ivakhnenko, 1975

Macrophon komiensis Ivakhnenko, 1975

See Figures 9.8C and 9.9D.

Diagnosis. A very high posterior wall of the maxilla, and upper molariform teeth that have transverse axes directed distolabially and mesolingually. The anterior edge of the medial excavation of the ascending maxillary process is level with the anterior rim of the maxillary foramen, and faces posteroventrally (Spencer and Storrs, 2000).

Holotype and locality. PIN 3361/1, part of upper jaw; Zheshart settlement, Vychegda River, Komi Republic.

Horizon. Gamskaya Svita, Yarenskian Gorizont, Lower Triassic.

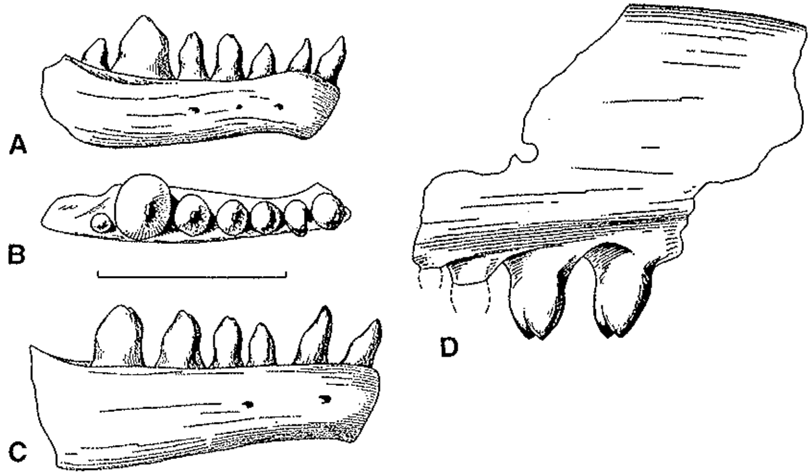

Figure 9.9. Anterior dentary fragments of *Kapes amaenus* Ivakhnenko, 1975 (PIN 3361/1; A, B), *Kapes majmesculae* (Otschev, 1968) (restored from SGU 104/3824 and PIN 4365/5; C), and partial left maxilla of *Kapes* (*Macrophon*) *komiensis* (Ivakhnenko, 1975) (PIN 3361/3; D) in lateral (A, C, D) and occlusal (B) views. Scale bars = 10 mm. (Modified from Ivakhnenko, 1979.)

Comments. This taxon is clearly like *Kapes* in its large size. However, it was said to differ from *Kapes* by the shape of its teeth (Ivakhnenko, 1975, p. 88), but that distinction is not clear. It is referred here to *Kapes* since it shares many of the characters noted as diagnostic of that genus by Novikov (1991), as indicated above. In addition, it shares some particular features with a new species of *Kapes* from the Otter Sandstone Formation of Devon, England (Spencer and Storrs, 2000): the upper molariform teeth are much broader than long, the M1–2 show a size increase distally, and the lingual cusp is higher than the labial cusp. The species *K. komiensis* (Ivakhnenko, 1975) appears to be valid, and distinct from other species of *Kapes*. It occurs at the same locality, and in the same horizon, as *Kapes amaenus*.

Orenburgia Ivakhnenko, 1975

Diagnosis. Medium-sized procolophonine. Skull up to 45 mm long, rounded-triangular, with concave lateral margins. Pineal foramen in front of posterior orbital margins, at the level of the middle of orbital length. Palate strongly curved longitudinally, with four short tooth rows. Interpterygoid notch narrow. Maxillary teeth: two incisiforms, four molariforms; premaxillary teeth: three incisiforms; dentary teeth: two incisiforms, five molariforms gradually becoming smaller backwards. Crowns of molariforms bicuspid, widened transversely, with the maximal width at the middle of height (for anterior teeth) or lower third (for posterior). Incisiforms highest in dental tooth row. Coronoid process of lower jaw rounded. (Ivakhnenko, 1975, p. 89; Novikov, 1991, p. 94).

Comments. This genus was established for *Tichvinskia enigmatica* Tchudinov and V'yushkov, 1956 and *T. majmesculae* Otschev, 1968, the latter later (Ivakhnenko, 1983) re-assigned to *Kapes*. The genus differs from other procolophonines in the shape of the molariform teeth, and in the 'character of differentiation of dentition and in dominance of quasi-incisors'. It differs from *Tichvinskia*, and other taxa, in the 'location of pineal aperture and large size of buccal notch' (Novikov, 1991, p. 94).

Orenburgia shares affinities with *Lestanshoria*, for example in the height distribution of teeth along the dentary, which is very similar in both taxa. These two genera, and *Samaria*, all resemble *Kapes* in many

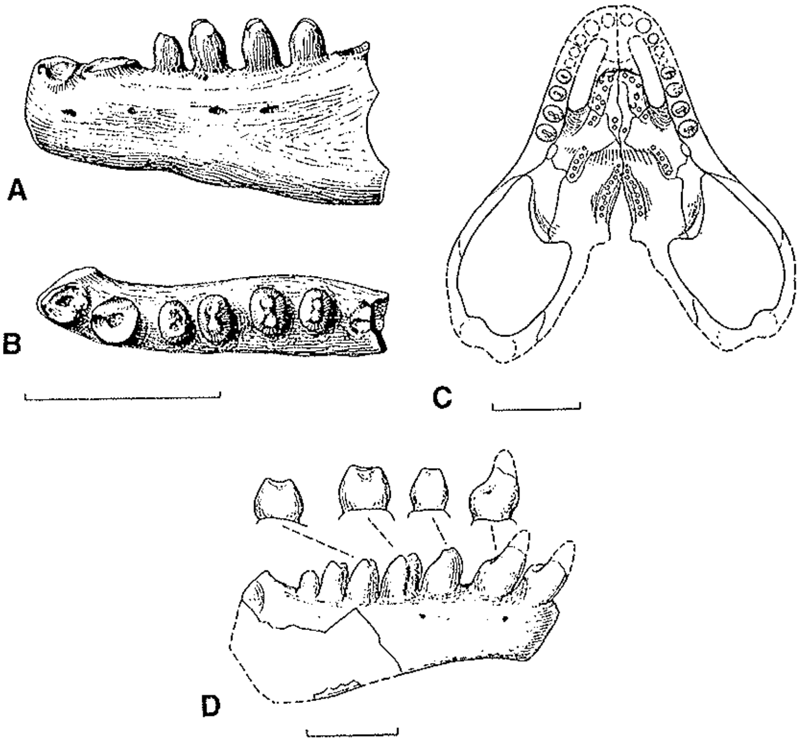

Figure 9.10. Dentary fragments (A, B, D) and partial skull (C) of *Orenburgia enigmatica* (Tchudinov and Vjuschkov, 1956) (A, B) and *Orenburgia bruma* Ivakhnenko, 1983 (C, D) in lateral (A, D) and occlusal/ ventral (B, C) views. A, B, PIN 1043/1; C, restored from PIN 3951/1 and 3952/2, D, PIN 4370/3. Scale bars = 10 mm. (Modified from Novikov, 1991.)

respects, and it could be that the small morphological differences are merely examples of individual variation within a single taxon (Spencer and Storrs, 2000).

O. enigmatica (Tchudinov and Vjuschkov, 1956)

See Figures 9.8D and 9.10A, B.

Diagnosis. 'Height of teeth similar to height of tooth-bearing element. Last tooth of lower jaw not much bigger than the second last.' (Ivakhnenko, 1979, p. 19).

Holotype and locality. PIN 1043/1, left dentary; Lipovaya Balka hollow, Don River basin, Volgograd Province.

Horizon. Lipovskaya Svita, Yarenskian Gorizont, Lower Triassic.

Comments. This species is probably a *nomen nudum*. The holotype dentary, the sole specimen, is damaged, seemingly abraded during transport, and several of the teeth are broken (Figure 9.10A, B). It lacks diagnostic characters sufficient to distinguish it from other taxa. It seems very like *Tichvinskia vjatkensis* (cf. Figure 9.5E), except that the teeth are more widely spaced. It lacks the enlarged penultimate molariform of *Kapes* (cf. Figure 9.9A–C). The holotype has been lost.

O. bruma Ivakhnenko, 1983

See Figure 9.10C, D.

Diagnosis. Autapomorphies include a short jugal with dorsoventrally expanded anterior and posterior ends, the anterior portion of the tooth ridge on the palatine is edentulous and reaches the choana, and each vomer has a transverse expansion anteriorly bearing a diagonal row of three small teeth.

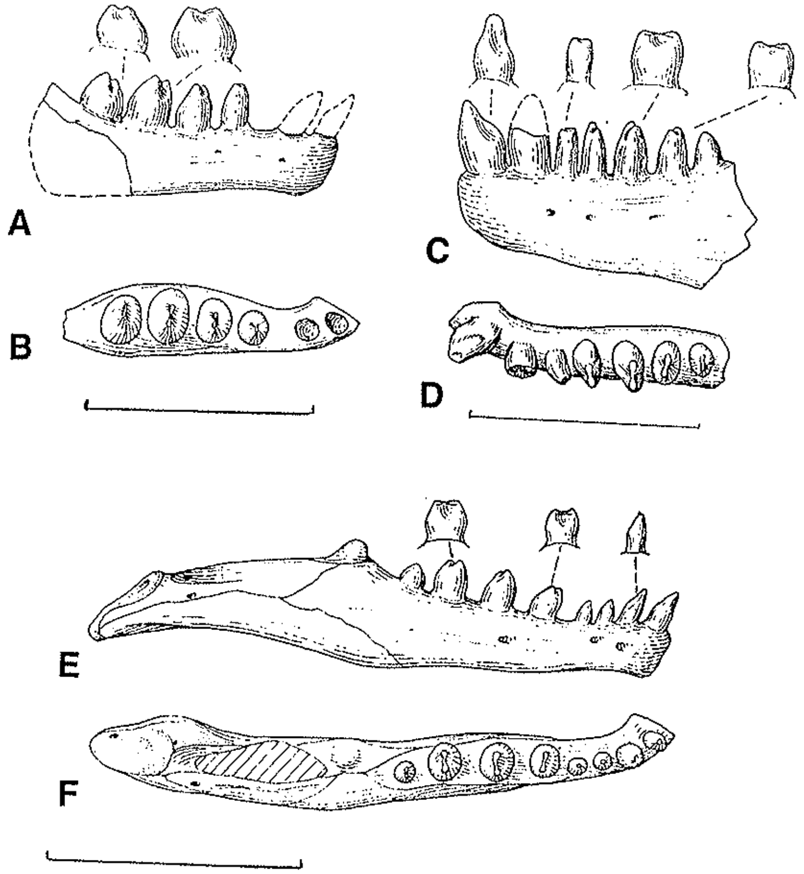

Figure 9.11. Lower jaws of *Samaria concinna* (Ivakhnenko, 1975), PIN 3362/1 (A, B), *Lestanshoria massiva* Novikov, 1991, PIN 4370/4 (C, D), and *Timanophon raridentatus* Novikov, 1991, PIN 3359/11 (E, F) in lateral (A, C, E) and occlusal (B, D, F) views. Scale bars = 10 mm. (Modified from Novikov, 1991.)

Holotype and locality. PIN 3952/1, incomplete skull; Cape Nikolaya, Admiralteistva Peninsula, Severnii Island, Novaya Zemlya Archipelago.

Horizon. Admiralteistva Svita, Ustmylian Gorizont, Lower Triassic.

Paratype. PIN 3952/2, an incomplete skull, from the same locality; PIN 4370/3, a partial dentary from Khei-Yaga River basin.

Comments. The distribution and shapes of dentary teeth are similar to *Kapes* (cf. Figure 9.9A–C), except that *O. bruma* lacks the enlarged penultimate molariform tooth. The ventral view of the skull (Figure 9.10C) is, in its preserved parts, similar to *Tichvinskia* (Figure 9.5B). *O. bruma* is distinct from *Tichvinskia* in having widely spaced teeth, and from *Kapes* in lacking the enlarged penultimate molariform.

Samaria Novikov, 1991

Samaria concinna (Ivakhnenko, 1975)

See Figure 9.11A, B.

Diagnosis. Coronoid eminence very high; tooth ridge flanking interpterygoid vacuity with widely spaced denicles (Spencer and Sues, 2000).

Holotype and locality. PIN 3362/1, skull fragment with lower jaw; Markovka village, Soroka River, Samara River basin, Orenburg Province.

Horizon. Kzylsaiskaya Svita, Sludkian Gorizont, Lower Triassic.

Comments. This species was established as belonging to the genus *Orenburgia* by Ivakhnenko (1975, pp. 89–90), and was differentiated from the other species of that genus 'by the lesser height of the dentary relative to the height of the teeth and by the presence of a longitudinal depression on its anterior–inferior margin. Teeth slightly more obviously bicuspid.' It was made the type species of *Samaria* by Novikov (1991, pp. 101–102), and distinguished from other genera by the shape of the molariform teeth, by the reduction of palatal tooth rows, the relative height of the dentary, and possibly by the overall skull shape.

The taxon is most comparable to *Orenburgia* (Spencer and Storrs, 2000) from which it differs in only minor features that are subject to individual variation (cf. Figures 9.10D and 9.11A, B). Of the features listed in the diagnosis above, the coronoid is not preserved in the currently available material of *Orenburgia* for comparison. The dentary tooth morphology of *Samaria* is very similar to that of *Lestanshoria.*

Lestanshoria Novikov, 1991

Lestanshoria massiva Novikov, 1991

See Figure 9.11C, D.

Diagnosis. Medium-sized procolophonid. Skull short and massive (based on observation of lower jaw). Dentary teeth: two incisiforms, five molariforms (the third highest). Crowns of molariforms bicuspid, strongly widened, flattened longitudinally, with the maximal width at the middle of tooth height, narrowing slightly toward apex. Cusps of molariforms broadly placed. (Based on Novikov, 1991, pp. 102–103.)

Holotype and locality. PIN 4370/4, dentary; Lestanshor Creek, Khei-Yaga River, Nenetskii National District, Korotaikha River basin, Arkhangel'sk Province.

Horizon. Lestanshorskaya Svita, Ustmylian Gorizont, Lower Triassic.

Comments. Novikov (1991, p. 103) differentiated *Lestanshoria* from other procolophonids on the basis of the character of the differentiation of the teeth, the shape of the molariform teeth, the dominance of the incisiforms, and the purportedly more massive and shorter skull. However, this genus appears to lack diagnostic criteria, and it strongly resembles *Orenburgia* (cf. Figure 9.10D), especially in the incremental height increase of the molariform teeth forwards to the mid row, the presence of five molariforms (inclusive of the mesial and distal intermediate molariforms), and the two massive anterior incisiform teeth (Novikov, 1991). *Lestanshoria* is probably a junior synonym of *Orenburgia.*

Timanophon Novikov, 1991

Timanophon raridentatus Novikov, 1991

See Figure 9.11E, F.

Diagnosis. Medium-sized procolophonine. Skull up to 30 mm long, egg-shaped, with almost straight lateral margins. Interorbital depression slight. Posterior margins of orbits and of pineal foramen at the same level. Frontal contributes to orbital margin. Postfrontal separated from parietal by suture. No lateral process on quadratojugal. Palate strongly curved longitudinally, with four short tooth rows. Interpterygoid notch wide. Maxillary teeth: two incisiforms, four molariforms; dentary teeth: three of four incisiforms, four molariforms (the second and third highest and equal in height). Crowns of molariforms bicuspid, widened transversely, with the maximal width on the middle of tooth height, narrowing evenly toward base and apex. Coronoid process of lower jaw rounded, broader than long. (Based on Novikov, 1991, p. 100.)

Holotype and locality. PIN 3359/11, incomplete skeleton with skull and lower jaw; Pizhmo-Mezen' River; Mezen' River basin, Arkhangel'sk Province.

Horizon. Pizhmomezen'skaya Svita, Ustmylian Gorizont, Lower Triassic.

Paratypes. Additional tooth-bearing elements from localities in the Mezen' River basin listed by Novikov (1991, p. 101).

Comments. *Timanophon* is superficially similar to *Orenburgia* (cf. Figure 9.10D), but it differs in the possession of three, rather than two, dentary incisiform teeth. However, *Timanophon* appears to represent a metataxon, being only distinguished by possession of a unique combination of primitive characters and autapomorphies (Spencer and Sues, 2000).

Insulophon Novikov, 1992

Insulophon morachovskayae Novikov, 1992

Diagnosis. Autapomorphies include: adductor fossa extremely narrow and straight; coronoid eminence with steeply angled posterior face formed by the posterodorsal process of the coronoid and surangular (Spencer and Sues, 2000).

Holotype and locality. TsNIGRI 842/10, incomplete skull with lower jaw fragment; borehole 23, Kolguev Island, Arkhangel'sk Province.

Horizon. Charkabozhskaya Svita, Sludkian(?) Gorizont, Lower Triassic.

Paratype. TsNIGRI 842/11, a partial disarticulated postcranial skeleton, from the type locality.

Comment. This specimen was obtained from an exploration borehole on Kolguev Island, in the Russian Arctic. Such boreholes had also yielded the prolacertiform *Boreopricea* from similar buried Triassic strata (Tatarinov, 1978; Benton and Allen, 1997). *Insulophon* is said to differ from other procolophonines in the form of the quasi-molars, in general skull shape, in the form of the coronoid process and of the adductor notch (Novikov and Orlov, 1992, pp. 182–183). Features of the palate and teeth seem, however, to be indistinguishable from *Orenburgia bruma* (cf. Novikov, 1994, figs. 10, 13).

Taxa provisionally removed from the Procolophonoidea

Vitalia Ivakhnenko, 1973a

Vitalia grata Ivakhnenko, 1973a

Diagnosis. 'Lower jaw low at the symphysis, teeth elongate-conical, with weakly expanded crowns, with blunt lateral cusps.' (Ivakhnenko, 1979, p. 21).

Holotype and locality. PIN 104/3105, lower jaw with teeth; Lipov hollow, Don River basin, Volgograd Province.

Horizon. Lipovskaya Svita, Yarenskian Gorizont, Lower Triassic.

Comments. Vitalia was described by Ivakhnenko (1973a) as a procolophonid, and specifically as a procolophonine (Ivakhnenko, 1979, p. 21). However, its dentition is unusual, unlike any fully identified procolophonid. A new specimen (PIN unnumb.) displays a better preserved crown morphology than the holotype, and confirms its unusual nature.

The crown structure has no parallel in any definitely assignable procolophonoid. There are two transversely expanded terminal cusps on each side of the teeth, set inside a flattened, transversely expanded terminal basin. The posteriormost two teeth are larger, and, viewed occlusally, are more equidimensional, with narrow mesial and distal hollows, which represent the parts of the terminal basin of more anterior teeth behind and in front of the central cusp.

Beyond exhibiting transversely expanded marginal teeth (seen in several other groups), there are no unequivocal characters supporting inclusion of *Vitalia* in Procolophonoidea. It is not possible to place *Vitalia* in another group: such obscure broad-toothed amniote remains are not uncommon in the Permo-Triassic. Some may belong to procolophonid relatives, others to trilophosaurids (archosauromorph diapsids), others to synapsids, or to other as yet incompletely known groups (e.g. Sues and Olsen, 1993).

Coelodontognathus Otschev, 1967

Coelodontognathus ricovi Otschev, 1967

Coelodontognathus donensis Otschev, 1967

Diagnosis. 'Skull 60 mm long. Lower jaw relatively low and elongate. Teeth transversely widened, and regularly serrated. First and last teeth of the lower jaw expanded and without serrations. In each half of the lower jaw, as well as, apparently, in the upper jaw, there were about 10 teeth.' (Ochev, 1967, p. 15)

Holotypes and locality. SGU 104/3101 (*C. ricovi*), right dentary; SGU 104/3103 (*C. donensis*), right dentary and nine teeth, and a further left and right dentary (SGU 104/3104, 3105); Lipovaya Balka, Don River basin, Volgograd Province.

Horizon. Lipovskaya Svita, Yarenskian Gorizont, Lower Triassic.

Comments. Coelodontognathus is almost certainly not a procolophonoid for basically the same reasons outlined for *Vitalia* above. The only character that seems to have been used to suggest procolophonid affinities is transversely expanded cheek teeth. However, expanded cheek teeth occur in other unrelated groups. The rest of the morphology of *Coelodontognathus* is quite unlike a procolophonoid.

Discussion

Over the years, 20 species and 14 genera of procolophonoids have been described from the Russian Permo-Triassic. Many of these are distinctive, and they attest to an important evolutionary radiation of the group in Eastern Europe. However, many of the taxa have been founded on rather incomplete materials, and comparisons among taxa have been difficult. Thorough revision is required, but a survey of the available specimens in PIN has suggested that the true diversity of described procolophonoids from Russia may be rather lower, at most six genera and 13 species (listed stratigraphically).

Upper Permian
  Severodvinskian Gorizont
    Microphon exiguus Ivakhnenko, 1983
Lower Triassic
  Vokhmian Gorizont
    Phaanthosaurus ignatjevi Tchudinov and Vjuschkov, 1956
    Phaanthosaurus simus (Ivakhnenko, 1974) [incl. *Contritosaurus*, *C. convector*]
  Rybinskian Gorizont
    '*Tichvinskia jugensis*' Vjuschkov and Tchudinov, 1956
(Procolophonoidea *incertae familiae*)
  Sludkian Gorizont
    Orenburgia concinna Ivakhnenko, 1975 [incl. *Samaria* Novikov, 1991; *Lestanshoria massiva* Novikov, 1991; *Insulophon morachovskayae* Novikov, 1992]
  Ustmylian Gorizont
    Orenburgia bruma Ivakhnenko, 1983
    Timanophon raridentatus Novikov, 1991
  Yarenskian Gorizont
    Tichvinskia vjatkensis Tchudinov and Vjuschkov, 1956
    Kapes amaenus Ivakhnenko, 1975
    Kapes majmesculae (Otschev, 1968)
    Kapes komiensis (Ivakhnenko, 1975) [incl. *Macrophon* Ivakhnenko, 1975]
    Orenburgia enigmaticus (Tchudinov and Vjuschkov, 1956)
  Donguz Gorizont
    Kapes majmesculae (Otschev, 1968) [incl. *Kapes serotinus* Novikov, 1991]

This tentative revision confirms that there was generally one taxon of procolophonid present in each gorizont in the Russian Upper Permian to Middle Triassic sequence (Chapter 7), except during the time of deposition of the Yarenskian Gorizont, when as many as four genera and six species may have occupied European parts of Russia.

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