A SMALL LEPIDOSAUROMORPH REPTILE FROM THE EARLY TRIASSIC OF POLAND

SUSAN E. EVANS and MAGDALENA BORSUK-BIAŁYNICKA

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The Early Triassic karst deposits of Czatkowice quarry near Kraków, southern Poland, has yielded a diversity of fish, amphibians and small reptiles. Two of these reptiles are lepidosauromorphs, a group otherwise very poorly represented in the Triassic record. The smaller of them, *Sophineta cracoviensis* gen. et sp. n., is described here. In *Sophineta* the unspecialised vertebral column is associated with the fairly derived skull structure, including the tall facial process of the maxilla, reduced lacrimal, and pleurodonty, that all resemble those of early crown-group lepidosaurs rather then stem-taxa. Cladistic analysis places this new genus as the sister group of Lepidosauria, displacing the relictual Middle Jurassic genus *Marmoretta* and bringing the origins of Lepidosauria closer to a realistic time frame.

Key words: Reptilia, Lepidosauria, Triassic, phylogeny, Czatkowice, Poland.

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INTRODUCTION

Amongst living reptiles, lepidosaurs (snakes, lizards, amphisbaenians, and tuatara) form the largest and most successful group with more than 7 000 widely distributed species. The two main lepidosaurian clades are Rhynchocephalia (the living *Sphenodon* and its extinct relatives) and Squamata (lizards, snakes and amphisbaenians). Currently, the earliest recorded rhynchocephalians are of early Late Triassic age (Carnian, Scotland and Germany, Fraser and Benton 1989), but these taxa are already quite derived, and it is clear that rhynchocephalian evolution began well before this time (Evans 2003). Similarly, although the earliest true lizards are from the Late Triassic (Datta and Ray 2006) and Early Jurassic (Evans *et al.* 2002), of India, and the Mid Jurassic of Britain (*e.g.*, Evans 1993, 1994a, 1998), their diversity at this time provides clear evidence of an earlier origin. On current evidence, therefore, we would predict that Rhynchocephalia and Squamata had diversified from more basal lepidosauromorphs by at least the Mid Triassic. Frustratingly, virtually nothing is known of this Early–Mid Triassic period of lepidosauromorph history, barring two very incomplete specimens from the Permo-Triassic of South Africa — *Paliguana* (a partial skull, Broom 1903; Carroll 1975) and *Saurosternon* (a postcranial skeleton, Carroll 1975, 1977, but see Müller 2004 for a different phylogenetic hypothesis). Furthermore, only four other taxa are currently placed on the lepidosaurian stem (*i.e.*, within Lepidosauromorpha but outside crown-group Lepidosauria). These are the Middle Jurassic *Marmoretta* (Evans, 1991) and the Late Triassic gliding kuehneosaurs (*Kuehneosaurus*, *Kuehneosuchus*, *Icarosaurus*; Robinson 1962, 1967a, b; Colbert 1966, 1970). All four are survivors of an earlier period in lepidosauromorph history. Of the many other taxa previously referred to the group from the Permian and Triassic (*e.g.*, *Coelurosauravus* Carroll, 1978; *Fulengia* Carroll *et* Galton, 1977; *Colubrifer* Carroll, 1982; *Lacertulus* Carroll *et* Thompson, 1982; *Blomosaurus* Tatarinov, 1978; *Santaisaurus* Sun, Li, Ye, Dong, *et* Hou, 1992; *Kudnu* Bartholomai, 1979), none are recognised as lepidosauromorphs and most can be attributed to other reptilian groups (*e.g.*, archosaurs, Evans and Milner 1989; procolophonians, Evans 2001). The Mid Jurassic *Tamaulipasaurus* (Clark and Hernandez 1994) is a problematic and highly specialized taxon, the affinities of which remain uncertain.

The Early Triassic microvertebrate assemblage of Czatkowice 1 is therefore unusual in containing two lepidosauromorphs. One, an early kuehneosaurid, is described elsewhere in this volume (Evans 2009); the other is smaller and more delicate. It is described here.

Institutional abbreviation. — ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

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MATERIAL AND METHODS

The original Czatkowice 1 material is karstic bone breccia from which bone is extracted by solution in weak acetic acid and the resulting residues sorted carefully. As outlined elsewhere, dentitions were first recognised and then matched (maxilla to dentary and to premaxilla) using high power Scanning Electron Microscopy (SEM) images of tooth morphology. Attribution of other elements is more tentative, but relies primarily on matching facets, sculpture pattern, and adult size, and to a lesser degree on relative commonality of the elements. For the small lepidosauromorph described in this paper, we are confident of our attribution of jaw elements to one another, and of the attribution of one set of small, delicately built vertebrae. Other elements of the skull and postcranial skeleton also figure in the description. Their attribution depends on a combination of size (consistent small size with little or no range), sculpture pattern, and fit.

Over the whole text, the term "relictual" is used to describe late survivors of basal phylogenetic lineages that co-occur with representatives of more derived lineages. The term "early" refers to the stratigraphic occurence of the discussed taxa. "Primitive" is used to refer to characters, and to taxa situated at or near the base of the lineage in question.

SYSTEMATIC PALEONTOLOGY

Clade Neodiapsida Benton, 1985

Clade Lepidosauromorpha Gauthier, 1984

Family uncertain

Genus *Sophineta* gen. n.

Type and only species: *Sophineta cracoviensis*.

Derivation of the name: To honour Professor Zofia Kielan-Jaworowska of the Instytut Paleobiologii PAN. Greek *sophia* (wisdom) is the classical root of the name Zofia.

Diagnosis. — As for type and only species.

Sophineta cracoviensis sp. n.

Derivation of the name: From *Cracovia*, the Latin name for Kraków, the closest major Polish city to the Czatkowice 1 locality, and also to recognise researchers at the University of Kraków (Drs Paszkowski and Wieczorek) for their pioneering work at the locality.

Holotype: ZPAL RV/175, a nearly complete right maxilla.

Type locality and horizon: Czatkowice 1 dated as Early Triassic (earliest Late Olenekian) based on local geology (the upper limit is the Röt transgression at the end of the Early Triassic) and faunal analysis (Shishkin and Sulej 2009).

Diagnosis. — A small lepidosauromorph that differs from Late Triassic kuehneosaurs, *Marmoretta* and the Czatkowice 1 kuehneosaur (Evans 2009) in having short notochordal vertebrae without transverse processes; differs from all kuehneosaurs in tooth implantation (pleurodont rather than subthecodont), the presence of paired rather than confluent nares, the presence of weakly developed zygosphenoidal articulations on the vertebrae, the possession of notochordal rather than amphiplatyan vertebrae, and tooth morphology (compressed keeled tooth tips rather than simple cones); differs from the Permo-Triassic *Paliguana* in having a deeper facial process on the maxilla and a much smaller lacrimal (as deduced from facets on the maxilla); differs from *Marmoretta* in that the latter has a specialised maxillary/premaxillary overlap whereby a long process from the maxilla fits into a slot in the lateral surface of the dorso-ventrally compressed premaxilla; resembles lepidosaurs in having weak zygosphenes, short vertebrae and single-headed ribs throughout the column, but differs in having a shallower pleurodont tooth implantation and the apparent absence of both a thyroid fenestra and functional caudal autotomy.

Referred specimens. — ZPAL RV/226–230, 445, 1086 (frontals); ZPAL RV/231, 232, 443 (parietals); ZPAL RV/1056 (prefrontal); ZPAL RV/233–235, 966, 967, 1060 (postfrontals); ZPAL RV/236–238, 1058, 1062 (postorbitals); ZPAL RV/10, 239–244, 965, 1054, 1059 (jugals); ZPAL RV/245–249, 1055, 1057, 1069 (squamosals); ZPAL RV/968–973 (pterygoids); ZPAL RV/13, and 974 (quadrates); ZPAL RV/3, 7, 174–178, 455, 472, 493, 823, 824 (maxillae); ZPAL RV/1061 (premaxilla); ZPAL RV/174, 189, 392, 493, 512, 1101 (dentaries); ZPAL RV/23, 627, 628, 1079, 1080, 1098, 1108, 1110, 1121 (vertebrae); ZPAL RV/948–950, 952, 959, 1053, 1063 (ilia).

Note. — Based on the dimensions of the holotype maxilla and comparative skull proportions in *Marmoretta* (Evans 1991), the total skull length is estimated as about 10 mm in *Sophineta*, with a body length (without tail) of about 30 mm. The skull to body (without tail) ratio in the early Jurassic basal rhynchocephalian *Gephyrosaurus* is 1/3 (Evans 1981).

SKULL BONES

As reconstructed (Fig. 1), the skull of *Sophineta* is that of a modified diapsid with a relatively short preorbital region. The orbits, narial openings and upper temporal fenestrae are large, and the lower temporal fenestrae are open ventrally. The quadrate was firmly held by its attachments to the pterygoid and squamosal but its arched posterior margin suggests the presence of a tympanic membrane. Although a pterygoid has been attributed to *Sophineta*, there is currently insufficient information to permit a palatal reconstruction.

Premaxilla. — The attributed premaxilla (Fig. 2B) has a long, dorsal nasal process that is anteroposteriorly deeper at the base than it is wide. It differs from that of the Czatkowice 1 protorosaur-grade diapsid (Borsuk-Białynicka and Evans 2009b) in having a nasal process with a broad, planar medial surface that met the opposite premaxilla in a firm joint. Posterolaterally, a slender process separates from the alveolar margin of the bone and clearly ran along the medial side of the maxilla. It bears a facet dorsally between itself and the alveolar margin. Presumably the tip of the maxilla overlapped the premaxilla at this point. There were four small teeth.

Maxilla. — The maxilla of *Sophineta* is best represented by the holotype ZPAL RV/175 (Fig. 2A), a nearly complete right bone, ca. 5 mm in total length. This shows a deep facial process that precludes the possibility of a large lacrimal contributing to the antorbital skull wall. The premaxillary process is short and vertical in orientation, with clearly distinct medial and lateral surfaces. There are 22–26 tooth positions.

The lateral surface of the maxilla (Figs 2A$_4$, 3A) is smooth with a basal row of nutrient foramina and, above these, isolated subsidiary openings. There is no sculpture. Seen in medial view (Figs 2A$_3$, 3B) the anterior, narial margin of the bone is gently curved and carries a shallow groove. Behind it, the maxilla formed the sidewall of the nasal chamber and bears a concavity to house parts of the nasal glands. Above this concavity the facial process is relatively tall with a rounded shape. The medial surface of the process bears three clear facets: anterior, central and posterior (Figs 2A$_3$, 3A). The first of these extends over the anterior half of the facial process and must have received the nasal. Behind it there is a facet of similar size covering the posterior half of the facial process. Posteroventral to it, as a narrow band along the descending posterior margin, is a third facet. The only two bones that lie in this position in other reptiles are the prefrontal and the lacrimal. Where the lacrimal is large (*e.g.*, *Kuehneosaurus*), the prefrontal may have only a small posterior contact with the maxilla behind the lacrimal. In this case, the major facet on this margin of the maxilla would be that for the lacrimal. In the case of *Sophineta* this cannot be the arrangement because if the central facet were for the lacrimal it would form a small element wedged between the nasal and an extensive ventral process of the prefrontal (meeting the long facet on the posterior margin). It is more likely that the central facet is for a narrow prefrontal process with a shallow lacrimal extending medially along the posterior margin of the maxilla. Either way, the lacrimal did not make a significant contribution to the antorbital skull wall.

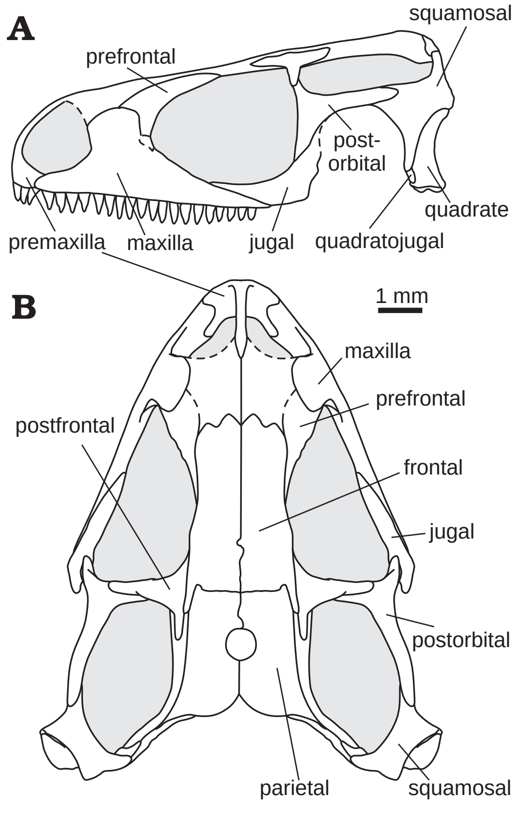

Fig. 1. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Skull reconstruction in lateral (A) and dorsal (B) views.

The maxilla shows a steady decrease in height posteriorly and the posterior three-quarters of the bone form an elongate shallow triangle with a straight ventral margin and a long sloping dorsal rim that formed the posterior, orbital, process. Medially (Figs 2A$_3$, 3B), a strong shelf develops above the tooth row, and this is perforated by a large ovoid foramen that carried the maxillary nerve and accompanying blood vessels onto the superior alveolar canal of the maxilla. Between the second and fifth tooth positions posterior to this opening, the medial side of the alveolar shelf bears a

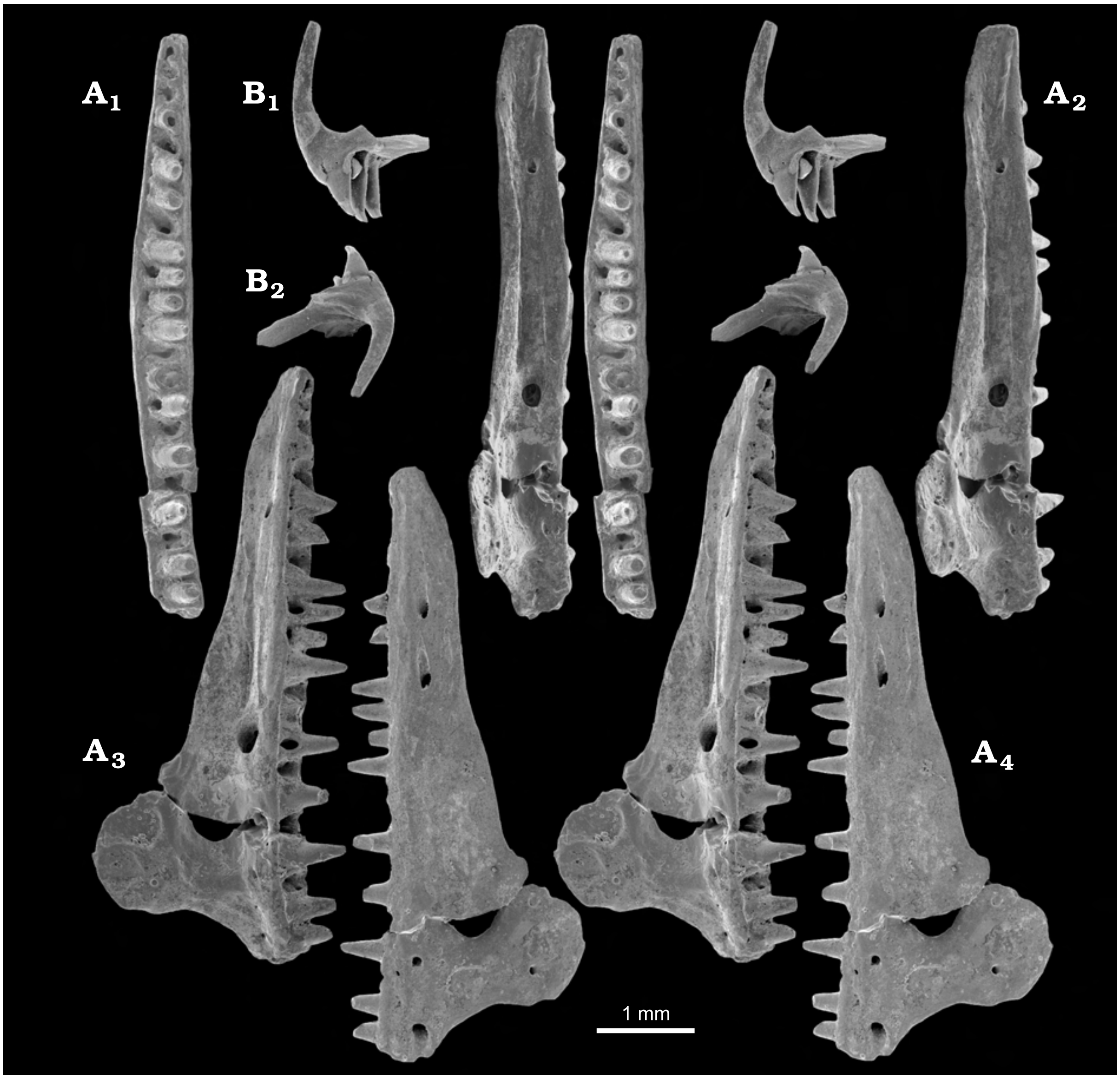

Fig. 2. *Sophineta cracowiensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Right maxilla ZPAL RV/175, the holotype, in occlusal (A_1), dorsomedial (A_2), medial (A_3), and lateral (A_4) views. **B**. Right premaxilla ZPAL RV/1061, in medial (B_1) and dorsal (B_2) views. SEM stereo-pairs.

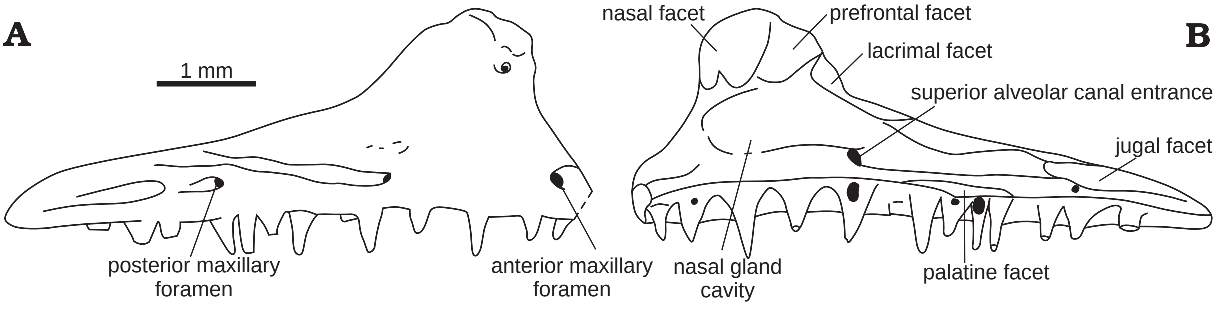

Fig. 3. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right maxilla in lateral (A) and medial (B) views. Mainly on the basis of ZPAL RV/175.

shallow facet for the maxillary process of the palatine (Fig. 3B). Further posteriorly, the supraalveolar shelf develops a gutter-like facet for the anterior process of the jugal. The remainder of the facet extends inside the dorsal lamina of the maxilla and its anterior limit is clearly circumscribed. The jugal did not reach the anterior orbital margin and formed only the posterior and posteroventral margin of the orbit.

Frontal. — Several paired frontals and parietals are known from the Czatkowice 1 assemblage and attributing them to the jaw species relies on a combination of matched sculpture, facets, size, and distribution. The frontal attributed to *Sophineta* is well-represented by both right (Fig. 4A) and left bones (Fig. 4G). The frontal is slender and lightly sculptured dorsally with a pattern of low rounded ridges and tubercles. The bone is dense and solid. Ventrally (Figs 4A, $5A_1$) the frontal is divided into medial and lateral parts by a strong crista cranii (subolfactory process). The medial half is narrowest between the orbits and widens anteriorly and posteriorly. It is concave, with the concavity deepening anteriorly in the region of the olfactory chamber. Laterally (Fig. $4A_2$) the orbital margin slopes dorso-laterally and bears strong deep facets for the prefrontal and postfrontal. The medial suture forms a simple joint anteriorly, with a small right-over-left overlap and a weakly interdigitating edge posteriorly (Figs $4A_1$, $5A_1$). There is an anterior shelf facet for the nasal, flanked laterally by a slender facet for the prefrontal that is almost confluent with the nasal facet. The nasal facet has the shape of an inverted "W" (Fig. $5A_1$) with each frontal sending a triangular process into the back of the nasal bone. Posterolaterally, the prefrontal facet extends onto the lateral surface (Fig. $4A_1$). Posteriorly the frontal is drawn into medial and lateral processes separated by a strong incision (Fig. 4G). The lateral process bears a strong ventral facet (Fig. $4A_1$) and covers the anterolateral surface of the parietal. It is notched along its outer margin by the postfrontal. The medial process varies in shape and appears to have abutted rather than overlapped the corresponding part of the parietal. Thus the frontoparietal margin was "M" shaped (Fig. 4G).

Variation: The frontals referred to *Sophineta* vary in their level of sculpture (some are unsculptured), in the degree of lateral separation of the prefrontal and postfrontal facets (the separation is greatest in small specimens, *e.g.*, Fig. 4G), and least in more mature specimens, *e.g.*, Fig. 4A), and in the precise shape of the posterior margin (with a triangular or squared median process), but there is a gradation between morphologies and it seems likely that these differences are due to age and sex rather than being taxonomically significant.

Parietal. — ZPAL RV/443 (Fig. 4C) is a well-preserved right parietal with a dorsal sculpture pattern matching that of the frontal (Fig 4C, D_2). The bone has a relatively long anterior plate and a long tapering postparietal process that extends laterally, and slightly ventrally, at roughly 45° to the main axis of the bone. The median area of the bone is usually damaged but is clearly seen to enclose a large parietal foramen. Behind this, the parietals seem to be separated in many specimens as the medial edges are angled Fig. $4D_2$). Whether this is a developmental feature or indicates the presence of postparietals is not clear. Anteriorly, the parietal bears incised lateral facets (Figs $4D_1$, 5F) for the frontal and postfrontal, but centrally the bone is serrate. The lateral margins are vertical with small adductor surfaces but no development of ventral crests. The postparietal process has a distal slot facet for the squamosal.

Variation: Parietals of *Sophineta* display a size-related variation in their level of sculpture (more in larger specimens), in the shape of the posteromedial edge, and in the extent of the facet for the squamosal/supratemporal. The shape of the posteromedial edge seems to depend on the extent of a thin bony flange running medially from the base of the postparietal process. In some specimens (*e.g.*, ZPAL RV/232), this appears to be a separate ossification and it is possible that it represents a remnant of a postparietal centre. Laterally, the slot facet for the squamosal varies in position from well along the postparietal process (large specimens, Fig. 4C) to close to the base of the process (small specimens, *e.g.*, Fig. $4D_2$). However, there is again a gradation in structure and this seems to depend on the degree of ossification over what begins as an open groove on the dorsal face of the process. The groove gradually closes in a proximodistal direction during growth, pushing the proximal limit of the facet closer to the end of the process, but whether this simply reflects ossification into the periosteum or the gradual ossification of a supratemporal centre is not clear.

Prefrontal. — Prefrontals are attributed only tentatively to *Sophineta* on the basis of size, rarity, and consistency of form in relation to the maxilla. This bone, represented by ZPAL RV/1056, has a shallow orbital margin and a thin facial lamina with two facets. The posterior facet (probably for a small lacrimal) is more shallow that the anterior one (for the facial process of the maxilla).

Postfrontal. — The postfrontal (Figs 4F, 5C, D) is attributed on a combination of fit and sculpture pattern (*e.g.*, ZPAL RV/233–235 and 1060). It is a roughly triangular bone, broadest dorsally and tapering ventrally.

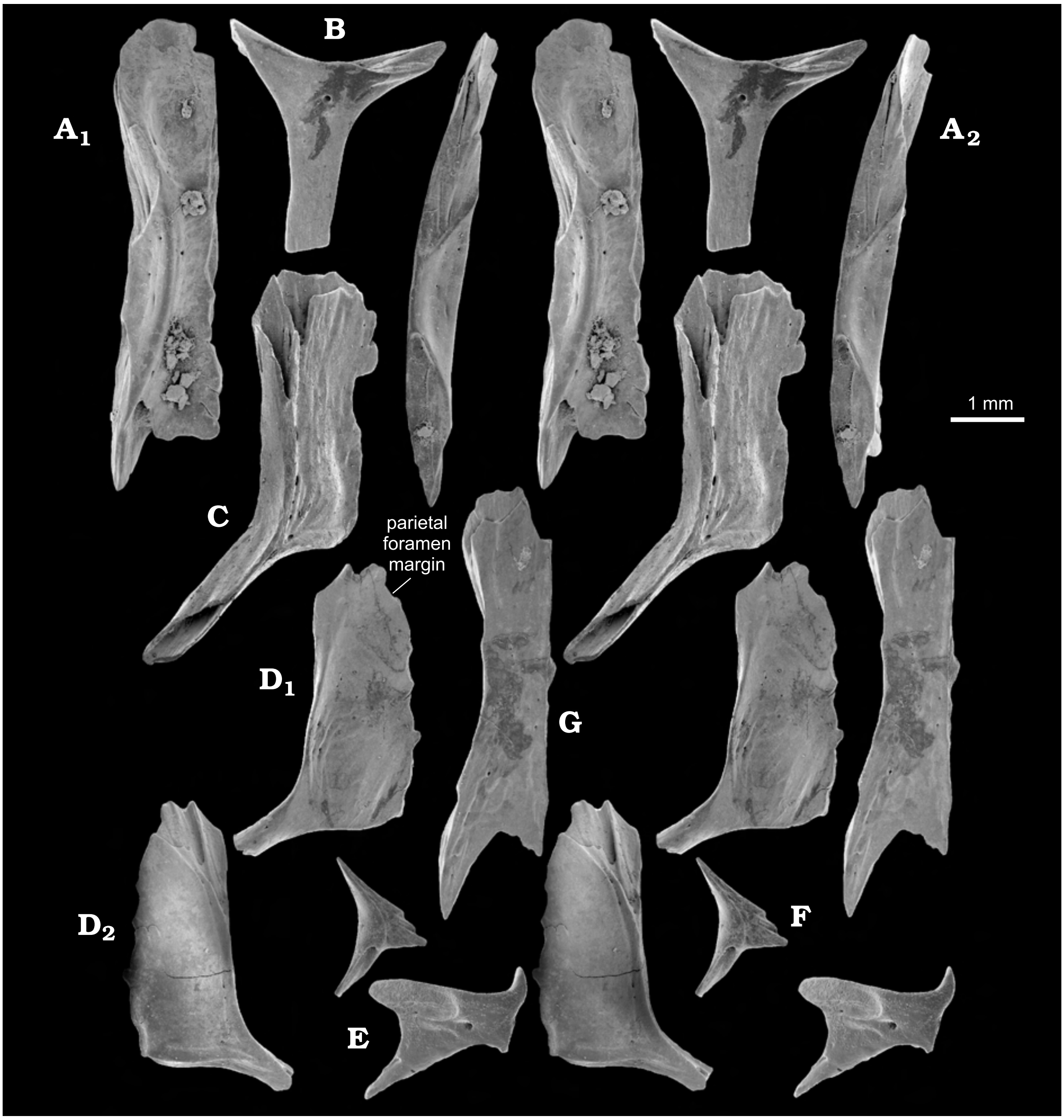

Fig. 4. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Right frontal ZPAL RV/227, in ventral (A_1) and lateral (A_2) views. **B**. Right postorbital ZPAL RV/237, in lateral view. **C**. Left parietal ZPAL RV/443, in dorsal view. **D**. Right parietal ZPAL RV/231, in ventral (D_1) and dorsal (D_2) views. **E**. Left squamosal ZPAL RV/245, in dorsal view. **F**. Left postfrontal ZPAL RV/233, in dorsal view. **G**. Right frontal ZPAL RV/226, in dorsal view. SEM stereo-pairs.

The dorsal part is divided into two short tapering processes that fit into corresponding recesses on the frontal and parietal respectively. The ventrolateral process is longer and more slender. It carries a posteroventral slot facet for the postorbital (Fig. 5C). The parietal and postorbital facets are separated for short distance and the postfrontal thus entered, though only slightly, the margin of the upper temporal fenestra.

Postorbital. —This triradiate bone is attributed on the basis of fit and bone type (Figs 4B, 5G). It is quite common and is represented by more than 20 specimens (*e.g.*, ZPAL RV/236, 237, 1058, and 1062). The bone is characterised by short dorsal (postfrontal) and ventral (jugal) processes and a long slender posterior (squamosal) process, although this is broken in many specimens. The postfrontal process bears a flat anterior facet that receives the postfrontal, the pointed tip slotting into a small recess in the back of that bone. The ventral process forms another simple overlap with the anterior margin of the jugal. The squamosal process is

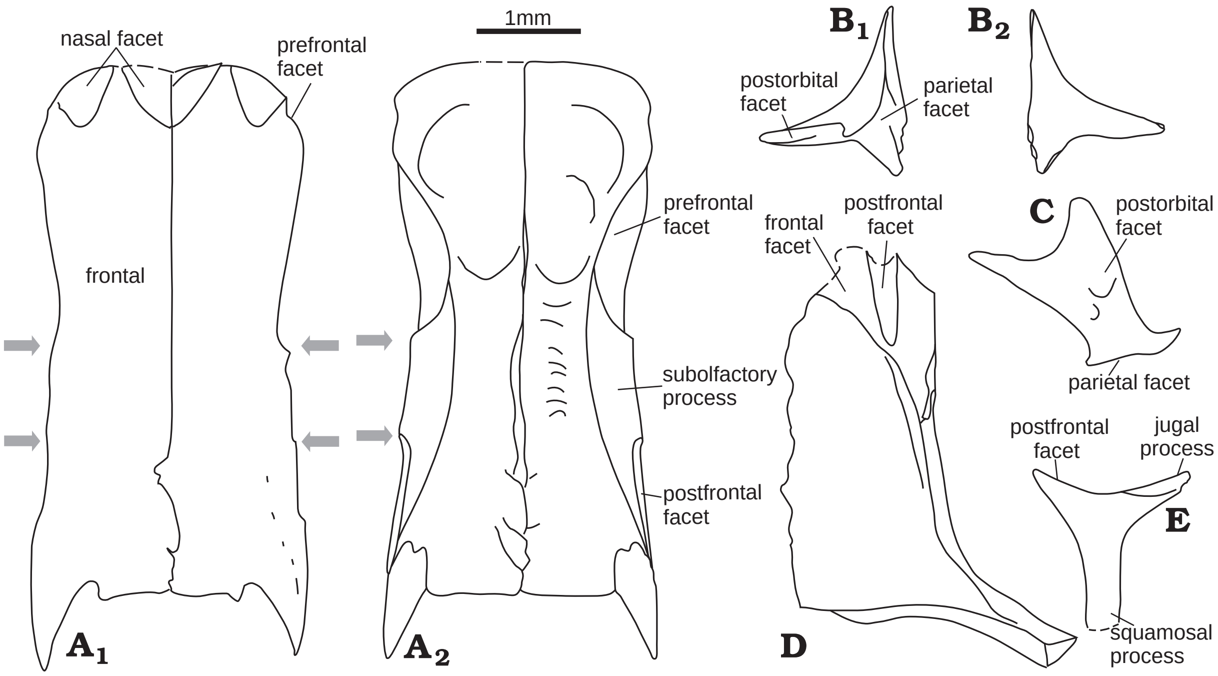

Fig. 5. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Reconstruction of skull bones. **A**. Frontals, in dorsal (A_1) and ventral (A_2) views. **B**. Right postfrontal ZPAL RV/233, in ventral (B_1) and dorsal (B_2) views. **C**. Left squamosal ZPAL RV/245, in dorsal view. **D**. Right parietal ZPAL RV/231, in dorsal view. **E**. Right postorbital ZPAL RV/237, in lateral view.

long and mediolaterally flattened, with a long, tongue-like squamosal facet at its tip. The jugal and squamosal facets are well separated from one another. This and the long postorbital are consistent with the general elongation of the medial margins of the upper temporal fenestra due to the long postparietal process.

Jugal. — Jugals are rare elements at Czatkowice 1. Amongst the small elements, there are two types of jugal. In a previous paper (Borsuk-Białynicka *et al.* 1999), one of these (ZPAL RV/10) was tentatively attributed to the smaller of the two Czatkowice 1 lepidosauromorphs, and the recovery of further specimens lends support to this (some of the larger jugals of this type bear the characteristic sculpture pattern found on other attributed bones). These are the commonest type of jugal and come in a range of sizes (Fig. 6). The smallest specimens are essentially biradiate with an anterior maxillary process, a posterodorsal postorbital process, a central, flanged body, and a very small posteroventral spur (Fig. 6B). The latter feature becomes less pronounced in the largest specimen ZPAL RV/1059 (Fig. 6C) as the main body of the bone thickens. In the latter specimen, considered mature, the sculpture has become exaggerated along the posterior edge giving a scalloped edge to the bone that is completely natural. The postorbital process carries a facet along its anterior margin for the postorbital bone (Fig. $6C_2$). This facet slots into the corresponding "wrap-around" facet on the postorbital, and is divided into two surfaces — a small anterolateral surface and a wider anteromedial surface. There is no trace of a squamosal facet apically and the jugal and squamosal probably did not meet. The maxillary process bears a convex ventromedial facet for the orbital process of the maxilla. At the medial junction of the anterior and dorsal processes, there is a large rugose facet for the ectopterygoid (Fig. $6C_2$).

Variation: the main variation is in the size of the posterior spur and the depth of the ectopterygoid facet (shallow in small specimens). Given the likelihood of some time-averaging for the Czatkowice 1 assemblage, the possibility that some of these differences might be taxonomically significant cannot be excluded. However, the differences between the specimens in size, thickness, outline and surface sculpture falls within the range of ontogenetic variation in extant lizards (see *e.g*, Stephenson 1960; Presch 1969; Rieppel and Crumly 1997; Barahona and Barbadillo 1998). It has no effect on either the phylogenetic analysis or the reconstruction.

Squamosal. — Several tiny quadriradiate squamosals (*e.g.*, ZPAL RV/245–249) are tentatively attributed to *Sophineta* (the Czatkowice 1 kuehneosaur has a reduced squamosal). They are similar to the bones of basal diapsids, but also to those basal rhynchocephalians (*e.g.*, *Gephyrosaurus*) in having a short

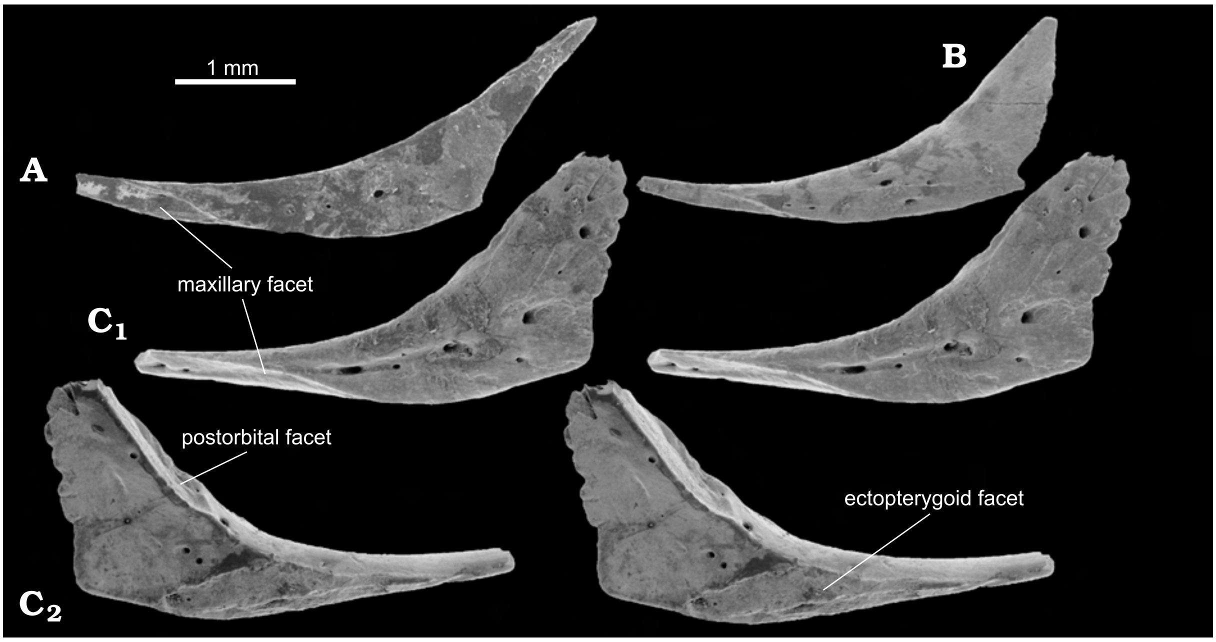

Fig. 6. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Juvenile left jugal ZPAL RV/10, in lateral view. **B**. Mature right jugal ZPAL RV/243, in lateral view. **C**. Mature left jugal ZPAL RV/1059, in lateral (C_1) and medial (C_2) views. SEM micrographs; C stereo-pairs.

posteroventral process contributing to the dorsal rim of the tympanic membrane, a dorsomedial process that bears a short posterior groove facet that probably abutted a supratemporal, itself forming the link between squamosal and parietal (because it does not fit into the parietal slot facet); an anteroventral process meeting the anterior quadrate rim; and an anterior process to the postorbital (Figs 4E, 5E). The latter is elongate with a long anterodorsal facet suggesting the squamosal formed the major part of the ventrolateral and dorsal margins of the upper and lower temporal fenestrae respectively. Where preserved (*e.g.*, ZPAL RV/245), the tip of the anteroventral process carries a narrow facet that must be for a small quadratojugal. Although it is possible that these small bones represent juvenile elements of either the archosauriform, *Osmolskina*, or the protorosaurian-grade reptile, their relatively robust build and finished bone surfaces suggest they are not immature.

Quadrate. — Of the non-archosauriform quadrates of the Czatkowice 1 material, one type is common and clearly belongs to the protorosaur-grade reptile (Borsuk-Białynicka and Evans 2009b). Two other morphotypes, distinguished from the latter by their smaller size and finer structure, are associated here with the lepidosauromorph material. The first of these, represented by several specimens, is described elsewhere (Evans 2009) and recognized as the kuehneosaurid type. Specimens of the second morphotype are very rare, but are readily distinguished from the others and are tentatively attributed to *Sophineta*. Represented by specimens ZPAL RV/13 (Fig. 7A), and possibly ZPAL RV/974 (Fig. 7B_1, B_2), the *Sophineta* quadrate has a shorter, wider posterior pillar; less angulation of the medial wing and lateral conch (so that the anterior surface is flat rather than deeply grooved in contrast to the kuehneosaurid reptile from the same material); a wider dorsal head; and a deeper ventral condyle. The lateral quadratojugal notch is more open and rounded than that of the kuehneosaurid quadrate, and either bears a distinct quadratojugal facet on its ventral margin, or has a quadratojugal partially fused in place (ZPAL RV/13, Fig. 7A_2), as sometimes occurs in the basal rhynchocephalian, *Gephyrosaurus* (Evans 1980). In addition, the dorsal head bears a narrow anterolateral facet for the descending process of the squamosal. The morphology of the quadrate is thus compatible with that of the attributed squamosal, which also has a narrow ventral facet for a quadratojugal. In all its details, the bone is strikingly similar to that of *Gephyrosaurus*.

Pterygoid. — A series of small pterygoids are tentatively attributed to *Sophineta* on the basis of a consistent small size. Most specimens preserve the mid-section of the bone comprising the posterior part of the palatal plate, the basipterygoid joint, and the anterior part of the quadrate ramus. Together, specimens ZPAL

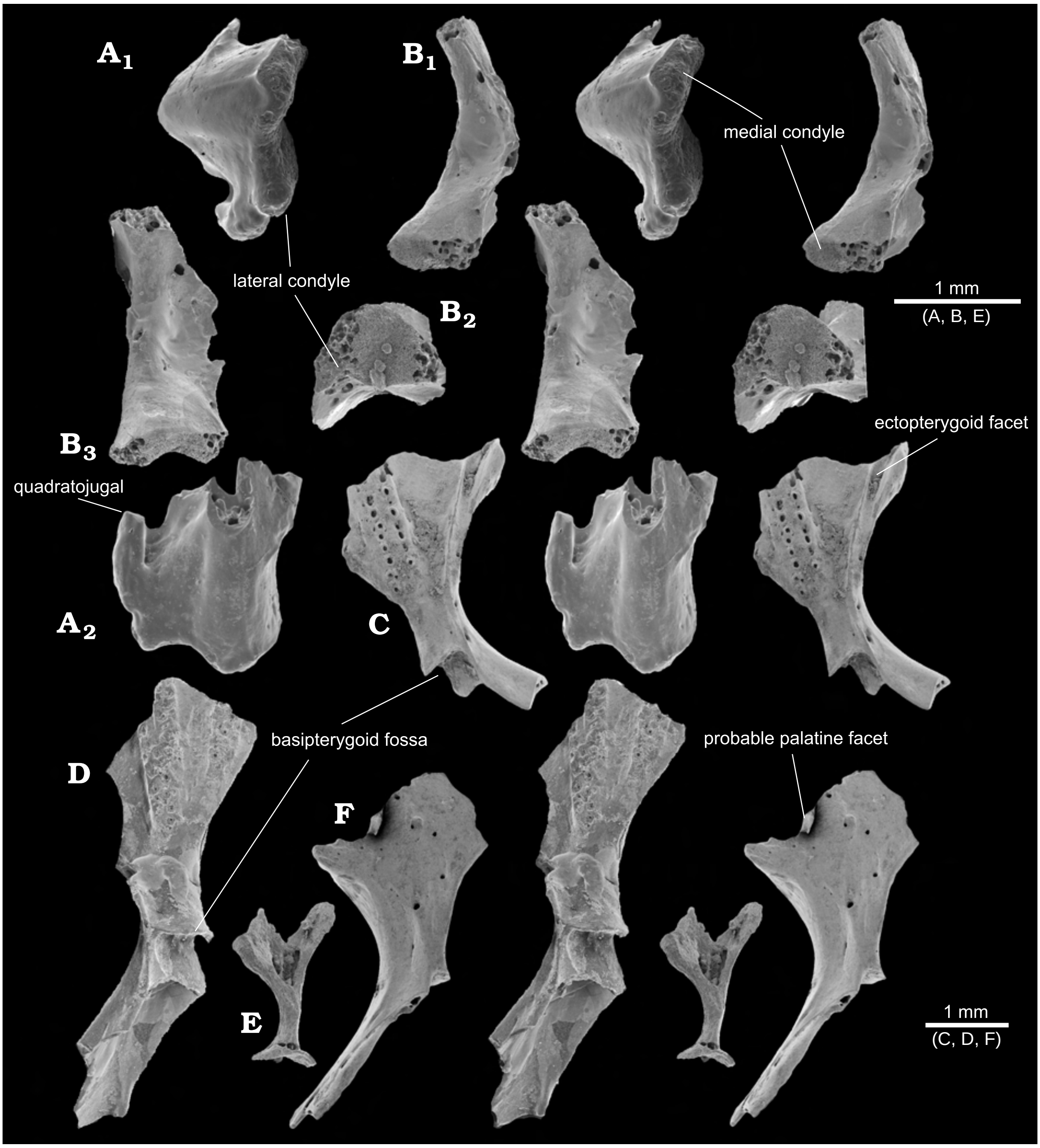

Fig. 7. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Distal end of a left quadrate and quadratojugal ZPAL RV/13, in distal (A_1) and posterior (A_2) views. **B**. Left quadrate ZPAL RV/974, in medial (B_1) and posterior (B_2) views; distal condyle of the same (B_3, posterior to the right, lateral toward the bottom). **C**. Left pterygoid ZPAL RV/968, in ventral view. **D**. Right pterygoid ZPAL RV/746, in ventral view. **E**. Left ectopterygoid ZPAL RV/1142, in dorsal view. **F**. Left pterygoid ZPAL RV/969, in dorsal view. SEM stereo-pairs.

RV/968, 746, and 969 provide most details (Fig. 7C, D, F, respectively). The central part of the bone comprises the recess for the basipterygoid process of the sphenoid. If the palatal plate is oriented horizontally, then the basipterygoid fossa appears to open as much ventrally as medially. It seems likely therefore that in life the pterygoid was rotated slightly about its long axis so that the medial and lateral margins of the palatal plate were actually dorsomedial and ventrolateral in position. Posterior to the basipterygoid fossa, the bone extends into a narrow quadrate process that bears an elongate medial concavity for the pterygoideus attachment. Just behind the basipterygoid fossa in ZPAL RV/968 (Fig. 7C) the dorsal margin of the bone expands slightly into a weak epipterygoid eminence but there is, at best, only a weak indication of a facet on this spec-

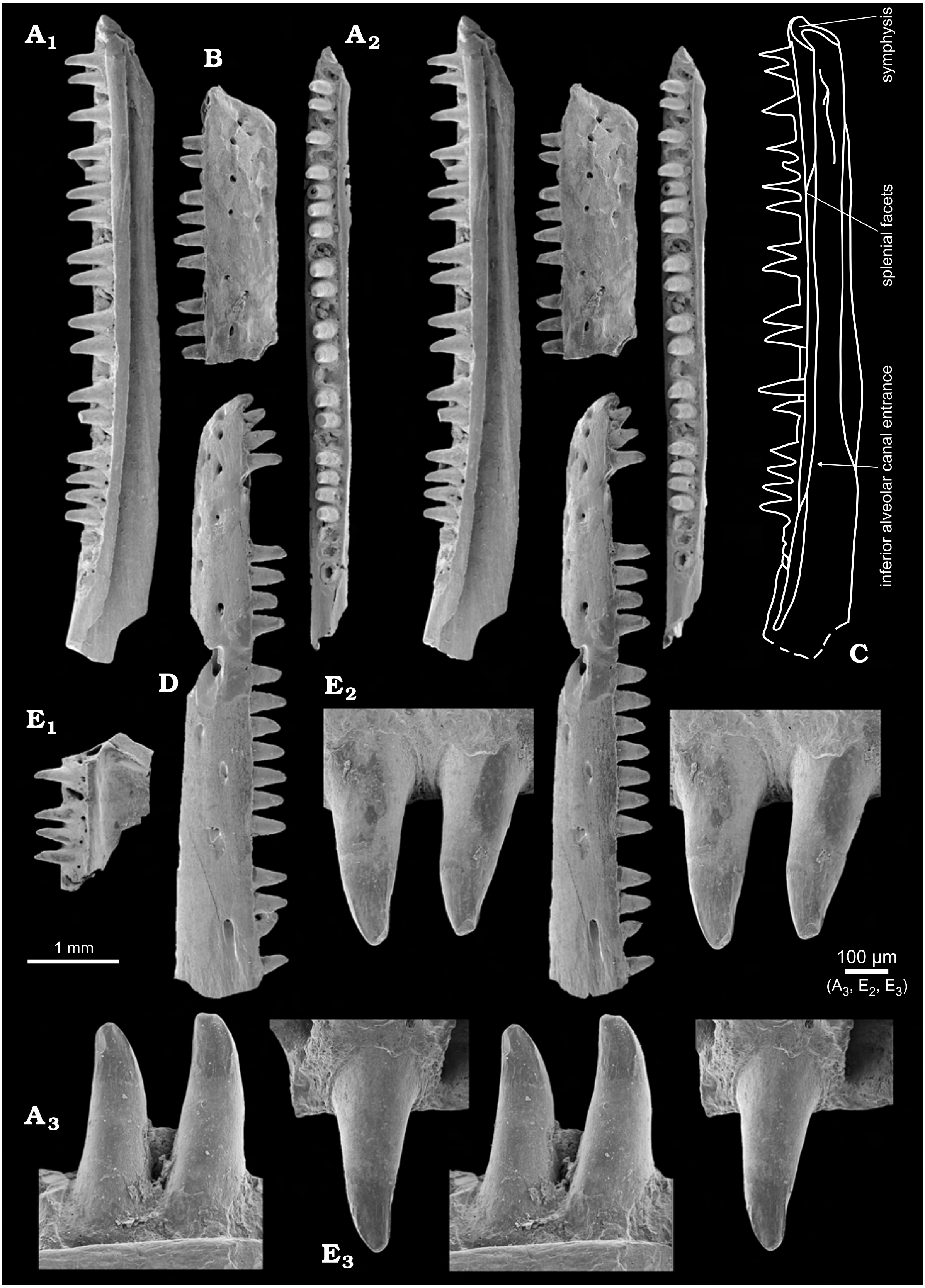

Fig. 8. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left dentary ZPAL RV/1101, in lingual (A_1) and occlusal A_2) views; two teeth of the same in lingual view (A_3). **B**. Anterior part of the right dentary ZPAL RV/174, in labial view. **C**. Left dentary reconstruction, in lingual view. **D**. Left dentary ZPAL RV/493, in labial view. **E**. Fragment of right maxilla ZPAL RV/176, in lingual (E_1) view; E_2, E_3 isolated teeth of the same. All but C SEM micrographs; all but C, E_1 stereo-pairs.

imen. Anterior to the basipterygoid fossa, the palatal plate fans out both medially and laterally. On the palatal surface traces of four tooth rows are preserved, the two lateral and two medial rows each running parallel to one another, but with the medial and lateral pairs separated from one another by a diverging gap. The medial rows begin on the inner edge of the pterygoid, but run directly anteriorly as the edge extends medially. They thus become increasingly separated from this edge. Laterally the bone expands into a pterygoid flange that ends in a deeper, flattened tuberosity. The flange bears dorsolateral and ventrolateral facets for the ectopterygoid. Further medially, the dorsal surface of the bone bears facets for the palatine — but the thinner, more anterior parts of these facetted surfaces are broken away.

Ectopterygoid. — ZPAL RV/1142 is a small left ectopterygoid (Fig. 7E) tentatively attributed to *Sophineta* on the basis of size, robusticity and fit. It closely resembles the ectopterygoid of *Gephyrosaurus* (Evans 1980) and other generalised lepidosaurs. The bone has a small, deep lateral head that met the jugal and an expanded, bifurcate medial head that slotted into the lateral margin of the pterygoid and bears anterior and posterior facets for that bone. Together the ectopterygoid and pterygoid formed a vertical flange that guided movements of the lower jaw. Between the medial and lateral heads is a slender neck that formed the posterior margin of the suborbital fenestra.

Braincase. — There are many small fragments of braincase bones, some of which must pertain to *Sophineta*. However, distinguishing these from juvenile bones of the other non-archosaurian diapsids is proving difficult and requires a more detailed survey of early lepidosauromorph braincase morphology than is possible here.

Dentary. — The dentaries (Fig. 8A–C) are relatively abundant in the material (*e.g.*, ZPAL RV/174, 189, 391, 512, and 1101) but are slender and usually break into several pieces. There were an estimated 25–30 tooth positions. The symphysis (Fig. $8A_2$) is deep but only the upper half carries an articular surface; the lower half is a sharp blade. In medial view, the subdental ridge is moderately developed and of constant height with a clear facet for the splenial. The Meckelian fossa is fairly deep and is without a clear ventral rim, although this margin does carry a shallow facet through most of its length, either for the angular or the lower margin of the splenial. Behind the tooth row, the subdental ridge continues backward for some distance and bears a narrow horizontal facet for the coronoid. Close to the symphysial end, below tooth position 7, there is a consistent small foramen. The lateral surface is perforated by large nutrient foramina in a double row. The inferior alveolar canal enters the bone through a foramen towards the rear of the tooth row.

Dentition. — The teeth appear simple and conical but under scanning electron microscopy (Fig. $8A_1$, A_3, E_2) are shown to have compressed and slightly keeled tips. This morphology assists in the attribution of elements from upper and lower jaws. The implantation is weakly pleurodont with the teeth attached to a labial jaw margin that is deeper than the lingual one. In many specimens there is a build up of ankylosing bone around the bases of these teeth (*e.g.*, Fig. $8A_2$), perhaps to increase the robusticity. Teeth underwent continued replacement from the lingual surface, as shown by the pattern of replacement pits.

POSTCRANIAL SKELETON

Axial skeleton. — A subset of the Czatkowice 1 vertebrae are small and show a distinctive morphology (Figs 9, 10), very similar to that of the Jurassic *Gephyrosaurus* and of the living *Sphenodon*. All display a fully notochordal amphicoelous centrum but closed neurocentral sutures in all but the smallest specimens. All bear single headed rib facets (*e.g.*, Fig. 9C, E) without any development of transverse processes on trunk vertebrae, and all have strong zygapophyses with a weak medially angled component that matches the rudimentary zygosphene-zygantrum (Fig. $9D_1$) system found in *Sphenodon* and *Gephyrosaurus*. The neural spines, though broken, have a broad base.

Cervical (ZPAL RV/1121) and dorsal (*e.g.*, ZPAL RV/1098, 1099,1108, and 1109) vertebrae have a keeled centrum, though more broadly so in the dorsals. There is no clearcut evidence of intercentra, but they are likely to have been present since they are retained in rhynchocephalians and in some basal squamates. In the sacral region, the ribs are usually fused to the centrum but, as in *Gephyrosaurus*, the suture lines are still visible in some specimens, and in juveniles they have separated (ZPAL RV/628, Fig. 10). ZPAL RV/627

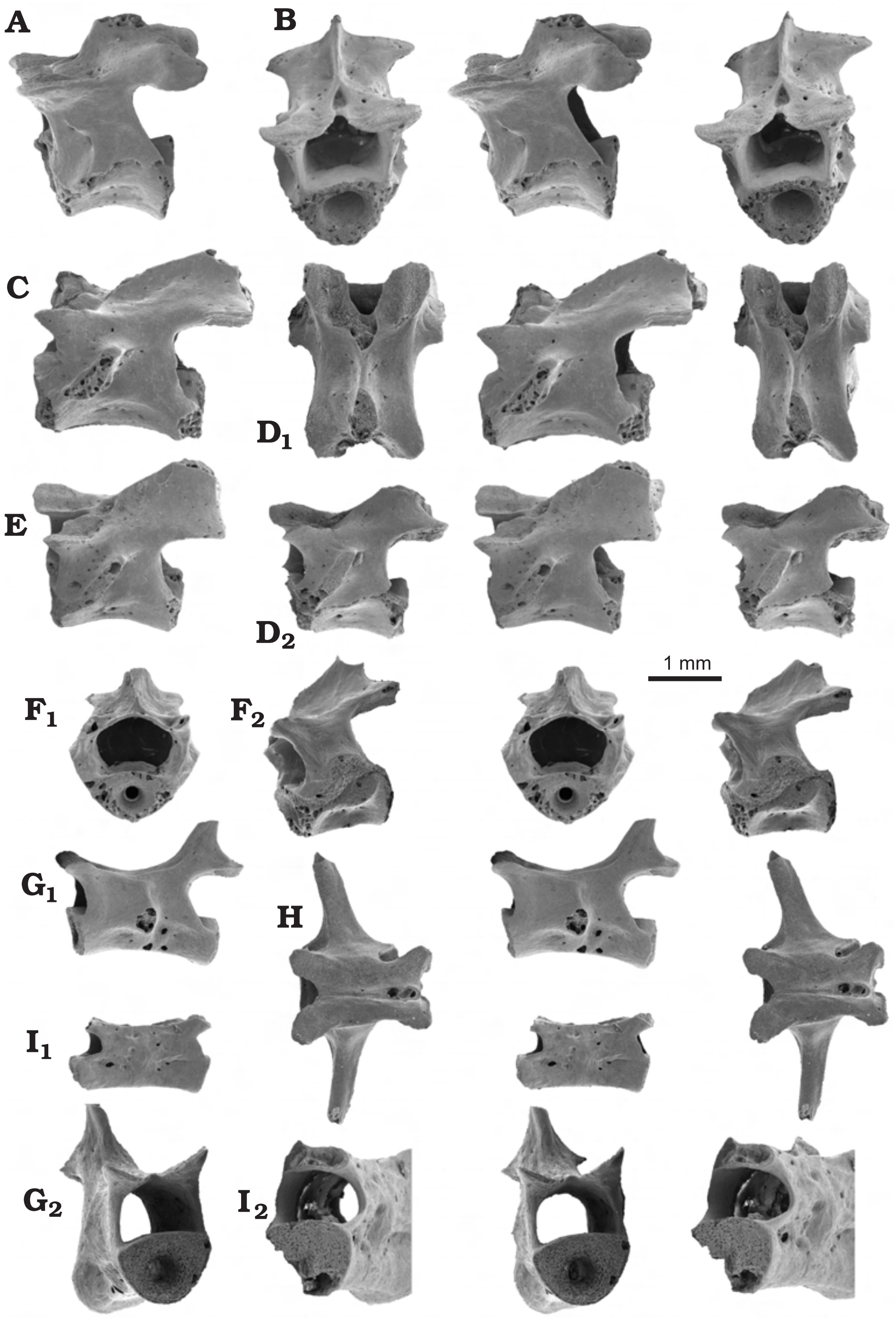

Fig. 9. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae. **A**. Cervical ZPAL 1121. **B**. Anterior dorsal ZPAL RV/1108. **C**. Dorsal ZPAL RV/1098. **D**. Juvenile dorsal ZPAL RV/1110. **E**. Dorsal ZPAL RV/1109. **F**. Sacral. **G**. Caudal ZPAL RV/1080. **H**. Anterior caudal ZPAL RV/627. **I**. Posterior caudal ZPAL RV/1079. Left side (A, C, D_2, E, F_2, G_1), cranial (B, F_1, G_2), dorsal (D_1, H), right side (I_1), and caudal (I_2) views. SEM stereo-pairs.

(Figs 9H, 11D) appears to be an anterior caudal (probably caudal 2), with long, transverse processes that have a slight anterior angulation. Further posteriorly, the transverse processes remain long but become narrower and lose the angulation. ZPAL RV/1079, 1080 (Fig. 9G, I) are more posterior caudals, showing reduction of the transverse process, and elongation and a slight grooving of the midventral surface of the centrum. Although these vertebrae lack fully developed autotomy septa, some (*e.g.*, ZPAL RV/1079) show a disruption

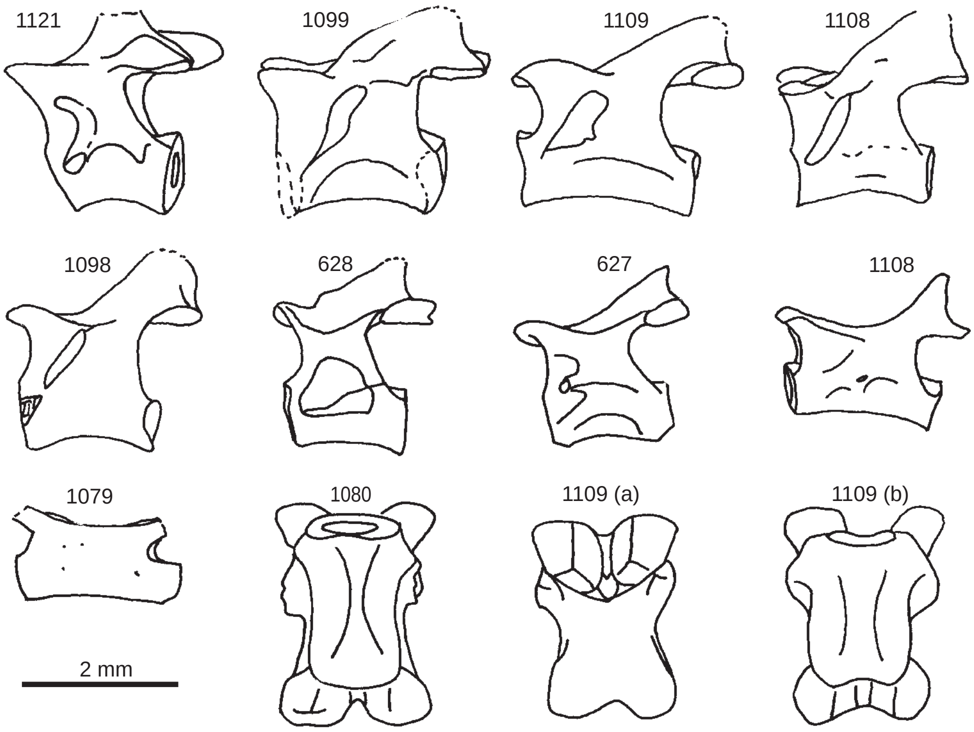

Fig. 10. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. Vertebrae from ZPAL RV/1121 to 1080 in a possible life sequence. Mostly those illustrated in Fig. 9. All but 1108, 1109 in left lateral view; 1108 and 1109 (b) in ventral view, 1109 (a) in dorsal view.

of the midventral groove similar to that in lepidosaurian vertebrae just anterior in position to the first with a fully developed fracture plane.

Forelimb. — The Czatkowice 1 remains include several humeri (mostly distal ends) but these differ in size and in the presence or absence of an entepicondylar foramen or groove. The smallest and most gracile of these elements probably, but not certainly, pertain to *Sophineta* and have a distinct elongate entepicondylar foramen (Fig. 11B). Whether or not the ectepicondylar foramen was completely enclosed is unclear since the distal end of the bone is usually poorly ossified or damaged.

Hind limb. — There are five distinct types of ilia in the Czatkowice 1 assemblage, including morphotypes that clearly fit into the archosauromorph or procolophonoid pattern. However, members of one set (*e.g.*, ZPAL RV/948–950, 952, 959, 1053, and 1063) (Fig. 11A, C, E, F) are uniformly small and broadly match the iliac type of relatively unspecialised basal rhynchocephalians such as *Gephyrosaurus* (Evans, 1981) and *Diphydontosaurus* (SEE personal observation). These ilia almost certainly belong to *Sophineta*. Each has an elongated blade set at roughly 45° to the horizontal but with a slight posteroventral curvature. The acetabulum is rather shallow and there is only a weak supraacetabular buttress. Anteroventrally, in good specimens, the margin is drawn out into a slender tapering prepubic process (Fig. 11E). On the medial aspect, the facets for the first and second sacral ribs are seen to lie fully on the iliac blade, with their long axes following the line of the blade.

As yet, no ventral pelvic elements have been attributed to *Sophineta*, but none of the numerous small ischia and pubes from the Czatkowice 1 material suggests any emargination of the puboischiadic suture. There is thus no evidence for the presence of a thyroid fenestra.

Variation: There is some ontogenetic/size variation in the shape of the iliac blade and the presence or absence of an anterior tubercle. In very small individuals, the blade is of fairly uniform width but in larger individuals the posteroventral border of the shaft expands a little, probably in concert with a strengthening of the sacroiliac joint (Fig. $11E_1$). Similarly, some specimens have an almost straight anterodorsal margin (Fig. 11C), some are more arched (Fig. 11A). The largest specimens can bear a distinct tubercle (Fig. 11E) marking the position of the iliopubic ligament and its associated musculature.

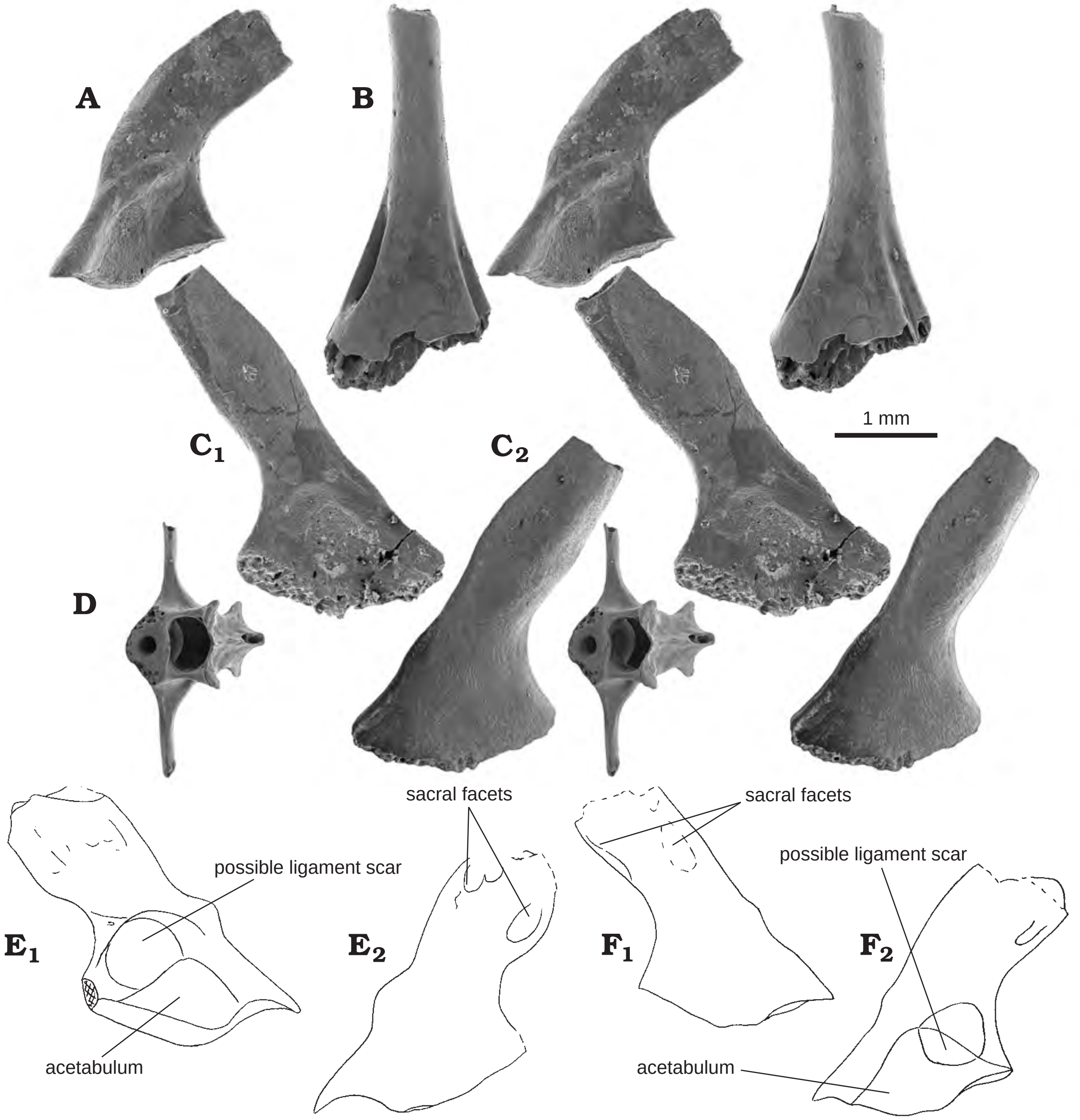

Fig. 11. *Sophineta cracoviensis* gen. et sp. n., Early Triassic of Czatkowice 1, Poland. **A**. Left ilium ZPAL RV/876, in lateral view. **B**. Right humerus ZPAL RV/1145, in distal dorsal view. **C**. Right ilium ZPAL RV/959, in lateral (C_1) and medial (C_2) views. **D**. Anterior caudal ZPAL RV/627, in anterior view. **E**. Right ilium ZPAL RV/1053, in lateral (E_1) and medial (E_2) views. **F**. Left ilium ZPAL RV/1063, in medial (F_1) and lateral (F_2) views. A–D SEM stereo-pairs.

DISCUSSION

PHYLOGENETIC ANALYSIS

A matrix of 77 characters (Waldman and Evans, 1994) and 11 taxa: *Petrolacosaurus*, *Coelurosauravus*, and *Youngina*, representing basal diapsids; *Prolacerta* representing archosauromorphs; *Saurosternon*, *Paliguana*, *Kuehneosaurus*, and *Marmoretta* considered basal lepidosauromorphs; *Gephyrosaurus* (a basal rhynchocephalian) and Squamata representing crown-group lepidosaurs; and *Sophineta* (Appendix 1) has been used for a phylogenetic analysis using PAUP version 3.1 (Swofford, 1993). A branch-and-bound search yielded 5 most parsimonious trees (MPT's) (Tree length [L] = 129; Consistency Index [CI] = 0.736; and

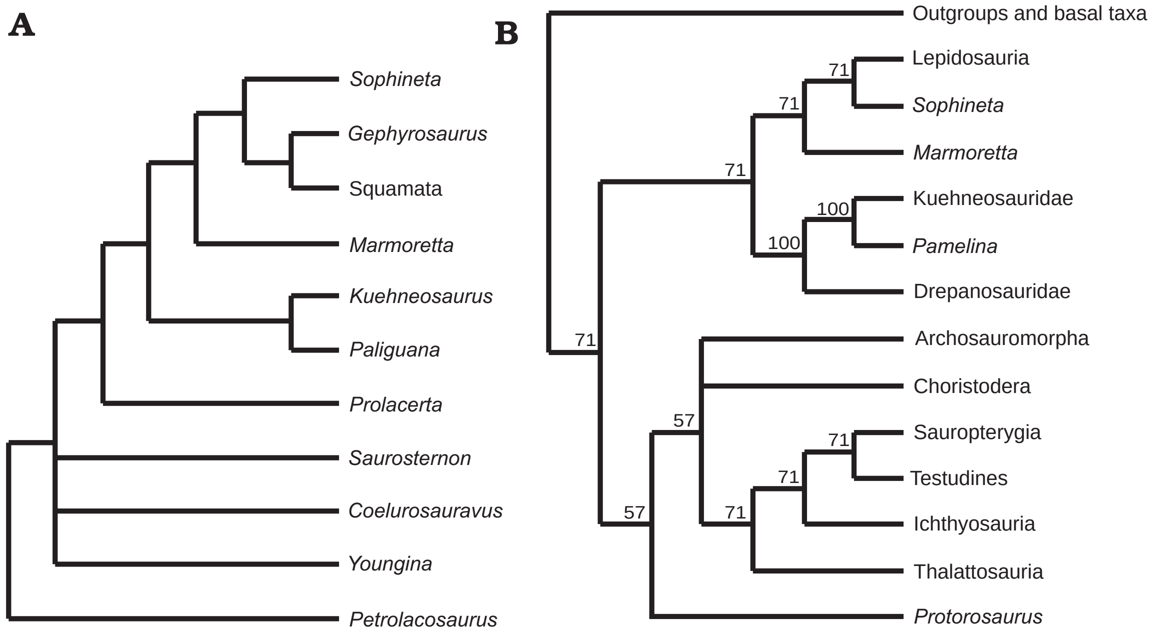

Fig. 12. **A**. The strict consensus tree of the diapsid interrelationships based on Waldman and Evans' (1994) matrix with *Sophineta* added. **B**. The 50% Majority Rule Tree based on Müller's (2004) matrix with *Sophineta* added.

Rescaled Consistency Index [RC] = 0.458). In all trees, *Sophineta* emerged as the sister group of Lepidosauria, one node above the Middle–Late Jurassic *Marmoretta*. Fig. 12A shows the strict consensus tree. Thus *Sophineta* is not a lepidosaur, but is close to the base of this important clade.

Recently, Müller (2004) published a detailed phylogenetic analysis of diapsids in which the kuehneosaurs, generally regarded as lepidosauromorphs, emerged as the sister taxon to the arboreal drepanosaurs at the base of neodiapsids. *Marmoretta*, *Sophineta*, and the Czatkowice 1 kuehneosaur (Evans 2009) have been added to the matrix (Appendix 2), including new data on kuehneosaurs and with some correction of the codings for rhynchocephalians and squamates (see Appendix 3). One of us (SEE) ran a Heuristic search (Random addition sequence, Tree-bisection-reconnection [TBR] branch swapping, replicates, rooted with outgroups, Seymouriidae, Synapsida, multistate characters treated as polymorphism: the matrix is too large to run a Branch and Bound search). This resulted in seven equally parsimonious trees with weak support values (L = 998, Consistency Index = 0.428, Rescaled Consistency Index = 0.234). The Strict Consensus of these trees is almost completely unresolved above the Araeoscelida, but the 50% Majority Rule Tree (Fig. 12B) places *Sophineta* as the sister group of Lepidosauria, with *Marmoretta*, and then kuehneosaurs as consecutive outgroups. The addition of Czatkowice 1 protorosaur (Borsuk-Białynicka and Evans 2009b) to the matrix resulted in three equally parsimonious trees (L = 1008; CI = 0.425; RC = 0.232), the Strict Consensus of which was better resolved and, for the lepidosauromorph at least, is identical to the cladogram shown in Fig. 12B. The differences are with respect to the relationships between archosauromorphs, testudines, choristoderes, ichthyosaurs, sauropterygians and thalattosaurs, and that is not at issue here.

IMPLICATIONS

The early history of lepidosaurs is very poorly known. On the stem of Archosauria, there are a series of relatively well known groups — rhynchosaurs, trilophosaurs, "protorosaurs", stem archosaurs (basal Archosauriformes), all of which help in understanding the structural and functional evolution of the group. For Lepidosauria, the only known stem taxa are the specialised Triassic kuehneosaurs (but see Müller 2004; and Evans 2009), the Middle Jurassic *Marmoretta*, and the very fragmentary Permo-Triassic *Paliguana* and *Saurosternon*. Currently, the most primitive known crown-group lepidosaur is the basal rhynchocephalian *Gephyrosaurus* (Evans 1980, 1981), but it has been difficult to know which of its skull characters are genuinely plesiomorphic, which autapomorphic (since the states in outgroups are obscure), and which already approaching the derived rhynchocephalian condition (*e.g.*, the posterior process on the jugal; the quadriradiate squamosal).

Sophineta thus provides an important point of comparison, both from its Early Triassic age and its position close to the base of Lepidosauria (Fig. 13). It appears to be unspecialised as far as its postcranium is known — unlike gliding kuehneosaurs or the possibly aquatic *Marmoretta*. *Sophineta* vertebrae are almost indistinguishable from those of the primitive rhynchocephalian *Gephyrosaurus* (low synapophyses, notochordal centrum, weak zygosphene/zygantral system), whereas those of *Marmoretta* are more like those of kuehneosaurs in having a solid, platycoelous centrum and in retaining transverse processes (albeit very short ones). In contrast, the skull characters of *Sophineta,* including the tall facial process of the maxilla, reduced lacrimal, and pleurodonty all resemble those of early crown-group lepidosaurs rather than those of stem-taxa. In *Sophineta* the unspecialized vertebral column is thus associated with the fairly derived skull structure, whereas kuehneosaurs combine a highly derived postcranial morphology with a skull that retains many plesiomorphic states (including a large lacrimal, low facial process of the maxilla, teeth on the pterygoid flange, teeth on the parasphenoid, and a weak subthecodont form of tooth implantation). The late surviving *Marmoretta* (Mid Jurassic, UK: Evans 1991; Late Jurassic, Portugal: SE personal observation), apparently positioned one step crownward of kuehneosaurs, represents a level of organisation not dissimilar to that of the Early Triassic *Sophineta* in terms of some skull characters (dental, maxillary, lacrimal and jugal traits), while showing autapomorphies in others (*e.g.*, the parietal crest and deep vertical parietal flanges, Evans 1991).

CHARACTER EVOLUTION IN LEPIDOSAUROMORPH REPTILES

As noted above, the description of *Sophineta* and its interpretation as a lepidosauromorph close to the origin of Lepidosauria provides an opportunity to reassess character evolution within the group. In the following section, key characters are examined and discussed in the light of the new data, and areas needing further work are highlighted.

Paired dorsal roofing bones. — All the small non-archosauriform reptiles from Czatkowice 1 have paired frontals and parietals, a trait regarded as plesiomorphic. This is the condition found in basal taxa like *Petrolacosaurus* (Reisz 1981), *Araeoscelis* (Reisz, Berman, *et* Scott, 1984), and *Youngina* (Gow 1975); in archosauromorphs (*e.g.*, *Prolacerta*, Gow 1975); and in lepidosauromorphs (*e.g.*, *Paliguana*, kuehneosaurs, Carroll 1975, 1977; Colbert 1966, 1970). It was probably also the condition in basal lepidosaurs as the frontals and parietals are paired in *Sphenodon* and the frontals are paired in many modern lizards, and the parietals are paired in the primitive Late Jurassic lizard *Bavarisaurus* (Evans 1994b). The fusion of the frontals and of the parietals in the basal rhynchocephalian *Gephyrosaurus* (Evans 1980) and in *Marmoretta* (Evans 1991) is therefore probably a derived condition.

Retention of parietal foramen. — An open parietal foramen placed in the mid-parietal suture, well back from the fronto-parietal suture, is the primitive diapsid condition (*e.g.*, Gow 1975; Reisz 1981). This is a plesiomorphic character state in *Sophineta*. Robinson (1962, 1967a) suggested a fronto-parietal position for the parietal foramen in *Kuehneosaurus* but the supposed foramen is simply a gap in the midline between the paired frontals and paired parietals (SEE personal observation). Thus kuehneosaurs are specialised in lacking a parietal foramen.

Size of the facial process of the maxilla and size of the lacrimal. — In primitive diapsids, the lacrimal is a large bone that spans much of the antorbital region from the orbit to the naris above a low maxilla. In the lepidosauromorph lineage there is a gradual reduction in the size of this bone and a concomitant increase in the size of the facial process of the maxilla. In the Triassic kuehneosaurs, the lacrimal remains large, above and behind a relatively low maxilla (Robinson 1962, 1967a; Colbert 1970); in the Mid Jurassic genus *Marmoretta*, the facial process of the maxilla is taller and the lacrimal apparently reduced (Evans 1991). In *Gephyrosaurus* (Evans 1980), as an example of a relatively basal lepidosaur, the facial process of the maxilla is tall and the lacrimal confined to the orbital rim. The lacrimal of *Sophineta* has not been recovered, but the facial process of the maxilla is relatively tall and there appears to have been only a small facet here, and on the prefrontal, for a lacrimal.

Maxilla enters orbital margin. — The primitive diapsid condition seems to be for the jugal to extend along the ventral edge of the orbital margin (*e.g.*, *Petrolacosaurus*), contacting the lacrimal or prefrontal anteriorly. In *Sophineta*, the facets on the posterior process of the maxilla make it clear that the maxilla made a major contribution to the ventral border of the orbit which is thus a derived condition.

Postfrontal enters margins of upper temporal fenestra. —This was a character listed by Gauthier *et al.* (1988) as diagnostic of lepidosauromorphs, the postfrontal being excluded both in basal diapsids and in archosauromorphs by the contact of the dorsal ramus of the postorbital with the parietal. The reassessment of the position of *Youngina* as a basal diapsid rather than a lepidosauromorph renders this character problematic. It reflects the enlargement of the upper temporal fenestra, and perhaps a reduction in the degree to which its anterior margin (or the posterior margin of the orbit) is braced. Facets on the postfrontal of *Sophineta* suggest the postfrontal made a small entry into the margin of the upper temporal fenestra.

Incomplete lower temporal arcade. — "Loss" of the lower temporal arcade was once considered to be a unique derived character of squamates and their immediate ancestors. With the recognition that a complete lower temporal arcade is absent in a number of small diapsids with no relationship to lepidosauromorphs (*e.g.*, *Prolacerta*, Parrington 1935; Gow 1975; *Tanystropheus* Wild 1973; *Coelurosauravus*, Evans 1982), it is generally accepted that the bar was either lost several times independently, or is a synapomorphy at the level of Neodiapsida (or earlier) with subsequent reacquisition in several lineages. The latter view is the more parsimonious.

Kuehneosaurus and *Marmoretta* both have a fairly large jugal with a strong body but no posterior process. This may mean that the longer posterior jugal process of *Gephyrosaurus* was actually a derived character, associated with a trend that eventually led to the re-establishment of the lower temporal bar in many later rhynchocephalian lineages (Whiteside 1986) and in at least one squamate (Lü *et al.* 2008). *Sophineta* has a gracile jugal with only a very slight posterior angle which would be thus plesiomorphic.

Reduction of the anteroventral process of the squamosal. — In diapsids, the squamosal is primitively quadriradiate, with a posterodorsal process to the parietal/ supratemporal, a posteroventral process overhanging the quadrate and contributing to the frame for the tympanic membrane, an anterior process to the postorbital, and an anteroventral process that runs along the anterior margin of the quadrate and may meet the quadratojugal if this is retained. Rhynchocephalians retain the plesiomorphic squamosal morphology; kuehneosaurs have modified it, reducing the squamosal to a narrow bar in a manner analogous to the squamosal reduction in squamates. The functional reasons for this are not yet clear. The quadrate of kuehneosaurs is not streptostylic in the squamate sense since it retains a strong pterygoid/quadrate suture (SEE personal observation). The condition in *Sophineta*, as interpreted here, is plesiomorphic.

Retention of the quadrate/pterygoid overlap. — Squamate streptostyly involves changes in the dorsal and ventral attachments of the quadrate to the bony skull by reduction of the squamosal, modification of the supratemporal and paroccipital so that they contribute to the support of the quadrate head, loss of the quadratojugal, and extreme reduction of the quadrate/pterygoid overlap. Kuehneosaurs have modified the dorsal articulation, by changing the shape of the squamosal (but they lose the supratemporal, and the paroccipital process is not involved, Robinson 1967a), but the pterygoid/quadrate overlap remains extensive. In *Sophineta*, a strong pterygoid/quadrate overlap seems also to have been retained.

Quadrate conch. — One of the features considered diagnostic for Lepidosauromorpha is the presence of an expanded lateral quadrate conch (*e.g.*, Gauthier *et al.* 1988). This conch is present in *Paliguana* (SEE personal observation), in kuehneosaurs, in lizards, and in *Gephyrosaurus* and many other rhynchocephalians (but secondarily lost in *Sphenodon*), although it is sometimes a composite of the quadrate and quadratojugal (*e.g.*, some rhynchocephalians). In *Paliguana* there is no trace of a separate quadratojugal, but the presence of a large foramen perforating the lateral part of the conch suggests the quadrate may, indeed, be composite. In the Late Triassic kuehneosaurs, there is no trace of a foramen, but it is possible that a quadratojugal was incorporated into the ventrolateral margin of the conch (see also the description of the Czatkowice 1 kuehneosaur, Evans 2009). The quadrate attributed to *Sophineta* has composite conch, with a quadratojugal foramen enclosed between the quadrate and a reduced quadratojugal. This was probably the primitive lepidosaurian condition.

Palatal dentition. — Early diapsid reptiles have an extensive palatal dentition with multiple rows of teeth on the vomers, palatines, pterygoids and parasphenoid. The Triassic kuehneosaurs also have an extensive palatal dentition, although it is not clearly organised into rows (SEE personal observation). In more crownward lepidosauromorphs, no teeth are present on the parasphenoid or the pterygoid flange, but basal rhynchocephalians like *Gephyrosaurus* retain an essentially primitive pattern, except for the enlargement of the lateral palatine row, a derived character of all rhynchocephalians. In squamates, the palatal dentition is much reduced, with only a scatter of pterygoid teeth (and more rarely palatine and vomerine teeth) in many taxa, or none at all. This loss of the palatal dentition must be related in some way to changes in feeding efficiency, since palatal teeth serve to increase the frictional resistance of the palate and thus aid grip. *Sophineta* has a pterygoid dentition similar to that of *Gephyrosaurus*, but the palatine is not known. Like *Gephyrosaurus*, but unlike *Kuehneosaurus*, it lacks teeth on the pterygoid flange.

Parasphenoid teeth. — In some primitive taxa, the parasphenoid — as a dermal element — bears small palatal teeth. This condition is present in both *Icarosaurus* and *Kuehneosaurus* (probably as a secondary condition, see Evans 2009) but not in either *Marmoretta* or *Gephyrosaurus*. The condition is still to be determined in *Sophineta* because no parasphenoid has been identified as yet (but equally, we have not recovered any toothed parasphenoids from the deposit).

The following braincase characters have not yet been reorganized in *Sophineta*, but we note them here as a basis for future work.

Parabasisphenoid, **development of the dorsum sella and the presence of abducens foramina**. — In modern lizards and rhynchocephalians, the hypophysial fossa is walled posteriorly by a strong ridge, the dorsum sellae, that contains paired concavities for the origin of ocular muscles and is perforated by foramina for branches of the abducens nerve. In kuehneosaurs the dorsum sellae is much lower and the abducens nerves presumably passed through soft tissue above it. The morphology of the parasphenoid in *Sophineta* is still unknown.

Parabasisphenoid — closure of vidian canal. — In extant lizards, the lateral edges of the parasphenoid are extended and co-ossified with the overlying basisphenoid to enclose bilateral vidian canals for the palatine ramus of the facial nerve and the internal carotid artery. In rhynchocephalians, basal lepidosauromorphs including kuehneosaurs, and also basal diapsids, the lateral margins of the parasphenoid remain as raised crests, leaving open grooves for the contents of the vidian canal.

Prootic — crista prootica and alary processes. — In extant lizards, the anterodorsal corner of the prootic is usually developed into a process or flange of varying length (the alar process of the prootic). This process is absent or at most rudimentary in rhynchocephalians but is developed to a small degree in the Late Triassic *Kuehneosaurus* (SEE personal observation). Similarly, in extant lizards, a distinct bony flange, the crista prootica, usually overhangs and protects the lateral foramen for the facial nerve, forming a canal for the anterior (palatine) and posterior (hyomandibular) branches of that nerve. In modern lizards, the crest also gives attachment to part of the protractor pterygoid musculature. A small crest exists in kuehneosaurs (SEE personal observation).

Opisthotic — ventral ramus. — Robinson (1962, 1967a) listed the ventral ramus of the opisthotic as a character linking “prolacertiforms” (then thought to be related to the ancestry of lizards) and kuehneosaurs. However, the ventral ramus is more widespread in its distribution (*e.g.*, in basal rhynchosaurs, Evans 1986 and basal archosauriforms *e.g.*, *Osmolskina* see Borsuk-Białynicka and Evans 2009a).

Basioccipital and exoccipital. — In primitive diapsids, the basioccipital and paired exoccipitals are separate ossifications enclosing all or most of the foramen magnum. In squamates, the exoccipital becomes co-ossified at an early stage with the opisthotic to form a composite oto-occipital. A similar co-ossification also occurs in *Sphenodon*, although later and to a less extensive degree (*i.e.*, the two bones join dorsally above the metotic fissure, but not ventrally). In *Gephyrosaurus*, however, and also in *Marmoretta* and *Kuehneosaurus*, the exoccipital may be co-ossified with the basioccipital, having a suture with the opisthotic dorsally, but not fusing with it (the same ossification style occurs in the protorosaurid grade reptile from Czatkowice 1; Borsuk-Białynicka and Evans 2009b). This radically different pattern of ossification may be related to enclosure and subdivision of the metotic fissure in squamates. However, dorsal fusion of the opisthotic and exoccipital (like that of *Sphenodon*) also occurs independently in the archosauriform *Osmolskina* (Borsuk-Białynicka and Evans 2009a), and there is evidently some variation in this character within diapsids that would merit further investigation.

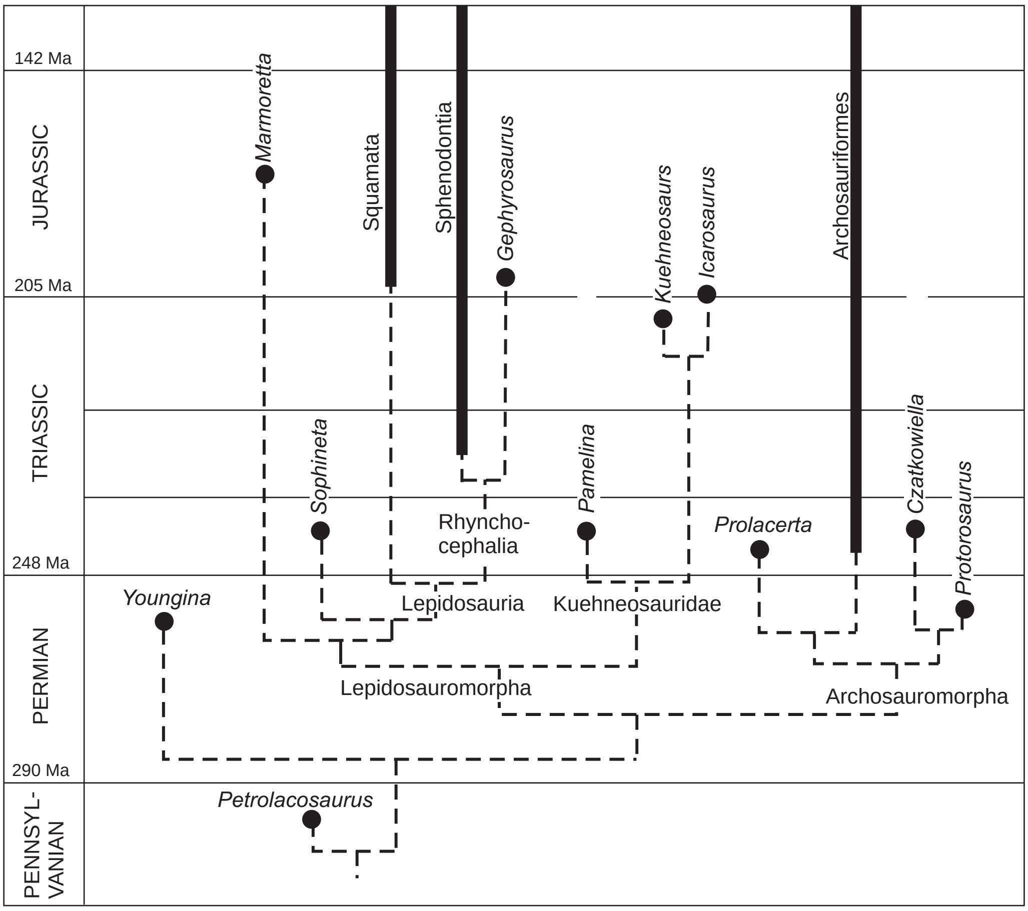

Fig. 13. Phylogenetic tree of basal diapsids in geological time based on the most parsimonious result of the present analysis.

Dentary symphysis. — The symphysial surface of the dentary is large and ovoid in *Gephyrosaurus* and *Marmoretta*, but is less extensive in both squamates and derived rhynchocephalians. However, the symphysis is also very weak in kuehneosaurs and in *Sophineta*, suggesting that this, rather than a massive symphysis, may be the plesiomorphic condition inherited by early lepidosaurs.

Vertebral morphology. — In rhynchocephalians, the vertebral centra are relatively short and retain an open notochordal canal. Since this condition is also found in *Youngina*, it was thought to be plesiomorphic for lepidosauromorphs as a whole. However, based on the condition in *Marmoretta* and kuehneosaurs, where the centra are weakly amphicoelous but solid, it is possible that the basal lepidosaurian condition represents a secondarily acquired (paedomorphic) trait. The vertebrae attributed to *Sophineta* resemble those of *Gephyrosaurus* in being notochordal and amphicoelous with a small zygosphene-zygantral system and a low, single synapophysis. *Marmoretta* and kuehneosaurs differ in having rather elongate vertebrae, lacking zygosphenes, and in having at least some development of transverse processes.

Lepidosaurs are also characterised by the presence of an autotomy septum in the caudal vertebrae, although this has been lost secondarily in some squamate taxa. None of the many small caudal vertebrae in the Czatkowice 1 bone assemblage shows a fully developed autotomy plane, but some of the caudals in *Sophineta* resemble *Gephyrosaurus* caudals in which the septum had not quite developed (*i.e.*, vertebrae lying just in front of the first with an autotomy septum). It may be, therefore, that the caudals of *Sophineta* show an incipient development of autotomy, although the developmental basis of this character is poorly understood.

Pelvis. — The ilium attributed to *Sophineta* has a relatively small acetabulum, and a simple angled blade like that of some basal lepidosaurs. It also shows the distinctive prepubic process found in some lepidosaurs (*e.g.*, *Gephyrosaurus*, *Sphenodon*). However, it seems unlikely that *Sophineta* pelvis had a thyroid fenestra since none of the small ischia or pubes in the collection show any trace of emargination. In lepidosaurs, this foramen emarginates the ventral midline, separating the pubis and ischium at the symphysis.

CONCLUSIONS

Skeletal morphology and phylogenetic analysis support the hypothesis that *Sophineta* is a lepidosauromorph close to the base of crown-group Lepidosauria. Although our knowledge of the genus remains incomplete, the structure of its skull and postcranial skeleton may help in establishing the polarity of lepidosaurian and lepidosauromorph characters in primitive lepidosaurs. *Sophineta* suggests that the quadriradiate condition of the squamosal and the presence of a small quadratojugal contribution to the quadrate conch were characters inherited by basal lepidosaurs, as was the long slender jaw with many small teeth, but the strong dentary symphysis in *Gephyrosaurus* may be a derived rather than plesiomorphic feature, as may the distinct posterior process on the jugal. In addition, some features of typical lepidosaurian postcranial structure (single headed-ribs, zygosphene-zygantrum, the prepubic process on the ilum) may characterise a more inclusive group, while others (caudal autotomy, thyroid fenestra) remain limited to the crown-group.

On the basis of the rhynchocephalian and squamate fossil records, the origins of crown-group Lepidosauria have been predicted to lie in the Late Permian or Early Triassic (*e.g.*, Evans 2003). However the paucity of basal lepidosauromorph remains left a significant gap in the fossil record for this important period. Until now, the only real clues to this key stage in lepidosauromorph evolution have come from relictual Jurassic taxa like *Gephyrosaurus* and *Marmoretta*. The Early Triassic *Sophineta* is important not only in filling a major temporal gap in the lepidosauromorph record, but also a morphological one, since it lies between the lepidosauromorph *Marmoretta* and the basal rhynchocephalian *Gephyrosaurus*, and provides a glimpse of the stem lepidosaurian condition.

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APPENDIX 1

Matrix of 77 characters used in the analysis as listed in Waldman and Evans (1994). Letters represent variable states as follows: A = 0&1&2; B = 0&1; C = 0&2

Petrolacosaurus	00000 00000 00000 00000 00100 00001 00000 000?0 ?0000 0000? ?0000 00000 1000? 00000 000?0 10
Youngina	01000 00000 00000 00000 00000 01101 00000 00000 00010 00000 ?0000 00010 00000 ????? ?0?00 00
Paliguana	00000 00000 ???01 ?10?? ????? 1?0?0 ?0?0? ??1?? ????? ????? ????? ????? ????? ????? ????? ??
Saurosternon	????? ????? ????? ????? ????? ????? ????? ????? ?0000 0000? 1010? 0???? ?000? ?0000 00?1? 00
Kuehneosaurus	00012? 100?0 11?11 11100 00100 10000 00100 01100 ?0000 12311 ?011? 11000 11001 00??? ?1?01 00
Marmoretta	1?02? ?0010 0??00 000?1 01??? 00010 01011 01?11 0000? 111?? ????? ?11?? 1?0?? ????? ????0 0?
Sophineta	1?001 10110 0000? 010?? ????? 110?0 0??0? ????2 0100? 001?? ????? ????? ???0? ????? ????0 0?
Gephyrosaurus	11001 11110 01?00 01001 1110? 11010 01111 01112 01100 00000 ?010? ?1101 11011 ?11?? 12?20 00
Squamata	111A1 10B?0 10111 01111 11112 11010 B12B0 11112 11101 201B1 21111 21101 12011 11111 12120 00
Prolacerta	000C1 11001 00000 00000 01001 10001 00000 011?0 ?0001 1100? ?0010 01000 00000 00100 11?01 11

APPENDIX 2

Character codings for *Sophineta* in the Müller (2004) analysis. See that reference for full character list and taxon matrix.

Sophineta	00000 11010 00011 02001 00??? 11?1? 1000? 01310 0??10 00??0 ????? ????? ????? ??0?? ????? ????? ?0000 0?001 20000 ????0 ??01? ?1??? ????? 000?? ?0?00 10111 10??? ????0 ????? ????? ?0000 11??? ???1? ???0? ?0010 ??210 00?1

APPENDIX 3

Characters changed in the codings of Müller (2004)

Rhynchocephalia

2: 0 to 0&1. Premaxilla without (0) or with (1) postnarial process. Within rhynchocephalians, clevosaurs and some other isolated taxa have a strong postnarial process that restricts entry of the maxilla into the margin of the narial opening. The score should therefore be 0&1

16: 1 to 0&1. Jugal extending no further than mid-cheek (0) or nearly to posterior end of skull. This is a variable character. First there is no differentiation as to whether the dorsal or ventral part of the jugal is involved — or both. The ventral ramus of the jugal does not extend posteriorly in *Pleurosaurus*, and there is no ventral ramus in *Priosphenodon*. The jugal is more extensive dorsally in these taxa, but this is not the same character.

57: 1 to 0&1 Supraglenoid buttress present (0) or absent (1) on scapulocoracoid. There is a buttress at least in *Gephyrosaurus* so it should be 0&1

100: 1 to 0&1.Teeth present (0) or absent (1) on palatine ramus of pterygoid. Primitive rhynchocephalians (*Gephyrosaurus*, *Diphydontosaurus*, *Planocephalosaurus* etc.) have teeth on the palatine ramus of the pterygoid. The coding should therefore be 0&1

105: 0 to 0&1. Second sacral rib not bifurcate (0) or bifurcate (1). It is slightly flanged rather than bifurcate in *Gephyrosaurus*, and it is not bifurcate in *Sphenodon*.

131: 1 to 0&1. Postorbital terminates prior to reaching posterior limit of parietal (0) or extends at least to posterior limit of parietal. This is presumably a mistake since even in *Sphenodon* it terminates anteriorly.

137: ? to 0&1. Floor of braincase with gap between basioccipital and basisphenoid (0) or elements fused to floor of brain cavity. Both conditions exist in rhynchocephalians, the primitive state in *Gephyrosaurus*, the derived one in *Sphenodon*.

144: ? to 1. Atlantal ribs are ossified (0) or not (1). They are not ossified.

161: 0&1 to 0. Medial wall of inner ear is unossified (0) or ossified (1). It is not ossified in any known rhynchocephalian.

182: 1 to 1&0. Lacrimal enters orbital margin (0) or remains excluded by prefrontal-maxillary contact. In *Gephyrosaurus* a very small lacrimal enters the orbital rim (0).

10/184 — 5.4%

Squamata

93: 1 to 0&1. Contact between ectopterygoid and jugal; restricted, equal or less than contact of pterygoid and ectopterygoid (0) or expanded caudally (1). Both states occur in squamates.

96: 1 to 0&1. Basipterygoid processes oriented anterolaterally (0) or laterally (1). The angle of the processes differs and in some (*e.g.*, *Uromastyx*) they are certainly anterolateral.

113: 1 to 0&1. Dorsal margin of ilium without (0) or with an anterior process (1). This feature varies in squamates according to locomotor style, *e.g.*, *Heloderma*, many anguids and some scincids lack the process.

115: 0 to 0&1. Supratemporal stout and short (0) or long and slender projecting far anteriorly (1). In varanoid lizards, a long supratemporal extends anteriorly along the margin of the parietal.

131: 1 to 0. Postorbital terminates prior to reaching posterior limit of parietal (0) or extends at least to posterior limit of parietal. As with rhynchocephalians, this is presumably a mistake, or poorly explained. The postorbital only rarely reaches back that far posteriorly.

137: 0 to 1. Floor of braincase with gap between basioccipital and basisphenoid (0) or elements fused to floor of brain cavity. This is perhaps poorly explained, because the basioccipital and basisphenoid meet in squamates to floor the brain cavity.

146: 1 to 0&1: Humeral distal articulations, distinct trochlea and capitellum (0) or low double condyle (1). At least some lizards seem to have a pronounced trochlea and capitellum.

161: 1 to 0&1. Medial wall of middle ear is unossified (0) or ossified (1). Squamates do generally have the derived condition, but an opening in the medial wall is found in some taxa where the lateral opening of the recessus scala tympani is reduced.

166: 1 to 0&1. Lateral shelf on the surangular is absent (0) or present (1). This is variable in squamates.

9/184 — 5%