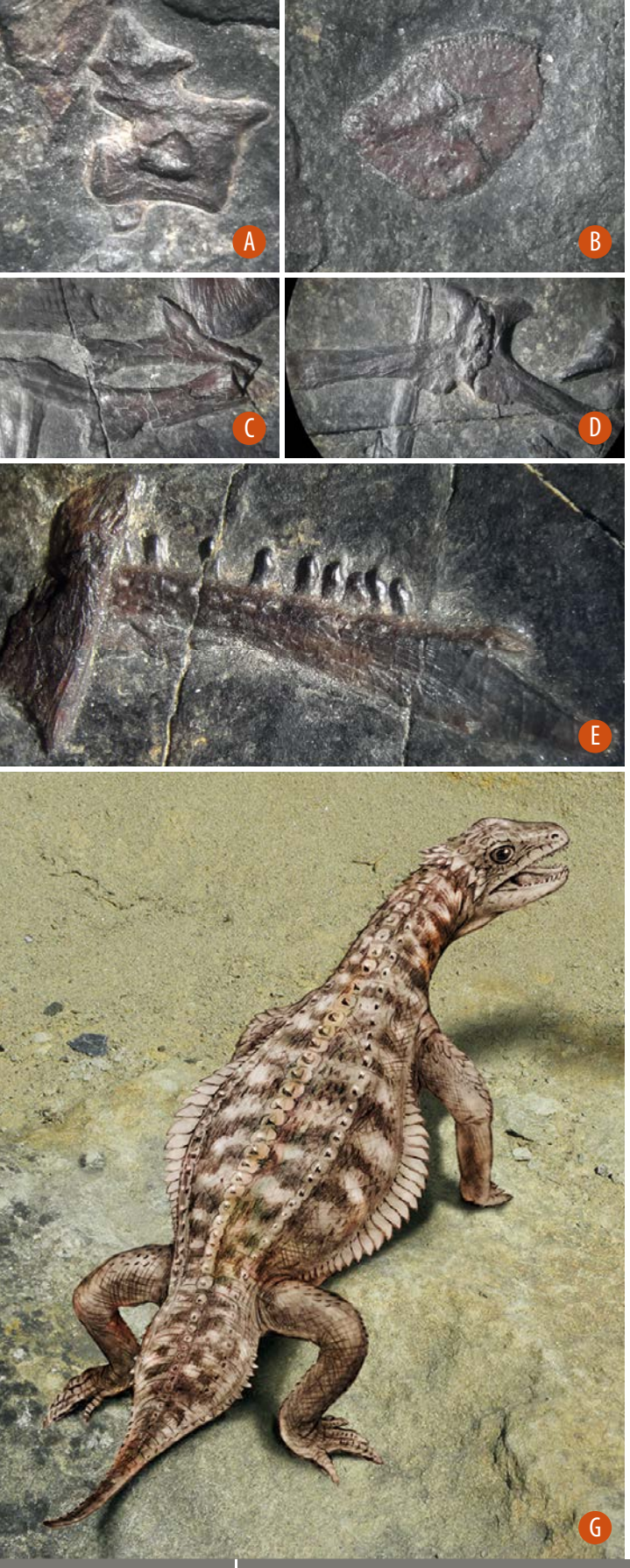

FIGURE 1. | *Specimens of* Eusaurosphargis dalsassoi *from the Middle Triassic of the Alpine region. A-E, selected bones (not to scale) of the holotype specimen BES SC 390 from Besano, Italy. A, caudal (tail) vertebra with conical osteoderm sitting on the neural spine. B, isolated osteoderm from the lateral side of the trunk. C, two anterior thoracic ribs with wide uncinate processes. D, thoracic vertebra with elongated transverse processes in dorsal (top) view. E, dentary of the left lower jaw carrying characteristic teeth with distinctive curved crowns. F, specimen PIMUZ A/III 4380 from the Ducan area, Switzerland (Image from Scheyer* et al., *2017). G, life reconstruction of* Eusaurosphargis, *mainly based on PIMUZ A/III 4380. Note that the article of Scheyer* et al. *(2017) and its online supplement were published by Scientific Reports under Creative Commons Attribution 4.0 International License and can be accessed freely via https://doi.org/10.1038/s41598-017-04514-x.*

With plates and spikes - the heavily armoured *Eusaurosphargis* aff. *dalsassoi*

U vindt een samenvatting aan het eind van dit artikel.

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Besides the wealth of nothosaur and pachypleurosaur fossils from the Vossenveld Formation, there are findings of bones that show very peculiar shapes, not easily attributable to the aforementioned groups. Among these are vertebrae with very long transverse processes, curved dorsal ribs with broadened portions known as uncinate processes, and peculiar shaped dermal armour (generally referred to as osteoderms), usually in the form of small bony cones. For a long time, the identity of these bones remained obscure, but lately, there is increasing evidence that all those materials belong to a single enigmatic diapsid, *Eusaurosphargis*, known from several European fossil localities.

Previous works

In a previous overview work on the fauna recovered in the sediments exposed in Winterswijk, the peculiarly shaped bones mentioned above were thought to possibly belong to *'Saurosphargis'* (e.g., Oosterink *et al*., 2003). This was accompanied by a note that this taxon, *'Saurosphargis'*, might be synonymous with the placodont *Paraplacodus broilii* Peyer, 1931, which is well known from the Middle Triassic World Heritage Site Monte San Giorgio, Ticino, Switzerland (Peyer, 1931; Kuhn-Schnyder, 1942; Rieppel, 2000). Unfortunately, the holotype of *Saurosphargis volzi* Huene, 1936, a partial postcranial skeleton preserving mostly part of the trunk, was lost during WWII and thus cannot be studied anymore. Furthermore, due to the lack of diagnostic features of that partial skeleton, some authors consider the genus and species as a 'nomen dubium' (e.g., Nosotti & Rieppel, 2003; Scheyer *et al*., 2017). Concerning Oosterink *et al*.'s (2003) statement above, it is noteworthy that both *Paraplacodus* and *'Saurosphargis'* share similarities in vertebral and rib anatomy, but they also differ in an important aspect. For example, both taxa have trunk ribs carrying uncinate processes (Huene, 1936; Rieppel, 2000), but whereas dermal armour is completely lacking in all known specimens of *Paraplacodus*, the holotype of *'Saurosphargis'* had osteoderms associated with the uncinate processes of its ribs.

With the description of a new *'Saurosphargis'*-like taxon from the early Middle Triassic of southern China, *Sinosaurosphargis yunguiensis* (Li *et al*., 2011), the species *'Saurosphargis volzi'* was recently resurrected and the family Saurosphargidae was erected (Li *et al*., 2011). In that study, yet undescribed material proposedly referable to *'Saurosphargis'* from the Lower Muschelkalk of Winterswijk was mentioned as "(Paul Albers, pers. comm.)". Since then, the additional saurosphargid taxa *Largocephalosaurus polycarpon* (Cheng *et al*., 2012) and *L. qianensis* (Li *et al*., 2014) have been described from the Middle Triassic of Yunnan and Guizhou Provinces in southern China, which are very similar in anatomy to the European *'Saurosphargis'*.

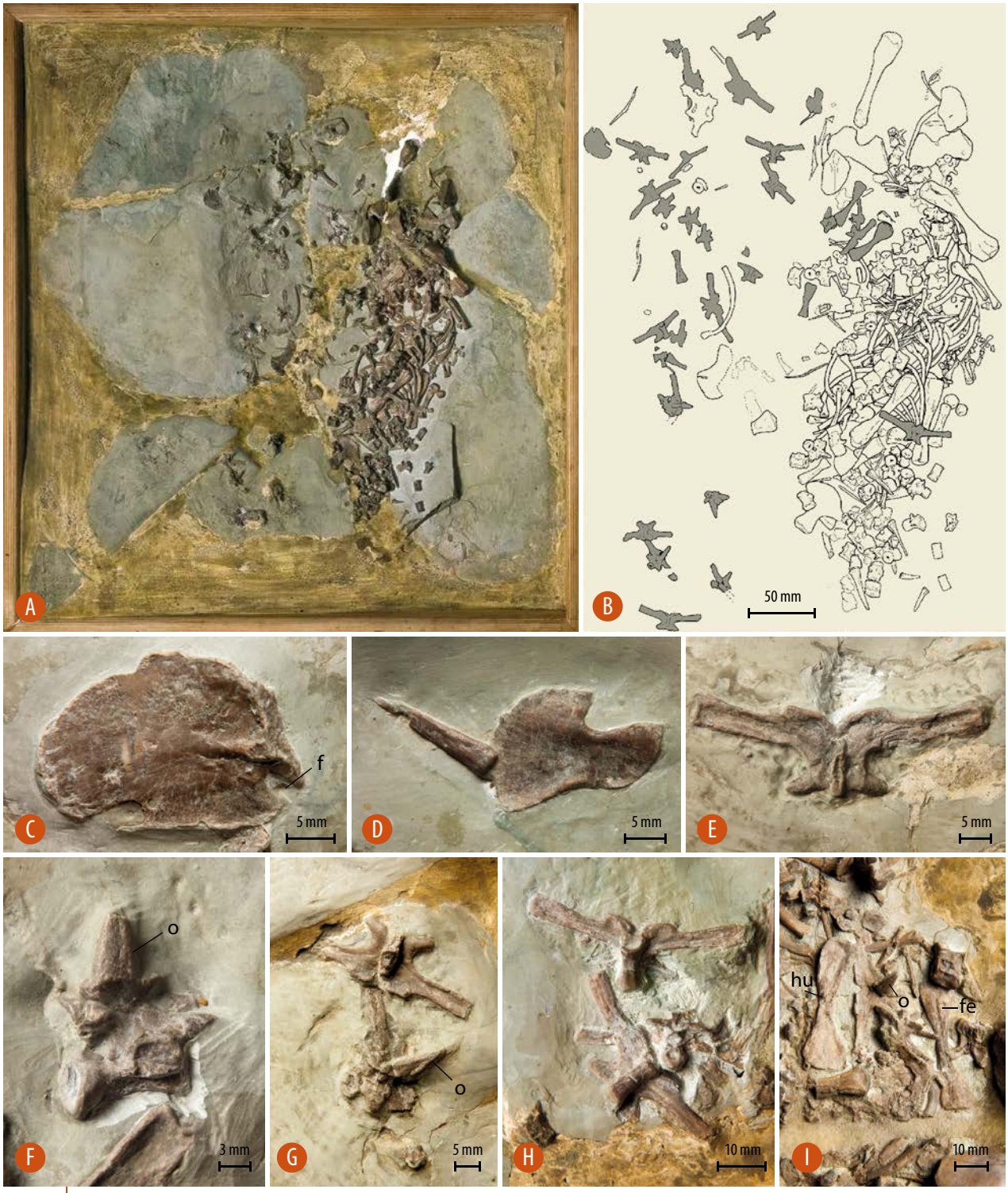

FIGURE 2. | *Main matrix block NMNHL RGM 449487 with bone accumulation including a basal pistosauroid skeleton, a skull fragment of* Anarosaurus heterodontus, *as well as scattered postcranial bones identifiable as belonging to* Eusaurosphargis *(see also Sander* et al.*, 2014: Fig. 3). A, photograph of the matrix block. B, sketch of the bones with the bones of* Eusaurosphargis *highlighted in grey. C, kidney-shaped coracoid with the notch of the (open) coracoid 'foramen' on the right side. D, left ischium with strongly concave anteromedial margin. The bone is partially overlapped by a rod-like bone (possibly a caudal transverse process). E, thoracic vertebra with elongated transverse processes in dorsal view (anterior is towards the top). F, caudal (tail) vertebra with conical osteoderm sitting on the neural spine. G, two thoracic vertebrae, the upper one in dorsal view, the lower in angled view, topped by a conical osteoderm. H, two thoracic vertebrae with elongated transverse processes in ventral (bottom) view. I, long bones (femur and humerus), with a thoracic vertebra with osteoderm lying in between. Abbreviations: f, foramen; fe, femur; hu, humerus; o, osteoderm.*

In 2014, a study by a Dutch-German research team lead by Martin Sander from the University of Bonn was published, focussing on associated skeletal remains being preserved close together on one slab (NMNHL RGM 449487). Sander *et al.* (2014) identified three taxa: articulated remains were found pertaining to the pistosauroid cf. *Cymatosaurus*,

an isolated fragmentary skull belonging to the pachypleurosaur *Anarosaurus heterodontus*, and the remaining scattered postcranial bones belonging to the enigmatic diapsid aff. *Eusaurosphargis*. The latter taxon was identified based on the vertebrae carrying elongated transverse processes and the presence of conical osteoderms. The authors provided a solid anatomical description and comparison, which supports their taxonomic interpretation of the fossils. Sander *et al.* (2014) thus also refuted a previous assessment of the very same fossils by Diedrich and Gradinaru (2013) to taxa known mostly from the Alpine Triassic. In the same year, two types of isolated broadened dorsal rib morphologies from Winterswijk with more or less strongly developed uncinate processes were identified and compared to other European fossil material (Klein & Sichelschmidt, 2014). The authors concluded that the majority of the ribs were referable to *Eusaurosphargis* as well. The question arises of course what this enigmatic *Eusaurosphargis* really is and whether part of specimen NMNHL RGM 449487, as well as the other remains from Winterswijk displaying this peculiar vertebral and rib morphology, can be confidently referred to this taxon.

Current taxonomic identification

So far, *Eusaurosphargis* was mainly described from Alpine Triassic localities (Fig. 1). The genus and species *Eusaurosphargis dalsassoi*, a small to medium-sized animal that might have reached 1.5 to 2 m in body length, was first described based on scattered remains of a sub-adult specimen (BES SC 390) found in the Middle Triassic of Besano, Italy (Nosotti & Rieppel, 2003). Although much of the anatomy of the species became thus known, other aspects remained obscure due to incomplete and scattered preservation of the bones. A complete and well-preserved skeleton (except the skull) from a small individual (PIMUZ A/III 4380) from the Middle Triassic sediments (Prosanto Formation) of the Ducan area, Switzerland, was found to increase the overall understanding of the species' anatomy further and allowed, for the first time, a life reconstruction and better interpretation of its palaeoecology (Scheyer *et al.*, 2017). Based on the extreme scarcity of *Eusaurosphargis* in Alpine Triassic localities in Switzerland and Italy that yielded hundreds of other, similar-sized marine reptiles (i.e., pachypleurosaurs, nothosaurs), as well as osteological features including stout limbs with widened terminal phalanges, the authors argued for a terrestrial lifestyle.

The study of Scheyer *et al.* (2017) also relied to a large degree on facilitating micro-computed tomography scanning of the fossil and subsequent three-dimensional reconstruction and modelling on powerful computer workstations. Due to the excellent and almost completely undisturbed preservation of PIMUZ A/III 4380, the association of the different aspects of the complex dermal armour and the underlying endoskeletal bones could be studied in detail. As such, conical or spiked osteoderms were found associated with vertebrae, ribs, and the girdles, whereas flat or keeled osteoderms were found associated with the forelimbs and the lateral edges of the gastralia. Previous systematic works found *Eusaurosphargis* either as sister taxon to the large and enigmatic marine reptile *Helveticosaurus* from the Besano Formation at Monte San Giorgio, Switzerland (Nosotti & Rieppel 2003; Li *et al.*, 2011), or to *Hanosaurus* from the Early to Middle Triassic Jialingjiang Formation of China (Neenan *et al.*, 2013; Cheng *et al.*, 2016). The latest phylogenetic analysis, following the discovery and description of PIMUZ A/III 4380, recovered *Helveticosaurus* and *Eusaurosphargis*, not in a monophyletic clade but as successive sister taxa to Sauropterygia (Scheyer *et al.*, 2017). Accordingly, though it has a similar name, these analyses do not find *Eusaurosphargis* forming a natural group (i.e., a monophyletic clade) with other Saurosphargidae known mainly from the Middle Triassic of China.

Eusaurosphargis from Winterswijk

Based on the above, several specimens from Winterswijk can be assigned to *Eusaurosphargis*. Until the Winterswijk material is further studied in detail, however, it is best to assign the materials to *Eusaurosphargis* aff. *dalsassoi*. These materials include disarticulated long bones, vertebrae, ribs, and osteoderms that are associated with the basal pistosauroid on slab NMNHL RGM 449487 (Sander *et al.*, 2014). The collection number NMNHL RGM 449487 refers to a main matrix block (Fig. 2) of a bone accumulation to which several smaller slabs belong that largely contain further bones of *Eusaurosphargis* and which are housed in Naturalis. In addition, numerous remains of isolated vertebrae with elongated transverse processes with or without associated osteoderms, ribs with uncinate processes, as well as isolated osteoderms are known that are housed in the collections of Naturalis and TWE or private collections.

There are several groups of animals that show elongated transverse processes of their dorsal vertebrae. Among extant reptiles, the mid- and posterior trunk vertebrae can become quite elongated in crocodylians. In the fossil record, however, the armoured placodonts (i.e., *Cyamodus* spp.) within Sauropterygia might be viewed as an extreme form, with most of their trunk below the wide carapace being supported by the transverse processes rather than ribs; the latter can be rudiments restricted to the lateral body wall (Scheyer, 2010). In *Eusaurosphargis*, the transverse processes are also strongly elongated, but the ribs are not reduced as in *Cyamodus* but rather robust, carrying isolated osteoderms atop their uncinate processes. In this regard, *Eusaurosphargis* resembles more closely the condition seen in the Chinese saurosphargids *Sinosaurosphargis* and *Largocephalosaurus* (Cheng *et al.*, 2012; Li *et al.*, 2014). One might speculate that the elongation of the transverse processes could be linked to the development of body armour as this would increase rigidity in the dorsal part of the trunk and likely serve as muscle attachment sites in the aforementioned groups, but to our knowledge the elongation of transverse processes and its functional implications has so far received little attention.

Eusaurosphargis further shares with the non-cyamodontoid placodont *Placodus* the presence of a single row of osteoderms over the neural spines (Drevermann, 1933; Jiang *et al.*, 2008). In *Placodus*, however, the triangular-shaped osteoderms fit within the space between two adjacent transverse processes, whereas in *Eusaurosphargis* the osteoderms sit directly on top of the flat and low neural spines of the precaudal vertebrae.

Finally, it is noteworthy that some of the *Eusaurosphargis* materials recovered from Winterswijk, as exemplified by the

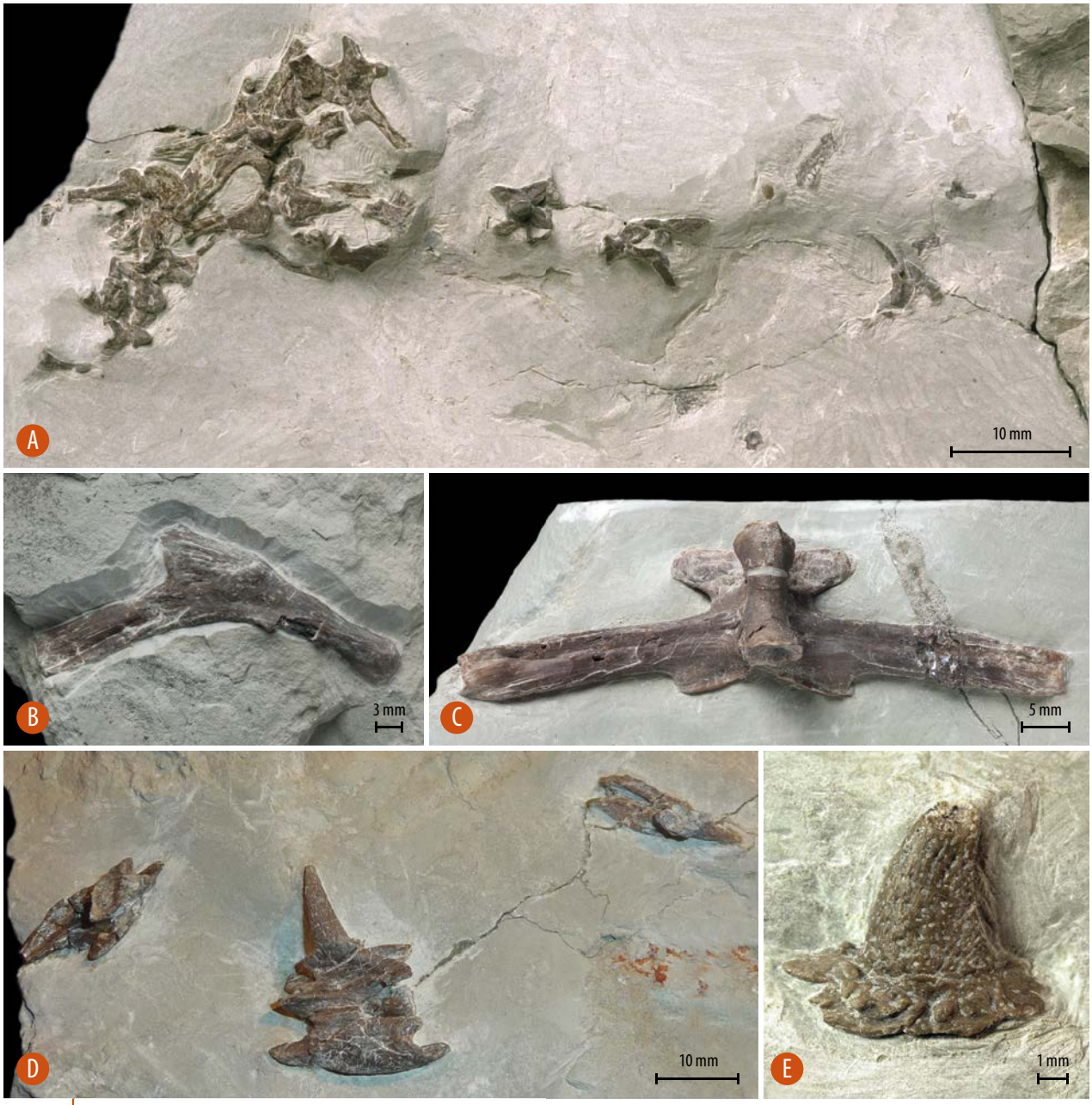

FIGURE 3. | *Additional material assignable to* Eusaurosphargis *from Winterswijk stored at Naturalis. A, associated postcranial bones. B, thoracic rib with wide uncinate process. C, isolated thoracic vertebra with elongated transverse processes in ventral view. D, cervical vertebra (middle) with conical osteoderm and attached neck rib in left lateral view. Next to the vertebra, isolated neck ribs are visible. E, isolated conical osteoderm, possibly from the shoulder region, showing broad sculptured base.*

bones on slab NMNHL RGM 449487, are distinctly larger than the material from Italy and Switzerland and thus likely represent different ontogenetic stages of this animal. For the holotype of *E. dalsassoi*, originally described as a subadult, the width of the larger trunk vertebrae measured over the transverse processes would be 31-33 mm (see Nosotti & Rieppel, 2003); that of a mid-trunk vertebra in the juvenile specimen from Ducan area ca. 23 mm. In contrast, the larger, well-preserved trunk vertebrae known from NMNHL RGM 449487 measure about 45 mm (see Sander *et al.*, 2014), indicating that this specimen is more than 30 % larger than the holotype specimen BES SC 390. Other material from Winterswijk (Fig. 3) is comparable in size to the Ducan specimen from Switzerland.

In conclusion, although no complete skeleton has been recovered in Winterswijk so far, and even partially associated materials are rare, there are several specimens known that can be assigned to the diapsid *Eusaurosphargis* aff. *dalsassoi* (Nosotti & Rieppel, 2003) based on their peculiar morphology.

Abbreviations

BES, Palaeontological Collection of the Museo Civico di Storia Naturale di Milano, Italy; **NMNHL**, National Museum of Natural History (NCB Naturalis), Leiden, The Netherlands; **PIMUZ**, University of Zurich, Palaeontological Institute and Museum, Zurich, Switzerland; **TWE**, Museum TwentseWelle, Enschede, The Netherlands.

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Abstract

Saurosphargis voltzi was described based on a fragmentary specimen, which was lost during WWII. Because of this, the nature of this taxon and its exact relationships, particularly to the placodont *Paraplacodus broilii* to which it was considered to be closely related, are unclear. However, since then, a much more complete fossil has emerged from Monte San Georgio that exhibits striking similarities with *Saurosphargis*. This complete but disarticulated fossil was assigned to the new taxon *Eusaurosphargis dalsassoi*. Recently, a fossil assigned to this species from the Prosanto Formation has been found in the Ducan region of Switzerland. The postcranial skeleton is completely intact, allowing us a good insight into the appearance of the animal. Further knowledge about this species comes from comparison with fossils from China, such as *Sinosaurosphargis* and *Largocephalosaurus*. These Chinese fossils help us understand how the characteristic armour of these animals, with the transversely elongated vertebral processes, bone plates, and spines, is functionally put together. In the Vossenveld Formation of Winterswijk, fossils are found that we can best describe as *Eusaurosphargis* aff. *dalsassoi*. Further research may change this, in particular, because many of the fossils from Winterswijk are much larger than the specimens known from *E. dalsassoi*.

Samenvatting

Saurosphargis voltzi is beschreven op basis van een fragmentarisch exemplaar dat verloren is gegaan tijdens WOII. Hierdoor is er veel onduidelijkheid over dit taxon en zijn verwantschappen aan andere taxa, in het bijzonder aan de placodont *Paraplacodus broilii*, waar het nauw verwant aan wordt geacht. Sindsdien is er echter een veel completer fossiel ontdekt op de Monte San Georgio met opvallende overeenkomsten met *Saurosphargis*. Dit complete maar verspoelde fossiel is toegewezen aan het nieuwe taxon *Eusaurosphargis dalsassoi*. Recentelijk is een nieuw fossiel van deze soort in de Prosanto Formatie in de Ducan regio in Zwitserland ontdekt. Het postcraniale skelet is compleet en gearticuleerd, wat ons een goed beeld van het uiterlijk van dit dier geeft. Verdere kennis omtrent deze soort komt uit vergelijkingen met fossielen uit China, zoals *Sinosaurosphargis* en *Largocephalosaurus*. Deze Chinese fossielen helpen ons te begrijpen hoe de karakteristieke bepantsering van deze dieren, met de zijdelings uitgegroeide wervels, beenplaten en stekels, functioneel in elkaar zit. In de Vossenveld Formatie van Winterswijk worden fossielen gevonden die we het beste kunnen beschrijven als *Eusaurosphargis* aff. *dalsassoi*. Verder onderzoek zal daar mogelijk verandering in brengen, met name omdat nogal wat fossielen uit Winterswijk veel groter zijn dan de exemplaren die van *E. dalsassoi* bekend zijn.

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The full list of references can be found at: http://www.geologienederland.nl > Grondboor & Hamer > Staringia 16.
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