Anarosaurus heterodontus
– the least aquatic pachypleurosaur

U vindt een samenvatting aan het eind van de tekst.

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Abstract | Pachypleurosauria are small-bodied (50 cm-120 cm) basal Eosauropterygia inhabiting epicontinental seas and intraplatform basins of the Tethys Ocean during the latest Early to late Middle Triassic (late Olenekian-Ladinian). Ladinian taxa show a paedomorphic and pachyostotic skeleton, both resulting from secondary aquatic adaptations. Some taxa occur in high individual numbers, which allowed for documenting viviparity and sexual dimorphism, the latter expressed in morphological differences. Pachypleurosaurs are a very diverse clade with currently 7 genera containing about 10 species. Some of these are well known, whereas others are so far only documented by one or two individuals. However, the origin of pachypleurosaurs, their position within Sauropterygia and the phylogenetic relationships between the European clade and the eastern Tethyan taxa are not well understood. *Anarosaurus heterodontus*, the pachypleurosaur occurring in Winterswijk, is one of the oldest pachypleurosaurs from a stratigraphical perspective. Regarding its morphology, it is one of the least aquatic adapted pachypleurosaurs, which might be the result of its lifestyle: living in near coastal, shallow marine habitats. *A. heterodontus* differs from other pachypleurosaurs in its special bone histology indicating – when compared to other pachypleurosaurs and modern reptiles – fast growth rates.

A specimen of A. heterodontus *projected onto the surface of layer 4 with polygonal cracks in the Winterswijk Quarry to reconstruct/visualize the possible situation of the carcass before fossilization (by Dorothea Kranz, IGPB).*

Paleogeography, Distributions and Phylogeny of Pachypleurosauria

Stratigraphic Occurrences

Pachypleurosaurs have a mainly Anisian-Ladinian (Middle Triassic) distribution. *Keichousaurus* was long considered to be of Carnian age (e.g., Rieppel, 2000; Liu *et al*., 2011; Benton *et al.,* 2014), but this is still under discussion because a late Ladinian age of the locality is favored by others (Zou *et al*., 2015; Sun *et al*., 2016). Pachypleurosaurs inhabited shallow marine environments of epicontinental seas and intraplatform basins of the Tethys Ocean (Rieppel, 2000), i.e., the Germanic Basin, the Alpine Triassic and the eastern Tethys Ocean that is present-day China. Renesto *et al.* (2014) and Černansky *et al.* (2018) specified their preferred environment to lagoonal and/or temporarily slightly hypersaline carbonate platforms. The oldest occurrences of the clade are in the Germanic Basin and are latest Early Triassic in age (Kowal-Linka & Bodzioch, 2017). New finds from Myanmar might be older but the stratigraphy of those fossil-bearing sediments needs to be revised (Khaing *et al*., 2019). *Dactylosaurus* and *Anarosaurus,* from Muschelkalk sediments of the Germanic Basin, both exhibit a plesiomorphic morphology when compared to stratigraphically younger pachypleurosaurs from the Alpine Triassic and China, but also when compared to the finds of Myanmar (see below). Stratigraphical occurrence, as well as morphology, thus point to an origin of the clade in or close to the Germanic Basin. However, the currently favored hypothesis is that of an eastern Tethyan origin of pachypleurosaurs and their migration into the western Tethyan faunal province (Liu *et al*., 2011; Renesto *et al*., 2014; Khaing *et al*., 2019).

The Western Tethyan Realm

During Anisian and Ladinian times, central and southern Europe was dominated by two marine depositional environments: the epicontinental sea that is nowadays represented by Muschelkalk sediments of the Germanic Basin and the intraplatform basin that hosted formation of the black shales of the so-called Alpine Triassic, exposed in Italy and Switzerland. The Germanic Basin is interpreted as a shallow marine epicontinental sea, which experienced irregularly alternating regression and transgression intervals, salinity fluctuations and numerous storm events (e.g., Fischer *et al*., 2012). The locality of Winterswijk lies at the western margin of the Germanic Basin (i.e. Rhenish Massif) and represents a vast carbonate mudflat, the Vosssenfeld Formation, with near coastal conditions, low water depth, and occasional drying of the sediment.

The Alpine Triassic consists of lagoonal to shallow shelf environments, with at least partially connected seaways to the Tethys (i.e., open/deeper sea). It is thought that the climate in the Middle Triassic was subtropically warm with alternating dry and wet seasons (mega-monsoonal intervals).

The Eastern Tethyan Realm

The third region that has produced pachypleurosaurs is the southwestern Chinese province of Guizhou and neighboring Yunnan Province. Here, a thick section of mainly shallow marine carbonates of Anisian to Ladinian age was deposited on the Yangtze platform, which is part of the South China Block. This section contains a horizon succession with marine reptiles (Benton *et al*., 2014) that have been extensively collected since the beginning of this millennium. Pachypleurosaurs are mainly known from the late Ladinian Xingji Biota. They occur in laminated, organic-rich limestones that are strikingly similar in lithology to the pachypleurosaur-bearing beds of the Western Tethyan Realm, such as the Meride Limestones (Sander, 1989). As in the Meride Limestones, these beds show a high abundance of pachypleurosaurs but only rarely yield finds of other marine reptiles or fishes. There are almost no invertebrate fossils except for mass accumulation of the small shrimp *Schimperella*. The lamination suggests hostile bottom conditions, and the lack of invertebrates indicates an unfavorable water chemistry (e.g. hypersalinity). *Schimperella* and other small arthropods are known to

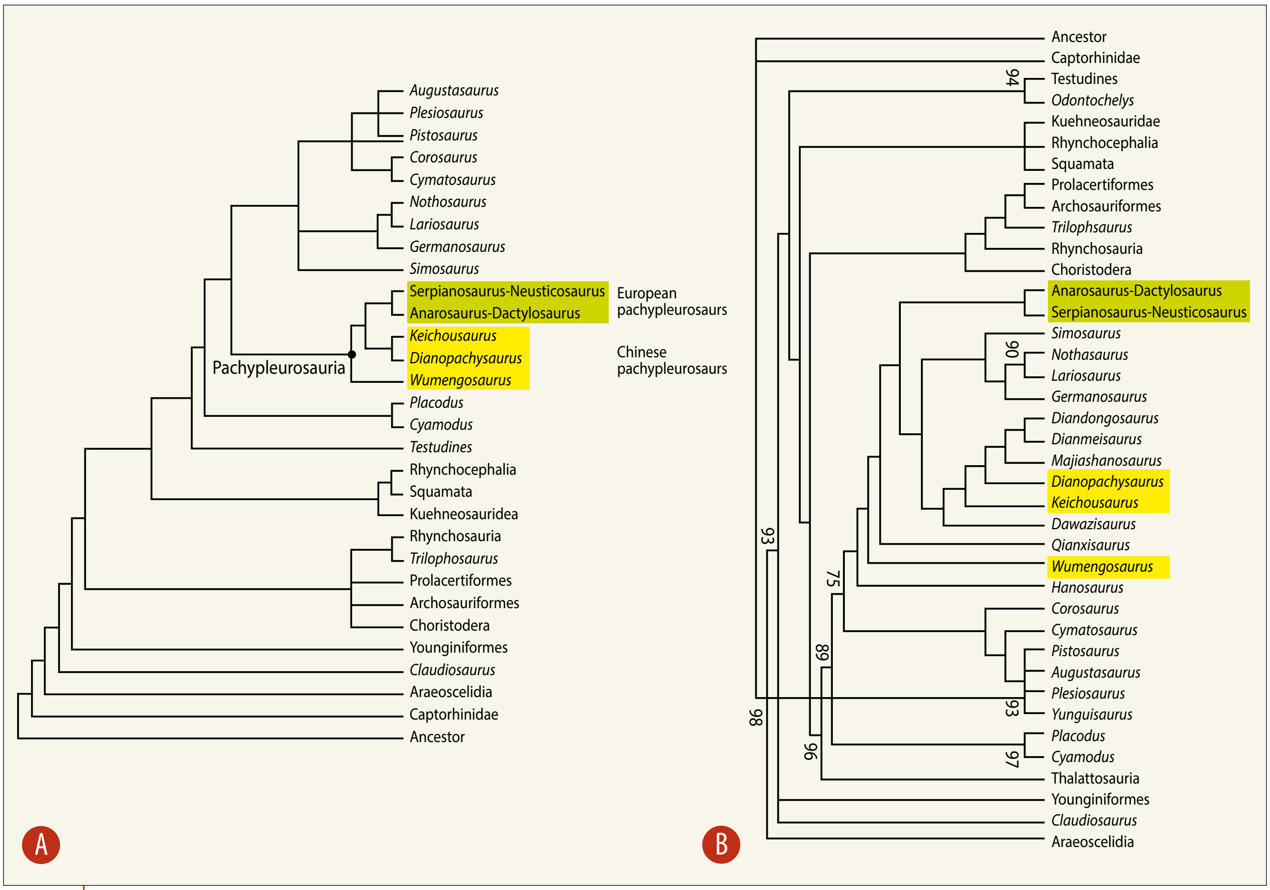

Figure 1. | *A, Cladogram depicting phylogenetic relationships of pachypleurosaurs after Liu* et al. *(2011), which supports a monophyletic Pachypleurosauria with a sister group relationship of Chinese and European pachypleurosaurs.*
B, Cladogram depicting the phylogenetic relationships of pachypleurosaurs after Shang et al. *(2017) in which Chinese pachypleurosaurs and other basal eosauropterygians are more closely related to Nothosauroidea than to European pachypleurosaurs.*

tolerate hypersaline conditions to the exclusion of most other marine invertebrates. This suggests that the Tethys pachypleurosaurs of the Ladinian were specialized arthropod feeders living in hypersaline lagoons. This feeding adaptation may have also applied to the Lower Muschelkalk pachypleurosaurs, particularly at Winterswijk, where there is ample evidence for shallow, hypersaline waters (e.g., Dülfer & Klein, 2006; Heijne *et al.*, 2019), explaining the abundance and good preservation of the *Anarosaurus* specimens in Winterswijk.

Phylogeny

The phylogenetic position of Pachypleurosauria within Sauropterygia is controversial (e.g., Rieppel, 2000; Holmes *et al.*, 2008; Liu *et al.*, 2011; Shang *et al.*, 2017), but they are generally accepted as members of the Eosauropterygia. Phylogenetic controversy largely arose from several eosauropterygian taxa from the Middle Triassic of China described in the last decade, which exhibit a mosaic of pachypleurosaurian and nothosaurian characters that questions the monophyly of Pachypleurosauria (e.g. Voeten *et al.*, this volume page 234). In most phylogenetic analyses, the European taxa from the Germanic Basin (*Dactylosaurus, Anarosaurus, Neusticosaurus*) and from the Alpine Triassic (*Odoiporosaurus-Serpianosaurus-Neusticosaurus*) usually form a clade, which has a sister-group relationship to the Chinese pachypleurosaurs, the Keichousauridae (*Keichousaurus-Dianopachysaurus*) with the eosauropterygian *Wumengosaurus* occupying the most basal position within a monophyletic Pachypleurosauria (Liu *et al.*, 2011) (Fig. 1A). However, other phylogenetic hypotheses place the European Pachypleurosauria as the sister group to Nothosauroidea and to a clade consisting of Chinese pachypleurosaurs and eosauropterygians (*Diandongosaurus* (*Dianmeisaurus* (*Majiashanosaurus* (*Dianopachysaurus* (*Keichousaurus* (*Dawazisaurus* (*Qianxisaurus* (*Wumengosaurus* (*Hanosaurus*)))))))) (Shang *et al.*, 2017) (Fig. 1B). Under the latter phylogenetic hypothesis, the Chinese pachypleurosaurs and other basal eosauropterygians are more closely related to Nothosauroidea than to European pachypleurosaurs (Shang *et al.*, 2017). Nothosauroid affinities of *Keichousaurus* had been already proposed by Holmes *et al.* (2008).

Keichousaurus yuananensis Young, 1965 and *Hanosaurus hupehensis* Young, 1972 from China, as well as two species of *Neusticosaurus* (*N. staubi* Kuhn-Schnyder, 1959; *N. toeplitschi* Nopcsa, 1928) from the Alpine Triassic, are all only based on a single incomplete specimen, making their validity questionable (Rieppel, 2000).

Due to different phylogenetic hypotheses, depending which taxa from China are included, the possibility remains that the pachypleurosaurs as traditionally understood (the *Anarosaurus-Dactylosaurus* clade and the *Odoiporosaurus-Serpianosaurus-Neusticosaurus* clade) represent a strictly European radiation, which did not include the taxa from the eastern Tethyan faunal province (Rieppel, 2019).

European Pachypleurosaurs

Pachypleurosaurs from the Germanic Basin

The first pachypleurosaur that was described historically is also the stratigraphically oldest. *Dactylosaurus gracilis* Gürich, 1884 (Fig. 2D, E) was found in the early Anisian (Lower Muschelkalk) of Poland but some isolated pachypleurosaur bones are even older, i.e., from the late Olenekian (Kowal-Linka & Bodzioch, 2012, 2017). A great number of isolated bones – mainly small bones from the Lower Muschelkalk of Poland – have since then been assigned to *Dactylosaurus* (e.g., Kowal-Linka & Bodzioch, 2012, 2017; Klein & Griebeler, 2018), but only three incomplete skeletons with an articulated skull are known (Fig. 2A-E). These are the holotype of *D. schroederi* Nopcsa, 1928 (BGR, uncatalogued; Fig. 2A, B), a not yet described specimen in the collection of the GPIT (Fig. 2C), and the very incomplete holotype of *D. gracilis* (Fig. 2D, E), which most likely represents a juvenile individual (Rieppel, 2000; MGU Wr 3871s). Thus, diagnostic material is rare and the description of the taxon is largely based on a single specimen (BGR, uncatalogued; Fig. 2A-B).

The holotype and only specimen of *Anarosaurus pumilio* Dames, 1890, an articulated but incomplete skeleton preserving the skull, was lost during WWII and only casts of different quality are available today (Fig. 2F, G). *A. pumilio* was found in Anisian Middle Muschelkalk sediments from Saxony-Anhalt, Germany. Isolated bones from the Middle Muschelkalk of southern Germany have been tentatively assigned to *A. pumilio* (Hagdorn & Simon, 1993). The species *Anarosaurus heterodontus* Rieppel & Lin, 1995 was erected based on a right dentary displaying the typical heterodont dentition of the species. The holotype was found in Lower Muschelkalk sediments (middle Anisian) close to Freyburg along the Unstrut river, Germany. Rieppel & Lin (1995) also referred the material from Winterswijk to *Anarosaurus heterodontus*. However, they did not select the type specimen in this material because, at that time, the Winterswijk finds were not housed in public collections. Later, skulls of *A. heterodontus* from Winterswijk were donated (Kolstee collection, now in TwentseWelle, Enschede) to a public collection. Other material was found during joint scientific excavations consisting of Naturalis, Leiden, the University of Utrecht, the University of Bonn, and the Workgroup Muschelkalk Winterswijk, or was made available by private collectors for scientific study by depositing casts in public collections. These developments finally allowed a detailed and comprehensive description of the morphology of *A. heterodontus* (Klein, 2009, 2010, 2012; Klein *et al.*, 2015) (Fig. 3). The abundant material of *A. heterodontus* from Winterswijk was also included in a taphonomical study (Heijne *et al.*, 2019), which again highlighted the special character of the Winterswijk locality.

Dactylosaurus and *Anarosaurus* differ in several features, such as in the morphology of the teeth and the number of cervical vertebrae, which is higher in *Anarosaurus* than in *Dactylosaurus*. *A. pumilio* and *A. heterodontus* differ, as far as comparable, in only a few morphological features (Klein, 2012) but mainly in size: *A. heterodontus* is twice as large as *A. pumilio* (Rieppel, 2000). Furthermore, *A. heterodontus*, as the species name implies, has a specialized heterodont dentition in addition to a massive posterior lower jaw.

The deposits of the Germanic Basin also have yielded several articulated pachypleurosaur skeletons from the Hoheneck Limestone of early Ladinian age in southern Germany. These were described as *Neusticosaurus pusillus* (Seeley, 1882), a taxon later recognized and described in detail from the southern Alpine Middle Triassic (Sander, 1989). The Hoheneck Limestone is a marine transgressive unit in the otherwise marginally marine and brackish sediments of the Lettenkeuper, the lower part of the thick Keuper succession. The presence of *N. pusillus* in southern Germany thus indicates a marine transgression (Fraas, 1881; Schoch, 2015) that must have connected the epicontinental realm with the Tethys, allowing the immigration of this pachypleurosaur. Isolated bones of pachypleurosaurs are also characteristic components of many Upper Muschelkalk localities and of the Muschelkalk-Keuper Grenzbonebed in southern Germany (pers. comm. Hagdorn, 2019; pers. obs. in the field in southern Germany of NK).

Pachypleurosaurs from the Alpine Triassic

The black shale deposits of the Alpine Triassic of Monte San Giorgio (Switzerland and Italy; Sander, 1989; Rieppel, 1989) contain concentrations of pachypleurosaurs, the *Serpianosaurus-Neusticosaurus* clade, that number in the hundreds. Four taxa are described, which subsequently appear one after the other in a stratigraphical sequence from the late Anisian/early Ladinian Besano Formation (= Grenzbitumenzone of the older German literature) to the middle Ladinian Lower Meride Limestone (Sander, 1989). The Besano Formation taxon is *Serpianosaurus mirigiolensis* (Rieppel, 1989). The oldest Meride Limestone taxon is *Neusticosaurus pusillus* (Seeley, 1882) which was found in the beds of the Cava Inferiore horizon. *N. peyeri* (Sander, 1989) occurs in the Cava Superiore horizon, and the stratigraphically youngest taxon, *N. edwardsii* (Cornalia, 1854), is preserved only in the Alla Cascina horizon (summarized in Sander, 1989 and Hugi *et al.*, 2011).

N. pusillus is of particular importance because it allows the correlation of the Tethyan southern Alpine section with the epicontinental Muschelkalk deposits (see above). This plethora of specimens has allowed detailed studies of morphology and ontogenetic and intraspecific variation, including growth using bone histology (Sander, 1989, 1990) and ossification patterns (Sander, 1989; Hugi & Scheyer, 2012). Among others, sexual dimorphism was documented (Sander, 1988, 1989; Rieppel, 1989) and an isolated embryo of *Neusticosaurus peyeri* was identified (Sander, 1988), first raising the possibility of vivipary in sauropterygians. Vivipary was later confirmed by Cheng *et al.* (2004) for *Keichousaurus* through the finds of pregnant females.

The taphonomy of these pachypleurosaurs was studied by Beardmore & Furrer (2016).

Recently, a new genus and species, *Odoiporosaurus teruzzii* Renesto *et al.*, 2014, was described from the middle Anisian of the Besano Formation. *Odoiporosaurus* is thus the oldest pachypleurosaur taxon from the Alpine Triassic. It is the sister taxon to the *Serpianosaurus-Neusticosaurus*-clade but also shares some primitive characters with the *Dactylosaurus*/*Anarosaurus* clade. According to the authors, the presence of *Odoiporosaurus* supports the hypothesis of an eastern origin of Pachypleurosauria, with ancestors of *Dactylosaurus*/*Anarosaurus* immigrating into the Germanic Basin from the eastern Tethys. In the western Tethys, they then diversified and invaded the intraplatform basin of the South Alpine realm (Renesto *et al*., 2014).

In addition to finds in the classical Muschelkalk deposits (i.e., the Germanic Basin) and the Alpine Triassic, remains of pachypleurosaurs had been described from Spain (Rieppel & Hagdorn, 1998; Fortuny *et al*., 2011) and the Western Carpathians (Čerňanský *et al*., 2018).

Pachypleurosaurs from the Eastern Tethyan Realm (Guizhou Province, China)

The first Triassic marine reptile taxon that was ever described from China was the pachypleurosaur *Keichousaurus hui* Young, 1958. *Keichousaurus* is found in the Zhuganpo Member of the Falang Formation (late Ladinian or early Carnian) in a wide area ranging from Dingxiao and Wusha (Xingyi County, Guizhou Province) to Fuyuan County (Yunnan Province) (Li, 2006; Benton *et al*., 2014). The number of excavated *Keichousaurus* individuals is estimated at many thousands. Due to this high number, the morphology could be studied in detail and interesting life history traits identified, such as ontogenetic and intraspecific variation and sexual dimorphism (Rieppel & Lin, 1995; Lin & Rieppel, 1998; Cheng *et al*., 2009; Xue *et al*., 2015). Due to the find of pregnant females, sexually dimorphic morphological features can for the first time be assigned to a certain sex (Cheng *et al*., 2004), showing that sex A of Sander (1988) and sex X of Sander (1989) & Rieppel (1989) is the female. This enabled researchers to identify males as the sex that becomes larger and has the more plesiomorphic humerus (among many other differences) (see also Sander, 1988, 1989).

A few years ago, a new pachypleurosaur genus and species, *Dianopachysaurus dingi* Liu *et al*., 2011 from the Anisian of Luoping County, Yunnan Province, was erected (see also Benton *et al.,* 2014). Contrary to the numerous individuals of *Keichousaurus, Dianopachysaurus* is so far only known from a single, nearly complete and articulated specimen. In spite of its small size (~ 20 cm), the authors argue for a mature ontogenetic stage (Liu *et al*., 2011). Together with *Keichousaurus, Dianopachysaurus* forms the Keichousauridae (Liu *et al*., 2011).

Besides these two valid pachypleurosaur taxa, the Middle Triassic (Anisian) of China has yielded a variety of taxa that show a mixture of pachypleurosaur and nothosaur features, leaving them as eosauropterygians of unclear phylogenetic affinities. *Wumengosaurus delicatomandibularis* Jiang *et al*., 2008 is known from about five, more or less complete specimens from the middle Anisian of Xinmin, Panxian County, Guizhou Province, China. *Wumengosaurus* has a very special dentition and highly differentiated 'pincers jaws', which are typically used to secure prey with a laterally directed snapping bite (Jiang *et al*., 2008). In some phylogenetic analyses, *Wumengosaurus* is found as sister taxon to pachypleurosaurs (Fig. 1A) whereas other authors treat it as an eosauropterygian of unclear affinities (Fig. 1B).

From various Anisian localities in the Yunnan Province, China, which also had yielded the pachypleurosaur *Dianopachysaurus*, three more small eosauropterygians are described: *Diandongosaurus acutidentatus,* Shang *et al*., 2011 (see also Liu *et al*., 2017), *Dianmeisaurus gracilis*, Shang and Li, 2015, and *Dawazisaurus brevis,* Cheng

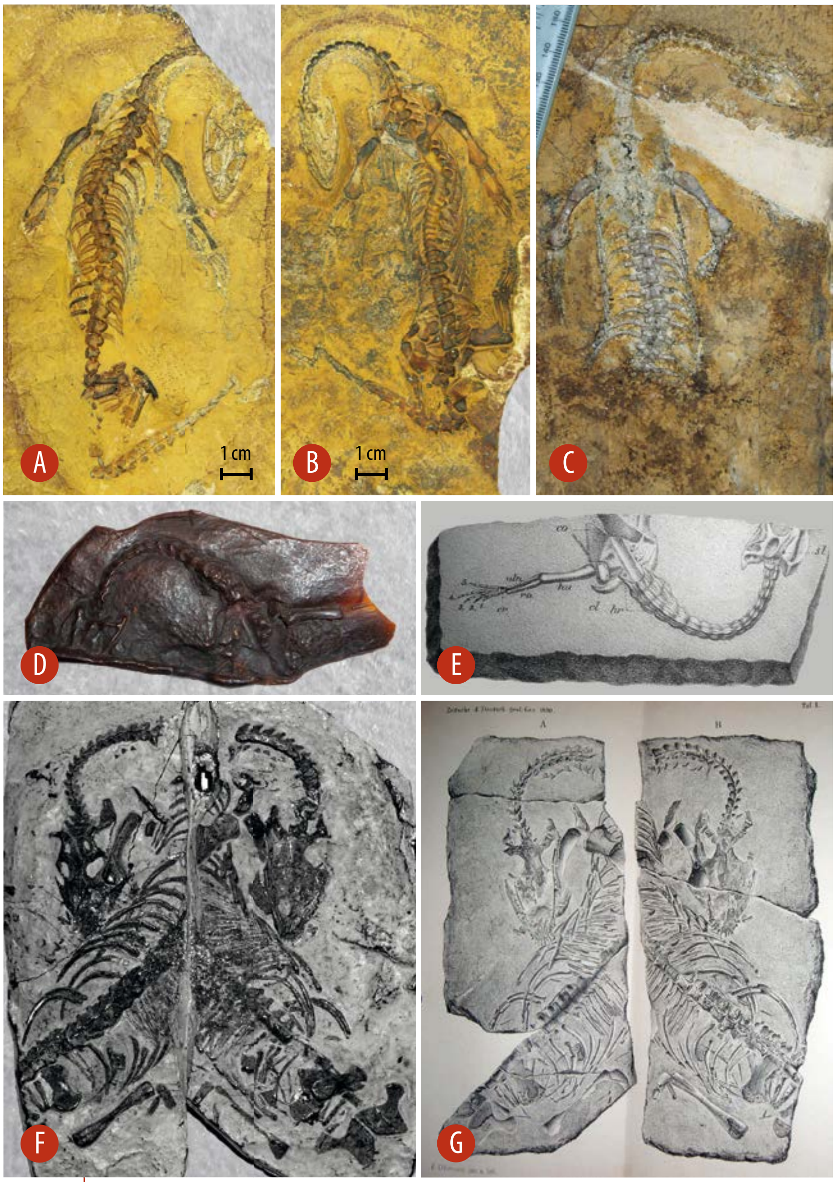

FIGURE 2. | *A, B, Holotype of* Dactylosaurus schroederi *(Nopsca, 1928) (BGR uncatalogued) in dorsal (A) and ventral (B) view (part and counterpart, natural mold).*

C, Skeleton of aff. Dactylosaurus *(GPIT/RE/01867).*

D, Cast of the holotype of Dactylosaurus gracilis *(Gürich, 1884).*

E, Interpretive drawing of Dactylosaurus gracilis taken from Gürich (1884).

F, Cast of the lost holotype of Anarosaurus pumilio *(IGWH / M4/12).*

G, Interpretive drawing of Anarosaurus pumilio *taken from Dames (1890).*

et al., 2016. These taxa all share a similar small size range with the keichousaurids (body size < 50 cm) but differ from these pachypleurosaurs and from each other in several morphological aspects. However, only one or two specimens of each of these new taxa are known, limiting morphological information.

Recently, two pachypleurosaur specimens have been described from the Triassic of Myanmar (Khaing *et al.*, 2019). Although they are unequivocally assignable to Pachypleurosauria, their preservation does not allow a further taxonomical assignment or a test of phylogenetic relationships. The most diagnostic feature of the Myanmar pachypleurosaur is the distinctly curved humerus, which is unknown in other pachypleurosaurs except for *Dianopachysaurus* (Liu *et al.*, 2011; Khaing *et al.*, 2019). The flat and curved humerus disagrees with the plesiomorphic condition and can be interpreted as an advanced adaptation to an aquatic lifestyle. Although the exact stratigraphy of the fossil-bearing units is in need of revision, the pachypleurosaurs from Myanmar 'may be among the oldest pachypleurosaurs globally, potentially corroborating biogeographic scenarios that posit an eastern Tethyan origin for pachypleurosaurs' (Khaing *et al.*, 2019:1).

Morphology

Most pachypleurosaurs stayed rather small, i.e., below 50 cm in total body length. *Keichousaurus* males grew larger than females and could have reached 40 cm, although most stayed smaller (25-30 cm). The maximum body length of *Serpianosaurus* according to Rieppel (1989) is 2 m but most individuals reached only 1-1.5 m. The body length of *N. edwardsii* was around 1.2 m (Caroll & Gaskill, 1985; Sander, 1989) and that of *A. heterodontus* is estimated to reach about 1 m (Klein, 2012).

Pachypleurosaurs have a generalized postcranial skeleton. All share the typical elongated body shape with a small head on a long neck, an elongated trunk region, and a long tail. Limbs are rather short in relation to the body length. Shoulder girdle and pelvic girdle are modified, and coracoid, ischium and pubis are plate-like elements (Fig. 3F).

Except for their trunk shape and body ratios, pachypleurosaurs from the Germanic Basin do not show any further special aquatic adaptations apart from a slight tendency towards pachyostosis in the dorsal vertebrae and proximal dorsal ribs in *Dactylosaurus* and *A. pumilio*. Pachyostosis, however, is not documented in the skeleton of *A. heterodontus*. In contrast, stratigraphically younger pachypleurosaurs from the Alpine Triassic and China show progressive morphological adaptations to an aquatic life, such as simplification of limb bones, reduction of carpal and tarsal bones, and pronounced pachyostosis of vertebrae and ribs as well as osteosclerosis in most of their bones. The Alpine and Chinese taxa were thus more adapted to an aquatic environment than those from the Germanic Basin, which is most likely the result of differences between environments (near coastal vs. shallow marine).

Pachypleurosaurs are thought to have swum by lateral undulation (anguilliform swimmers) with the forelimbs applied to the body and the main propulsion effected via the tail (Caroll & Gaskill, 1985). The hindlimbs may have served in steering. The increase in bone mass via pachyosteosclerosis documented in pachypleurosaurs from the Alpine Triassic (*Neusticosaurus* and *Serpianosaurus*) (Sander, 1989, 1990; Hugi *et al.*, 2011) and pachyostosis in *Keichousaurus* (Li & Rieppel, 1998) when compared to *Dactylosaurus* and *Anarosaurus*, increased their body mass to cope with buoyancy.

The skull of pachypleurosaurs is dorsoventrally flat and paedomorphic due to the very large orbits (Fig. 3A-C). The skull clearly differs from that of Eusauropterygia by the very small upper temporal fenestra but shares the closed occiput. The snout is relatively short and not constricted. Except for *A. heterodontus,* pachypleurosaurs have a homodont dentition consisting of numerous small teeth. As the species name suggests, *A. heterodontus* has the anterior premaxillary and dentary teeth relatively enlarged (Fig. 3B, C). Contrary to other pachypleurosaurs, *A. heterodontus* has a massive posterior part of the skull and lower jaw (Fig. 3B), most likely enabling it to crush hard-shelled prey such as arthropods. All other pachypleurosaurs are interpreted to have been suction feeders that hunted for small fishes and cephalopods (Rieppel, 2002). Contrary to nothosaurs, *Anarosaurus* and *Neusticosaurus* have scleral ossicles (Fig. 3C) and this probably applies to all pachypleurosaurs.

The Winterswijk pachypleurosaur: *Anarosaurus heterodontus*

The pachypleurosaur *A. heterodontus* was the most common vertebrate in the Lower Muschelkalk of Winterswijk considering the amount of its fossilized remains that have been found. Several incomplete but articulated and/or associated skeletons (Klein, 2012; Heijne *et al.*, 2019) and about 25 skulls (or even more) are noted (Klein, 2009; Heijne *et al.*, 2019; Fig. 3) The large number found in Winterswijk contrasts with the extremely rare occurrence of *A. heterodontus* elsewhere in the Germanic Basin- at least when considering diagnostic/ unequivocally assignable material. Only isolated finds such as the holotype (right dentary) from Remkersleben (housed in the IGWH) and an isolated maxilla from the Lower Muschelkalk of Rüdersdorf (Berlin) (housed in the collection of the BGR; pers. obs. NK) are so far documented. To our knowledge, *A. heterodontus* is not known outside the Germanic Basin, neither is *Dactylosaurus* nor *A. pumilio*.

The skeleton of *A. heterodontus* shows the least aquatic adaptations among all pachypleurosaurs. This means that it is plesiomorphic, i.e., closer to the unknown terrestrial ancestor. The humerus morphology of *A. heterodontus* is simple, i.e., it is less complex when compared to *Dactylosaurus* (Fig. 3E, F). Furthermore, humeral microanatomy reveals a lesser degree of bone mass increase (i.e., less aquatic adaptation) in *A. heterodontus* when compared to *Dactylosaurus*. The plesiomorphic morphology and low degree of aquatic adaptation in *A. heterodontus* could be interpreted as consistent with its early stratigraphical occurrence (but see Liu *et al.*, 2011; Renesto *et al.*, 2014; Khaing *et al.*, 2019) or might be related to function, i.e., a lifestyle in a near-coastal, shallow marine environment as indicated by the sediments in Winterswijk. However, an eastern Tethyan origin of pachypleurosaurs would imply a gap in the fossil record. A possible explanation could be that the first pachypleurosaurs were still terrestrial or semiaquatic and dispersed largely through fluviatile environments. A second (but less likely) hypothesis is that paleogeographical ideas about seaways and landmasses need improvement. However, new finds, from older sediments (pre-Anisian) and further studies are necessary to answer

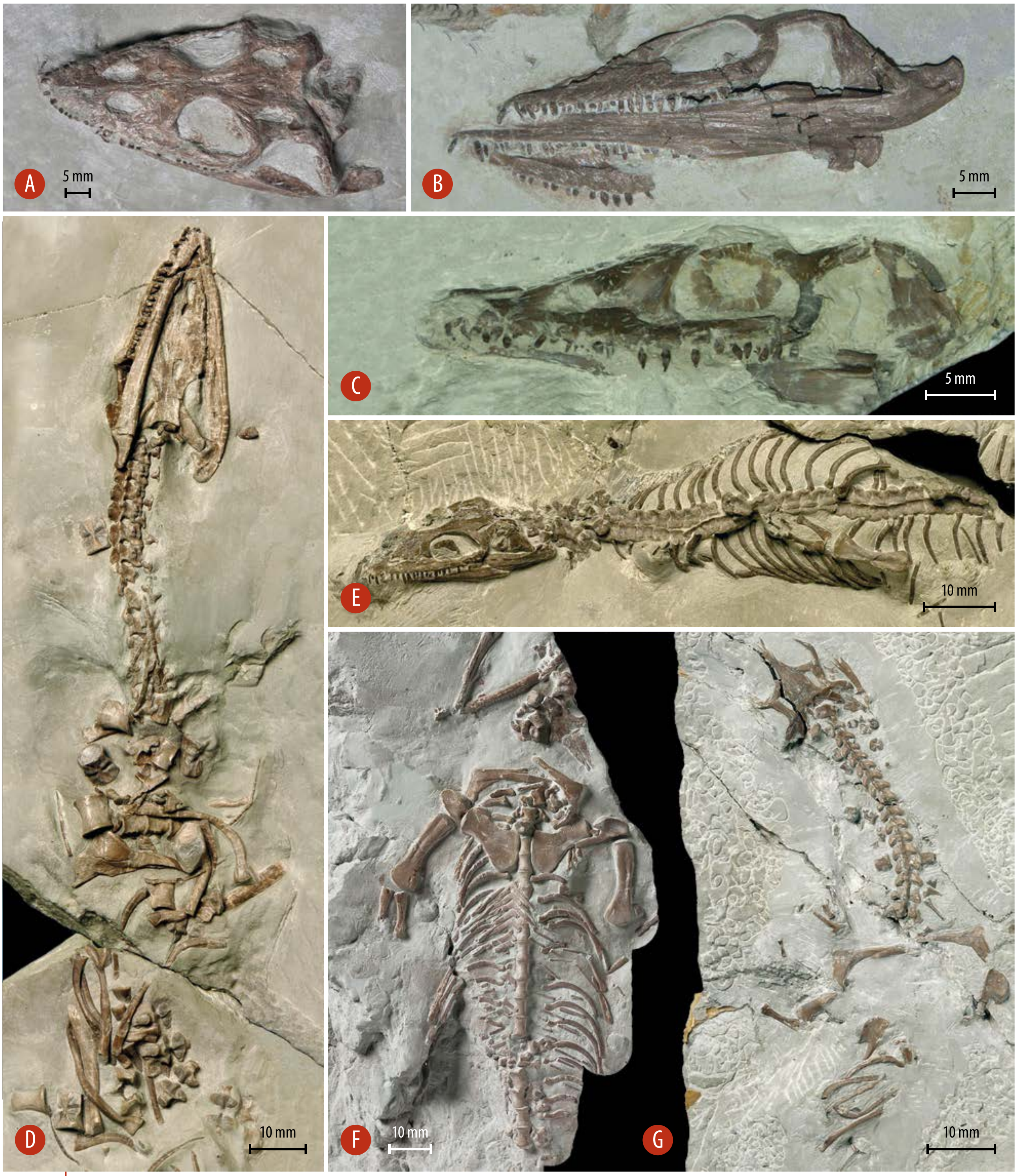

FIGURE 3. | *A, Skull of* Anarosaurus heterodontus *in dorsolateral view showing the characteristic wide shape of the posterior skull and lower jaw. The specimen was found by Wim Berkelder, Winterswijk and is now in the collection of TwentseWelle, Enschede (TWE 480000476). B, Skull of* Anarosaurus heterodontus *in ventrolateral view depicting the heterodont dentition in the upper and lower jaws. The massive posterior part of the lower jaw implies strong muscles and thus biting forces. The specimen was found by and is housed in the collection of Jos Lankamp, Borne. C, Skull of* Anarosaurus heterodontus *in lateral view nicely exhibiting the heterodont dentition as well as being one of the rare finds that has the scleral ossicles preserved. The specimen was found by and is housed in the collection of Henk Oosterink, Winterswijk. D, Skull, neck and disarticulated shoulder region of* Anarosaurus heterodontus *in ventral view. The specimen was found by and is housed in the collection of Jan van den Berg, Schoonhoven. E, Articulated skull and incomplete anterior trunk region of* Anarosaurus heterodontus *in dorsolateral view found during a joint excavation by the University of Bonn, the Winterswijk workgroup, Naturalis and the University of Utrecht in 2007 and is now housed in the collection of Naturalis, Leiden (NMNHL RGM 443858). F,* Anarosaurus heterodontus*, lower jaws, disarticulated neck region, and trunk region with the shoulder girdle and upper arms still articulated, in ventral view. The specimen was found by and is housed in the collection of Jos Lankamp, Borne. G, Incomplete skull, articulated neck, and parts of the shoulder girdle of a very young individual of* Anarosaurus heterodontus *in dorsal view. The specimen was found by and is housed in the collection of Herman Winkelhorst, Aalten.*

the question about the origin of Sauropterygia and Pachypleurosauria, respectively. *A. heterodontus* also differs from all other pachypleurosaurs in its bone histology. Whereas *Dactylosaurus* (Klein & Griebeler, 2018), *Serpianosaurus, Neusticosaurus* (Hugi *et al*., 2011), and *Keichousaurus* (pers. comm. Qiang Li 2019) share a typical lamellar-zonal bone tissue type, *Anarosaurus heterodontus* displays a tissue type more similar to that of cf. *Cymatosaurus* (Klein, 2010; Klein & Griebeler, 2018). The cortex of *A. heterodontus* was much more vascularized and the tissue faster deposited when compared to all other pachypleurosaurs and even when compared to nothosaurs (Klein, 2010; Klein *et al*., 2016). This indicates an increased growth rate and a higher metabolic rate, similar to what is documented in long bones of cf. *Cymatosaurus* from the Lower Muschelkalk (Klein, 2010). Due to size and morphological differences as well as mathematical modeling of growth, it can be largely excluded that *A. heterodontus* is the juvenile of cf. *Cymatosaurus* (See the pistosauroidea work by Klein on page 245). However, new finds can always change scientific ideas and hypotheses.

Abbreviations

BGR, Bundesanstalt für Geowissenschaften und Rohstoffe, Berlin, Germany.
GPIT, Geologisch-Paläontologisches Institut, Univeristät Tübingen, Germany.
IGWH, Institut für Geowissenschaften, Martin-Luther-Universität, Halle/Saale, Germany.
MGU Wr, Institute of Geological Sciences, University of Wraclaw, Poland.

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Samenvatting

Pachypleurosauria zijn kleine (50 cm – 120 cm lichaamslengte), basale Eosauropterygia die de ondiepe continentale zeeën en de kustgebieden van de Tethys Oceaan bewoonden. Pachypleurosauria kwamen voor tussen de laatste periode van het Vroeg-Trias tot aan het einde van het Midden-Trias (Laat-Olenekien tot Ladinien). Soorten uit het Ladinien bezaten een skelet met pedomorfe (volwassen dieren hadden eigenschappen die we bij jongere dieren verwachten) en pachyostotische (verdikte botten om drijfvermogen tegen te gaan) kenmerken. Deze eigenschappen zijn beide het gevolg van aanpassing aan het leven in water. Van sommige soorten zijn zeer veel individuen bekend, waardoor levendbarendheid en geslachtsdimorfie (fysieke verschillen tussen de geslachten) kon worden herkend. Pachypleurosauriërs vormen een zeer diverse groep die tegenwoordig 7 genera en 10 goed bekende soorten bevat. Desalniettemin konden hun oorsprong, hun onderlinge relaties, en in het bijzonder de relaties tussen Europese soorten en pachypleurosauriërs uit de oostelijke Tethys, nog niet worden opgehelderd. *Anarosaurus heterodontus*, de pachypleurosauriër die in Winterswijk wordt aangetroffen, is stratigrafisch gezien een van de oudste pachypleurosauriërs. Binnen de groep laat deze soort ook nog de minste aanpassingen aan een leven in water zien. *A. heterodontus* verschilt van andere pachypleurosauriërs door een speciale botstructuur die wijst op verhoogde groeisnelheden.

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