*Journal of the Marine Biological Association of the United Kingdom*, 2013, 93(7), 1857–1869. 
doi:10.1017/S0025315413000404

# Phylogeography of the horse mussel *Modiolus modiolus*

KENNETH M. HALANYCH[1], E. THURÓCZY VODOTI[2], PER SUNDBERG[2] AND THOMAS G. DAHLGREN[2,3]

[1]Department of Biological Sciences, Auburn University, Auburn, AL, USA, [2]University of Gothenburg, Department of Biological and Environmental Sciences, PO Box 463, SE-405 30 Göteborg, Sweden, [3]Uni Research, Thormøhlensgate 55, Bergen, Norway

*Phylogeographic inferences concerning marine species are largely based on intertidal species. In high latitudes, intertidal species have been affected by ice coverage and ice scour, and therefore show northern range limitations during glaciations. In this study, we use the subtidal horse mussel (*Modiolus modiolus*) to investigate whether generalizations about genetic structure of high latititude intertidal species, specifically in the North Atlantic, are representative of other near shore taxa. We analysed genetic diversity, molecular variance, and geographical patterns of genetic relatedness using data from the mtDNA CO1 gene. Although we do find little to no haplotype structure in the North Atlantic, our results show that north-eastern Pacific individuals represent a different haplotype network with no haplotypes in common with Atlantic individuals. Thus,* M. modiolus *in the Pacific may represent an unrecognized species. Genetic diversity and population expansion times suggest a Pacific origin is most likely, with subsequent dispersal to the Atlantic. The lack of genetic structure in the Atlantic suggests that a rapid range expansion occurred less than 50 KYA, rather than a stepping stone mode of dispersal.*

**Keywords:** genetic structure, dispersal, refugia, North Atlantic, *Modiolus*

Submitted 8 November 2012; accepted 19 February 2013; first published online 31 May 2013

## INTRODUCTION

The horse mussel, *Modiolus modiolus* (Linnaeus, 1758), is a boreal species occurring in the northern hemisphere (Figure 1). Sensitivity to changes in temperature and salinity make horse mussels dependent on deeper, subtidal waters from a few metres down to 100 m of depth, although individuals have been reported at 280 m (Schweinitz & Lutz, 1976) as well as in the intertidal (Davenport & Kjorsvik, 1982). These mussels often form biogenic reefs, which can sustain large numbers of associated invertebrate taxa (Brown & Seed, 1977; Ojeda & Dearborn, 1989). The species is gonochoristic and has a generation time of 5–10 years with sexual maturity reached around 3–8 years of age (Jasmin & Brand, 1989). Individuals can reach 100 years old, although an age span of 20–35 years is more commonly reported (Anwar *et al.*, 1990). Spawning is sporadic and several years can pass without recruitment. The larval phase can be up to six months, and thus there is potential for long distance dispersal. Temperature requirements for adult specimens have been rather poorly investigated, but available data suggest an optimal growth temperature of around 7–10°C with an upper limit of around 15–20°C (Davenport & Kjørsvik, 1982), and a tolerance for below-zero temperatures for an extended period of time (e.g. during winter in the White Sea population; Howland *et al.*, 1999).

Biology of the horse mussel (e.g. the need of subtidal habitat, resistance to freezing) makes the species a suitable indicator of how shallow subtidal marine areas have been affected by climate change, including temperature and sea level fluctuations. As opposed to genetic studies focusing on North Atlantic intertidal species (e.g. Muhlin & Brawley, 2009; Campo *et al.*, 2010; Marko *et al.*, 2010), patterns of shallow subtidal organisms can reveal information about an extended geographical range and duration of climate changes in the North Atlantic because subtidal organisms were presumably exposed to lower rates of localized extinction from, for example, ice scour. Additionally, such data provide insight to identification of source populations, historical species ranges, climate refugia and probable re-colonization routes. For instance, communities that have experienced prior extinctions are generally poor in species or have populations that are not highly specialized in terms of, for example, competition, predation and disease, and they are the ones most easily replaced (Vermeij, 1996).

Most intertidal animals in the North Atlantic have limited genetic structure and evidence of recent population expansion (see Wares, 2001; Wares & Cunningham, 2001). Thus to test this generalization with a subtidal taxon, we investigated intraspecific genetic patterns of *M. modiolus* using partial mitochondrial gene cytochrome oxidase subunit 1 (CO1) data from several localities in the North Atlantic and one in the north-east Pacific. Results here provide insight as to how glaciation may have impacted near shore marine fauna that are not primarily intertidal in nature.

## MATERIALS AND METHODS

### Data collection

*Modiolus modiolus* specimens were collected during 2000–2005 in the north-east Pacific (San Juan Island, Washington, USA) and the North Atlantic (Figure 1; Table 1). DNA was extracted

**Corresponding authors:**
K.M. Halanych and T.G. Dahlgren
Emails: ken@auburn.edu & thomas.dahlgren@uni.no

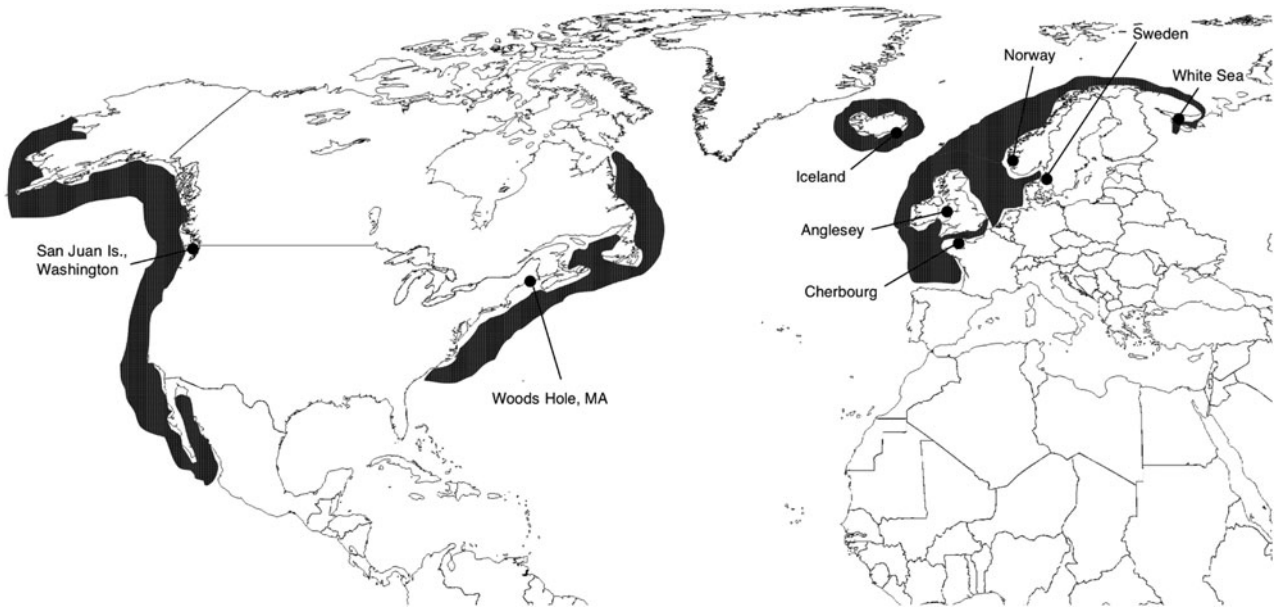


**Fig. 1.** *Modiolus modiolus*: map showing the eight sample sites. Dark-grey areas indicate the current species distribution.

from large adductor muscle tissue from a total of 123 individuals with E.Z.N.A® Tissue DNA Kit II (200) from Omega Bio-Tek and then stored at −20°C. The mitochondrial cytochrome oxidase subunit 1 (CO1) gene was amplified using the LCO 1490/HCO 2198 (Folmer *et al.*, 1994) primer combination and standard recommendations of Illustra PuReTaq Ready-To-Go PCR Beads kit from GE Healthcare. Polymerase chain reactions (PCR) were run initially for 5 min at 95°C followed by 40 cycles of (95°C 40 s, 45°C 45 s, 72°C 30 s), and ended with 72°C 5 min. Completed PCR-reactions were purified with Qiagen™ Qiaquick Kit. Sequencing was performed by the genetic service facilities of Macrogen (Seoul, Korea) using the same primers as for PCR. Sequences were proofread in SeqMan, saved in EditSeq-format, aligned in MegAlign 5.51 (DNASTAR Inc.) with Clustal W implementation (Thompson *et al.*, 1994), and confirmed by eye. Further editing of PHYLIP and NEXUS format files for subsequent analyses was performed in MacClade 4.07 (Maddison & Maddison, 2005). The aligned data set is deposited as a population study at GenBank with haplotypes M01-M052 under Accession numbers KC119336–KC119387, respectively.

## Genetic variation and population analyses

We applied a statistical parsimony algorithm (Templeton *et al.*, 1992) in TCS v.1.21 (Clement *et al.*, 2000) to reconstruct genetic relatedness among haplotypes as a network. MrModeltest2 (Nylander, 2004) was used to determine the most appropriate model of nucleotide substitution as judged by the Akaike information criterion (AIC). Genetic statistics were conducted in DNAsp v.4.0 software (Rozas & Rozas, 1999), and Arlequin software v.3.1 (Excoffier *et al.*, 2005). We used the ratio of non-synonymous and synonymous substitutions, $d_N/d_S$, to test for positive selection and Tajima's D statistic (Tajima 1989) for selective neutrality. Fu and Li's F-statistic (Fu & Li, 1993) was used to test for deviations from a constant population-size. Further, we estimated haplotype diversity (Hd) and nucleotide diversity ($\pi$). Using only populations showing expansion (as judged by Tajima's D and Fu and Li's F statistics), the time ($t$) of onset of population expansion was inferred from tau ($\tau$) as estimated from a mismatch analysis as $t = \tau/2u$ (Rogers & Harpending 1992), where $u = m_T\mu$ ($m_T$ = number of nucleotides investigated, $\mu$ = mutation rate nucleotide-site$^{-1}$). Confidence intervals of $\tau$ and the sum of squared deviation, which estimates the validity of the assumed stepwise expansion model, were generated by a parametric bootstrap (10,000 replicates). The raggedness statistic ($r$) that measures the smoothness of the mismatch distribution (Harpending, 1994), and its significance were also calculated. In population expansion calculations based on $\tau$ from the mismatch analysis, we used the hitherto estimated range of the CO1 gene divergence rates of 1–5.1% MY$^{-1}$ for a number of marine bivalves (Marko & Moran, 2002; Luttikhuisen *et al.*, 2003; Won *et al.*, 2003). In addition, we also estimated divergence rates in *M. modiolus* for different codon positions in the Atlantic clade alone (see below), calibrated with the estimation of the trans-Arctic interchange based on *Astarte* bivalves of 5.32 million years ago (MYA) (Gladenkov *et al.*, 2002). Because this is considered one of the earliest stages of the Bering Strait opening, our calculations will represent minimum estimates of nucleotide change.

Population pairwise $F_{ST}$ values were estimated between all sample sites (10,000 permutations for significance testing) with Tamura–Nei distance implementation (given by

**Table 1.** *Modiolus modiolus*. Collection information.

| Locality | Collection method | Lat | Long | Depth (m) | Number |
|---|---|---|---|---|---|
| Anglesey | Dredge | 53°22′N | 04°59′W | 55–67 | 16 |
| Cherbourg | Dredge | 49°50′N | 01°51′W | 60–70 | 3 |
| Iceland | SCUBA | 64°17′N | 22°17′W | 25 | 19 |
| Norway | Dredge | 63°27′N | 10°19′E | 30–35 | 12 |
| Sweden | Dredge | 58°53′N | 11°05′E | 15–20 | 26 |
| White Sea | Dredge | 66°19′N | 33°40′E | 15 | 14 |
| Woods Hole | Dredge | 41°21′N | 70°56′W | 28–30 | 18 |
| Washington | Dredge | 48°32′N | 122°59′W | 20–23 | 15 |

https://doi.org/10.1017/S0025315413000404 Published online by Cambridge University Press

MrModeltest2, results not presented). Correlation analysis (Mantel test) was performed between the estimated $F_{ST}$ values and the geographical distances in kilometres between all Atlantic sample sites (the Pacific site was too divergent be meaningful in the Mantel test). Distances were estimated by using the ruler function in Google Earth software (http://earth.google.com/) by tracing coastlines with shortest distances trajectories between sampling sites.

## RESULTS

The aligned data set consisted of 598 bp (no indels present) for 123 individuals of *Modiolus modiolus*. Out of 98 (16.4%) variable sites, 70 (11.7%) sites were parsimony informative and a total of 70 synonymous and 31 non-synonymous changes were found (see Appendix). A total of 20 of the 31 non-synonymous changes were found in the Washington sample alone. Within each ocean basin, no more than five amino acids were different between any two individuals. The 52 haplotypes identified possessed uncorrected differences of 0.17–11%. TCS analysis with a 95% cut-off value produced two separate networks, one representing Pacific samples and one representing all Atlantic samples. No shared haplotypes were recovered between the Pacific and Atlantic (Figure 2; Table 2). From here on, we will refer to these two networks as the Pacific clade and the Atlantic clade. We found weak spatial genetic structuring in the Atlantic clade, seen as large, deeply nested haplotypes comprising all or most of the sample sites, but we also found a considerable number of private haplotypes. We chose to analyse the Pacific and the Atlantic samples separately where appropriate, to avoid biased results because of the apparently old separation between the two clades.

Statistics relating to nucleotide and haplotype diversity and mismatch analyses are given in Table 3. Variable nucleotide sites within the Pacific clade (0.17–3%) were greater than in the Atlantic clade (0.17–1.50%). Nucleotide diversity ranged from 0.0021–0.0045 in the Atlantic (Iceland/Anglesey–White Sea), to 0.0127 in the Pacific sample. When analysed as a single sample, the Atlantic clade had a haplotype diversity of 0.837 (SD 0.034), and a nucleotide diversity of 0.0033 (SD $3.1{\cdot}10^{-4}$). Sweden, the White Sea and Woods Hole display the highest haplotype diversities, while Iceland had the lowest value. Compared to Atlantic populations, the Pacific clade has all private alleles (100%) and all haplotypes were represented by single individuals (except for the Mo15 haplotype represented twice). This pattern stands in stark contrast to the Atlantic network illustrating a 'star shape' network with several singletons radiating from the two major and widely shared haplotype groups Mo4 and Mo5 that were found in all the Atlantic populations except Cherbourg (Figure 2;

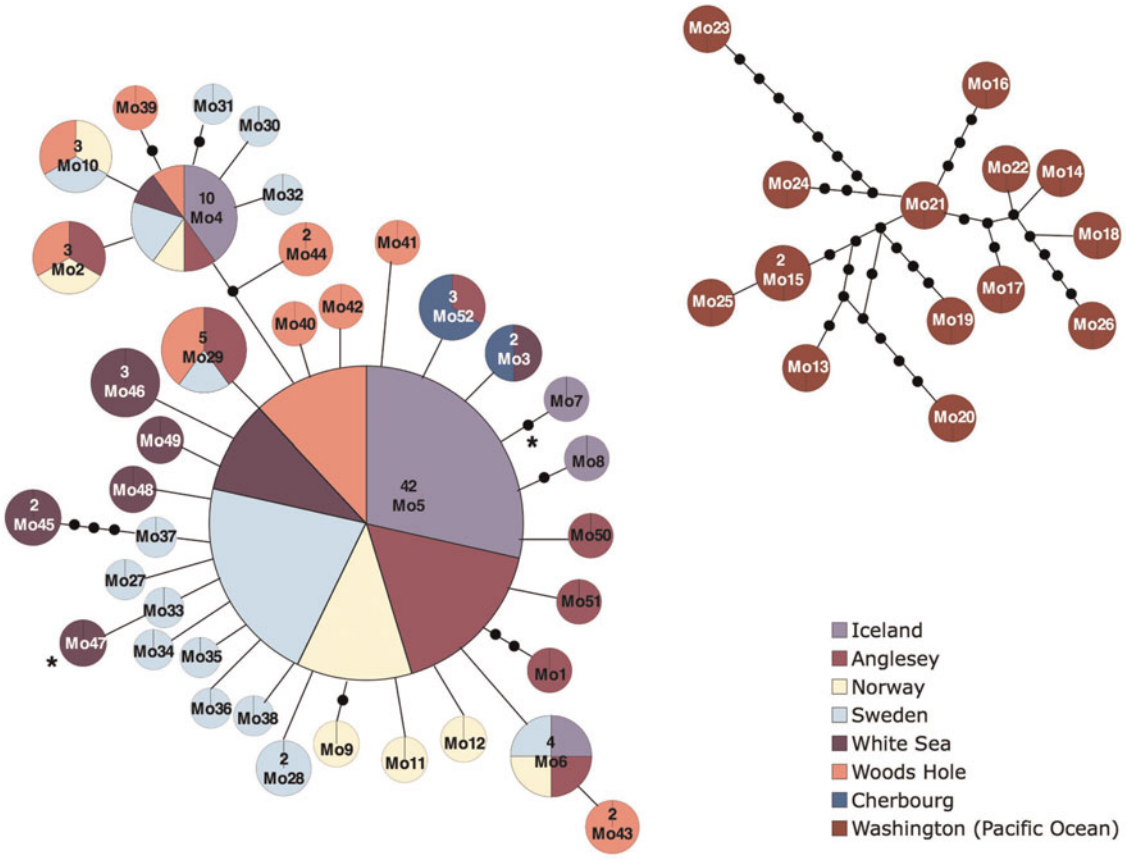


**Fig. 2.** *Modiolus modiolus:* TCS parsimony haplotype network. Legend denotes the different sample sites shown in Figure 1. Each circle represents a unique haplotype and shows the haplotype ID (2; Appendix). The relative sizes of circles indicates number of included specimens, which is also shown above the haplotype ID (e.g. 42/Mo5). An empty line connecting haplotypes represents a single mutational change; each black dot on a line represents one mutational change (a missing intermediate specimen). The 95% connecting limit was estimated to 21 steps. *, indicates one mutational change between the Mo47 haplotype and a missing intermediate.

https://doi.org/10.1017/S0025315413000404 Published online by Cambridge University Press

**Table 2.** *Modiolus modiolus*: haplotypes recovered at each sampling site. Private alleles are totalled.

| Haplotype ID | Anglesey | Cherbourg | Iceland | Norway | Sweden | White Sea | Woods Hole | Washington State | Genbank Access. No. |
|---|---|---|---|---|---|---|---|---|---|
| Mo1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | KC119336 |
| Mo2 | 1 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | KC119337 |
| Mo3 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | KC119338 |
| Mo4 | 1 | 0 | 4 | 1 | 2 | 1 | 1 | 0 | KC119339 |
| Mo5 | 7 | 0 | 12 | 5 | 9 | 4 | 5 | 0 | KC119340 |
| Mo6 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | KC119341 |
| Mo7 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | KC119342 |
| Mo8 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | KC119343 |
| Mo9 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | KC119344 |
| Mo10 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | KC119345 |
| Mo11 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | KC119346 |
| Mo12 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | KC119347 |
| Mo13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119348 |
| Mo14 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119349 |
| Mo15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | KC119350 |
| Mo16 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119351 |
| Mo17 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119352 |
| Mo18 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119353 |
| Mo19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119354 |
| Mo20 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119355 |
| Mo21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119356 |
| Mo22 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119357 |
| Mo23 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119358 |
| Mo24 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119359 |
| Mo25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119360 |
| Mo26 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | KC119361 |
| Mo27 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119362 |
| Mo28 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | KC119363 |
| Mo29 | 2 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | KC119364 |
| Mo30 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119365 |
| Mo31 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119366 |
| Mo32 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119367 |
| Mo33 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119368 |
| Mo34 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119369 |
| Mo35 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119370 |
| Mo36 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119371 |
| Mo37 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119372 |
| Mo38 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | KC119373 |
| Mo39 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | KC119374 |
| Mo40 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | KC119375 |
| Mo41 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | KC119376 |
| Mo42 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | KC119377 |
| Mo43 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | KC119378 |
| Mo44 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | KC119379 |
| Mo45 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | KC119380 |
| Mo46 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | KC119381 |
| Mo47 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | KC119382 |
| Mo48 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | KC119383 |
| Mo49 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | KC119384 |
| Mo50 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | KC119385 |
| Mo51 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | KC119386 |
| Mo52 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | KC119387 |
| Total | 16 | 3 | 19 | 12 | 26 | 14 | 18 | 15 | |
| No. private alleles | 3 | 0 | 2 | 3 | 11 | 5 | 6 | 15 | |
| % private alleles | 18.8 | 0 | 10.5 | 25 | 42.3 | 35.7 | 33.3 | 100 | |

Table 2). For Mo4 and Mo5, the Icelandic population has a proportionally larger number of specimens represented while the White Sea population had the lowest.

No positive selection was revealed by $d_N/d_S$ values (0.14 and 0.16 for the Atlantic and Washington group, respectively). Tajima's D-value was not significant for separate populations, but highly significant for the Atlantic as a whole ($-2.40$; $P < 0.001$). The Pacific sample did not have a significant D-value ($-1.41$; $P = 0.071$). Fu and Li's F statistic was only significant for the Atlantic clade ($-4.34$; $P < 0.05$), demonstrating a deviation from the Wright–Fisher model of a constant-sized population (Hartl & Clark, 1997). The mismatch analysis showed an onset of population expansions in the Atlantic, based on the third codon position

https://doi.org/10.1017/S0025315413000404 Published online by Cambridge University Press

**Table 3.** Genetic statistics and results of the mismatch analysis for the inferred populations.

| | Anglesey | Cherbourg | Iceland | Norway | Sweden | White Sea | Woods Hole | Washington State |
|---|---|---|---|---|---|---|---|---|
| *N* | 16 | 3 | 19 | 12 | 26 | 14 | 18 | 15 |
| h | 9 | 2 | 5 | 8 | 16 | 8 | 11 | 14 |
| Hd | 0.817 (0.095) | 0.667 (0.314) | 0.579 (0.114) | 0.848 (0.104) | 0.883 (0.050) | 0.890 (0.060) | 0.915 (0.050) | 0.990 (0.028) |
| π | 0.0021 ($6{\cdot}10^{-4}$) | 0.0022 (0.0011) | 0.0021 ($5{\cdot}10^{-4}$) | 0.0033 ($7{\cdot}10^{-4}$) | 0.0033 ($5{\cdot}10^{-4}$) | 0.0045 (0.0011) | 0.0041 ($6{\cdot}10^{-4}$) | 0.0127 (0.0015) |

*N*, number of sampled specimens; h, number of haplotypes; Hd, haplotype diversity; π, nucleotide diversity.

divergence rate, of around 26 KYA, τ-value of 1.45 (95% CI 0.69–3.14). Previously published divergence rates roughly conform to our estimates (Table 4). We chose to use the third codon position divergence rate since it is least prone to selection as most mutations are synonymous, but in Table 4 we also present results from the second codon position, for comparison. The raggedness statistic and the sum of squared deviation of the mismatch analysis were both non-significant for all populations ($P \gg 0.05$). Analyses generated highly significant $F_{ST}$ values for the Washington clade as compared to all other sites (Table 5). The Mantel test of correlation between pairwise population $F_{ST}$ values and geographic distance was clearly non-significant between Atlantic populations ($-0.076$; $P = 0.490$).

## DISCUSSION

*Modiolus modiolus* samples from the north-east Pacific and the North Atlantic are genetically distinct, forming two separate clades with no shared haplotypes. The Pacific population from Washington displays considerably higher haplotype and nucleotide diversity as compared to the Atlantic, suggesting a more recent origin for the latter population. This finding is consistent with time estimates in Table 3 that indicates the expansion in diversity of the Pacific samples started roughly 132 KYA where as all such dates in the Altantic are less than 50 KYA. Importantly, this estimate is based off a single Pacific locality, San Juan Island, Washington, and is thus likely a significant underestimate of Pacific diversity. Thus, the Pacific populations likely coalesce at a much earlier date then indicated here.

Given these considerations, *M. modiolus* likely expanded from the Pacific into the Atlantic. Similar patterns of Pacific-to-Atlantic expansion of species are recorded from fossil data for a great number of marine invertebrate taxa (Vermeij, 1991; Cunningham & Collins, 1998; Luttikhuisen *et al.*, 2003). Based on fossil evidence, the horse mussel is estimated to have invaded the North Atlantic basin from the Pacific around 3 MYA–125 KYA, with a population increase during Late Pliocene (2 MYA) peaking at Early Pleistocene (1.5 MYA), but declining in Late Pleistocene (20 KYA) (Janssen *et al.*, 1984; Vermeij, 1989). Using divergence estimates for the CO1 third codon position, we calculated that *M. modilus* would have taken roughly 2.6–3.5 MYA to reach the 8–11% divergence observed between Atlantic and Pacific populations. This estimate is concordant with earlier estimates of bivalve and marine invertebrate divergence rates for the CO1 gene (Table 4). Thus genetic connectivity between Pacific and Atlantic populations appears to have been severed around the Pliocene/Pleistocene boundary (or just before) in agreement with the fossil data. The absence of genetic connectivity is further supported by the lack of shared haplotypes between the two oceans (but more Pacific sampling is needed).

In contrast, the Atlantic star-shaped network is indicative of relatively recent and rapid range expansions (Avise, 2001). Here, shared haplotypes Mo 4 and Mo 5 (found at all Atlantic sites except Cherbourg) are central and nested in the network (Figure 2). The sampling of deeply nested Atlantic haplotypes throughout the North Atlantic suggests a recent range expansion and migration across the region, i.e. the 'leading edge model', resulting in low overall genetic diversity, as opposed to a sequential colonization by founder groups, i.e. the 'stepping-stone' model (Hewitt 2000). This conclusion is bolstered by: (1) the non-significant raggedness and sum of square statistic from the mismatch analysis that indicate a recent demographic expansion (Rogers & Harpending, 1992), or a range expansion with high levels of individuals migrating between demes (Ray *et al.*, 2003); (2) both $F_{st}$ estimates and Mantel tests within the North Atlantic reported no significant differences between populations (Table 5); and (3) estimated onset of population expansion times varied only marginally across the Atlantic (Table 3) reflecting dispersal of individuals close in time.

**Table 4.** Approximate divergence rate estimates for the CO1 mtDNA gene in the Atlantic clade alone based on different codon positions and calibrated at the trans-Arctic interchange 5.32 MYA. Results are compared to previously published estimates for bivalves and the subsequent times of invasion based on the Atlantic τ-value from the mismatch analysis are presented. Finally, an estimate of the time needed for the Atlantic clade to acquire the found 8–11% divergence from the Pacific clade is shown. KYA, thousand years ago; MY, million years; MYA, million years ago.

| | Divergence (% $MY^{-1}$) | Divergence rate ($site^{-1}$ $year^{-1}$) ($\times 10^{-8}$) | Onset of population expansion (KYA) (95% CI) | Time to reach 8–11% clade divergence (MYA) |
|---|---|---|---|---|
| Codon pos 2 | 0.75 | 0.75 | 106 (51–230) | 10.7–14.7 |
| Codon pos 3 | 3.12 | 3.12 | 26 (12–55) | 2.6–3.5s |
| *Bathymodiolus** | 1–2† | – | 81 (38–175) | 5.3–7.3 |
| *M. edulis*** | 4.4 | – | 28 (13–60) | 1.8–2.5 |
| *Arcidae**** | 5.1 | – | 24 (11–51) | 1.6–2.2 |

*, Won *et al.*, 2003; **, Luttikhuisen *et al.*, 2003; ***, Marko & Moran 2002. †, here we use the mean value of 1.5.

https://doi.org/10.1017/S0025315413000404 Published online by Cambridge University Press

**Table 5.** Genetic structure analysis showing population pairwise $F_{ST}$ values (below diagonal) with Tamura–Nei distance implementation. Above diagonal shows geographical distance between sample sites (km) used in the Mantel test.

| | Anglesey | Cherbourg | Iceland | Norway | Sweden | White Sea | Woods Hole | Washington State |
|---|---|---|---|---|---|---|---|---|
| Anglesey | | 854 | 1413 | 1314 | 1660 | 3740 | 5136 | 10428 |
| Cherbourg | 0.1181 | | 2070 | 1397 | 1446 | 4224 | 5043 | 11468 |
| Iceland | −0.0124 | 0.2529 | | 1090 | 1650 | 3005 | 4333 | 8919 |
| Norway | −0.0147 | 0.1520 | −0.0347 | | 453 | 2857 | 5500 | 10213 |
| Sweden | −0.0083 | 0.1493 | −0.0227 | −0.0289 | | 3425 | 5920 | 11043 |
| White Sea | 0.0368 | 0.0686 | 0.0539 | 0.0426 | 0.0502 | | 7385 | 9154 |
| Woods Hole | −0.0004 | 0.1258 | −0.0075 | −0.0306 | −0.0082 | 0.0650 | | 12155 |
| Washington State | 0.9239* | 0.8897* | 0.9321* | 0.9147* | 0.9326* | 0.9133* | 0.9194* | |

*, shows a significant *P*-value (<0.01) estimated with 10, 000 permutations.

Our results show several private haplotypes, proportionally highest in Sweden and Woods Hole localities (~42%), followed by the White Sea (~36%) (Table 2; Figure 2). These locations also have the highest observed genetic diversity in the Atlantic (Table 3) indicating that populations may have been refugia, close to refugia, or at least source populations for the Atlantic population expansion. In general refugia in the North Atlantic (e.g. Dahlgren *et al.*, 2000; Addison & Hart, 2005), should display a higher proportion of unique haplotypes (Wares, 2002; Vermeij, 2005) with other areas in which a species have been expatriated should have a lower genetic diversity. However, Maggs *et al.* (2008) noted that low genetic diversity alone can be unreliable as an indicator of recently recolonized areas, because of issues like bottlenecks. Also, areas with high genetic diversity might be secondary contact zones instead of refugia, as seen in the coastal ice-cream cone worm *Pectinaria koreni* (Jolly *et al.*, 2006).

In the context of the present data, the White Sea has previously been hypothesized to host refuge populations (Audzijonyte & Väinölä, 2006). This region was covered by the eastern lobe of the Scandinavian Ice Sheet around 20 KYA (Svendsen *et al.*, 2004), and the horse mussel population may have survived in or in close vicinity to the White Sea. The first findings of horse mussel shells from northern Spitsbergen are dated to ~8.3 KYA, and indicate marine climatic optimum conditions further north (Salvigsen, 2002). Although the White Sea may have been a refugium, the genetic diversity may be due to repeated colonization events from other regions (Ingólfsson, 2009).

One other boreal subtidal species whose genetic structure has been examined in the North Atlantic is the ocean quahog, *Arctica islandica* (Linnaeus, 1767) (Dahlgren *et al.*, 2000; Weinberg, *et al.*, 2002). The ocean quahog's range does not differ markedly from that of the horse mussels in the North Atlantic, but it does not occur in the Pacific Ocean. The two species mostly differ in habitat preferences and life history. The ocean quahog occurs solely on sandy bottoms and therefore tolerates higher wave and tidal exposure (Sabatini & Pizzolla, 2008). Its larvae are long-lived and settle over a period of several months. Adults have a recorded longevity of more than 400 years and spawning can be intermittent on timescales of 10–20 years. Both adults and larvae of the horse mussel tolerate lower temperature than the ocean quahog, and have a high sensitivity to abrasion and decreased salinity (Tyler-Walters, 2007). Despite the overall similarities, phylogeographic patterns of the ocean quahog and the horse mussel differ. Specifically, ocean quahog populations show more east-to-west genetic structure in the North Atlantic. Additionally, the American east coast does not host any private haplotypes of the ocean quahog, while private haplotypes are abundant throughout the entire North Atlantic range of the horse mussel. On a smaller scale, however, gene flow does not seem to have been limited in the ocean quahog either (e.g. around Iceland and Nova Scotia).

In comparison with other North Atlantic subtidal organisms studied to date, the horse mussel haplotype diversity is comparable with the diversity found in the cone worm *Pectinaria koreni* (Jolly *et al.*, 2006) and the hermit crab *Pagurus longicarpus* (Young *et al.*, 2002) but much less than in the brittle star *Ophiothrix fragilis* where a high level of diversity is maintained by admixture of genetically differentiated cohorts produced from isolated populations (Muths *et al.*, 2009). The lower diversity in *M. modiolus* compared to other North Atlantic taxa might suggest that it only moved into the Atlantic recently.

Whether the Pacific and Atlantic populations of horse mussels should be separate species needs more consideration. In particular, mytilids are renowned for being extremely challenging taxonomically even when both molecular and morphological evidence are brought to bear. Herein we show that there are at least two lineages for as currently recognized *M. modiolus*, but how distinct they are will depend on future sampling in the Pacific. Our findings are in general agreement with palaeontological information on migration and expansion of this and other bivalves. But while there has been considerable work on the impacts of glaciation and climate change in the northern Atlantic, the northern Pacific has received less attention. Likewise, more efforts need to be devoted to subtidal shelf species to more accurately assess range shifts of continental shelf species during climatic changes.

## ACKNOWLEDGEMENTS

We are grateful to Inger Holmqvist who assisted with laboratory work. Help with collection of some of the samples was provided by Jan Sørensen, Christin Appelqvist, Matthías Bjarnason, Marc Taimour Jolly, Toril Moen and Mikhail Fokin. AU Marine Biology contribution number 100.

## FINANCIAL SUPPORT

Funding was provided by the Swedish Research Council (TGD & PS), and Magnus Bergvalls Foundation (TGD).

## REFERENCES


**Addison J.A. and Hart M.W.** (2005) Colonization, dispersal, and hybridization influence phylogeography of North Atlantic sea urchins (*Strongylocentrotus droebachiensis*). *Evolution* 59, 532–543.

**Anwar N.A., Richardson C.A. and Seed R.** (1990) Age determination growth rate and population structure of the horse mussel *Modiolus modiolus*. *Journal of the Marine Biological Association of the United Kingdom* 70, 441–457.

**Audzijonyte A. and Väinölä R.** (2006) Phylogeographic analyses of a circumarctic coastal and a boreal lacustrine mysid crustacean, and evidence of fast postglacial mtDNA rates. *Molecular Ecology* 15, 3287–3301.

**Avise J.C.** (2001) *Phylogeography. The history and formation of species*. 3rd edition. Cambridge, MA: Harvard University Press.

**Brown R.A. and Seed R.** (1977) *Modiolus modiolus* (L.). An autoecological study. In Keegan B.K., Cleidigh P.O. and Boddin P.J.S. (eds) *Biology of benthic organisms*. Oxford: Pergamon Press, pp. 93–100.

**Campo D., Molares J., Garcia L., Fernandez-Rueda P., Garcia-Gonzalez C. and Garcia-Vazquez E.** (2010) Phylogeography of the European stalked barnacle (*Pollicipes pollicipes*): identification of glacial refugia. *Marine Biology* 157, 147–156.

**Clement M., Posada D. and Crandall K.A.** (2000) TCS: a computer program to estimate gene genealogies. *Molecular Ecology* 9, 1657–1660.

**Cunningham C.W. and Collins T.M.** (1998) Beyond area relationships: extinction and recolonization in molecular marine biogeography. In Schierwater B., Streit B., Wagner G. and DeSalle R. (eds) *Molecular ecology and evolution: approaches and applications*. Basel: Birkhäuser, pp. 297–321.

**Dahlgren T.G., Weinberg J.R. and Halanych K.M.** (2000) Phylogeography of the ocean quahog (*Arctica islandica*): influence of paleoclimate on the diversity and species range. *Marine Biology* 137, 487–495.

**Davenport J. and Kjørsvik E.** (1982) Observations on a Norwegian intertidal population of the horse mussel *Modiolus modiolus* (L.). *Journal of Molluscan Studies* 48, 370–371.

**Excoffier L., Laval G. and Schneider S.** (2005) Arlequin ver. 3.0: an integrated software package for population genetic analysis. *Evolution and Bioinformatics Online* 1, 47–50.

**Folmer O., Black M., Hoeh W., Lutz R. and Vrijenhoek R.** (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit 1 from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3, 294–299.

**Fu Y.X. and Li W.H.** (1993) Statistical tests of neutrality of mutations. *Genetics* 133, 693–709.

**Gladenkov A.Y., Oleinik A.E., Marincovich L., Jr and Barinov K.B.** (2002) A refined age for the earliest opening of the Bering Strait. *Palaeogeography, Palaeoclimatology, Palaeoecology* 183, 321–328.

**Harpending H.C.** (1994) Signature of ancient population growth in a low-resolution mitochondrial DNA mismatch distribution. *Human Biology* 66, 591–600.

**Hartl D.L. and Clark A.G.** (1997) *Principles of population genetics*. 3rd edition. Sinauer Associates: Sunderland, MA.

**Hewitt G.** (2000) The genetic legacy of the Quarternary ice ages. *Nature* 405, 907–913.

**Howland R.J.M., Pantiulin A.N., Millward G.E. and Prego R.** (1999) The hydrography of the Chupa estuary, White Sea, Russia. *Estuarine, Coastal and Shelf Science* 48, 1–12.

**Ingólfsson A.** (2009) A marine refugium in Iceland during the last glacial maximum: fact or fiction? *Zoologica Scripta* 38, 663–665.

**Janssen A.W., Peeters G.A. and van der Slik L.** (1984) De fossiele schelpen van de Nederlandse stranden en zeegaten, tweede serie. VIII. *Basteria* 48, 91–219.

**Jasim A.K.N. and Brand A.R.** (1989) Observations on the reproduction of *Modiolus modiolus* in the Isle of Man. *Journal of the Marine Biological Association of the United Kingdom* 69, 373–385.

**Jolly M.T., Viard F., Gentil F., Thiebaut E. and Jollivet D.** (2006) Comparative phylogeography of two coastal polychaete tubeworms in the Northeast Atlantic supports shared history and vicariant events. *Molecular Ecology* 15, 1841–1855.

**Luttikhuisen P.C., Drent J. and Baker A.J.** (2003) Disjunct distribution of highly diverged mitochondrial lineage clade and population subdivision in a marine bivalve with pelagic larval dispersal. *Molecular Ecology* 12, 2215–2229.

**Maddison D.R. and Maddison W.P.** (2005) *MacClade*. Sunderland, MA: Sinauer Associates.

**Maggs C.A., Castilho R., Foltz D., Henzler C., Jolly M.T., Kelly J., Olsen J., Pereze K.E., Stam W., Vainola R., Viard F. and Wares J.** (2008) Evaluating signatures of glacial refugia for North Atlantic benthic marine taxa. *Ecology* 89, 108–122.

**Marko P.B., Hoffman J.M., Emme S.A., McGovern T.M., Keever C. and Cox L.N.** (2010) The 'Expansion–Contraction' model of Pleistocene biogeography: rocky shores suffer a sea change? *Molecular Ecology* 19, 146–169.

**Marko P.B. and Moran A.L.** (2002) Correlated evolutionary divergence of egg size and a mitochondrial protein across the Isthmus of Panama. *Evolution* 56, 1303–1309.

**Muhlin J.F. and Brawley S.H.** (2009) Recent versus relic: discerning the genetic signature of *Fucus vesiculosus* (Heterokontophyta; Phaeophyceae) in the Northwestern Atlantic. *Journal of Phycology* 45, 828–837.

**Muths D., Jollivet D., Gentil F. and Davoult D.** (2009) Large-scale genetic patchiness among NE Atlantic populations of the brittle star *Ophiothrix fragilis*. *Aquatic Biology* 5, 117–132.

**Nylander J.A.A.** (2004) MrModeltestv2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.

**Ojeda F.P. and Dearborn J.H.** (1989) Community structure of macroinvertebrates inhabiting the rocky subtidal zone in the Gulf of Maine: seasonal and bathymetric distribution. *Marine Ecology Progress Series* 57, 147–161.

**Ray N., Currat M. and Excoffier L.** (2003) Intra-deme molecular diversity in spatially expanding populations. *Molecular Biology and Evolution* 20, 76–86.

**Rogers A.R. and Harpending H.** (1992) Population growth makes waves in the distribution of pairwise genetic differences. *Molecular Biology and Evolution* 9, 552–569.

**Rozas J. and Rozas R.** (1999) DNAsp version 3: an integrated program for molecular population genetics and molecular evolution analysis. *Bioinformatics* 15, 174–175.

**Sabatini M. and Pizzolla P.** (2008) *Arctica islandica*. Icelandic cyprine. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme. Plymouth: Marine Biological Association of the United Kingdom. Available at: http://www.marlin.ac.uk/reproduction.php?speciesID=2588 (accessed 18 March 2013).

**Salvigsen O.** (2002) Radiocarbon-dated *Mytilus edulis* and *Modiolus modiolus* from northern Svalbard: climatic implications. *Norwegian Journal of Geography* 56, 56–61.


https://doi.org/10.1017/S0025315413000404 Published online by Cambridge University Press

**Schweinitz E.H. and Lutz R.A.** (1976) Larval development of the northern horse mussel *Modiolus modiolus* (L.), including a comparison with the larvae of *Mytilus edulis* L. as an aid in planktonic identification. *Biological Bulletin. Marine Biological Laboratory, Woods Hale* 150, 348–360.

**Svendsen J.I., Alexanderson H., Astakhov V.I., Demidov I., Dowedswell J.A., Funder S., Gataullin V., Henriksen M., Hjort C., Houmark-Nielsen M., Hubberten H.W., Ingolfsonn O., Jakobsson M., Kjaer K.H., Larsen E., Lokarntz H., Lunkka J.P., Lysa A., Mangerud J., Matiouchkov A., Murray A., Moller P., Niessen F., Nikolskaya O., Polyak L., Saarnisto M., Siergert C., Siegert M.J., Spielhagen R.F. and Stein R.** (2004) Late Quaternary ice sheet history of northern Eurasia. *Quaternary Science Reviews* 23, 1229–1271.

**Tajima F.** (1989) Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. *Genetics* 123, 585–593.

**Templeton A.R., Crandall K.A. and Sing C.F.** (1992) A cladistic analysis of phenotypic associations with haplotypes inferred from restriction endonuclease mapping and DNA sequence data. III. Cladogram estimation. *Genetics* 132, 619–633.

**Thompson J.D., Higgins D.G. and Gibson T.J.** (1994) CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position specific gap penalties and weight matrix choice. *Nucleic Acids Research*. 22, 4673–4680.

**Tyler-Walters H.** (2007) *Modiolus modiolus*. Horse mussel. *Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme*. Plymouth: Marine Biological Association of the United Kingdom. Available at: http://www.marlin.ac.uk/species/Modiolusmodiolus.htm (accessed 18 March 2013).

**Vermeij G.J.** (1989) Invasion and extinction: the last three million years of North Sea pelecypod history. *Conservation Biology* 3, 274–281.

**Vermeij G.J.** (1991) Anatomy of an invasion: the trans-Arctic interchange. *Paleobiology* 17, 281–307.

**Vermeij G.J.** (1996) An agenda for invasion biology. *Biological Conservation* 78, 3–9.

**Vermeij G.J.** (2005) From Europe to America: Pliocene to Recent trans-Atlantic expansion of cold-water North Atlantic mollluscs. *Proceedings of the Royal Society, B: Biological Sciences* 272, 2545–2550.

**Wares J.P.** (2002) Community genetics in the Northwestern Atlantic intertidal. *Molecular Ecology* 11, 1131–1144.

**Wares J.P. and Cunningham C.W.** (2001) Phylogeography and historical ecology of the north Atlantic intertidal. *Evolution* 55, 2455–2469.

**Weinberg J.R., Dahlgren T.G. and Halanych K.A.** (2002) Influence of rising sea temperature on commercial bivalve species of the US Atlantic Coast. *Fisheries in a Changing Climate* 32, 131–140.

**Won Y., Young C.R., Lutz R.A. and Vrijenhoek R.C.** (2003) Dispersal barriers and isolation among deep-sea mussel populations (Mytilidae: *Bathymodiolus*) from eastern Pacific hydrothermal vents. *Molecular Ecology* 12, 169–184.

and

**Young A.M., Torres C., Mack J.E. and Cunningham C.W.** (2002) Morphological and genetic evidence for vicariance and refugium in Atlantic and Gulf of Mexico populations of the hermit crab *Pagurus longicarpus*. *Marine Biology* 140, 1059–1066.

**Correspondence should be addressed to:**
K. Halanych
101 Life Sciences Building,
Department of Biological Sciences, Auburn University
Auburn, AL 36849 USA
email: ken@auburn.edu
or

T. Dahlgren
Uni Research
Thormøhlensgate 55
5008 Bergen, Norway
email: thomas.dahlgren@uni.no

https://doi.org/10.1017/S0025315413000404 Published online by Cambridge University Press

# APPENDIX

*Modiolus modiolus*. Variable positions in the 52 haplotypes (Mo1–Mo52; cf. Figure 2. Mo13–26 are from the Pacific). Numbers refer to the positions on the CO1 gene fragment. *Shaded columns* indicate first positions and **numbers in bold** indicate second positions, while all others are third positions. **Bases in bold** show non-synonymous changes.

| | 11 | 20 | 26 | 29 | 38 | 42 | **49** | 62 | 65 | **70** | 71 | 74 | 83 | 89 | **91** | 92 | 110 | **121** | 122 | 125 | **127** | 128 | 134 | 149 | 173 | 182 | 185 | 191 | 194 | 197 | 200 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mo1 | G | A | A | A | A | A | G | G | A | G | C | A | C | T | A | A | C | A | G | C | A | C | C | T | A | A | G | A | T | A | G | Mo1 |
| Mo2 | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo2 |
| Mo3 | – | – | – | – | – | – | – | – | – | A | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo3 |
| Mo4 | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo4 |
| Mo5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo5 |
| Mo6 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo6 |
| Mo7 | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | A | Mo7 |
| Mo8 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo8 |
| Mo9 | – | – | – | – | – | **T** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo9 |
| Mo10 | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo10 |
| Mo11 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo11 |
| Mo12 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo12 |
| Mo13 | A | **G** | – | – | G | – | **A** | A | – | – | A | – | **T** | C | **G** | – | T | – | **A** | T | – | T | T | C | – | **G** | – | – | – | G | A | Mo13 |
| Mo14 | A | **G** | – | G | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | T | **G** | T | T | C | – | **G** | – | – | – | G | A | Mo14 |
| Mo15 | A | **G** | – | – | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | T | **G** | T | T | C | – | **G** | – | – | – | C | A | Mo15 |
| Mo16 | – | **G** | – | – | G | – | **A** | A | – | – | A | – | - | – | **G** | – | T | – | **A** | – | **G** | T | T | C | – | **G** | – | – | – | G | A | Mo16 |
| Mo17 | – | **G** | – | – | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | T | **G** | T | T | C | – | **G** | – | – | – | G | A | Mo17 |
| Mo18 | A | **G** | – | – | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | T | **G** | T | T | C | – | **G** | – | – | – | G | A | Mo18 |
| Mo19 | A | **G** | – | – | G | – | **A** | A | – | A | A | – | **T** | – | **G** | – | T | – | **A** | – | **G** | T | T | C | **G** | **G** | – | – | – | G | A | Mo19 |
| Mo20 | A | **G** | – | – | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | – | - | T | T | C | – | **G** | – | – | – | G | A | Mo20 |
| Mo21 | – | **G** | – | – | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | – | **G** | T | T | C | – | **G** | – | – | – | G | A | Mo21 |
| Mo22 | A | **G** | – | – | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | T | **G** | T | T | C | – | **G** | – | – | – | G | A | Mo22 |
| Mo23 | – | **G** | – | – | – | – | **A** | A | – | – | A | – | **T** | – | **G** | G | T | – | **A** | – | **G** | T | T | C | – | **G** | – | – | – | – | A | Mo23 |
| Mo24 | – | **G** | – | – | – | – | **A** | – | – | – | A | – | **T** | – | – | – | T | – | **A** | – | **G** | T | T | C | – | **G** | – | – | – | G | A | Mo24 |
| Mo25 | A | **G** | – | – | G | – | **A** | A | – | – | G | – | **T** | – | **G** | – | T | – | **A** | T | **G** | T | T | C | – | **G** | – | – | – | C | A | Mo25 |
| Mo26 | A | – | – | – | G | – | **A** | A | – | – | A | – | **T** | – | **G** | – | T | – | **A** | – | **G** | T | T | C | – | **G** | – | – | – | C | A | Mo26 |
| Mo27 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | **G** | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo27 |
| Mo28 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo28 |
| Mo29 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo29 |
| Mo30 | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo30 |
| Mo31 | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo31 |
| Mo32 | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo32 |
| Mo33 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | **G** | – | A | Mo33 |
| Mo34 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo34 |
| Mo35 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | – | – | – | – | – | – | – | A | Mo35 |
| Mo36 | – | – | – | – | – | – | – | – | C | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo36 |
| Mo37 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo37 |
| Mo38 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo38 |
| Mo39 | A | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo39 |
| Mo40 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo40 |
| Mo41 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo41 |

| | 203 | 209 | 221 | **226** | **235** | 242 | 254 | 257 | 269 | 275 | 278 | **280** | 281 | 284 | 287 | 290 | 292 | 293 | 294 | 296 | 302 | 305 | 308 | **310** | 311 | 314 | 326 | **340** | 341 | 359 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mo01 | A | A | A | A | A | G | G | A | A | A | C | A | A | A | A | T | A | A | G | C | A | A | G | A | C | G | A | G | T | G | Mo01 |
| Mo02 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | A | – | – | – | – | – | – | – | Mo02 |
| Mo03 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo03 |
| Mo04 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo04 |
| Mo05 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo05 |
| Mo06 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo06 |
| Mo07 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo07 |
| Mo08 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | C | – | – | – | T | – | – | – | Mo08 |
| Mo09 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo09 |
| Mo10 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo10 |
| Mo11 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo11 |
| Mo12 | – | – | **G** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo12 |
| Mo13 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | – | Mo13 |
| Mo14 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo14 |
| Mo15 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo15 |
| Mo16 | **G** | G | – | – | **G** | **A** | A | C | G | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | G | A | – | **A** | C | A | Mo16 |
| Mo17 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | – | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo17 |
| Mo18 | **C** | – | – | – | **G** | – | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo18 |
| Mo19 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | T | – | G | C | – | – | – | T | G | – | T | – | A | A | – | - | C | A | Mo19 |
| Mo20 | **G** | – | **G** | – | **G** | **A** | A | C | – | – | – | G | – | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo20 |
| Mo21 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo21 |
| Mo22 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo22 |
| Mo23 | **G** | – | **G** | – | - | **A** | A | C | – | – | – | G | G | – | – | C | – | – | – | T | – | – | T | – | A | A | – | **A** | C | A | Mo23 |
| Mo24 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo24 |
| Mo25 | **G** | – | – | – | **G** | **A** | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo25 |
| Mo26 | **G** | – | – | – | **G** | – | A | C | – | – | – | G | G | – | G | C | – | – | – | T | G | – | T | – | A | A | – | **A** | C | A | Mo26 |
| Mo27 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo27 |
| Mo28 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo28 |
| Mo29 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo29 |
| Mo30 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo30 |
| Mo31 | – | – | – | **G** | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | Mo31 |
| Mo32 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo32 |
| Mo33 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo33 |
| Mo34 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | Mo34 |
| Mo35 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo35 |
| Mo36 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo36 |

https://doi.org/10.1017/S0025315413000404 Published online by Cambridge University Press

| | 365 | 368 | 371 | 374 | 380 | 389 | **391** | 401 | 404 | 410 | 416 | 431 | 435 | 443 | 446 | 449 | 455 | **457** | 467 | 488 | 491 | 494 | 500 | 503 | 506 | 509 | 512 | 515 | **517** | 524 | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mo1 | C | A | T | C | G | C | G | A | T | A | T | C | T | A | C | G | T | A | C | A | A | G | A | A | G | G | A | T | G | G | Mo1 |
| Mo2 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo2 |
| Mo3 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo3 |
| Mo4 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo4 |
| Mo5 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo5 |
| Mo6 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo6 |
| Mo7 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo7 |
| Mo8 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo8 |
| Mo9 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo9 |
| Mo10 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | **A** | – | – | – | – | – | – | – | – | Mo10 |
| Mo11 | – | – | – | – | – | – | **A** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo11 |
| Mo12 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo12 |
| Mo13 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo13 |
| Mo14 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | G | – | **A** | – | – | – | **A** | A | Mo14 |
| Mo15 | – | – | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo15 |
| Mo16 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo16 |
| Mo17 | – | G | C | T | A | A | – | – | C | **C** | – | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | **A** | A | Mo17 |
| Mo18 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | **A** | A | Mo18 |
| Mo19 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo19 |
| Mo20 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | C | C | **G** | T | – | G | **C** | – | – | **A** | A | – | – | – | A | Mo20 |
| Mo21 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo21 |
| Mo22 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | **A** | A | Mo22 |
| Mo23 | – | – | C | T | A | A | – | **G** | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo23 |
| Mo24 | – | G | C | T | A | A | – | – | C | – | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo24 |
| Mo25 | – | – | C | T | A | A | – | – | C | **C** | C | T | – | T | T | – | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | – | A | Mo25 |
| Mo26 | – | G | C | T | A | A | – | – | C | **C** | C | T | – | T | T | A | C | **G** | T | – | G | **C** | – | – | **A** | – | – | – | **A** | A | Mo26 |
| Mo27 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo27 |
| Mo28 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | C | – | – | – | – | – | – | – | – | – | – | Mo28 |
| Mo29 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | **C** | – | – | – | – | – | Mo29 |
| Mo30 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | A | Mo30 |
| Mo31 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo31 |
| Mo37 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo37 |
| Mo38 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo38 |
| Mo39 | – | – | – | – | – | – | A | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo39 |
| Mo40 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo40 |
| Mo41 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo41 |
| Mo42 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo42 |
| Mo43 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo43 |
| Mo44 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo44 |
| Mo45 | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo45 |
| Mo46 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo46 |
| Mo47 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo47 |
| Mo48 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | **G** | G | – | – | – | – | – | – | – | – | – | – | – | Mo48 |
| Mo49 | – | – | – | – | – | – | – | – | – | – | T | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo49 |
| Mo50 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo50 |
| Mo51 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo51 |
| Mo52 | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo52 |

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Mo32 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | **A** | – | – | – | – | – | Mo32 |
| Mo33 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo33 |
| Mo34 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo34 |
| Mo35 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo35 |
| Mo36 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo36 |
| Mo37 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | **A** | – | Mo37 |
| Mo38 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo38 |
| Mo39 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo39 |
| Mo40 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | C | – | – | Mo40 |
| Mo41 | – | – | – | – | – | – | – | – | – | – | – | – | T | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo41 |
| Mo42 | – | – | – | – | – | – | – | – | – | – | – | – | – | **A** | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo42 |
| Mo43 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | – | – | – | – | – | Mo43 |
| Mo44 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo44 |
| Mo45 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | G | – | **A** | – | Mo45 |
| Mo46 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo46 |
| Mo47 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo47 |
| Mo48 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo48 |
| Mo49 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo49 |
| Mo50 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo50 |
| Mo51 | T | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo51 |
| Mo52 | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | – | Mo52 |

| | **532** | 539 | 540 | 542 | 548 | 563 | 566 | 578 | 584 |
|---|---|---|---|---|---|---|---|---|---|
| Mo1 | **G** | T | C | A | A | A | T | A | C |
| Mo2 | A | – | – | – | – | – | – | – | – |
| Mo3 | A | – | – | – | – | – | – | – | – |
| Mo4 | A | – | – | – | – | – | – | – | – |
| Mo5 | A | – | – | – | – | – | – | – | – |
| Mo6 | A | – | – | – | – | – | C | – | – |
| Mo7 | A | – | – | – | – | – | – | – | – |
| Mo8 | A | – | – | – | – | – | – | – | – |
| Mo9 | A | – | **T** | – | – | – | – | – | – |
| Mo10 | A | – | – | – | – | – | – | – | – |
| Mo11 | A | – | – | – | – | – | – | – | – |
| Mo12 | A | – | – | – | – | – | – | – | – |
| Mo13 | A | – | – | T | G | G | – | **G** | A |
| Mo14 | A | – | – | T | G | – | – | **G** | A |
| Mo15 | A | – | – | T | G | – | – | **G** | A |
| Mo16 | A | – | – | T | G | – | – | **G** | A |
| Mo17 | A | – | – | T | G | – | – | **G** | A |
| Mo18 | A | – | – | T | G | – | – | **G** | A |
| Mo19 | A | – | – | T | G | – | – | **G** | A |
| Mo20 | A | – | – | T | G | G | – | **G** | A |
| Mo21 | A | – | – | T | G | – | – | **G** | A |
| Mo22 | A | – | – | T | – | – | – | **G** | A |
| Mo23 | A | – | – | T | G | – | – | **G** | A |
| Mo24 | A | – | – | T | G | – | – | **G** | A |
| Mo25 | A | – | – | T | G | – | – | **G** | A |
| Mo26 | A | – | – | T | G | – | – | **G** | A |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| M027 | A | – | – | – | – | – | – | – | – |
| M028 | A | – | – | – | – | – | – | – | – |
| M029 | A | – | – | – | – | – | – | – | – |
| M030 | A | – | – | – | – | – | – | – | – |
| M031 | A | – | – | – | – | – | – | – | – |
| M032 | A | – | – | – | – | – | – | – | – |
| M033 | A | – | – | – | – | – | – | – | – |
| M034 | A | – | – | – | – | – | – | – | – |
| M035 | A | – | – | – | – | – | – | – | – |
| M036 | A | – | – | – | – | – | – | – | – |
| M037 | A | – | – | – | – | – | – | – | – |
| M038 | A | C | – | – | – | – | – | – | – |
| M039 | A | – | – | – | – | – | – | – | – |
| M040 | A | – | – | – | – | – | – | – | – |
| M041 | A | – | – | – | – | – | – | – | – |
| M042 | A | – | – | – | – | – | – | – | – |
| M043 | A | – | – | – | – | – | C | – | – |
| M044 | A | – | – | – | – | – | – | – | – |
| M045 | A | – | – | – | – | – | – | – | – |
| M046 | A | – | – | – | – | – | – | – | – |
| M047 | A | – | – | – | – | – | – | – | – |
| M048 | A | – | – | – | – | – | – | – | – |
| M049 | A | – | – | – | – | – | – | – | – |
| M050 | A | – | – | – | – | – | – | – | – |
| M051 | A | – | – | – | – | – | – | – | – |
| M052 | A | – | – | – | – | – | – | – | – |